UNITED STATES OF AMERICA
DEPARTMENT OF COMMERCE
NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION

In re:	)	Administrative Law Judge
	)	Hon. George J. Jordan
Proposed Waiver and Regulations Governing the Taking of Eastern North Pacific Gray Whales by the Makah Indian Tribe	)	Docket No. 19-NMFS-0001
	)	
	)	RINs: 0648-BI58; 0648-XG84
	)	

DECLARATION OF DR. DAVID WELLER

I, Dr. David Weller, declare as follows:

1. I am a wildlife research biologist with the Marine Mammal and Turtle Division of the National Marine Fisheries Service (NMFS) Southwest Fisheries Science Center (SWFSC), within the National Oceanic and Atmospheric Administration. Within the Division, I conduct research as part of the Cetacean Health and Life History Program. The Marine Mammal and Turtle Division of the NMFS SWFSC, located in La Jolla, California, is the agency's lead for gray whale science, responsible for developing, collecting, and analyzing the best available scientific information to inform NMFS's management decisions. As a member of the Division, I am familiar with the policies and requirements of and NMFS's responsibilities under the Marine Mammal Protection Act (MMPA).

2. My professional training is in animal behavior, marine science, and wildlife and fisheries sciences. I am recognized as an expert on gray whales and have written extensively on and contributed to the scientific understanding of gray whales since 1997. I have authored or co-authored over 60 papers or reports on gray whales. These works include information on: gray whale abundance, occurrence, distribution, migration, reproduction, survival, behavior, genetics,

population structure, and interactions with human activities such as fishing gear and offshore oil and gas development. The geographic range of the topics covered in this scholarship encompasses the eastern and western North Pacific, including areas off the U.S., Mexico, Canada, Russia, Korea, Japan, and China. My major writings on gray whales within the past 10 years (2008-2018) are listed in my Curriculum Vitae, attached. NMFS Ex. 3-1.[1] I have been and continue to be engaged in research on gray whales including aspects of their distribution, abundance, movements, population structure, and calf production.

3. In addition to my written works on gray whales, during the past several decades I have studied gray whales in the field from boats, ships, shore stations, unmanned drones, and autonomous acoustic recorders. This work has included used of a number of methods, including: photography (boat, ship, shore, and aerial), satellite tagging, biopsying, underwater acoustic recording, infrared camera imaging, theodolite tracking, scat sampling, and visual observations. Also, as NMFS's lead for gray whale science, I review, evaluate, and contribute to the agency's official stock assessment reports (SARs) for gray whales, prepared in accordance with section 117 of the MMPA (16 U.S.C. § 1386). The MMPA's requirements pertaining to SARs and NMFS's procedures for preparing them are explained in the Declaration of Dr. Shannon Bettridge, filed herewith.

4. I am a member of the Society for Marine Mammalogy and the International Union for Conservation of Nature (IUCN) Western Gray Whale Advisory panel (*http://www.iucn.org/western-gray-whale-advisory-panel*). I also participate as a member of the U.S. delegation to the International Whaling Commission (IWC). The IWC is an inter-

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[1] NMFS's exhibits are labeled as follows: "NMFS Ex. 1-XX" for exhibits attached to the Declaration of Chris Yates; "NMFS Ex. 2-XX" for exhibits attached to the Declaration of Dr. Shannon Bettridge; "NMFS Ex. 3-XX" for exhibits attached to the Declaration of Dr. David Weller; and, "NMFS Ex. 4-XX" for exhibits attached to the Declaration of Dr. Jeffrey Moore.

governmental organization whose purpose is the conservation of whales and the management of whaling. The IWC implements the International Convention for the Regulation of Whaling (Convention), established in 1946. All signatories to the Convention are members of the IWC. Currently, the IWC membership comprises about 87 countries, including the United States. *See generally https://iwc.int/home.*

5. Since 2002, I have been a member, on behalf of the United States, of the IWC's Scientific Committee (SC) (*see https://iwc.int/scmain*). The IWC SC is composed of leading experts on cetaceans, including all baleen whales, and is charged with providing the best scientific advice to the IWC. I participate on several IWC SC working groups to address, among other things, the range-wide status of gray whales. As a member of the U.S. delegation to the IWC and from my experience participating in the IWC SC and various scientific working groups, I am familiar with and have developed expertise in the provisions of the Convention, the United States' positions with respect to implementation of the Convention, and the scientific underpinnings of the IWC's work.

6. Pursuant to the Convention, commercial whaling by member states has been banned since 1986. The IWC provides a framework for the take of whales by aborigines of member states for subsistence purposes. To obtain an IWC allocation for aboriginal subsistence whaling, a member state must identify a subsistence need and request a quota of whales from the relevant stock. The IWC SC has a standing working group tasked with providing scientific advice on the sustainability of catch limits for aboriginal subsistence whaling operations that takes into account scientific uncertainty and meets the IWC's management and conservation objectives. These conservation objectives focus on ensuring that requests for aboriginal subsistent hunts are sustainable and do not seriously increase the risk of extinction (highest

priority); enable hunts in perpetuity; and maintain stocks at the highest net recruitment level (or if they are below that level, ensure that they move toward it). The objective of the working group's assessment and evaluation process is to determine sustainable catch limits, by way of simulation modeling over a 100-year period. These simulations account for plausible levels of uncertainty regarding a large number of factors including knowledge of population structure, abundance and trends, historic and future catch levels, reproduction, survivorship, and environmental conditions. The computer simulations used by the working group are called strike limit algorithms (SLAs). Although SLAs are intended for long-term use, regular reviews (usually every five to six years) are undertaken to ensure that no new information has been obtained that suggests new testing is required. Together, these methods are referred to as aboriginal whaling management procedures. After consulting with the IWC SC, the IWC decides whether or not to endorse a requested catch limit. Catch limits that meet the IWC's conservation objectives are included in a legally binding "Schedule" to the Convention.

7. As explained in the Bettridge Declaration, NMFS currently recognizes two stocks of gray whales under the MMPA, the eastern North Pacific (ENP) stock and the western North Pacific (WNP) stock. Bettridge Decl. ¶¶ 16-18. The agency's determination to classify these two populations as separate stocks was informed, in part, by the findings of a 2012 NMFS task force composed of agency marine mammal experts convened to provide an objective scientific evaluation of gray whale stock structure as defined under the MMPA. I was asked to chair that task force and was lead author of a report documenting its deliberations and conclusions. *See* NMFS Ex. 3-2 (Weller *et al.* 2013). The task force report was internally peer reviewed and published as part of the NMFS technical memorandum series. The task force found that levels of genetic differentiation between WNP and ENP gray whales provided convincing evidence that

WNP gray whales and ENP gray whales should be recognized as separate stocks under the MMPA.

8. The IWC also recognizes ENP and WNP gray whales as separate stocks for evaluating catch limits, although the IWC's criteria for identifying and managing stocks are not the same as those used by NMFS under the MMPA. Generally, the IWC uses data regarding range, distribution, movements, genetic structure, mixing rates, and morphology to identify stocks. For management purposes, the IWC may identify a management stock or a management unit that may or may not be equivalent to a single biological stock; for example, a management unit may include animals that happen to be present in a defined region and defined season where management is taking place or is contemplated.

9. Since 1997, the United States has routinely requested an aboriginal subsistence whaling quota for ENP gray whales from the IWC on behalf of the Makah Indian Tribe. These requests have been made through a joint proposal with the Russian Federation. The IWC recently approved a 2018 joint request that became effective December 29, 2018. Article 13(b)(2) of the IWC Schedule establishes a seven-year catch limit of 980 ENP gray whales with an annual cap of 140 ENP gray whales. The catch limit runs for a seven year period from 2019 through 2025, when a status quo or modified request may be made for a new six-year term. NMFS Ex. 3-3 (IWC 2018a). A United States and Russian Federation bilateral agreement allocates the catch limit between the two countries and provides annual limits of up to five ENP gray whales for the Makah Tribe and 135 ENP gray whales for the Russian Federation. NMFS Ex. 3-4 (Fominykh and Wulff 2018). As provided for in the bilateral agreement, either country may initiate discussions on the transfer of unused strikes. *Id.* In the past, the United States has assigned all of its unused catch limit to Russia for use by Chukotka hunters. *See, e.g.*, NMFS Ex.

3-5 (Fominykh and Wulff 2017); NMFS Ex. 3-6 (Fominykh and Smith 2016); NMFS Ex. 3-7 (Ilyashenko and DeMaster 2012); NMFS Ex. 3-8 (Ilyashenko and Hogarth 2007).

10. I am familiar with the proposed waiver and regulations that are the subject of this proceeding and with the scientific evidence submitted by NMFS in support of the proposed waiver and regulations. Based on my experience as a gray whale scientist and a member of the IWC SC, it is my professional opinion that the scientific evidence submitted by NMFS in support of the proposed waiver and regulations represents the best available scientific information regarding gray whales.

OVERVIEW OF GRAY WHALE BIOLOGY AND SCIENCE

11. Given my expertise on gray whales, I participated in the development and drafting of the gray whale sections of the February 2015 Draft Environmental Impact Statement on the Makah Tribe Request to Hunt Gray Whales (2015 DEIS). The 2015 DEIS, Chapter 3, provides a thorough discussion of gray whale biology and ecology. The following paragraphs summarize the best available scientific information on gray whales.

ENP GRAY WHALE STOCK

12. The range of the ENP gray whale stock is vast and crosses many large marine ecosystems, including the Pacific Central American Coast, California Current, Gulf of Alaska, and Bering and Chukchi Seas. NMFS Ex. 3-9 (Longhurst 1998); NMFS Ex. 3-10 (Sherman and Alexander 1998). Most ENP gray whales spend the winter months off the Baja California Peninsula then migrate north along the coast of North America to their summer/fall feeding range, which extends as far north as the Chukchi, Beaufort, and northwestern Bering Seas for most of the population. *See* NMFS Ex. 1-7, at 3 Fig. 2 (NMFS 2019a).

13. The ENP gray whale stock's southward migration generally begins in late November, and most whales reach the wintering grounds in northern Mexico and southern California starting in late December through February. Whales begin migrating north to the summer feeding areas in February, with the final phase of the migration, composed primarily of females whales with their calves, winding down by late May. Migrating gray whales are steady swimmers during migration (estimated to travel between 3-6 miles (5-10 km) per hour) and often exhibit directed travel and predictable breathing and dive patterns. NMFS Ex. 3-11 (Jones and Swartz 2002). During migration, gray whales generally remain close to shore (especially where the continental shelf is narrow) and the best available information indicates that most northbound and southbound whales migrate within 27 miles (43 km) of shore. NMFS Ex. 3-12 (Green *et al.* 1995); NMFS Ex. 3-13 (Green *et al.* 1992); NMFS Ex. 3-14 (Pike 1962).

14. Mating can occur throughout the southward migration, with a mean conception date of December 5. NMFS Ex. 3-15, at 74 (Rice and Wolman 1971). Females that have not successfully bred may enter a second estrous cycle within 40 days, *id.* at 90, such that a few females may breed as late as the end of January while present on the winter grounds. NMFS Ex. 3-16 (Jones and Swartz 1984). Some ENP gray whales calve in the shallow, protected lagoons of Baja Mexico starting around late December and ending by approximately the beginning of March, although around one-quarter to one-half of calves are born north of Carmel, California during the southward migration. NMFS Ex. 3-17 (Swartz and Jones 1983); NMFS Ex. 3-18 (Sanchez-Pacheco 1998); NMFS Ex. 3-19, at 10-14 (Sheldon *et al.* 2004).

15. Gray whales feed on a wide variety of prey throughout their range using various feeding techniques, including suction feeding, also called benthic or bottom feeding, and engulfing or skimming prey in the water column and on the sea surface. Researchers have

observed gray whales aggregating in particular areas to feed where prey densities are high, especially in portions of the northern seas. *See, e.g.*, NMFS Ex. 3-20, at 11 (Berzin 1984); NMFS Ex. 3-21, at 5 (Yablokov and Bogoslovskaya, 1984); NMFS Ex. 3-22, at 4 (Clarke and Moore 2002); NMFS Ex. 3-23, at 1 (Moore *et al.*, 2000); NMFS Ex. 3-24, at 2 (Moore *et al.* 2003); NMFS Ex. 3-25, at 3 (Highsmith *et al.* 2007). Areas where whales congregate to feed on a regular basis have been referred to as "feeding grounds" or "feeding areas" *See, e.g.*, NMFS Ex. 3-20, at 7 (Berzin, 1984); NMFS Ex. 3-26, at 1 (Calambokidis *et al.* 2002); NMFS Ex. 3-24, at 1 (Moore *et al.* 2003); NMFS Ex. 3-27, at 3 (Calambokidis *et al.* 2004). Gray whales change location and habitat to exploit the optimum prey species at any one time, based on abundance, density, size, caloric content, and predation pressure. Such factors may vary by season and year, depending on environmental variability and the population dynamics of prey. NMFS Ex. 3-28, at 19-24 (Darling *et al.* 1998); NMFS Ex. 3-22 (Clarke and Moore 2002); NMFS Ex. 3-29 (Moore *et al.* 2007).

16. Not all ENP gray whales make the full migration every year to the northern feeding grounds in the Chukchi, Bering, and Beaufort Seas. Beginning in the 1970s, researchers observed that some gray whales spend summer/autumn months feeding off the coasts of Oregon, Washington, and Vancouver Island. *See, e.g.*, NMFS Ex. 3-30 (Hatler and Darling 1974); NMFS Ex. 3-31 (Darling 1984). Based on photo-identification studies, which NMFS has participated in and helped fund, researchers have identified individual whales that use these areas each year or most years, rather than continuing to the more northern feeding grounds. *See* NMFS Ex. 3-32 (Calambokidis *et al.* 2000); NMFS Ex. 3-26 (Calambokidis *et al.* 2002); NMFS Ex. 3-33, at 2-3 (Calambokidis *et al.* 2017). These whales have been referred to as the Pacific Coast Feeding Group, or PCFG. The IWC defines the PCFG as gray whales observed between

June 1 and November 30 within the region between northern California and northern Vancouver Island (from 41° N lat. to 52° N lat.) and photo-identified within this area during two or more years. *See* NMFS Ex. 3-34, at 18 (IWC 2011a); NMFS Ex. 3-35, at 7 (IWC 2011c). NMFS has adopted this definition. *See* NMFS Ex. 2-7, at 8 (Caretta *et al.* 2017). A majority of PCFG whales make the southern migration to the wintering grounds off Baja California along with the rest of the ENP stock.

17. One of the purposes of the 2012 NMFS task force described in paragraph 7 above was to consider whether the PCFG should be designated as a separate stock under the MMPA. The task force examined several lines of evidence, including genetics, photo-identification, tagging, and other studies, representing the best scientific evidence available regarding gray whale stock structure.

18. With respect to genetics, the task force found small but significant differences in patterns of mitochondrial DNA (*i.e.*, diversity in a form of DNA inherited only from the mother), between samples collected from whales meeting the PCFG definition and whales sampled in northern feeding areas, including Chukotka, Russia. NMFS Ex. 3-36, at 7 (Lang *et al.* 2011a). Similar results were found in an independent study comparing mtDNA diversity between whales sampled during summer on the PCFG feeding ground and samples collected from whales, most of which had stranded, between southern California and the Chukotka Peninsula. NMFS Ex. 3-37 (Frasier *et al.* 2011). However, when analyzing microsatellites of nuclear DNA, which is inherited from both parents, no significant differences were identified between whales from the different feeding areas or between whales sampled during summer on the PCFG feeding ground and whales sampled in one of the Mexican wintering lagoons. *See* NMFS Ex. 3-38, at 6 (D'Intino *et al.* 2013). Lang *et al.* (2011) concluded that these results indicate that: (1) structure

is present among gray whales using different feeding areas, (2) matrilineal fidelity plays a role in creating such structure, and (3) individuals from different feeding areas may interbreed. In other words, calves likely follow their mothers to feeding areas and to some extent they return to those feeding areas in subsequent years. There was no evidence, however, that whales that frequent one feeding area are reproductively isolated from whales that frequent other feeding areas. NMFS Ex. 3-36, at 7-9 (Lang *et al.* 2011a).

19. Based on the MMPA's requirements, NMFS's guidance, and the best available scientific information, the task force concluded that there is substantial uncertainty in the strength of the lines of evidence supporting demographic independence of the PCFG and that the status of the PCFG as a population stock remains unresolved. The task force recommended that research should continue. NMFS Ex. 3-2, at 47-48 (Weller *et al.* 2013). Key areas of research identified by the task force included expanding photo-identification and tagging efforts, assessing interactions with fishing gear, and exploring genetic relatedness to better understand recruitment to the PCFG. NMFS continues to fund photo-identification surveys and is leading analyses regarding the recruitment of PCFG whales and assessing human-caused injury and mortality affecting gray whales in the PCFG range. *See e.g.*, NMFS Ex. 3-33 Table 1 (Calambokidis *et al.* 2017); NMFS Ex. 2-10 (Carretta *et al.* 2018a).

20. Because the task force was unable to provide definitive advice as to whether the PCFG qualifies as a population stock, NMFS continues to recognize the PCFG as part of the larger ENP stock. *See* NMFS Ex. 3-2 (Weller *et al.* 2013); Bettridge Decl. ¶ 18.

21. Because the ENP gray whale migration corridor is close to shore, the ENP stock has been routinely studied and monitored for many years by scientists from the U.S., Mexico, Canada, Russia, and elsewhere. Consequently, more is known about this stock than about most

other large cetacean stocks. NMFS estimates the ENP gray whale population size based on systematic shore-based surveys conducted during the whales' southbound migration. NMFS has conducted these surveys since 1967. I have been a project leader of these abundance surveys since 2009. The survey methods and data have been reviewed and accepted by the IWC SC and have been published in peer-reviewed literature. *See* NMFS Ex. 3-39, at 31 (IWC 2018d); NMFS Ex. 3-40 (Durban *et al.* 2015).

22. An Unusual Mortality Event (UME) during the 1999/2000 season reduced the ENP stock by as much as one fourth. The stock recovered from that decline and has been increasing since then, and the current abundance estimate of about 27,000 is the highest that has been recorded in the 1967-2016 time series. Several factors following the die-off, including the aforementioned increasing trend in abundance, suggest that the event was short-term and acute and not a chronic situation. *See* NMFS Ex. 2-7, at 10 (Carretta *et al.* 2017).

23. As explained in the Bettridge Declaration and the Declaration of Dr. Jeffrey Moore, filed herewith, NMFS annually publishes stock assessment reports (SARs) for each marine mammal stock in U.S. waters. A SAR includes, among other data, an estimate of the stock's abundance, minimum abundance (Nmin), and potential biological removal (PBR) level. The most recent SARs for the ENP and WNP stocks are designated as the 2016 SARs. Bettridge Decl. ¶ 11. NMFS recently released draft 2017 SARs, which include updated information for the WNP and ENP stocks. NMFS Ex. 2-10 (Caretta *et al.* 2018).

24. The 2016 SAR for the ENP gray whale stock estimates abundance at 20,990 and concludes that the stock is within its optimum sustainable population level (OSP). The SAR estimates an annual PBR of 624 and average annual human-caused mortality for the period 2008-2012 of 133. Bettridge Decl. ¶ 19. The average annual human-caused mortality is due to:

Russian harvest (127); mortality and serious injury from commercial fisheries (4.45); and ship strikes (2.0). Concerns identified in the SAR include injuries due to fisheries interactions, ship strikes, and marine debris, as well as a number of habitat concerns such as industrialization, pollution, and shipping congestion throughout the nearshore migratory corridors. Climate change is likely to affect the availability of habitat and prey species, but species such as the gray whale (which feed on both benthic and pelagic prey) have been predicted in some studies, *see, e.g.*, NMFS Ex. 3-41, at 17 (Bluhm and Gradinger 2008), to adapt better than trophic specialists. Shipping and natural resource exploration and development activities (*e.g.*, for oil and gas deposits) are also expected to increase in the Arctic and elsewhere, which in turn could increase risks to whales from spills, ship strikes, and anthropogenic noise. The SAR does not indicate that these factors are a threat to the status of the ENP stock at this time.

25. The draft 2017 ENP gray whale SAR includes NMFS's current abundance estimate for the ENP stock, which is 26,960, based on data through the 2015/2016 migration season. NMFS Ex. 2-10, at 5 (Caretta *et al.* 2018); NMFS Ex. 3-42, at 4 (Durban *et al.* 2017). Based on our statistical methods of estimating abundance, there is 95 percent confidence that the true abundance is between 24,420 and 29,830. *Id.* In 2017 and 2018, the IWC SC reviewed the abundance estimate of 26,960 (from Durban *et al.* (2017)) and adopted it for use in the IWC SC assessment of aboriginal subsistence whaling for gray whales. *See* NMFS Ex. 3-39, at 31 Table 6b (IWC 2018d); NMFS Ex. 3-43, at 15, 99 (IWC 2018b). Durban *et al.* (2017) noted that a recent 22 percent increase in ENP gray whale abundance over 2010/2011 levels is consistent with high observed and estimated calf production between 2012 and 2016. NMFS Ex. 3-42, at 4 (Durban *et al*. 2017); *see also* NMFS Ex. 3-44, at 3 (Perryman *et al.* 2017). Recent increases in abundance also support hypotheses that gray whales may experience more favorable feeding

conditions in arctic waters due to an increase in ice-free habitat that might result in increased primary productivity in the region. NMFS Ex. 3-45 (Perryman *et al.* 2002); NMFS Ex. 3-46 (Moore 2016).

26. The ENP gray whale SARs have included abundance estimates for the PCFG as well as informational estimates of PBR for the group and other information. *See* Bettridge Decl. ¶ 21. The most recent abundance estimate of PCFG whales, which is reflected in the draft 2017 ENP gray whale SAR, is 243 whales with a minimum abundance (Nmin) of 228. NMFS Ex. 3-33, at 2, 11 (Calambokidis *et al.* 2017); NMFS Ex. 2-10, at 5 (Caretta *et al.* 2018). Calambokidis *et al.* (2017) also note that PCFG abundance estimates showed a high rate of increase in the late 1990s and early 2000s and "have been fairly stable since 2002 and recently increasing." NMFS Ex. 3-33, at 11 (Calambokidis *et al.* 2017). During this period of stability, the lowest abundance of 192 (Nmin of 171) occurred in 2007. *Id.* at 32.

27. The 2012 NMFS task force noted that the levels of internal versus external recruitment to the PCFG appear to be comparable, but these are not quantified well enough to determine if the population dynamics of the PCFG are more a consequence of births and deaths within the group (internal dynamics) rather than related to immigration and/or emigration (external dynamics). Data from photo-identification surveys between 1999 and 2014 indicate that an average of 14.9 whales per year were recruited (seen in a subsequent year) into the PCFG. NMFS Ex. 3-33, at 9 (Calambokidis *et al.* 2017). In addition to internal recruitment (*i.e.*, calves born to PCFG mothers), the annual coastal migration of the vast majority of ENP gray whales brings most individuals into contact with the habitat used by the PCFG, thereby serving as a substantial and continuous source of external recruitment into the PCFG. NMFS Ex. 3-2, at 46 (Weller *et al.* 2013). It has been estimated that about four new ENP gray whales immigrate to

the PCFG each year. NMFS Ex. 1-7, at 29 (NMFS 2019a); NMFS Ex. 3-47, at 7 (Lang and Martien 2012). From 2002 through 2015, the PCFG increased from 197 to 243 animals, which is an annual average increase of 3.5 whales over 13 years. NMFS Ex. 3-33, at 32 (Calambokidis *et al.* 2017).

28. Based on surveys during the past 20 years, about 48 percent of the 750 ENP gray whales identified in the proposed hunt area during the summer/fall feeding period (June 1 through November 30) are PCFG whales. NMFS Ex. 3-33, at 9 (Calambokidis *et al.* 2017). The other 52 percent are ENP gray whales that are seen once and not re-sighted. During the migration period (December 1 through May 31), 28 percent of ENP gray whales present in the proposed hunt area are currently estimated to be PCFG whales. NMFS Ex. 3-39, at 8 (IWC 2018d). Currently, we estimate that approximately 50 percent of PCFG whales are female. A. Lang, NMFS, personal communication, Oct. 17, 2017.

29. The photo-identification methods used to identify PCFG whales are well-developed and widely used in the management of large cetaceans. *See* NMFS Ex. 3-33 (Calambokidis *et al.* 2017); NMFS Ex. 3-39 (IWC 2018d). Photo-identification involves matching photographs of an individual whale based on the whale’s unique features and markings. Unique features used for individual identification of gray whales include the shape of the dorsal hump, spacing between ‘knuckles’ on the tail stock, and the mottled color patterns and scarring on the flukes and lateral flanks, which are visible when gray whales surface to breathe and arch to dive. Through photo-identification, researchers can track an individual whale’s location across years based on photographic evidence.

30. I have used photo-identification methods as part of my research on whales and dolphins since 1988. I have helped to create numerous photo-identification catalogs, including

catalogs for bottlenose dolphins, gray whales, humpback whales, and sperm whales, as well as related databases. I am personally familiar with the methods and procedures used to identify individual gray whales through photographs and genetic samples.

31. There are several photo-identification catalogs currently in use for identifying gray whales. For PCFG whales, the primary catalog is the Pacific Northwest Catalog, curated by the Cascadia Research Collective (Cascadia), located in Olympia, Washington. Cascadia is a non-profit scientific organization that has conducted research and education in the fields of marine mammal and bird biology, animal behavior, ecology, and toxicology for the past 39 years. The Pacific Northwest Catalog contains an extensive photographic database of gray whales (including PCFG and ENP whales) and other large cetaceans, and has on staff qualified individuals who can match new photos to photos in the database, if they exist. Several researcher groups collaborate on Cascadia's photo-identification program and provide photographs to Cascadia. Photographs taken by researchers under NMFS funding are also provided to the NMFS Marine Mammal Lab in Seattle, Washington. Cascadia has informed NMFS that matches can usually be made within 24 hours. J. Calambokidis, Cascadia Research Collective, personal communication, Jan. 23, 2017. Although there are no quantitative assessments regarding the error rate for either false positives or false negatives, a recent IWC workshop on North Pacific gray whales reviewed the Cascadia catalog data and estimated a combined error rate of 20 percent, resulting in 80 percent photo-matching accuracy. NMFS Ex. 3-39, at 9 (IWC 2018d).

32. In some cases, genetic data can also be used to identify PCFG and WNP whales by way of genotype matching. However, such cases require that the sample obtained (*e.g.*, tissue

residue obtained during aboriginal subsistence hunting or research) be an identical match to the genetic signature of an animal that has previously been sampled and its genotype cataloged.

WNP GRAY WHALE STOCK

33. The main feeding ground for the WNP gray whale stock is in the Okhotsk Sea off the northeastern coast of Sakhalin Island, Russia, but some animals occur off eastern Kamchatka and in other coastal waters of the northern Okhotsk Sea. NMFS Ex. 3-48 (Weller *et al.* 2002); NMFS Ex. 3-49 (Vertyankin *et al.* 2004); NMFS Ex. 3-50 (Tyurneva *et al.* 2010). Some WNP whales are thought to migrate south along the coast of Asia in the fall, but the migration route(s) and winter breeding ground(s) are poorly known. Information collected over the past century indicates that the range of the WNP stock is much more restricted at present than it was historically (NMFS Ex. 3-51 (Reeves *et al.* 2008)), and that whales migrated along the coasts of Japan and South Korea (NMFS Ex. 3-52 (Andrews 1914); NMFS Ex. 3-53 (Mizue 1951); NMFS Ex.3-54 (Omura 1984)), to wintering areas somewhere in the South China Sea, possibly near Hainan Island (NMFS Ex. 3-55 (Wang 1984).

34. Until recently, scientists believed that the WNP stock was geographically isolated from the ENP stock. In the past decade, however, photo-identification studies (NMFS Ex. 3-56 (Urbán *et al.* 2012); NMFS Ex. 3-57 (Weller *et al.* 2012)), genetic research (NMFS Ex. 3-58 (Lang *et al.* 2010); NMFS Ex. 3-59 (Lang *et al.* 2011b)), and telemetry studies (NMFS Ex. 3-60 (Mate *et al.* 2011); NMFS Ex. 3-61 (Mate *et al.* 2015)), have documented that some gray whales observed on the feeding grounds in the western North Pacific migrate to and from the eastern North Pacific Ocean. Such documentation includes: (1) six whales photographically matched between Sakhalin Island and southern Vancouver Island (during April and May); (2) two whales genetically matched from samples off of Sakhalin and off of Santa Barbara, California (March);

(3) thirteen whales photographically matched between Sakhalin Island and San Ignacio Lagoon, Mexico; and (4) three satellite-tagged whales that migrated east from Sakhalin Island to the west coast of North America. NMFS Ex. 3-61, at 2 Fig. 1 (Mate *et al.* 2015). Additional matching analyses are ongoing, and this work brings the total number of gray whales that have been recorded both at Sakhalin Island and in the eastern North Pacific to at least 30. Telemetry studies in 2010 to 2012 provide evidence of three whales migrating during the winter from the western North Pacific to the eastern North Pacific, with one whale tracked from the western North Pacific to Baja Mexico and back to the western North Pacific over the course of 408 days (August 2011 to October 2012). NMFS Ex. 3-60 (Mate *et al.* 2011); NMFS Ex. 3-62 (Marine Mammal Institute 2012).

35. Based on data showing that significant mtDNA and nuclear DNA differences exist between samples of whales summering in the western North Pacific and samples of those summering in the eastern North Pacific (NMFS Ex. 3-59 (Lang *et al.* 2011b)), and the fact that gray whales in the western and eastern North Pacific have exhibited different rates of recovery and levels of abundance following over-exploitation as a result of commercial harvest (NMFS Ex. 3-63 (Rugh *et al.* 1999); NMFS Ex. 3-64 (Swartz *et al.* 2000); NMFS Ex. 3-65 (Swartz *et al.* 2006)), NMFS has concluded that the gray whales identified the western North Pacific are members of the WNP gray whale stock that migrate to areas previously thought to have been occupied only by ENP gray whales.

36. The 2016 WNP gray whale SAR provides an abundance estimate of 140 non-calf animals in 2012. Bettridge Decl. ¶ 22. A more recent population assessment for the WNP stock estimates the population at 200 non-calf animals, with a 95 percent confidence interval of 187 to 212 individuals. NMFS Ex. 3-66, at 7 (Cooke 2018). The stock is estimated to have increased

from 1995 through 2015 at a rate of about five percent annually. *Id.* The 2016 SAR for the WNP stock calculates a PBR for U.S. waters of 0.06 whales per year or one whale every 17 years. Bettridge Decl. ¶ 22.

37. As with PCFG whales, WNP whales can be individually identified based on photographs. The primary catalogs for identifying WNP whales are the Western North Pacific Catalog I, often referred to as the U.S.-Russia Catalog, and the Western North Pacific Catalog II. Catalog I is curated by the Kamchatka Branch of the Pacific Institute of Geography, Russian Academy of Sciences, and Catalog II is curated by the National Scientific Centre for Marine Biology (formerly Institute of Marine Biology), Vladivostok, Russia. The Institute of Marine Biology also curates a Kamchatka Catalog, which contains additional WNP whale photographs. The International Whaling Commission is currently facilitating the development of a unified WNP catalog and related database to be held under the auspices of the IWC. *See* NMFS Ex. 3-67, at 5 (IWC 2017). In addition to these curators, researchers at Cascadia are capable of performing identifications of WNP whales with these catalogs. J. Calambokidis, Cascadia Research Collective, personal communication, Jan 23, 2017.

EFFECTS OF THE PROPOSED WAIVER AND REGULATIONS TO THE ENP GRAY WHALE STOCK

ABUNDANCE

38. I have reviewed and am familiar with NMFS's proposed waiver and regulations that would authorize the Makah Tribe to conduct a limited hunt for ENP gray whales. Under the proposed regulations, the maximum potential mortality of ENP gray whales would be three whales in even-year hunts and two whales in odd-year hunts or 2.5 whales per year on average, based on the strike limits. Over the 10-year duration of the proposed regulations, the maximum mortality of ENP gray whales would be 25.

39. Loss of 2.5 whales per year from the ENP stock would represent an average annual reduction of 0.009 percent. A total mortality of up to 25 whales over 10 years represents about one-tenth of one percent of the ENP stock, or 0.09 percent of the population of approximately 27,000 animals. The PBR level for the ENP stock from the 2016 SAR is 624, and based on the updated ENP stock abundance data, is estimated as 801 in the draft 2017 SAR. Bettridge Decl. ¶ 23. The 2016 SAR estimates average annual human-caused mortality and serious injury, including from the Chukotkan hunt, of 133 whales, and the draft 2017 SAR provides an estimate of 138 whales. *Id.* The level of mortality that could occur under the proposed hunt is a small fraction of the annual variability of the stock's abundance (between around 16,000 – 27,000 animals since the mid-1990s) and well below PBR estimates.

40. In my professional judgment, based on the best available scientific information, the level of mortality that could occur under the proposed waiver and regulations would have no discernable effect on the ENP stock's abundance or rate of growth and no effect on the ENP gray whale stock's abundance relative to OSP.

41. The proposed removal of an average of 2.5 ENP gray whales per year and maximum of five strikes in any calendar year is within the catch limits allocated by the IWC and defined in the bilateral agreement between the United States and Russia.

42. In 2018, the IWC Standing Work Group on Aboriginal Subsistence Whaling Management Procedures (AWMP) completed testing of the strike limit algorithm for ENP gray whales and concluded that harvest levels, including the U.S. proposal for a Makah tribal hunt, meet the IWC's conservation objectives for aboriginal subsistence whaling. NMFS Ex. 3-43, at 17-23 (IWC 2018b). After modelling the best available data, the AWMP agreed that the proposed hunt management plan for a Makah tribal hunt meets the IWC conservation objectives

for ENP gray whales as well as for PCFG and WNP whales. NMFS Ex. 3-43, at 17-23 (IWC 2018b). The IWC SC supported this conclusion. *Id.*

43. Further, as described in paragraph 9 above, the United States has a long-standing practice of transferring any unused IWC quota for ENP gray whales to the Russian Federation for use by Chukotkan native hunters, under the bilateral agreement between the two countries. As there is no reason to expect the United States to alter this practice in the future, the net effect on the ENP gray whale stock likely would be the same with or without the proposed waiver and regulations.

DISTRIBUTION AND MIGRATORY MOVEMENTS

44. Under the proposed regulations, some whales would be approached by hunt vessels, and some would be subjected to unsuccessful strike attempts or training harpoon throws, but would not be struck or killed. Hunt vessels proposed for use by the Tribe include a canoe and a motorized chase vessel.

45. The proposed regulations would allow a maximum of 353 approaches of ENP gray whales per calendar year by tribal training or hunting vessels, resulting in a maximum of 3,530 approaches over the 10 years of the regulations. Of the 353 annual approaches, not more than 142 per year could be approaches of PCFG whales. The regulations define an “approach” as causing a hunting or training vessel to be within 100 yards (91 meters) of a gray whale.

46. Based on my personal experience and research, I am familiar with how gray and other baleen whales react to vessel approaches. For example, I have spent nearly 30 years approaching whales and dolphins from small boats and ships for research purposes. Much of this work has been on baleen whales, particularly gray whales, and I have witnessed reactions or the lack thereof firsthand. Individual vessel approaches are likely to elicit a range of reactions from whales, from showing no response to whales diving, exhaling underwater and exposing only

their blowholes, fluke slapping, or changing direction and speed. Based on the literature (see, for example, the 2015 DEIS Sections 3.4 and 4.4) and my firsthand experience, these changes in whale behavior are generally short-term, meaning they do not have a lasting effect on the whale's health or behavior.

47. As an example, according to Calambokidis *et al.* (2017), between 1996 and 2015, researchers photographed 21,235 gray whales representing 1,638 unique individuals between southern California and Kodiak Island, an area that overlaps the PCFG range. NMFS Ex. 3-33. Obtaining a photograph of sufficient quality to make an identification requires a close approach. Notwithstanding these close approaches, ENP gray whales, including PCFG whales, continue to use these areas. Similarly, despite over a hundred gray whales being pursued and killed in native hunts off Chukotka each year (many of which are killed during the summer feeding months), there has not been a discernible change in the availability and location of hunted whales in that region. *See* NMFS Ex. 3-68, 3 (Zagrebelnyy 2018); NMFS Ex. 1-7, at 28 (NMFS 2019a). Based on the foregoing information and my firsthand observations, in my professional judgement 353 approaches of ENP gray whales per year, including up to 142 approaches per year of PCFG gray whales, would not have a lasting effect on the health or behavior of the affected whales.

48. The proposed regulations would also limit unsuccessful strike attempts and training harpoon throws, combined, to 18 during an even-year hunt and 12 during an odd-year hunt. Over the course of the 10 years of the regulations, there could be 90 unsuccessful strike attempts and training harpoon throws during even-year hunts and 60 during odd-year hunts (for a total of 150). An unsuccessful strike attempt, as defined in the regulations is an attempted strike that does not penetrate the skin of the whale. A training harpoon throw is defined as an attempt

to contact a gray whale with a blunted spear-like device that is not capable of penetrating the whale's skin.

49. Because an unsuccessful strike attempt or training harpoon throw would not penetrate a whale's skin, it would not result in death of the affected animal. It would likely result in temporary disturbance, but would not be expected to have a lasting effect on the whale's health or behavior, because of the whale's thick skin and blubber layer and the requirement to pad or blunt the tip of the training harpoon. It is uncertain how whales would react to unsuccessful strike attempts and training harpoon throws, but their reactions could be similar to those of whales that are tagged or biopsied for research purposes. In these instances, tags and biopsy darts are projected at whales using air-powered rifles or crossbows. With the exception of suction-cup tags, tracking devices are attached with cutting blades. In the case of biopsy sampling, a small coring device is used. In my experience and based on the available literature, tagging or biopsying whales elicits a range of responses from subtle to overt, including a brief startle or flinch, fluke slapping, quick submergence, rapid swimming, and breaching. *See, e.g.*, NMFS Ex. 3-69 (Harvey and Mate 1984); NMFS Ex. 3-70 (Clapham and Mattila 1993); NMFS Ex. 3-71 (Gauthier and Sears 1999).

50. Based on the best available scientific information, it is my professional opinion that any changes in gray whale behavior due to an unsuccessful strike attempt or training harpoon throw would likely be short-term and not have more than temporary effect on the affected whale's health or behavior. Given these considerations, and the relatively small number of training harpoon throws and unsuccessful strike attempts allowed under the proposed regulations, it is reasonable to expect that whales exposed to these hunt-related activities would experience them as temporary and localized events.

51. Even-year hunts and training exercises conducted from December through May would encounter mostly migrating whales that pass through the ocean portion of the Makah U&A. Migrating whales would be able to transit the widest portion of the Makah U&A (approximately 32 miles or 51 km north-south) in several hours. *See* NMFS Ex. 3-11 (Jones and Swartz 2002). As explained in the Declaration of Chris Yates, filed herewith, during even-year hunts, adverse weather conditions in the Makah U&A in winter and early spring coupled with shorter periods of daylight would keep most hunts and training exercises close to shore and of shorter duration than during the summer. It is reasonable to expect that the relatively small number of migrating whales subjected to non-lethal hunt encounters, including hunting or training approaches, unsuccessful strike attempts, or training harpoon throws, during the migration season would experience the encounter as temporary and localized near-shore events that would otherwise not affect their migration.

52. Odd-year hunts during July through October would likely encounter whales exhibiting feeding behavior, including milling in small, localized areas close to shore and typically within three miles (five km) of shore. NMFS Ex. 3-13 (Green *et al* 1992); NMFS Ex. 3-31 (Darling 1984); NMFS Ex. 3-72 (Sumich 1984); NMFS Ex. 3-73 (Mallonée 1991); NMFS Ex. 3-74 (Dunham and Duffus 2001); NMFS Ex. 3-75 (Scordino *et al.* 2011). Some animals have been seen clustering relatively far offshore (12-16 miles or 19-26 km) but these sightings are considered unusual. *See* NMFS Ex. 3-76 (Calambokidis *et al.* 2009). During summer hunts and training exercises, most gray whales would be found within the PCFG range from northern California to northern Vancouver Island, of which the hunt area is a small proportion (less than five percent of the coastline in the PCFG range). Whales are known to focus on specific areas within this range but also move extensively in search of food. NMFS Ex. 3-77 (Calambokidis *et*

al. 1999); NMFS Ex. 3-27 (Calambokidis *et al.* 2004);NMFS Ex. 3-78 (Calambokidis *et al.* 2014). The effects of hunt activities on feeding whales are likely to be temporary and limited to relatively small areas, resulting in negligible impacts on overall feeding opportunities and the nutritional state of the whales.

53. I am familiar with the provisions in the proposed regulations intended to limit the impacts of a tribal hunt on PCFG whales. The regulations limit the number of overall strikes of PCFG whales to 16 over the 10-year duration of the proposed waiver, and only 8 of those strikes may be of females. The strike limit on PCFG females is a precautionary measure given recent evidence that PCFG whales may be recruited through maternally-directed site fidelity (see paragraph 18 above), and based on the latest genetic data indicating a 1:1 sex ratio for PCFG whales. *See* NMFS Ex. 1-7, at 47 (NMFS 2019a).

54. Although the proposed waiver and regulations allow up to 16 strikes on PCFG whales over 10 years (average 1.6 whales per year), the actual number of PCFG whales killed is likely to be lower. As explained in the Yates Declaration, the proposed regulations would count all whales struck during odd-year hunts as PCFG whales, which is a conservative assumption. Currently, the best available estimate is that PCFG whales comprise approximately 48 percent of whales present in the hunt area during the months of odd-year hunts, so assuming that all strikes (10) were used, a total of 4.8 PCFG whales would be struck during odd-year hunts over 10 years. During even-year hunts, we estimate that PCFG whales comprise approximately 28 percent of whales in the hunt area. If all strikes (15) were used during even year hunts, a total of 4.2 PCFG whales would be struck over 10 years. Combining these totals provides an estimate of nine PCFG whales struck over the waiver period.

55. As explained in paragraph 27 above, PCFG abundance has increased by an average of 3.5 whales per year based on data from 2002 through 2015. This level of recruitment would exceed the level of removals authorized under the proposed regulations, meaning we would expect PCFG abundance to remain relatively stable or increase slightly, assuming that no broader environmental or ecological perturbations occur, over the duration of the proposed waiver.

56. In addition to the seasonal strike limits and the 10-year PCFG strike limits, the proposed regulations would not allow hunting in a given season if the estimated PCFG abundance for that season is below 192 whales, or if the minimum abundance estimate is below 171 whales. Published population estimates typically lag one or more years behind the most currently available survey data, so for purposes of the regulations, estimates for an upcoming hunting season would be projected using a population forecast model fit to the time series of data. The forecast model is explained in the Moore Declaration. The threshold values of 192 (and 171) represent the point estimate of PCFG abundance (and associated minimum 20th percentile estimate) in 2007. These thresholds represent the lowest values estimated for the population during the recent period of stability in abundance that started in 2002. Exhibit 3-33 (Calambokidis *et al.* 2017).

57. As explained in paragraphs 29 through 32 above, I am familiar with photo and genetic identification techniques for whales and with the PCFG catalogs and photo-matching expertise available through the Cascadia Research Collective. I have also reviewed the *NMFS Protocol for Identifying Gray Whales Encountered in Makah Hunts* proposed for use in managing the Makah hunt. NMFS Ex. 1-9 (NMFS 2019b). Based on my expertise, I conclude

that the photo-identification measures in the proposed regulations and the NMFS protocol are reasonable, feasible, and reliable methods for managing the strike limits for PCFG whales.

58. Under the proposed regulations, up to 142 PCFG whales annually could be approached by hunt vessels, and some PCFG whales would be subjected to unsuccessful strike attempts or training harpoon throws. There is the possibility that some of these encounters would be repeat encounters with the same whale. For the reasons described in paragraphs 44-50 above, I would not expect these approaches, unsuccessful strike attempts, and training harpoon throws to result in more than minor, temporary disturbance to the affected animals or to cause the affected whales to abandon the PCFG feeding area.

59. Based on the information above and my conclusions in paragraphs 40, 47, 50-52, and 58, it is my professional opinion that the proposed waiver and regulations would not have a meaningful effect on the distribution or migratory movements of the ENP gray whale stock, including distribution within the PCFG range.

BREEDING HABITS

60. As explained in paragraph 14 above, gray whale mating can occur throughout the southward migration. Under the proposed waiver and regulations, the expected time that hunting or hunt training would likely overlap with gray whale breeding would be in December-January. As explained in the Yates Declaration, NMFS expects that few if any hunt activities would occur in December-January due to inclement weather. While it is possible that hunt activities could occur in December-January and could encounter mating whales, I would not expect any adverse effects to the ENP stock due to the small portion of the migration corridor where hunt activities could occur, the limited level of hunt activity likely to occur, and given that any whales disturbed

but not struck would likely have additional opportunities to mate throughout the remainder of the southbound migration season.

EFFECTS OF THE PROPOSED WAIVER AND REGULATIONS TO WNP GRAY WHALES

61. As explained in paragraph 34 above, researchers have documented the presence of some WNP whales in the eastern North Pacific Ocean during the winter/spring migration season, including near the area where hunting would occur under the proposed waiver and regulations. I am familiar with the provisions in the proposed regulations intended to limit risks to WNP whales.

62. To assist NMFS in evaluating the risk to WNP whales from the proposed regulations and also at the request of the IWC SC, Dr. Jeffrey Moore and I conducted an analysis of the likelihood of Makah hunters encountering a WNP whale during an authorized hunt. We conducted this analysis first in 2013, and again in 2018 based on revisions made by NMFS to the initial hunt proposal. We published our most recent results in a NOAA Technical Memorandum. NMFS Ex. 4-8 (Moore and Weller 2018). Dr. Moore's Declaration explains in detail the results of our analysis.

63. The analysis in Moore and Weller (2018) addresses the risk of Makah hunters encountering a WNP gray whale during the December-May migration season. There is no evidence that WNP gray whales would be present in the hunt area during the summer/fall feeding season, when we expect that WNP gray whales would be feeding in the western North Pacific. Although we do not expect a WNP gray whale to be encountered by hunters during summer/fall odd-year hunt season, the proposed regulations establish photo-identification requirements, so that NMFS would look for matches between the WNP catalogs and any whales struck during odd-year hunts, and hunting would cease if NMFS determined that a WNP gray whale had been struck. Genetic data would also be used if available. For the reasons described

in paragraphs 29-32 above, it is my professional opinion that the proposed photo-identification measures are a reasonable and reliable method for determining whether a WNP gray whale has been struck.

64. As explained in the Declaration of Dr. Moore, our modelling indicated that Makah tribal hunters would approach about 14 WNP gray whales over the 10 years of the regulations, assuming that the full number of approaches were made each year, and all of them, including training approaches, occurred between December 1 and May 31, when WNP gray whales could be present in the hunt area. NMFS Ex. 4-8, at 5 note 3 (Moore and Weller 2018). This is an unlikely scenario. Realistically, we would expect a substantial number of approaches to occur during the summer and fall, when hunting conditions are more favorable *Id.*; *see* Yates Decl. ¶ 66. However, even if 1.4 WNP gray whales per year were approached by tribal hunters, I would not expect these approaches to have a lasting effect on the approached whale's health or behavior for the reasons explained in paragraphs 44-47 above.

65. In addition to being approached, there is about a 30 percent probability that one WNP whale would be subjected to an attempted strike or training harpoon throw over the 10 years of the regulations. If this were to occur, for the reasons explained above (see paragraphs 48-50), I would not expect it to lead to mortality injury, or more than temporary disturbance to the affected animal.

66. The IWC has not established a catch limit for WNP gray whales. The IWC recently reviewed the potential impact of the proposed waiver and regulations on WNP gray whales and, as described in paragraph 42 above, concluded the proposal meets the IWC conservation objectives for this group. NMFS Ex. 3-43 (IWC 2018b).

EFFECTS OF THE PROPOSED WAIVER AND REGULATIONS ON THE MARINE ECOSYSTEM

67. As stated in paragraph 1 above, I am familiar with the policies and requirements of the MMPA, including the policy that marine mammals should not be permitted to diminish beyond the point at which they cease to be a significant functioning element of their ecosystems and that the health and stability of marine ecosystems should be maintained.

68. As explained in paragraph 12 above, the range of the ENP gray whale stock is vast (*see* NMFS Ex. 1-7, at 3 Fig. 3 (NMFS 2019a)), and crosses many large marine ecosystems, including the Pacific Central American Coastal, California Current, Gulf of Alaska, and Bering and Chukchi Seas. The hunt area is within what oceanographers call the California Current System or Province (NMFS Ex. 3-10 (Sherman and Alexander 1989); NMFS Ex. 3-9 (Longhurst 1998)), a part of the North Pacific Gyre that moves cool ocean waters south along the western coast of North America, beginning off British Columbia, flowing southward past Washington, Oregon, and California, and ending off Baja California. Within that province, scientists regularly study and predict physical and biological features and processes in the northern California Current ecosystem, which is generally described as extending from northern California to Vancouver Island (*e.g.*, NMFS Ex. 3-79 (Field *et al.* 2001); NMFS Ex. 3-80 (Field *et al.* 2006); NMFS Ex. 3-81 (Hickey and Banas 2008); NMFS Ex. 3-82 (Sydeman and Elliott 2008); NMFS Ex. 3-83 (Harvey *et al.* 2017); NMFS Ex. 3-84 (Wells *et al.* 2017)), though some studies extend only to the U.S. Canada border in the north because of differing management regimes between the two countries (NMFS Ex. 3-79 (Field *et al.* 2001); NMFS Ex. 3-80 (Field *et al.* 2006)). The northern California Current ecosystem corresponds with the seasonal range of the PCFG and is the smallest recognized marine ecosystem that encompasses the area of the proposed hunt.

69. The ENP gray whale stock numbers between about 24,420 and 29,830, with a point estimate of 26,960. The potential impact of the proposed regulations on the ENP stock would thus be the annual removal of less than one tenth of one percent of the population. This level of removal, which is an order of magnitude less than the natural variability of the population, would be too small to have a perceptible effect on the functioning of ENP gray whales as an element of the large Pacific Central American Coastal, California Current, Gulf of Alaska, or Bering and Chukchi Seas ecosystems, or on the health of the ecosystems themselves.

70. For similar reasons, the proposed regulations will not result in gray whales ceasing to be a significant functioning element of the smaller northern California Current ecosystem. This ecosystem is shaped by dynamic, highly energetic, large-scale processes, including currents, upwelling, freshwater runoff, seasonal wind/storm patterns, and variable climate patterns such as El Niño, and the role of ENP gray whales in structuring these habitats is limited. *See* 2015 DEIS at 3-33 to 3-50. A hunt carried out under the proposed regulations is likely to result in a negligible decrease in the numbers of whales present in the northern California Current ecosystem or the northern Washington coastal environment. *Id.* at 4-51 to 4-61.

71. For the same reasons, although the northern Washington coast is not considered a separate ecosystem, even at the scale of the hunt area, the proposed hunt would not have a significant effect on the health or functioning of the marine environment. Also, the protections for PCFG whales in the proposed regulations would ensure that the hunt does not reduce PCFG abundance below recent stable levels, which would prevent any detectable changes in the marine habitat associated with the PCFG range.

72. As explained in the Yates Declaration, hunt-related activities associated with the proposed waiver and regulations could include operating motorized vessels and towing a carcass onto the shore, which would potentially disturb the pelagic, benthic, and nearshore environments. I would expect any such disturbance to be short-term and localized. The biological composition and productivity of these areas is diverse, variable, and generally patchily distributed owing to the dynamic physical processes, which differ across a spectrum of temporal and spatial scales. The dynamic nature of these processes results in variable biological productivity of both benthic and pelagic organisms. The magnitude of any hunt-related disturbance would also be extremely small in the northern California Current ecosystem or the northern Washington coastal environment, which are large areas characterized by constant, highly energetic, and large-scale physical disturbances as described above.

73. For these reasons, I conclude that hunt-related activities under the proposed waiver and regulations are unlikely to affect the health or stability of the marine ecosystem or the functioning of gray whales in their ecosystem at any relevant scale.

I declare under penalty of perjury under the laws of the United States that the foregoing is true and correct to the best of my knowledge, information, and belief.

David W. Weller

Dr. David Weller

Dated: 01 April 2019

DECLARATION OF DR. DAVID WELLER
EXHIBIT LIST

3-1	CV-D. Weller	Curriculum vitae for Dr. David Weller, NMFS
3-2	Weller et al. 2013	Weller, D. W., and 7 co-authors. 2013. Report of the National Marine Fisheries Service gray whale stock identification workshop. March 2013. NOAA Technical memorandum NOAA-TM-NMFS-SWFSC-507.
3-3	IWC 2018a	IWC. 2018a. International Convention for the regulation of Whaling, 1946. Schedule. As amended by the Commission at the 67th Meeting, Florianopolis, Brazil, September 2018.
3-4	Fominykh and Wulff 2018	Fominykh, I.B. and R. Wulff. 2018. Monitoring in 2019 by the Russian Federation and the United States of the Aboriginal Subsistence Quota for Gray Whales Set by the International Whaling Commission. Agreement signed November 28, 2018 and December 7, 2018.
3-5	Fominykh and Wulff 2017	Fominykh, I.B. and R. Wulff. 2017. Addendum to monitoring in 2017 by the Russian Federation and the United States of the Aboriginal Quota for Gray Whales Set by the International Whaling Commission. Agreement signed December 20 and 21, 2017.
3-6	Fominykh and Smith 2016	Fominykh, I.B. and R.F. Smith III. 2016. Addendum to monitoring by the Russian Federation and the United States of the aboriginal quota for gray whales set by the International Whaling Commission. Signed March 9, 2016, and February 29, 2016.
3-7	Ilyashenko and DeMaster 2012	Ilyashenko, V. and D. DeMaster. 2012. Addendum to monitoring in 2012 by the Russian Federation and the United States of the Aboriginal Quota for Gray Whales Set by the International Whaling Commission. Agreement signed July 6, 2012.
3-8	Ilyashenko and Hogarth 2007	Ilyashenko, V. and D. DeMaster. 2007. Addendum to monitoring in 2007 by the Russian Federation and the United States of the Aboriginal Quota for Gray Whales Set by the International Whaling Commission. Agreement signed May 20, 2007.
3-9	Longhurst 1998	Longhurst, A.R. 1998. Ecological Geography of the Sea, 1st edition. Academic Press Limited.
3-10	Sherman and Alexander 1989	Sherman, K. and L.M. Alexander 1989. Biomass Yields and geography of Large Marine Ecosystems, K Sherman and L.M. Alexander, 1989. ISBN: 0813378443.
3-11	Jones and Swartz 2002	Jones, M. L., and S. L. Swartz. 2002. Gray whale Eschrichtius robustus. Pages 524-36 in Perrin, W. F., B. Wursig, and J. G. M. Thewissen, editors. Encyclopedia of Marine Mammals. Academic Press, San Diego, CA.
3-12	Green et al. 1995	Green, G. A., J. J. Brueggeman, R. A. Grotefendt, and C. E. Bowlby. 1995. Offshore distances of gray whales migrating along the Oregon and Washington coasts, 1990. Northwest Science 69:223-227.

3-13	Green et al. 1992	Green, G. A., J. J. Brueggeman, R. A. Grotefendt, C. E. Bowlby, M. L. Bonnel, and K. C. Balcomb. 1992. Cetacean distribution and abundance off Oregon and Washington, 1989-1990. Pages 1-100 in J. J. Brueggeman, editor. Oregon and Washington Marine Mammal and Seabird Surveys. Final Rept. OCS study MMS 91-0093.
3-14	Pike 1962	Pike, G.C. 1962. Migration and feeding of the gray whale (Eschrichtius gibbosus). Journal of the Fisheries Research Board of Canada 19:815-838.
3-15	Rice and Wolman 1971	Rice, D. W. and A. A. Wolman. 1971. Life history and ecology of the gray whale, Eschrichtius robustus. American Society of Mammalogists Special Publication 3.
3-16	Jones and Swartz 1984	Jones, M. L., and S. L. Swartz. 1984. Demography and phenology of gray whales and evaluation of whale-watching activities in Laguna San Ignacio, Baja California Sur, Mexico. Pages 309-374 in Jones, M. L., S. L. Swartz, and S. Leatherwood, editors. The Gray Whale Eschrichtius robustus. Academic Press, Inc., Orlando, FL.
3-17	Swartz and Jones 1983	Swartz, S.L., and M.L. Jones. 1983. Gray Whale (Eschrichtius robustus) Calf Production and Mortality in the Winter Range. SC/34/PS4. Rep. Int. Whal. Comm. 33:503-507.
3-18	Sanchez Pacheco 1998	Sanchez Pacheco, J.A. 1998. Gray whale mortality at Ojo de Liebre and Guerrero Negro Lagoons, Baja California Sur, Mexico: 1984-1995. Marine Mammal Science 14(1):149-155.
3-19	Shelden et al. 2004	Shelden, K. E. W., D. J. Rugh, and A. Schulman-Janiger. 2004. Gray whales born north of Mexico: indicator of recovery or consequence of regime shift? Ecological Applications 14(6):1789-1805.
3-20	Berzin 1984	Berzin, A. A. 1984. Soviet studies on the distribution and numbers of the gray whale in the Bering and Chukchi Seas from 1968 to 1982. Pages 409-419 in Jones, M. L., S. L. Swartz, and S. Leatherwood, editors. The Gray Whale Eschrichtius robustus. Academic Press Inc., Orlando, FL.
3-21	Yablokov and Bogoslovskaya 1984	Yablokov, A.V. and L.S. Bogoslovskaya. 1984. A Review of Russian Research on the Biology and Commercial Whaling of the Gray Whale. Pages 465-485 in Jones, M. L., S. L. Swartz, and S. Leatherwood, editors. The Gray Whale Eschrichtius robustus. Academic Press Inc., Orlando, FL.
3-22	Clarke and Moore 2002	Clarke, J. T. and S. E. Moore. 2002. A note on observation of gray whales in the southern Chukchi and northern Bering Seas, August-November, 1980-89. Journal of Cetacean Research and Management 4(3):283-288.
3-23	Moore et al. 2000	Moore, S. E., J. M. Grebmeier and J. R. Davies. 2000. Gray whale foraging habitat in the northern Bering Sea: A GIS Based retrospective summary. Report presented to the International Whaling Commission SC/52/E3.
3-24	Moore et al. 2003	Moore, S. E., J. M. Grebmeier, and J.R. Davies. 2003. Gray whale distribution relative to forage habitat in the northern Bering Sea:

		current conditions and retrospective summary. Canadian Journal of Zoology 81:734-742.
3-25	Highsmith et al. 2007	Highsmith R. C., K. O. Coyle, B. A. Bluhm, and B. Konar. 2007. Gray Whales in the Bering and Chukchi Seas. Pages 303-313 in Estes, J., D. P. DeMaster, D. F. Doak, T. M. Williams, and R. L. Brownell, editors. Whales, Whaling, and Ocean Ecosystems. University of California Press, Berkley, CA.
3-26	Calambokidis et al. 2002	Calambokidis, J., J. D. Darling, V. Deecke, P. Gearin, M. Gosho, W. Megill, C. M. Tombach, D. Goley, C. Toropova, and B. Gisborne. 2002. Abundance, range and movements of a feeding aggregation of gray whales (Eschrichtius robustus) from California to southeast Alaska in 1998. Journal of Cetacean Research and Management 4(2):267-276.
3-27	Calambokidis et al. 2004	Calambokidis, J., R. Lumper, J. Laake, M. Gosho, and P. Gearin. 2004. Gray whale photographic identification in 1998-2003: collaborative research in the Pacific Northwest. Final Report prepared for National Marine Mammal Laboratory, Seattle, WA.
3-28	Darling et al. 1998	Darling, J. D., K. E. Keogh, and T. E. Steeves. 1998. Gray whale (Eschrichtius robustus) habitat utilization and prey species off Vancouver Island, B.C. Marine Mammal Science 14(4):692-720.
3-29	Moore et al. 2007	Moore, S. E., K. M. Wynne, J. C. Kinney, and J. M. Grebmeier. 2007. Gray whale occurrence and forage southeast of Kodiak Island, Alaska. Marine Mammal Science 23(2): 419-428.
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3-83	Harvey et al. 2017	Harvey, C.N., and 36 co-authors. 2017. Ecosystem Status Report of the California Current for 2017: A Summary of Ecosystem Indicators Compiled by the California Current Integrated Ecosystem Assessment Team (CCIEA). U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-139. https://doi.org/10.7289/V5/TM-NWFSC-139
3-84	Wells et al. 2017	Wells, B.K., and 43 co-authors. 2017. State of the California Current 2016-2017: Still anything but “normal” in the north. CalCOFI Rep., Vol. 58, 2017.

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EDUCATION, AFFILIATION AND RELEVANT EXPERIENCE

Education

1998
Ph.D. Wildlife & Fisheries Sciences, Texas A&M University

1991
M.A. San Diego State University

1986
B.A. University of Hawaii

Institutional Affiliation

1998-2019
Southwest Fisheries Science Center, NOAA, NMFS - *Research Wildlife Biologist (Marine Mammals)*

Professional Experience

2017-2019
International Whaling Commission - *Science Advisor to U.S. Commissioner*

2018-2019
International Whaling Commission – *Chairman, Ship Strike Working Group*

2006-2019
International Union for Conservation of Nature (IUCN) - *Member, IUCN Western Gray Whale Advisory Panel*

2002-2019
International Whaling Commission - *Member, U.S. Delegation to the IWC Scientific Committee*

1998-2019
San Diego State University - *Adjunct Professor*

2012-2013
NOAA Task Force on Gray Whale Stock Identification - *Chairman*

2007-2008
Cuyamaca College - *Instructor of Oceanography*

2003-2004
Journal of Mammalogy - *Associate Editor*

PEER-REVIEWED PUBLICATIONS, BOOK CHAPTERS AND BOOKS (2008-2018+)

Guazzo, R.A., **Weller**, D.W., Europe, H.M., Durban, J.W., D'Spain, G.L. and Hildebrand, J.A. In Review. Cue rates of migrating eastern North pacific gray whales estimated from acoustic recordings, infrared camera images and visual sightings. Scientific Reports.

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Burkanov, V.N., Lowry, L.F., **Weller**, D.W. and Reeves, R.R. 2017. Entanglement risk to western gray whales in Russian Far East fisheries. Paper SC/67a/HIM11 presented to the Scientific Committee of the International Whaling Commission, May 2017.

Cooke, J.G., **Weller**, D.W., Bradford, A.L., Sychenko, O.A., Burdin, A.M., Lang, A.R. and Brownell, R.L., Jr. 2017. Population assessment update for Sakhalin gray whales with reference to stock identity. Paper SC/67a/NH11 presented to the Scientific Committee of the International Whaling Commission, May 2017.

Durban, J.W., **Weller**, D.W. and Perryman, W.L. 2017. Gray whale abundance estimates from shore-based counts off California in 2014/2015 and 2015/2016. Paper SC/A17/GW/06 presented to the Scientific Committee of the International Whaling Commission, May 2017.

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PROFESSIONAL MEMBERSHIPS AND ACTIVITIES

Member - Society for Marine Mammalogy, Honor Society of Phi Kappa Phi

Reviewer - Academic Press, Animal Behaviour, Animal Behavior and Cognition, Aquatic Mammals, Bulletin of the Southern California Academy of Sciences, Canadian Journal of Fisheries and Aquatic Sciences, Evolutionary Biology, Fishery Bulletin, Frontiers in Endocrinology, International Union for Conservation of Nature (IUCN), Journal of Cetacean Research and Management, Journal of Mammalogy, Latin Journal of Aquatic Mammals, Mammalia, Marine Biology, Marine Mammal Science, National Science Foundation, PLOS ONE, Raffles Bulletin of Zoology, Scientia Marina

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U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
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NOAA Technical Memorandum NMFS

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REPORT OF THE NATIONAL MARINE FISHERIES SERVICE GRAY WHALE STOCK IDENTIFICATION WORKSHOP

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U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Southwest Fisheries Science Center

NOAA Technical Memorandum NMFS

The National Oceanic and Atmospheric Administration (NOAA), organized in 1970, has evolved into an agency that establishes national policies and manages and conserves our oceanic, coastal, and atmospheric resources. An organizational element within NOAA, the Office of Fisheries is responsible for fisheries policy and the direction of the National Marine Fisheries Service (NMFS).

In addition to its formal publications, the NMFS uses the NOAA Technical Memorandum series to issue informal scientific and technical publications when complete formal review and editorial processing are not appropriate or feasible. Documents within this series, however, reflect sound professional work and may be referenced in the formal scientific and technical literature.

SWFSC Technical Memorandums

SWFSC Technical Memorandums are available online at the SWFSC web site (http://swfsc.noaa.gov). Copies are also available from the National Technical Information Service, 5285 Port Royal Road, Springfield, VA 22161 (http://www.ntis.gov).

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Executive Summary

The Marine Mammal Protection Act of 1972 (MMPA) requires that the National Marine Fisheries Service (NMFS) and the Fish and Wildlife Service develop stock assessment reports for all marine mammal stocks in waters under U.S. jurisdiction. NMFS considers stock structure as part of these assessments and has developed guidance for delineating separate population stocks under the MMPA. A single population stock of gray whales (*Eschrichtius robustus*), referred to as the eastern North Pacific (ENP) stock, is presently recognized in U.S. waters (Carretta *et al*. 2013). New information, however, suggests the possibility of recognizing two additional stocks of gray whales in U.S. waters: the Pacific Coast Feeding Group (PCFG) and the western North Pacific (WNP) stock. To evaluate the currently recognized and potentially emerging characterization of gray whale stock structure, NMFS established a scientific Task Force (TF). The overarching objective of this TF was to provide an objective scientific evaluation of gray whale stock structure as defined under the MMPA and implemented through the NMFS Guidelines for Assessing Marine Mammal Stocks (GAMMS; NMFS 2005). More specifically, the TF was convened to provide advice on the primary question – "*Is the PCFG a "population stock" under the MMPA and GAMMS guidelines"?* In addition, the TF was asked to provide advice on a question of developing importance – "*Is the WNP stock a "population stock" under the MMPA and GAMMS guidelines"?*

Both of these questions have immediate management implications, including: (1) how future NMFS stock assessment reports will address gray whale stock structure in the North Pacific, and (2) how to interpret any new information in the context of the Makah Indian Tribe's MMPA waiver request to resume hunting gray whales off Washington State, USA.

As the agency lead for gray whale science, the Southwest Fisheries Science Center convened a meeting of the aforementioned TF from 31 July to 2 August 2012. Using the best scientific information available at the time of the workshop, the TF worked to: (1) review new information relevant to gray whale stock structure, and (2) provide advice on revisions to stock structure so as to be available for management consideration. The TF conducted its work as an advisory rather than prescriptive body and therefore its conclusions should viewed as scientific advice based on review and discussion of the available science.

The implications of new data pertinent to stock structure, including considerable information related to the PCFG and WNP gray whales, were thoroughly reviewed during the workshop. Evaluating the new findings relevant to the status of the PCFG proved particularly complex. After review of results from photo-identification, genetics, tagging, and other studies within the context of the GAMMS guidelines (NMFS 2005) there remains a substantial level of uncertainty in the strength of the lines of evidence supporting demographic independence of the PCFG. Consequently, the TF was unable to provide definitive advice as to whether the PCFG is a population stock under the MMPA and the GAMMS guidelines. Members of the TF ranged in their opinions from strongly agreeing to strongly disagreeing about whether the PCFG should be recognized as a separate stock.

In the case of WNP gray whales, the work of the TF was more straightforward. The mitochondrial DNA and nuclear DNA genetic differentiation found between the WNP and ENP stocks provided convincing evidence that resulted in the TF providing unambiguous advice that the WNP stock should be recognized as a population stock pursuant to the GAMMS guidelines and the MMPA.

Additional research may narrow the uncertainty associated with the question of whether the PCFG should be recognized as a population stock. To work towards this objective, the TF recommended further investigation of recruitment into the PCFG. Presently, both the photo-identification and genetics data indicate that the levels of internal versus external recruitment are comparable, but these are not quantified well enough to determine if the population dynamics of the PCFG are more a consequence of births and deaths within the group (internal dynamics) rather than related to immigration and/or emigration (external dynamics). The TF offered a number of research recommendations, using the existing photo-identification and genetics datasets, that could provide increased resolution on the issue of recruitment and, in turn, the question of stock identification.

While the need for additional data collection was apparent, especially with regard to recruitment into the PCFG, the purpose of the workshop was for the TF to determine whether the *existing* best available science was sufficient to advise that the PCFG be recognized as a population stock under the language of the MMPA and GAMMS guidelines. Therefore, the advice of the TF offered in this report should be viewed as a contemporary "snapshot" taken from an emerging and ever-changing body of knowledge regarding the PCFG.

The TF emphasizes that the PCFG is relatively small in number and utilizes a largely different ecosystem from that of the main ENP stock. While the status of the PCFG as a population stock has yet to be resolved, continued research on these whales should be undertaken with particular attention dedicated to collecting data relevant to the question of stock identification.

Table of Contents

List of Acronyms

AFSC	Alaska Fisheries Science Center
ALJ	Administrative Law Judge
AWMP	Aboriginal Whaling Management Procedure
BRT	Biological Review Team
DIPs	Demographically Independent Units
DPSs	Distinct Population Segments
EIS	Environmental Impact Statement
ENP	Eastern North Pacific
ESA	Endangered Species Act
FEMAT	Forest Ecosystem Management Assessment Team
GAMMS	Guidelines for Assessing Marine Mammal Stocks
HCM	Human Caused Mortality
HWE	Hardy-Weinberg equilibrium
IR	Implementation Review
IUCN	International Union for Conservation of Nature
IWC	International Whaling Commission
K	Carrying Capacity
Makah U&A	Makah Usual and Accustomed (Fishing Ground)
MMC	Marine Mammal Commission
MMPA	Marine Mammal Protection Act
MNPL	Maximum Net Productivity Level
MSA	Magnuson-Stevens Act
MSYR	Maximum Sustained Yield Rate
mtDNA	Mitochondrial DNA
nDNA	Nuclear DNA
NEPA	National Environmental Policy Act
NMFS	National Marine Fisheries Service
NOAA	National Oceanographic and Atmospheric Administration
NPS	Northern Puget Sound
NWR	Northwest Regional Office
OPR	Office of Protected Resources
OSP	Optimum Sustainable Population
PBR	Potential Biological Removal
PCFG	Pacific Coast Feeding Group
SAR	Stock Assessment Report(s)
SEFSC	Southeast Fisheries Science Center
SJF	Strait of Juan de Fuca
SRG	Scientific Review Group
SWFSC	Southwest Fisheries Science Center
SVI	Southern Vancouver Island
TF	Task Force
UME	Unusual Mortality Event
WNP	Western North Pacific

1. Introductory Remarks

Dr. Lisa Ballance, Director of the Marine Mammal and Turtle Division at Southwest Fisheries Science Center (SWFSC), welcomed the workshop participants. She noted that this workshop represented a significant event, in that it: (1) brings agency scientists together to review research that continues to evolve and reveal unexpected patterns, (2) provides results that will be relevant to management activities for the National Marine Fisheries Service (NMFS), and (3) typifies the ideal model for how NMFS works, illustrating science addressing management actions and highlighting the collaboration between NMFS scientists, regional offices, and headquarters.

The technical and scientific expertise required on the Task Force (TF) was determined by SWFSC in consultation with the NMFS Northwest Regional Office (NWR) and the NMFS Office of Protected Resources (OPR). TF members were experts in their respective fields with ample experience and ability to bridge scientific and policy issues related to marine mammal stock structure. Members of the TF included the following eight NMFS scientists:

Dr. Shannon Bettridge	NMFS – Office of Protected Resources
Dr. Robert L. Brownell, Jr.	NMFS – Southwest Fisheries Science Center
Dr. Jeffrey L. Laake	NMFS – Alaska Fisheries Science Center
Dr. Jeffrey E. Moore	NMFS – Southwest Fisheries Science Center
Dr. Patricia E. Rosel	NMFS – Southeast Fisheries Science Center
Dr. Barbara L. Taylor	NMFS – Southwest Fisheries Science Center
Dr. Paul R. Wade	NMFS – Alaska Fisheries Science Center
Dr. David W. Weller (Chairman)	NMFS – Southwest Fisheries Science Center

In addition to the TF, a number of agency scientists and NMFS affiliates (e.g., post-docs, contractors, etc.) attended the workshop to observe and provide information. These participants included: Eric Archer (SWFSC), Lisa Ballance (SWFSC), Laurie Beale (NOAA General Counsel), Jim Carretta (SWFSC), Donna Darm (NWR), Kirsten Erickson (NOAA General Counsel - by phone), Jason Foreman (NOAA General Counsel), Annette Henry (SWFSC), Aimee Lang (SWFSC), Karen Martien (SWFSC), Sarah Mesnick (SWFSC), Phil Morin (SWFSC), Vicki Pease (SWFSC), Bill Perrin (SWFSC), Wayne Perryman (SWFSC) and Steve Stone (NWR). At the request of the TF, several of these participants provided valuable information to the workshop in the form of expert knowledge, presentations and/or written documents. Aimee Lang and Annette Henry generously agreed to serve as workshop rapporteurs.

The agenda for the workshop was circulated amongst the TF for input in advance of the meeting (Appendix 1). It was agreed, however, that the agenda would serve to guide the workshop proceedings but be viewed as flexible so as not to constrain discussion. Documents for the workshop were made available on a file sharing website. Appendix 2 provides a list of the workshop documents available for review and consideration by the TF in preparation for the workshop.

1.1 Workshop objectives

NMFS presently recognizes a single stock of gray whales (*Eschrichtius robustus*) in U.S. waters that is referred to as the eastern North Pacific (ENP) stock (Carretta *et al*. 2013). New information, however, suggests the possibility of recognizing two additional stocks of gray whales in U.S. waters, including: (1) the Pacific Coast Feeding Group (PCFG) - defined as whales observed between 1 June to 30 November within the region between northern California and northern Vancouver Island (from 41°N to 52°N) and photo-identified within this area during two or more years (see section 3.3), and (2) western North Pacific (WNP) gray whales - defined as whales observed feeding during summer and fall off Sakhalin Island, Russia, and other areas in the WNP (see section 3.2). The main objective of the TF was to provide scientific advice regarding gray whale stock structure using the definitions given in the GAMMS guidelines (NMFS 2005; see also Moore and Merrick 2011). More specifically, the TF was convened to provide advice on two questions: (1) *Is the PCFG a "population stock" under the MMPA and GAMMS guidelines?*, and (2) *Is the WNP stock a "population stock" under the MMPA and GAMMS guidelines?* Both of these questions have immediate management implications, including: (1) how future NMFS stock assessment reports (SAR) will address gray whale stock structure in the North Pacific, and (2) how to interpret any new information in the context of the Makah Indian Tribe's MMPA waiver request to resume hunting gray whales off Washington State, USA.

1.2 Workshop relationship to stock assessment reports

At the request of the TF, Carretta (SWFSC) summarized the relationship of the workshop to future gray whale stock assessment reports (SARs). The current eastern North Pacific gray whale SAR (Carretta *et al*. 2013) provides a summary of present knowledge but is expected to evolve based on the input received at this workshop as well as from input from the scientific review groups (SRG)[1], NWR and OPR. The TF expected that the outcome of the workshop would influence how the SAR is structured in the future, including how various data sources (i.e., genetics, movements, distribution) are evaluated for future stock designation. The workshop report will also serve as a useful SRG background document on gray whale stock structure.

1.3 Workshop relationship to Makah waiver request

Newly available information from genetic, photo-identification and tagging studies suggests that more than one stock of gray whales may occur in U.S. waters (Lang *et al*. 2010; Frasier *et al.* 2011; Lang *et al.* 2011a; Lang *et al*. 2011b; Mate *et al*. 2011; Calambokidis *et al.* 2012; Weller *et al*. 2012). With that in mind, the TF requested that Darm (NWR) present a summary of the Makah Indian Tribe's request to hunt gray whales off northwest Washington State, USA.

The Makah's right to hunt whales is secured by the 1855 Treaty of Neah Bay, where the Makah ceded lands to the U.S. government but reserved the right to hunt, fish, seal and whale. The Ninth Circuit Court of Appeals decision in 2004 (Anderson v. Evans) held that for the Makah to exercise their right to hunt whales they must comply with the requirements of the MMPA. In 2005, the Makah requested authorization from NOAA/NMFS, under the MMPA and the Whaling Convention Act, to resume limited hunting of gray whales for ceremonial and subsistence purposes in the coastal portion of their usual and accustomed (U&A) fishing grounds off the coast of Washington State (NMFS 2008). The spatial overlap of the Makah U&A with the summer distribution of PCFG whales has management implications. The proposal by the Makah Tribe includes time/area restrictions designed to reduce the probability of killing a PCFG whale and to focus the hunt on whales migrating to/from feeding areas to the north.

The NWR was assigned responsibility for evaluating the Tribe's request under the MMPA and National Environmental Policy Act (NEPA) process. Section 101(a) of the MMPA imposes a

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[1] Pursuant to Sec. 117 of the MMPA, independent scientific review groups, representing Alaska, and the Pacific and Atlantic coasts, were established in 1994. These groups consist of individuals with expertise in marine mammal biology and ecology, population dynamics and modeling, commercial fishing technology and practices, and stocks taken under section 101(b).

moratorium on the take of all marine mammals, although the statute provides for certain exemptions allowing the take of marine mammals. Section 101(a)(3)(A) allows for a waiver of the take prohibition; this exemption applies to a specific stock and is only authorized to the extent provided for in the waiver. Determination of whether the waiver will be granted must be made based on the best scientific information, in consultation with the Marine Mammal Commission, and with due regard to the distribution, abundance, breeding habits, and movements of the stock in question. For the waiver to be granted there must also be a finding that the requested take is in accord with sound principles of resources protection and conservation as provided for in the MMPA.

Unlike most rulemaking by the agency, this determination will entail a formal rulemaking process in which the agency presents evidence before an administrative law judge (ALJ) to support the rule. This process may involve presenting evidence on the status of relevant stocks, including their optimum sustainable population level (OSP)[2], and whether the stocks are at or below that level (i.e., depleted).

Although the NWR made substantial progress in evaluating the waiver request during the past few years, this progress had been slowed by: (1) new information pertinent to the question of whether the PCFG is a separate stock, and (2) the potential implications of movements of whales between the WNP and ENP. Therefore, the advice of the TF will provide a collective “best professional judgment” useful to the ongoing evaluation of the waiver by the NWR.

In discussion, the TF asked Darm if there would be a potential need to get more than one waiver to the MMPA if it was determined that three stocks of gray whales occur in U.S. waters (i.e., ENP, PCFG and WNP stocks). In that case, Darm replied that there would be some possibility of needing to request multiple exemptions (waivers). However, the need for a waiver would be informed by the likelihood of take and obtaining a waiver for WNP gray whales (if the group is recognized as a stock) is highly unlikely given that they are listed as endangered under the Endangered Species Act (ESA) and as such, would be considered depleted under the MMPA.

2. Overview of MMPA Language, GAMMS Guidelines and Related Key Concepts

From the outset of the workshop, the TF concurred that it was important to review the existing language of the MMPA and GAMMS with regard to the definition of “population stock”. In addition, it was also agreed important to discuss three key concepts inherent to defining a population stock, including: (1) “demographic independence”, (2) “interbreed when mature”, and (3) “functioning element of the ecosystem”.

Under the MMPA, population stock (used interchangeably with “stock” and “population” hereafter) is the fundamental conservation unit. The MMPA (Sec. 3) defines population stock as: “*a group of marine mammals of the same species or smaller taxa in a common spatial arrangement, that interbreed when mature.*” The purposes and polices underlying the stated definition, as follows, are found in Sec. 2(2) and Sec. 2(6) of the MMPA:

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[2] The maximum net productivity level is described in the National Marine Fisheries Service's definition of "optimum sustainable population" (OSP) (50 CFR 216.3) as the abundance level that results in the greatest net annual increment in population numbers or biomass resulting from additions to the population due to reproduction and/or growth less losses due to natural mortality. Under the U.S. Marine Mammal Protection Act, populations above MNPL are considered to be at OSP; populations below MNPL can be designated as ‘depleted’ and are afforded a greater level of protection.

(1) *"[marine mammal] species and population stocks should not be permitted to diminish beyond the point at which they cease to be a significant functioning element in the ecosystem of which they are a part, and, consistent with this major objective, they should not be permitted to diminish below their optimum sustainable population."*

(2) *"… the primary objective of their management should be to maintain the health and stability of the marine ecosystem."*

Acknowledging the above definitions and objectives of the MMPA, the TF then considered the related guidelines contained in the "Definition of Stock" section of the GAMMS guidelines (NMFS 2005):

(1) *"For the purposes of management under the MMPA, a stock is recognized as being a management unit that identifies a demographically isolated biological population."*

(2) *"Demographic isolation means that the population dynamics of the affected group is more a consequence of births and deaths within the group (internal dynamics) rather than immigration or emigration (external dynamics). Thus, the exchange of individuals between population stocks is not great enough to prevent the depletion of one of the populations as a result of increased mortality or lower birth rates."*

The TF noted that within the broader field of population biology, the term "isolation" generally implies little or no exchange (emigration or immigration of individuals) between stocks and is a criterion commonly used to distinguish taxonomic units higher than that of a population (e.g., species, subspecies). In contrast, the GAMMS guidelines and definition of stock clearly allow for the "*exchange of individuals between population stocks"* (NMFS 2005), a distinction more in line with use of the term "demographic independence" rather than "demographic isolation". The use of the term "independence" as opposed to "isolation" is potentially confusing and has been noted by a number of NMFS reviewers and workshops (Eagle *et al*. 2008). To avoid this confusion, Eagle *et al*. (2008) suggested that the term "demographic isolation" be replaced by "demographic independence".

Moore (SWFSC) provided the TF with an overview of the GAMMS III workshop, convened by NMFS in February 2011, which also noted the potential confusion over the use of "isolation" as opposed to "independence". The GAMMS III workshop recommended revising the SAR guidelines to reflect that the intent of the GAMMS II guidelines (NMFS 2005) was to base stock identification on demographic independence as noted in Eagle *et al.* (2008) and proposed that the term demographic isolation be replaced with "demographic independence" as follows:

(1) *"For the purposes of management under the MMPA, a stock is recognized as being a management unit that identifies a demographically independent biological population."*

(2) *"Demographic independence means that the population dynamics of the affected group is more a consequence of births and deaths within the group (internal dynamics) rather than immigration or emigration (external dynamics). Thus, the exchange of individuals between population stocks is not great enough to prevent the depletion of one of the populations as a result of increased mortality or lower birth rates."*

In other words, the participants at the GAMMS III workshop viewed this as a semantic issue where the term demographic independence is a better description for the current GAMMS guidelines definition than is the term demographic isolation.

2.1 Discussion of "demographic independence"

This interpretation of "isolation" differs substantively from how it is used within the GAMMS guidelines definition above, wherein allowance is made for some level of exchange of individuals between stocks. The TF concurred that in spite of using the term "isolation", the actual definitions under the current GAMMS guidelines (see above) are more consistent with MMPA objectives to protect population stocks than with the objective of protecting just subspecies and species.

Given that the draft GAMMS guideline revisions from the GAMMS III workshop have not yet been formally approved, the TF agreed to use the current GAMMS guidelines definition (NMFS 2005) for the purposes of their discussions and deliberations but noted that the actual definition used in the two versions (for demographic isolation and demographic independence) is essentially the same in that neither implies true "isolation" within the context of the MMPA.

2.2 Discussion of "interbreed when mature"

Bettridge (OPR) presented a brief overview of relevant language under the MMPA and GAMMS guidelines pertaining to NMFS interpretation of "interbreed when mature". She explained that the draft second revision to the SAR guidelines (from the GAMMS II workshop held in Seattle in 2003) included a definition of interbreed when mature. This term was interpreted to mean cases in which either:

(1) "*mating occurs primarily among members of the same demographically isolated group*"

or

(2) "*the group migrates seasonally to a breeding ground where its members breed with members of the same group as well as with members of other demographically distinct groups which have migrated to the same breeding ground from a different feeding ground.*"

When comments were solicited on the draft GAMMS II guidelines (69 FR 67541, 18 November 2004), the Marine Mammal Commission (MMC) supported the aforementioned interpretations, but suggested that a more rigorous analysis was needed of how the revisions fit with the language of the MMPA. Additionally, the MMC stated that NMFS should develop criteria for applying the modified guidelines to determine when a population is demographically isolated to an extent that it is a discrete group that warrants recognition as a separate stock.

In its response to comments on this issue (70 FR 35397, 20 June 2005), NMFS stated that public comments were sufficient to raise questions about the proposed interpretation, and the agency removed the proposed text pertaining to "interbreed when mature" from the final GAMMS II guidelines.

Subsequent NMFS review and consultation with MMC staff and NOAA General Counsel suggest that the GAMMS II workshop definition of "interbreed when mature" is consistent with NMFS GAMMS guidelines and the review undertaken in Eagle *et al.* (2008, see below). In those forums NMFS has consistently interpreted a population stock not as one that is completely reproductively isolated but rather as something less restrictive.

Regarding the MMC request for scientific criteria for how much interbreeding would be consistent with the proposed GAMMS II guidelines definition, the TF noted that specific quantitative criteria would be impractical to apply consistently across all contexts of uncertain stock definition and that determining whether a population is demographically independent or an isolated unit would likely have to be conducted on a case-specific basis. Some TF members felt that the “interbreed when mature” component of the MMPA definition of stock should merely be viewed as a necessary but not sufficient criterion for defining a stock. In other words, individuals “in a common spatial arrangement” would not constitute a stock unless there is some interbreeding (satisfying the need criterion), but this would not preclude individuals of a stock from also breeding with members of other stocks.

For the purposes of the workshop, the TF agreed they would continue to interpret “interbreed when mature” consistent with “demographic independence” as suggested by Eagle *et al*. (2008) and GAMMS II (NMFS 2005), with the minor change of “isolation” being replaced with “independence”.

2.3 Discussion of “functioning element of the ecosystem”

Sec. 2 of the MMPA states that marine mammals are “resources of great international significance, esthetic and recreational as well as economic” and “that the primary objective of their management should be to maintain the health and stability of the marine ecosystem”. The TF therefore considered whether the functioning element of the ecosystem criteria is aesthetically or ecologically based (or both) but no clear resolution on how to best define functioning element of the ecosystem was reached by the TF.

The TF then focused its discussion on defining the ecosystem and appropriate scale of management with respect to gray whales. The TF agreed the matter was complex given the species’ seasonal use of different ecosystems. In general, the TF agreed that the Chukotka Peninsula/Bering Strait feeding areas were not part of the same ecosystem as that found off the Pacific Northwest and used by the PCFG. In discussion of this concept, it was noted by some TF members that even for the largest-scale classification system for marine ecosystems (Longhurst 1998, discussed in Moore and Merrick 2011), it could be argued that the PCFG is in a different ecosystem than other gray whales. Other TF members pointed out, however, that this was only true for part of the year, and that the interpretation was complicated because non-PCFG animals migrate through the area defined for PCFG whales and, in some cases, may feed there in a given year but not return in a subsequent year.

2.4 Additional information on the definition of “population” for marine mammals

In addition to applying the MMPA language and GAMMS guidelines definitions, the TF considered two documents relevant to the question of stock definition under the MMPA. In the first (Taylor 1997), simulation analyses were used to explore the potential consequences, in terms of the risk of violating MMPA ecosystem function objectives, of defining a population stock as a unit akin to an evolutionarily significant unit or reproductively isolated group. Briefly, this analysis considered scenarios in which a single reproductively isolated population was distributed as a network of discrete groups occupying distinct habitat areas throughout its range, with some level of dispersal between discrete groups. The major analytical finding was that, if allowable human caused mortality (HCM) for the entire population (i.e., sum of all discrete groups) were to act disproportionately on certain groups, those groups could be extirpated, depending on whether the amount of immigration from other groups was below a certain dispersal rate threshold (which varied with simulation conditions). In conclusion, to achieve MMPA objectives of maintaining marine mammals as “functioning elements of their ecosystem”, distinct groups should be managed as separate stocks if their connectivity to other groups via dispersal is low, although how low is context specific.

Taylor (1997) provides several examples (Figure 1) where localized removals lead to local extirpation which arguably violates the ecosystem goals of the MMPA. For all of the models tested, when dispersal fell below a few percentage of the population per year, recruitment into the population with HCM was insufficient to compensate for removal, and population levels declined below those sought by management objectives. Therefore, populations should be managed separately if dispersal between them is less than several percent per year.

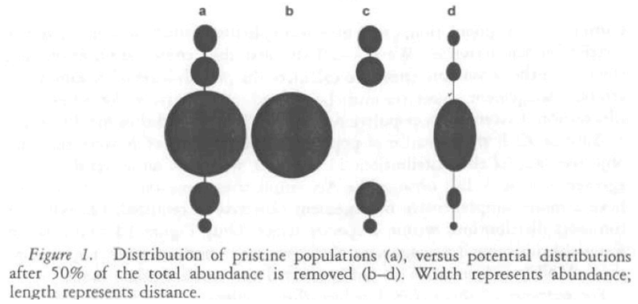

Figure 1. Distribution of pristine populations (a), versus potential distributions after 50% of the total abundance is removed (b–d). Width represents abundance; length represents distance.

Figure 1. Original figure from Taylor (1997).

Taylor (SWFSC) cautioned the TF, however, that it is impossible to have a "one number fits all" criterion and that a better approach would be to have an objective that states what is important in terms of maintaining the extent and connectivity of the range. There are some cases where it is obvious that a stock is no longer a functioning element of its ecosystem, such as example C in Figure 1 where the large central group is extirpated. Extirpation of the PCFG would be more analogous to removing one of the smaller groups outside of the main group (e.g., example B). Further discussion is needed to better define the intent of the MMPA with respect to maintaining marine mammals within different parts of their range.

The second document discussed by the TF, as pertains to the agency's definition of population stock, was the report of a 2006 workshop entitled "Conservation Units of Managed Fish, Threatened or Endangered Species, and Marine Mammals" (Eagle *et al.* 2008). This workshop was convened by NMFS with the objective of bringing together scientists, managers and policy advisers to discuss differences and recommend revisions to how NMFS defines units to conserve under three statutes – the MMPA, ESA and Magnuson-Stevens Act (MSA). The workshop sought to address two overarching questions: (1) why are conservation units different under the three statutes? and (2) is there a biological paradigm that can be used to explain the differences?

In brief, it was agreed by the participants of the 2006 workshop that the differences in how NMFS defines conservation units under the three statutes are appropriate given the differing objectives of the three laws. Under the ESA, major objectives are to prevent *species* extinction and preserve evolutionary potential. Thus, conservation units under this Act should be substantially reproductively isolated. Under the MMPA, objectives correspond to maintaining population and ecosystem goals. Therefore, conservation units align with demographically independent units (DIPs), which are demographically discrete from other populations but not necessarily genetically discrete due to a low but sufficient degree of interbreeding between them. Participants of the 2006 workshop concluded that while the GAMMS guidelines "*…clearly support the use of DIPs as stocks of marine mammals […] the MMPA does not indicate to what extent breeding should occur within a stock instead of among stocks*" and that future revisions to the GAMMS guidelines "*should, therefore, include a rationalization for recognizing DIPs as stocks in cases where males from one stock may breed with females from the same and other stocks*".

There was discussion amongst the TF regarding where to reasonably draw the line in defining small stocks, given that for some marine mammal species very small groups of animals could be considered DIPs. For example, individual pods of killer whales (*Orcinus orca*) could potentially be considered demographically independent. However, other TF members noted that the intent of the GAMMS guidelines was not to recognize very small population units – such as individual killer whale pods or a small group of animals occupying a small habitat fragment – as population stocks. It was similarly suggested that other criteria besides demographic independence, such as whether the unit can be considered a significant functioning element of the ecosystem, should also be considered in defining stocks. The TF understood that most biological "populations" and "stocks" do not exist as truly distinct groups, nor are individuals within the same population typically part of a truly panmictic group (Waples and Gaggiotti 2006). Rather, population differentiation occurs along a continuum, and placing discrete boundaries along this continuum for management purposes is a challenge. The TF acknowledged that marine mammal social structure can further complicate determining whether a unit should be considered demographically independent. In these areas of uncertainty, decisions will likely be case specific, and ultimately rely on scientific judgment and the factors identified for consideration in the MMPA and GAMMS guidelines.

The TF considered the report by Eagle *et al.* (2008) and the recommendations from that workshop as support for the NMFS interpretation of "interbreed when mature" as one that includes cases where individuals interbreed primarily within their stock but occasional interbreeding amongst stocks may occur and agreed to use such as the operational definition for the purposes of their work.

3. Overview of Eastern, Western and Pacific Coast Feeding Group Gray Whales

Like many species of baleen whales, gray whales exhibit seasonal movements between high-latitude summer feeding grounds and low- latitude wintering areas. The current distribution of this species is limited to the North Pacific, where a small western population (<150 individuals) and a much larger eastern population (~19,000 individuals) are recognized.(Reilly *et al.* 2008).

Lang (SWFSC) presented a brief overview of information on the biology of ENP, WNP, and PCFG gray whales. The purpose of this overview was not to discuss gray whale stock structure in detail but rather to provide a summary of relevant background information.

3.1 Eastern North Pacific (ENP) gray whales

During summer and fall most ENP whales feed in the Chukchi, Beaufort and northwestern Bering Seas (Figure 2). An exception is the relatively small number (100s) of whales that summer and feed along the Pacific coast between Kodiak Island, Alaska and northern California (Darling 1984; Calambokidis *et al.* 2002; 2012; Gosho *et al.* 2011). By late November, the southbound migration of the ENP stock is underway as whales begin to travel from summer feeding areas to winter calving areas off the west coast of Baja California, Mexico (Rugh *et al.* 2001; Swartz *et al.* 2006). The southbound migration is segregated by age, sex and reproductive condition (Rice and Wolman 1971). The northbound migration begins about mid-February and is also segregated by age, sex and reproductive condition.

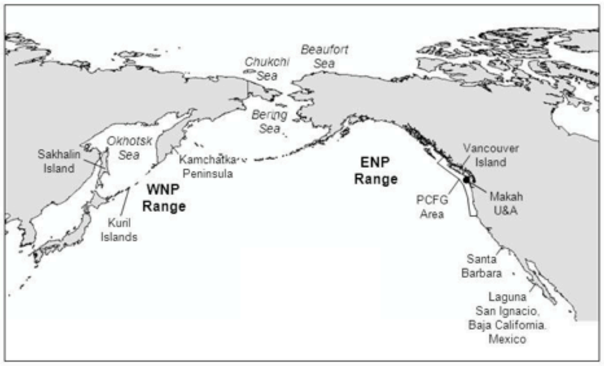

Figure 2. Geographic range of ENP, WNP and PCFG whales. In summer, WNP whales are typically found in feeding areas off the coasts of Sakhalin Island and the Kamchatka Peninsula, in Russia. Most ENP whales are typically found in summer north of St. Lawrence Island (in the northern Bering Sea), including the Bering Strait, the Chukotka Peninsula in Russia, the Chukchi Sea, and along the Beaufort Sea coast (north slope) of Alaska. Additional summer ENP feeding areas include Kodiak, AK, and areas between Southeast Alaska and Northern California. ENP whales migrate to the Baja Peninsula, Mexico in the autumn and return to feeding areas in the spring. The region used by the PCFG is defined to be the area between northern California and northern Vancouver Island (from 41°N to 52°N).

Gray whale breeding and calving are seasonal and closely synchronized with migratory timing. Sexual maturity is attained between 6 and 12 years of age (Rice 1990; Rice and Wolman 1971). Gestation is estimated to be 13 months, with calving beginning in late December and continuing to early February (Rice and Wolman 1971). Some calves are born during the southbound migration while others are born near or on the wintering grounds (Shelden *et al.* 2004). Females produce a single calf, on average, every 2 years (Jones 1990). Calves are weaned and become independent by six to eight months of age while on the summer feeding ground (Rice and Wolman 1971). Three primary calving lagoons in the ENP are utilized during winter, and some females are known to make repeated returns to specific lagoons (Jones 1990).

The abundance of the ENP population, which includes the PCFG, is presently estimated to be about 19,000 whales (Laake *et al.* 2012). The potential biological removal (PBR) level for the ENP stock of gray whales is calculated as the minimum (20th percentile) estimate of population size, times one-half of the maximum theoretical net population growth rate (½ x 6.2% = 3.1%), times a recovery factor of 1.0 for a stock above its maximum net productivity level (MNPL) (Punt and Wade 2012). The minimum population estimate (N_{MIN}) for the ENP stock is calculated from Equation 1 from the PBR Guidelines (Wade and Angliss 1997): $N_{MIN} = N/\exp(0.842\times[\ln(1 + [CV(N)]^2)]^{1/2})$. Using the 2006/07 abundance estimate of 19,126 and its associated CV of 0.071, N_{MIN} for this stock is 18,017. Therefore, PBR is 558 animals. A recent analysis conducted by Punt and Wade (2012) estimated a probability of 0.884 that the ENP gray whale stock is above its MNPL, which means there is a 0.884 probability that it is at its OSP as defined by the MMPA.

Genetic studies suggest some sub-structuring may occur on the wintering grounds, with significant differences in mitochondrial DNA (mtDNA) haplotype frequencies found between females (mothers with calves) utilizing two of the primary calving lagoons and females sampled in other areas (Goerlitz *et al.* 2003). Other research, employing both mtDNA and microsatellites, identified significant departure from panmixia between two of the lagoons using nuclear data, although no significant differences using mtDNA were observed (Alter *et al.* 2009). Significant mtDNA and nuclear (nDNA) genetic differences have been found between whales in the WNP and those in the ENP (LeDuc *et al*. 2002; Lang *et al.*, 2011b).

In discussion, the TF agreed that the information presented by Lang represented an up to date overview of the ENP population and had no follow up questions.

3.2 Western North Pacific (WNP) gray whales

Information on the distribution and migration patterns of gray whales in the WNP is incomplete. There is no doubt that the historical distribution of gray whales in the Okhotsk Sea once greatly exceeded what is found at present (Reeves *et al*. 2008). Today, the main feeding ground is in the Okhotsk Sea off the northeastern coast of Sakhalin Island, Russia (Figure 2) but some animals also occur off eastern Kamchatka and in other coastal waters of the northern Okhotsk Sea (Weller *et al.* 2002; Vertyankin *et al.* 2004; Tyurneva *et al.* 2010). Whales associated with the Sakhalin feeding area can be absent for all or part of a given feeding season (Bradford *et al.* 2008), indicating they probably use other areas during the summer and fall feeding period. For example, some whales observed off Sakhalin have been sighted off the northern Kuril Islands in the eastern Okhotsk Sea and Bering Island in the western Bering Sea (Weller *et al*. 2003).

The WNP migration route(s) and winter breeding ground(s) are poorly known (Weller *et al*. 2002; Weller and Brownell 2012). Information collected over the past century indicates that whales migrated along the coasts of Japan and South Korea (Andrews 1914; Mizue 1951; Omura 1984) to wintering areas somewhere in the South China Sea, possibly near Hainan Island (Wang 1984). At present, observations of gray whales off Japan are rare. Nambu *et al*. (2010) reported 13 known sighting or stranding records in Japanese waters between 1990 and 2007. Between 2005 and 2007, four female gray whales were fatally entrapped in set nets along the Pacific coast of Honshu, Japan. One of these females, entrapped in January 2007, was matched to earlier photographs of it as a calf (with its mother) while on the Sakhalin feeding ground in July and August 2006 (Weller *et al*. 2008). This match provided the most contemporary link between the summer feeding ground off Sakhalin and a winter location along the coast of Asia. More recently, in March 2012 a gray whale was sighted and photographed in Mikawa Bay (Aichi Prefecture), east of Ise Bay near Nagoya on the Pacific coast of Honshu (Japan Times, 3 May 2012).

Observations of gray whales in China are also exceptionally rare. Although 24 capture, sighting or stranding records exist since 1933 (Wang 1984; Zhu 2002), including observations of two mother-calf pairs, some of these (especially the sightings) have not been reported in sufficient detail to validate species identification. More recently, an 11.5 m female stranded live at Zhuanghe (Bohai Sea ca. 39˚N) in December 1996 (Zhao 1997) and a 13 m female gray whale was taken in fishing gear offshore of Baiqingxiang (Pingtan County), in the Taiwan Strait in November 2011 (Zhu 2012). The last known sighting of a gray whale off Korea was in 1977 (Park 1995).

The WNP gray whale population is redlisted by the IUCN as Critically Endangered. The most recent population assessment (for 2012), using a Bayesian individually-based stage- structured model, resulted in a median 1+ (non-calf) estimate of 155 individuals, with 95% CI = 142-165 (IUCN 2012). A collaborative Russia-U.S. research program on WNP gray whales summering off northeastern Sakhalin Island, Russia, has been ongoing since the mid-1990s. When data collected between 1994-2011 are combined, a catalog of 200 photo-identified individuals has been compiled. Beginning in 2002, photo-identification studies off Sakhalin have also been conducted by Russia scientists working with oil and gas companies (Tyurneva *et al*. 2010). This research largely corroborates the work of the Russia-U.S. team and in some cases collaborative analyses utilizing combined datasets have been conducted.

Recently, results from photo-identification (Urbán *et al.* 2012; Weller *et al.* 2012), genetic (Lang 2010; Lang *et al.* 2011b), and telemetry studies (Mate *et al.* 2011) have documented spatial and temporal overlap between WNP and ENP gray whales. Observations of such overlap include: (1) six whales photographically matched from Sakhalin Island to southern Vancouver Island, (2) two whales genetically matched from Sakhalin to Santa Barbara, California, (3) 13 whales photographically matched from Sakhalin Island to San Ignacio Lagoon, Mexico, and (4) 2 satellite tagged whales that migrated from Sakhalin Island to the west coast of North America. In combination, these studies have recorded a total of 23 gray whales observed in both the WNP and ENP. Despite this overlap, significant mtDNA and nDNA differences are found between whales in the WNP and those summering in the ENP (Lang *et al.* 2011b). Although it is clear that some whales feeding off Sakhalin Island during the summer/fall migrate to the west coast of North America during the winter/spring, past and present observations of gray whales in the WNP off Japan, Korea and China during the winter/spring suggest that not all gray whales in the WNP share a common wintering ground (Weller and Brownell 2012).

In discussion, the TF agreed that the occurrence of WNP gray whales in U.S. waters presented previously unexpected implications with respect to the SAR process and the Makah waiver request. More specifically, two questions were discussed at length, including: (1) given the occurrence of WNP gray whales in U.S. waters, is a WNP gray whale SAR required? and (2) given the potential occurrence of WNP gray whales in the proposed Makah hunt area, what are the implications regarding the existing wavier request?

TF members also noted that these new findings of gray whales moving between Sakhalin Island and the ENP had significance to our understanding of the status of gray whales in the WNP. That is, given that some of the whales sighted off Sakhalin appear to overwinter in the ENP, the number of animals remaining in the WNP year-round may be much smaller and of greater conservation concern than is currently recognized (Weller and Brownell 2012).

3.3 Pacific Coast Feeding Group (PCFG)

Gray whales using the Pacific Northwest area during summer and autumn include two components: (1) whales that return frequently and account for most of the sightings between 1 June and 30 November, and (2) whales that are sighted only in one year, tend to be seen for shorter time periods in that year, and are encountered in more limited areas. For the purposes of their work to evaluate the proposed Makah Indian Tribe gray whale hunt, the International Whaling Commission (IWC) defined PCFG gray whales as: whales observed between 1 June to 30 November within the region between northern California and northern Vancouver Island (from 41°N to 52°N) and photo-identified within this area during two or more years (IWC 2011; IWC 2012a). This same definition has been adopted in the analyses of Calambokidis *et al.* (2012). In this report, the TF defines "PCFG whales" following the IWC definition.

Recent research has provided new information on movements and habitat utilization of PCFG whales (for example Frasier *et al.* 2011; Lang *et al.* 2011a; Calambokidis *et al.* 2012). While PCFG whales are known to feed during summer and fall off the Pacific coast between northern California and southeastern Alaska, they also occasionally occur as far north as Kodiak (Gosho *et al.* 2011) and Barrow, Alaska (Calambokidis *et al.* 2012). The sighting from Barrow suggests that some PCFG whales (meaning whales seen in summer in the defined area used by the PCFG and in more than one year), at least occasionally occur in one of the most northern gray whale feeding areas in the ENP (Calambokidis *et al.* 2012). Similarly, of the 121 whales identified off Kodiak from 1998-2010, there have been 30 sightings of 17 individuals between June-November in areas extending from northern California to northern British Columbia (Table 9, Calambokidis *et al.* 2012). These observations indicate that at least some PCFG whales have used both the Kodiak feeding area in addition to the 41°N to 52°N area defined for the PCFG.

Satellite tagging studies between 3 September and 4 December 2009 off Oregon and California provide additional movement data for whales considered to be part of the PCFG (Mate *et al.* 2010). While duration of tag attachment differed between individuals, some whales remained in relatively small areas within the larger PCFG seasonal range while others traveled more widely. All six individuals whose tags continued to transmit through the southbound migration utilized the wintering area within and adjacent to Laguna Ojo de Liebre (Scammon´s lagoon). Three whales were tracked north from Ojo de Liebre and displayed the following movement patterns: (1) one whale traveled at least as far as Icy Bay, Alaska, and (2) two whales were tracked to coastal waters off Washington (Olympic Peninsula) and California (Cape Mendocino). In combination, satellite tag and photo-identification data suggest that the range of the PCFG may, at least for some individuals, exceed the pre-defined 41°N to 52°N boundaries that have been used in a number of PCFG-related analyses (e.g., abundance estimation).

Further support of the PCFG range extending beyond the pre-defined 41°N to 52°N boundaries comes from a study of six whales satellite tagged off the central west coast of Vancouver Island in March. This study was designed to determine northern migration routes in the greater Vancouver Island area (Ford *et al.* 2012). Three of the tagged whales had been previously sighted within the seasonal range used by PCFG whales (41°N to 52°N) and two had multi-year sighting histories there. These three whales moved north to between ~55°N to 57° N before their tags stopped transmitting. One of these whales was later observed in the seasonal range of the PCFG off southern Vancouver Island. These findings suggest that in the spring at least some PCFG whales may migrate northward, past the defined seasonal range used by the PCFG, along with the larger ENP stock before “circling back” to within the range of the PCFG summer feeding area.

It is unknown how long gray whales have used the PCFG area in summer and autumn; it may have been colonized as recently as the last century or during the Little Ice Age (~1540-1850) or other glacial periods when it was difficult or impossible for gray whales to feed further north. Records of gray whales feeding between northern California and Alaska during summer/fall date back to at least 1926 (Howell and Huey 1930), including reports of whales feeding on the southern feeding ground during the 1940s, 1950s, and 1960s (Gilmore 1960; Pike and MacAskie 1969; Rice and Wolman 1971). The consistent return of individuals to the southwestern coast of Vancouver Island, British Columbia, was first documented in the early 1970s (Hatler and Darling 1974).

A unique characteristic of PCFG whales is an apparent flexibility in their feeding habits. That is, whales summering in the seasonal range of the PCFG consume a varied diet including mysids, amphipods, crab larvae, and herring eggs/larvae. This is in contrast (generally speaking) to gray whales feeding in the arctic where they seem to be more focused on an amphipod food base (Nerini 1984). That being said, whales that utilize the seasonal range of the PCFG in only a single year (i.e., non-PCFG whales) must also be flexible, at least to some degree, in their feeding habits.

Abundance estimates of PCFG gray whales reported by Calambokidis *et al.* (2012) show a high rate of increase in the late 1990s and early 2000s, but have been relatively stable, albeit with some decline, since about 2003. No statistical analysis of trends in abundance is currently available for this population. The PCFG is estimated to contain about 200 individuals (Calambokidis *et al*. 2012). As stated in the 2012 gray whale SAR "because the PCFG appears to be a distinct feeding aggregation and may warrant consideration as a distinct stock in the future, a separate PBR was calculated" (Carretta *et al*. 2013). Calculation of a PBR for the PCFG allows NMFS to assess whether levels of HCM are likely to cause local depletion of this group. In keeping with that management objective, NMFS used the 2008 abundance estimate of 194 (SE = 17.0)[3] from Calambokidis *et al*. (2010) and the range of the PCFG (between 41°N to 52°N) as defined by the IWC to calculate a potential PBR for PCFG whales (Carretta *et al*. 2013). This calculation used the minimum population size (180 animals), times one half the maximum theoretical net population growth rate (½ x 6.2% = 3.1%), times a recovery factor of 0.5 (for a population of unknown status), resulting in a PBR of 2.8 animals (NMFS 2012). Further, a review of annual HCM in the PCFG between 2006 and 2010 was estimated and averaged 0.6 animals/year known deaths (Carretta *et al*. 2013).

In discussion, the TF asked Lang if there was any evidence that oceanographic changes have influenced the abundance or recruitment of whales into the PCFG. Lang replied that Calambokidis *et al.* (2012) reported a higher than usual "pulse" of animals recruited into the PCFG in the years following the 1999-2000 gray whale Unusual Mortality Event (UME). This UME has been theorized to be the result of limited food resources on the northern feeding grounds (see Gulland *et al.* 2005), and as such, this "pulse" of gray whale immigration[4] into the PCFG could potentially be considered a response to oceanographic changes. Given that the photo-identification effort on PCFG whales expanded greatly in 1998 (data from years prior to 1998 exist but not at the same level of effort), coinciding closely in time with the UME, it makes it impossible to resolve with certainty the occurrence or magnitude of the hypothesized pulse recruitment.

In response to the observations of PCFG whales in northern areas such as Kodiak and Barrow, Alaska, some members of the TF asked why the boundaries of the PCFG area defined by the IWC were not extended further north? The TF noted that the IWC definition was not intended to define the stock but rather to provide a conservative basis on which to evaluate the gray whale hunt proposed by the Makah Indian Tribe. With respect to low survey effort north of 52°N, the TF agreed that the PCFG could have a higher abundance than currently estimated and that this might affect a number of analyses including determination of annual sighting patterns of individual whales (e.g., a PCFG whale may have been present in a larger area but not photographed because it was located in an region not surveyed). The TF concurred that these issues are important to assignments of PCFG whales (i.e., those seen in two or more years between 41°N and 52°N) and highlighted the importance of expanding the spatial and temporal coverage of the photo-identification effort. In addition, further satellite tagging of known PCFG whales would also help to better define habitat use and delineate the seasonal feeding range.

Additional discussion was devoted to addressing the possibility that HCM (e.g., ship strikes and commercial fisheries bycatch) for whales in the PCFG area could be higher than for whales that migrate through the area. That is, PCFG whales spend more time near shore where ship traffic and fishing gear are concentrated. Despite this concern, little information is available on where

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[3] This estimate will be updated in the 2013 SAR to include the now available 1999-2010 time series presented in Calambokidis *et al*. (2012).

[4] Immigration, as used here, means a permanent change of feeding ground fidelity and is considered interchangeable with "external recruitment".

HCM actually occurs. The TF asked Carretta how whales were classified as being PCFG in his analysis. He replied that the estimate was based on NMFS stranding data for the most recent 5-year period and included whales that stranded within the defined PCFG time period (1 June and 30 November) and range (41°N to 52°N). Carretta noted that his estimate of 0.6 animals/year, based on only the most current 5-year period (as per protocol of the SAR guidelines), is lower than the 20-year average of 1.5 animals/year reported elsewhere (IWC 2012a). The TF agreed that both of these estimates of HCM for the PCFG were likely to represent minimum estimates because there is no correction for incidents that go unobserved or unreported.

Related to the issue of HCM, the TF also discussed the results presented in Connor *et al.* (2011), which found that PCFG whales had higher rates of scarring than other gray whales. It was noted that crab pots are common off the Washington and Oregon coasts and as such may pose an increased threat in some parts of the PCFG range. Carretta noted that when looking through the HCM records, a fair number of southern California crab pot interactions were reported, which suggests that fisheries interactions of this nature could be a pervasive issue along the coast. The TF noted that PCFG animals could have more interactions (compared to non-PCFG whales) with crab pots and coastal fishing gear given their extended residency in nearshore areas. Therefore, the TF recommended that the existing photo-identification time series be used to examine scarring patterns of PCFG whales to possibly provide a better assessment of their interactions with fishing gear.

4. Population Dynamics of the Pacific Coast Feeding Group

Laake (AFSC) provided a summary of information regarding the PCFG (following the IWC definition) based on photo-identification research as described in Calambokidis *et al.* (2012). Photo-identification studies from 1998 to 2010 between northern California and northern British Columbia have categorized gray whales using that region during summer and autumn in two components: (1) whales that frequently return to the area, are seen in more than one year between 1 June and 30 November, and account for most of the sightings during that time period, and (2) whales that are sighted only in one year, tend to be seen for shorter time periods in that year, and are encountered in more limited areas.

4.1 Definition of Pacific Coast Feeding Group whales based on timing and area

Defining the PCFG involves analysis that spans both time and space. The temporal component of the PCFG range is better defined than the spatial component, but neither can be considered absolute. As mentioned previously, the IWC defines the PCFG as: gray whales observed between 1 June to 30 November within the region between northern California and northern Vancouver Island (from 41°N to 52°N) and photo-identified within this area during two or more years (IWC 2012a). The spatial boundaries of the PCFG range under the IWC definition were chosen for the following reasons: (1) samples used for the genetic analyses were taken from whales across this range, (2) the work of Calambokidis *et al.* (2012) showed movements of whales throughout the area (Figure 3), (3) only a small number of PCFG whales have been observed north or south of the area during the 1 June to 30 November time period, and (4) few if any whales are still migrating north through the 41°N to 52° N region from 1 June to 30 November. The temporal definition (1 June to 30 November) was based, in part, on the disparity in sighting rates across months. Whales observed after 1 June were more likely to be sighted (i.e., photographed) more than one time, in more than one year, and in more than one region (Figure 4).

In discussion, the TF asked whether the results presented in Figure 3 were effort-corrected. Laake explained that the proportions are only dependent on the effort in the region from the Makah U&A to Southern Vancouver Island (SVI) and not in the other areas. Variation in effort in areas outside of the Makah U&A-SVI region will change the sample size that could be detected in the Makah U&A-SVI but not the proportion of individuals resighted in the Makah U&A-SVI.

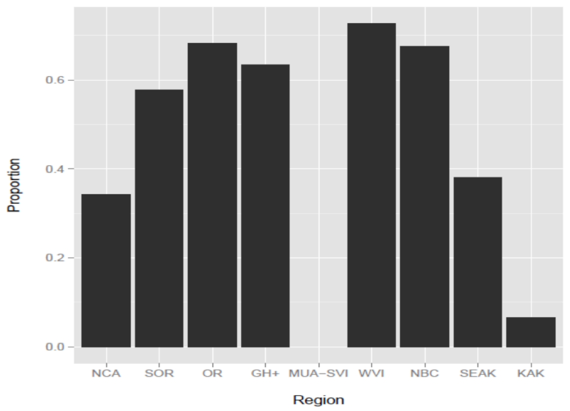

Figure 3. Proportion of whales sighted in the MUA-SVI region of whales seen in the identified areas. MUA and SVI were collapsed due to their proximity and high exchange rate. NCA = Northern California, SOR = Southern Oregon, OR = Central Oregon, GH+ = Gray's Harbor and surrounding coastal waters, MUA-SVI – Makah Usual and Accustomed Area to Southern Vancouver Island, WVI = West Vancouver Island, NBC = Northen Vancouver Island and coastal areas of British Columbia, SEAK = Southeast Alaska, KAK = Kodiak, Alaska.

The spatial range of PCFG whales was then discussed by the TF, including apparent gaps in survey coverage. Surveys in the seasonal range of the PCFG tend to focus on regions where gray whales have been seen and so the surveys are not randomly designed to cover the entire possible range. There is a large gap in survey effort north of 52° N (i.e., between northern Vancouver Island and Kodiak, Alaska). Because only a limited amount of gray whale survey effort has been undertaken in this region, it is unknown whether this area represents a true distributional gap. Even with this limitation, it is nevertheless possible to document observed movements of known individuals and estimate a related minimum range. Figure 5 presents the observed range of maximum distances between sighting locations for individual whales. Overall, approximately 40% of PCFG whales are known to have utilized areas spanning at least one degree of latitude. Further, there are documented movements of PCFG whales to Kodiak (Gosho *et al.* 2011) and Point Barrow, Alaska (Calambokidis *et al.* 2012), in years they were not seen in the PCFG area. Finally, information from tagging (see section above) also supports the idea that the range of some PCFG whales extends outside of the presently defined boundaries.

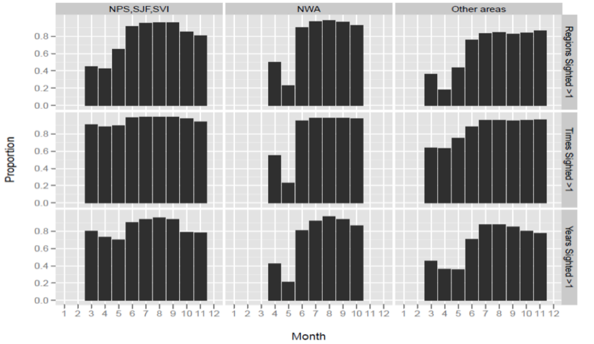

Figure 4. Proportion of whales sighted in more than one region (top), on more than one day (center) and in more than one year (bottom) as defined by the region and month they were seen. NPS = Northern Puget Sound, SJF = Strait of Juan de Fuca, SVI = Southern Vancouver Island, NWA = Northern Washington Coast.

It was noted by the TF that site fidelity of known reproductive mothers to the WNP Sakhalin Island feeding area is very strong (Weller *et al.* 2002). The TF therefore recommended that the existing PCFG photo-identification data be examined to see if moms/calves demonstrate higher levels of fidelity than other whales.

4.2 Pacific Coast Feeding Group abundance and survival

The photo-identification data collected annually in the seasonal range of PCFG whales (following the IWC definition) between 1998 and 2010 have been used to estimate abundance. In these analyses, the term “transient whale” was used to refer to whales seen in only one year and never seen again in any other year, and “non-transient whale” was used to refer to whales seen in at least two years, such that an estimate of the number of non-transient whales would be equivalent to an estimate of the number of whales defined to be in the area used by the PCFG. The total number of gray whales in the area used by the PCFG in summer would include both transient and non-transient whales, and is therefore higher than the number of defined PCFG whales in the area. In the following discussion of abundance estimates, whether an estimate is biased or not is relative to the true number of defined PCFG whales (not to the total number of gray whales in the area).

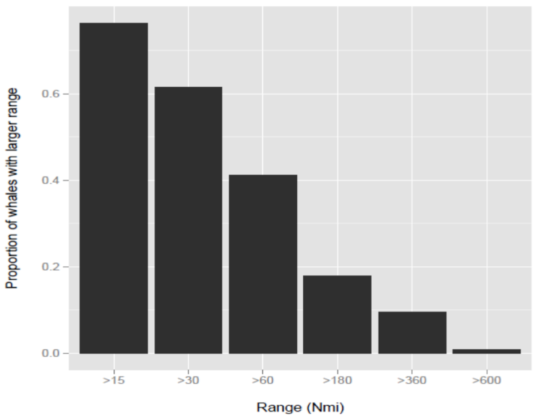

Figure 5. Distribution of maximum distance, in nautical miles, between photo-id locations for PCFG gray whales during 1 June – 30 November 1998-2010. The distance for 40% of the whales exceeded 1 degree latitude (60 nautical miles).

A number of different estimators were used including: (1) Lincoln-Peterson (LP), (2) Limited Lincoln-Peterson (LLP), and (3) Modified Jolly-Seber (JS1). The first two estimators constructed estimates from consecutive years of data. The LP estimator assumes a closed population and is unbiased if there are only losses or only gains. There are both losses and gains to the PCFG due to transient whales and therefore induces a positive bias. The LLP estimator removes the positive bias of the LP estimator by restricting the data to whales seen during the 2-year period but also in another year prior or after the 2-year period. This restriction eliminates whales that were transients in either of the years. The JS1 estimator is an open population model that estimates the abundance of non-transient whales. A fourth estimator, JS2, is an alternate JS modification that produced similar results except at the end of the time series (Calambokidis *et al*. 2012).

Calambokidis *et al.* (2012) considered the JS1 estimator to be the best suited for analysis of the PCFG (Figure 6). The Jolly Seber 1 (JS1) estimator assumes that any gray whale joining the PCFG is seen the first year it enters. The assumption is made to model the data adequately with the strong relationship between minimum tenure (time between first and last sighting in the year) and the probability it remains in the PCFG. The magnitude and trend of the LP abundance estimates do not match up well with the limited LP and the JS1 estimates; this is due to the fact that the LP

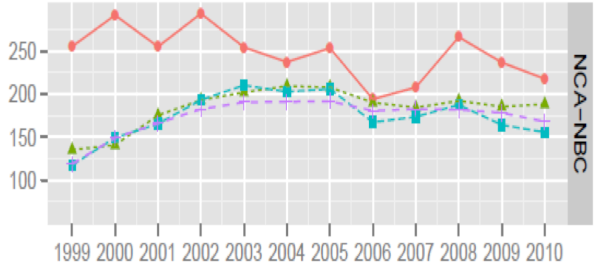

Figure 6. Estimates of the abundance of PCFG gray whales between northern California and northern British Columbia (NCA – NBC) using four different estimators based on photo-id data collected annually between 1998 and 2010. LP = Red Circle, JS1=Green Triangle, LLP=Blue Square, JS2=Purple Dotted Line

estimator was positively biased and the bias was greater at the beginning of the time series when there was more immigration and emigration into and out of the area used by the PCFG.

In discussion, the TF focused on whether the increase in the JS1 abundance estimates from 1999-2002 (Figure 6) was real or a reflection of the discovery of "new" whales that were present in the area used by the PCFG but not observed (i.e., photographed). Some of that discussion also focused on the related topic of recruitment described below. Laake responded that there were 13 whales not sighted in 1998 that were seen after 1998 (most of them were sighted in 1999) and were in the catalog for sightings prior to 1998. These results indicate that the assumption of JS1 (i.e., that any gray whale joining the PCFG is seen the first year it enters) was not met entirely. That being said, Laake argued that the bias was small or negligible after 1999 for the following reasons: (1) values from the JS1 estimator correspond closely to the value from the limited LP estimator which does not make the same assumption, (2) simulation results using similar values for capture probability estimated from the data showed a minimal amount of bias after 1999, and (3) the UME in 1999-2000 provides a plausible explanation for the coincident increase in PCFG abundance.

4.3 Pacific Coast Feeding Group IWC implementation review

Wade (AFSC) presented a brief overview of the status of the Implementation Review (IR) process conducted by the IWC. The IR includes trials based on three hypotheses: (1) Hypothesis P (Pulse) assumes that there is no bias in the PCFG abundance estimates (but dropping 1998) and that a pulse of immigration occurred in 1999 and 2000; (B) Hypothesis B (Bias) assumes a strong time-varying bias in the abundance estimate but no pulse of immigration; and (3) Hypothesis I (Intermediate) includes a moderate time-varying bias in the abundance estimates and a pulse of 10 immigrants into the PCFG in both 1999 and 2000. These hypotheses were evaluated because the model used in the IWC IR trials could not produce simulated abundance trajectories that fit the abundance estimates without incorporating a pulse or a bias into their model. For these trials the IWC Scientific Committee agreed that a sufficient fit to the data could be achieved with maximum annual immigration of up to six animals.

Wade noted that for the most part there was broad similarity between the population trajectories in the IWC trials and the population trajectories in the OSP determinations performed by Moore and Punt (pers. comm.), which only use Hypothesis P (a pulse of immigrants in 1999 and 2000, see related item below). The IWC implementation trials produce final statistics related to conservation status and catches.

There was some discussion about the need to evaluate trials that produced worrying conservation statistics and that it would be valuable to look at what the depletion level could be in those trials. Wade noted that the trials incorporating a low growth rate with little immigration or the trials in which the probability of taking a PCFG whale were doubled were the trials which do not do well with respect to conservation statistics such as final depletion level. Note that "final depletion level" is defined by the IWC to be the final population level as a percent of K. This is related to, but can be slightly different from, the U.S. MMPA definition of "depletion", which is defined to be a population level below the Maximum Net Productivity Level (MNPL). In U.S. MMPA depletion determinations, MNPL is generally assumed to either be a range from 50-70% of K, or a single value such as 50% or 60% of K. The only practical difference occurs when a range is used in MMPA determinations, where one calculates the probability a population is below MNPL over a range of percentages of K. If a single value is used for MNPL (e.g., 60%), than the IWC final depletion level is identical.

Some of the simulations conducted by the IWC with worrisome conservation performance (with respect to final depletion below 60%) are those using Maximum Sustained Yield Rate (MSYR) of 1% or 2%, implying a relatively low maximum population growth rate (Annex E, IWC 2012b). Note that the IWC Scientific Committee parameterizes population models with MSYR rather than Rmax (used in U.S. MMPA calculations). MSYR is the population growth rate at the Maximum Sustained Yield level, which is equivalent to MNPL if human-caused removals are unbiased with respect to age. Therefore, if MNPL is 50% of K, a population with an MSYR of 2% has an Rmax of 4%, and a population with an MSYR of 1% has an Rmax of 2%. Taylor noted that although she would have initially thought population growth rates that low were unlikely, after seeing some of the results presented she felt that relatively low population growth rates cannot be ruled out. She also noted that all trials in the table (which was a summary of trials that performed poorly with respect to conservation statistics) have annual immigration = 0 to 2, at the low end of the range considered. It appears that rates of annual immigration higher than 2 provide just enough of an offset to low MSYR rates of 1 or 2%.

The TF asked how the rescaled final depletion level was related to final depletion level in the IWC results. The rescaled final depletion statistic is used by IWC in trials whose specifications cause the population to decline even in the absence of catches. To evaluate those trials, the final population level for the trial (with catches) is compared to the final population level that would have been obtained in the absence of catches. That ratio is termed the rescaled final depletion, and represents the fraction of the population size that would have been obtained in the absence of catches. Since a low MSYR rate results in low population growth, the IWC found it is useful to compare depletion levels both with and without catches. The rescaled final depletion results for the PCFG only differ from the final depletion statistic for trials with a low value for MSYR, where the PCFG would decline and become depleted regardless of whether a hunt occurred due to the combination of a low population growth rate and bycatch.

4.4 Pacific Coast Feeding Group recruitment

Although new whales are identified each year in the range of the PCFG, about 50% of these individuals are seen in only one year and considered "transients" or "visitors" (Figure 7). Other whales are resighted in subsequent years and are considered "recruits" into the PCFG. Whales with a longer minimum tenure in the first year they were sighted have higher first year apparent survival and higher probability of return (i.e., do not permanently emigrate). This relationship might be expected given a hypothesis that whales are more likely to return if they find a suitable prey base during their first year in the seasonal range of the PCFG.

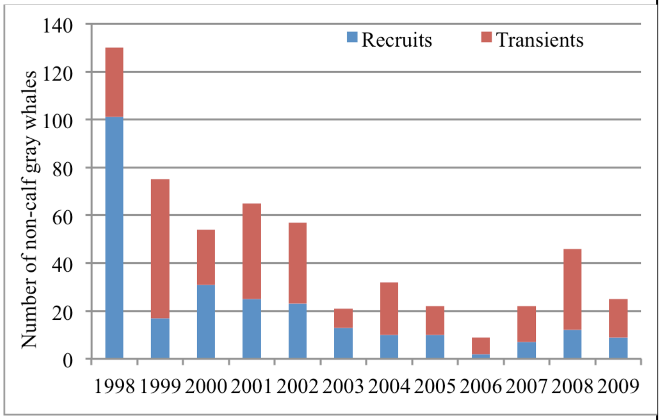

Figure 7. Number of "new" whales seen each year in the PCFG area that are transients (only seen in one year) and recruits (seen in more than one year).

Whales that recruited into the PCFG in 1999 or a subsequent year had lower first year apparent survival than whales that were first identified in 1998. Approximately 75% of the whales whose minimum tenure was 100 days or more in 1999 or later were resighted in a following year. For whales identified in 1998 (the first year of the study) whose minimum tenure was 100 days, nearly 100% were

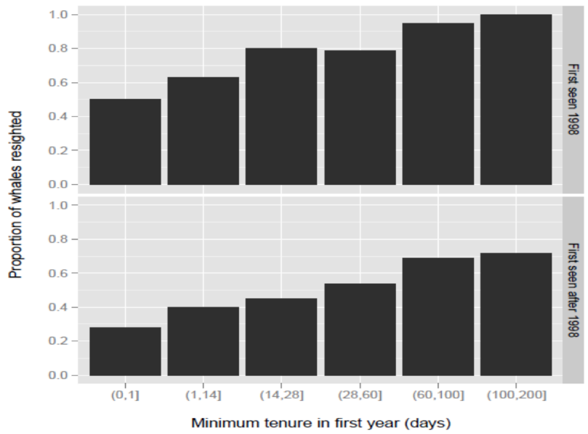

Figure 8. Relationship between minimum tenure in first year (# of days between first and last sighting plus 1) and the proportion resighted in at least one following year. The data series starts in 1998 so all whales are "new" so while the pattern is similar, the proportions are higher for 1998 because most whales are not truly new to the PCFG.

resighted in a following year (Figure 8). This suggests that some of the animals that recruited into the PCFG in 1999 or later may have subsequently emigrated out; this could explain why the abundance has declined somewhat in the later years (Figure 6). The high number of new whales identified in the seasonal range of the PCFG between 1999 and 2002 is hypothesized to have been in response to the 1999-2000 UME.

The TF discussed several alternative explanations for the relatively high numbers of recruits into the PCFG in the early part of the time series (1999-2002). For example, whether the increase in abundance during early years could be due to a "discovery" effect, such that it took a number of years for all the whales which were part of the PCFG to be photographed and "discovered". Alternatively, the heterogeneity in survey coverage over time and space could lead to some animals being considered "new" in a given year even if they had been utilizing areas with limited or no survey coverage in previous years. However, overall capture probabilities are high, suggesting it is unlikely a whale would be in the area for several years and not photographed. The TF concurred that on an annual basis, whales observed in the area used by the PCFG could be characterized as a collection of individuals whose residence patterns vary along a continuum such that some whales use the area for a single year (e.g., transients), some for a few years, and others on a consistent long-term basis.

By way of an analogy, Laake characterized the PCFG as a "leaky bucket", in that some whales are immigrating in while others are emigrating out. The "leaky bucket" phenomenon is not a random process, however, because a "core group" of whales appear to stay in the bucket over time. The dataset cannot discriminate between PCFG whales that die versus those that emigrate. Animals that recruit into the PCFG as non-calves may be more likely to emigrate out of the area than calves recruited to the PCFG in the year they were born. That is, calves of the year have been taught to feed on prey types common to the PCFG area (various swarming prey for instance) by their mothers and may obtain "local knowledge" that allows them to be successful long-term inhabitants of the PCFG area. To evaluate this, the TF recommended that the existing PCFG photo-identification time series be examined to see if moms/calves demonstrate higher degrees of fidelity than other whales.

In thinking about the "core group" of PCFG whales that return to the area on a consistent basis, the TF questioned if biopsy efforts in the area could be potentially biased towards these whales. If sampling efforts are unintentionally concentrating on the "core group" of PCFG whales, then the results of genetic comparisons may be driven by matrilineal fidelity of this "core group". In addition, the biopsy efforts are not spread evenly over time and space (more heterogeneity than the photo-identification survey efforts). If "core group" animals predominantly use the areas with high biopsy effort, then this potential bias could be magnified.

Some newly seen whales are calves with their mothers (Figure 9). As described in Calambokidis *et al.* (2012), much of the sighting effort occurs in August and later when many calves are likely to already be weaned and thereby more difficult to identify as a calf (versus a yearling). The TF noted that many of the whales identified as calves off Sakhalin Island in the WNP are not resighted for many years subsequent to their birth year but eventually they are again resighted in the area. This pattern suggests that young animals (1+ years old) may use other areas to feed during their first several years. Therefore, in the case of the PCFG, if a whale was not seen as a calf but returned in a later year it would appear to be an external rather than internal recruit. With that in mind, the TF recommended that the existing PCFG photo-identification time series be examined following a protocol developed by Bradford et al. (2011) that uses barnacle and pigmentation characteristics on young gray whales to reliably distinguish calves of the year from yearlings.

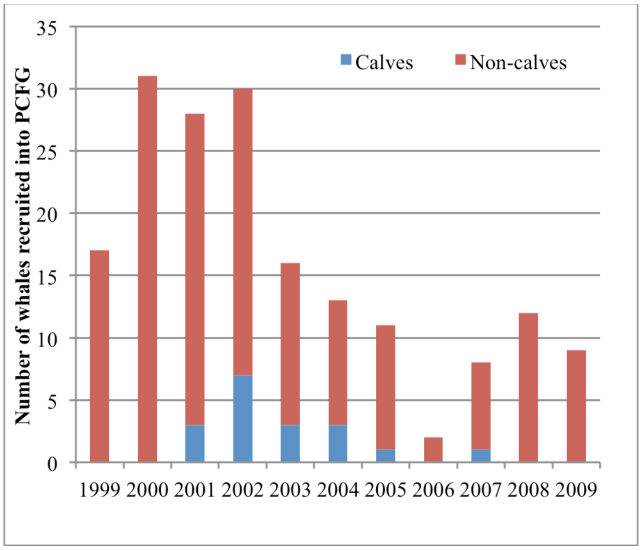

Figure 9. Number of whales first seen and recruited (seen in a following year) by year and calf and non-calf designation.

In summary, the TF discussion about the magnitude and source of recruitment into the PCFG focused on: (1) incomplete survey coverage of the entire seasonal range used by the PCFG and the potential for whales to be missed and then “recruited” in a subsequent year, (2) the proportion of “recruited” whales that were calves of mothers from the PCFG that may have been missed as a calf or misidentified as an external recruit, (3) the potential of the 1999/2000 UME to create a pulse of immigration into the PCFG, (4) to what degree gray whales recruited in 1999 or later were either emigrating back to the northern feeding areas or experiencing higher mortality, and (5) whether the biopsy sampling effort was prone to sample whales that spent more time in the range used by the PCFG.

All of these issues are relevant to assessing the amount of external recruitment into the PCFG and thereby especially pertinent to determining if it should be recognized as a population stock under the MMPA and GAMMS guidelines. That is, if the PCFG experiences little external recruitment then it would be considered demographically independent and should be recognized as a stock. If most of the recruitment into the PCFG were external, however, then it would not be considered demographically independent and would not be recognized as a stock. The TF concurred that the resolution of the existing photo-identification data in combination with uncertainly surrounding the accuracy of assigning whales as external or internal recruits prevent this question from being fully resolved. Increased genetic sampling in tandem with increased photo-id effort over both space and time may be the only way to better address this question.

4.5 Pacific Coast Feeding Group trend and optimum sustainable population determination

Moore presented an update on work he conducted in collaboration with Andre Punt (University of Washington) to determine if the PCFG, as a putative stock, is at OSP. The OSP assessment is based on the two-stock population model that has been developed as part of the IWC gray whale

Implementation Review (see section 4.3). Both assessments use the same definition for a PCFG whale. There are some differences, however, between the IWC model framework and the one used for the OSP assessment. First, in the OSP analysis, a Bayesian approach is used in which prior distributions are specified for input parameters and the time series of abundance estimates (for the ENP and PCFG) are used to the update priors and output posterior distributions. This contrasts with the IWC approach of generating outputs for many models each based on alternative fixed combinations of values for some parameters. Second, the IWC trials consider several hypotheses that attempt to explain the rapid increase in abundance estimates in the first few years of the time series; these include bias in the early abundance estimates, a pulse of immigration, and a combination of these two factors. In the OSP assessment, only the pulse immigration hypothesis is considered, based on work by Calambokidis *et al.* (2012) which suggested that the most recent abundance estimates should be fairly unbiased apart from the first estimate in 1998, which is not used in the OSP analysis.

At the time of the workshop, the OSP analysis considered two hypotheses pertaining to the regular annual immigration rate: one in which there is no immigration (PCFG is closed) and one in which the annual immigration rate is estimated, given a uniform prior distributed between 0 and 6 individuals per year. Different versions of the model allow the density-dependent (or inflection point) parameter θ to be estimated separately for each putative stock (PCFG vs. rest of the ENP) or to be constrained so that the two groups share a common θ. Outputs from both versions and immigration rate considerations (none vs. U[0, 6]) are similar in models run thus far. The primary parameter of interest in the OSP assessment is the probability that PCFG abundance is above MNPL (MSYL in IWC terms).

The analysis was not able to generate useful assessment results because, apart from the rapid population increase in the late 1990s attributed to an immigration pulse, the abundance time series is fairly flat and therefore not very informative for estimating *in situ* population growth parameters. The data have also not been informative for estimating population carrying capacity (K), a parameter necessary to determine whether current abundance is above MNPL. Posterior distributions for K have been strongly dependent on the upper bound used for the prior. Given that the abundance has been stable throughout most of the 2000s, it appears to be regulated at this level (of around 200 - 250 animals) by some factor, and thus it is somewhat puzzling that the data do not seem more informative with respect to estimating K. Moore suggested that annual levels of incidental take included in the model (about 2 animals per year) could be making it difficult to estimate whether the population is being regulated at K or some level below K, given that the data do not inform the estimates of MSYR (the population growth parameter in IWC models). For example, given annual bycatch mortality of 1%, a combination of being well below K and having a low MSYR may describe the data equally well as being close to K and having a high MSYR, since in both cases, the realized value for population growth would be low and potentially balanced by the additive mortality. It was also suggested that the population might be regulated at its current level as a result of emigration and bycatch offsetting the combination of immigration and *in situ* growth.

Moore and Punt were continuing to troubleshoot the problem by running alternative models that, for example, exclude incidental take from the model or constrain estimates of MSYR for the PCFG to be equal to those of the ENP. The goal of this troubleshooting is to explain why estimates of K and hence probability of being at OSP are elusive, which in turn may enable a decision as to whether an OSP assessment may be possible.

The TF thanked Moore and Punt for their work on this complicated matter and raised several points for clarification. It was asked where the estimates of incidental mortality for the model had come from. Moore reported that the bycatch estimate being used is based on a summary compiled at the 2011 IWC Aboriginal Whaling Management Procedure (AWMP) intersessional workshop (IWC 2012a). Carretta clarified that those estimates included data from over a 20-year period that tried to assign animals as being part of the PCFG (or not) based on time and space. Carretta also noted that the bycatch values used in the OSP analysis (as well as the SARs) account for only observed bycatch, which is likely to be an underestimate of actual bycatch.

It was also noted that emigration is a possible explanation for the difficulty in estimating K in spite of apparent PCFG population size stability. That is, all recruits are assumed in the model to have the same annual survival rate but as discussed above, whales that recruited into the PCFG in 1999 or later had lower first year survival than whales that were first identified in 1998. Not including this extra survival parameter may explain some of the lack of fit of the model to the abundance time series (plots show that the model underestimates abundance in the first half of the time series and overestimates abundance in the second half of the series).

The TF asked if the model assumed immigration was constant across years in the assessment given that in reality immigration into the PCFG is thought to vary across years. In the model, immigration to the PCFG occurs at a constant rate, with the number of immigrants being proportional to the northern stock (non-calf) abundance. The rate is equal to the estimated immigration parameter (I, specified with the uniform [0,6] prior) divided by 20,000. In other words, for recent abundance levels of the northern stock, annual immigration to the PCFG is approximately I individuals. Emigration from the PCFG group is similarly assumed to occur at a constant rate, specified by an additional survival parameter ($1 - S$), with the number of emigrants proportional to PCFG abundance. S is set so that when both stocks (northern and PCFG) are at carrying capacity, immigration and emigration to the PCFG is balanced, i.e., $IK_{\mathrm{north}}/20000 = (1 - S)K_{\mathrm{PCFG.}}$

Some members of the TF commented that based on this model it seems plausible that the pulse of immigration into the PCFG is larger than what the IWC is modeling or what the genetic simulations have modeled. If that were the case, then the estimates of regular annual immigration would be lower than estimated in the genetic simulations. In the light of this discussion, the TF noted that the genetic simulations should try pulses of 30 animals to see if that is consistent with the empirical genetic data. This line of thinking led to additional discussion as to how common pulse immigration events might be, and whether, for the purposes of the workshop and deliberations on internal versus external recruitment, the TF should be considering the pulse as part of the average level of immigration or if the pulse should be considered a one-time event and only annual immigration should be considered (in assessing how demographically independent the PCFG is).

It was further noted that if a UME event the size of the one in 1999-2000 had occurred previously, some record of it would be expected. Wade noted that it was due to this reasoning that they did not incorporate additional mortality events in the northern stock OSP analysis conducted by Punt and Wade (2012). Wade also noted, however, that there had been a drop in the northern stock abundance in earlier years of the time series but these were not accompanied by a record of increased strandings. The TF suggested that pulses could occur regularly on decadal time scales or as a result of a variety of other environmental or anthropogenic factors.

The TF discussed if the genetic data may reflect a sampling bias toward "core" PCFG animals. This follows other lines of evidence showing that there is a relationship between minimum tenure and probability of photographically capturing animals in the PCFG area (see section 4.4 above). If "core" PCFG whales are more approachable, then they are potentially more likely to be biopsied, meaning that these whales may be disproportionately selected for in the biopsy process.

Lang noted that she had looked at the current genetic sample set to see if the rare haplotypes found in the PCFG sample set came from animals that were sighted in 1999 or later, which might suggest that they were immigrants as the expectation would be that immigrants would be likely to bring in rare haplotypes. The results were mixed, with some rare haplotypes found in long-term PCFG whales while others were found in animals that came into the PCFG in 1999 or later.

This led to a discussion about what additional information might help the PCFG OSP assessment and improve inference generally about the level of internal versus external recruitment to the PCFG. The TF agreed that additional genetic sampling to improve estimates of immigration and residency times (emigration), and improved estimates of incidental mortality would be useful.

5. Probability of a Western North Pacific Gray Whale Being Taken by the Makah

Mixing of whales identified in the WNP and ENP has recently been reported (Weller *et al.* 2012). Lang (2010) reported that two adult individuals from the WNP, sampled off Sakhalin in 1998 and 2004, matched the microsatellite genotypes, mtDNA haplotypes, and sexes (one male, one female) of two whales sampled off Santa Barbara, California in March 1995. In 2010 and 2011, Mate and colleagues (Mate *et al.* 2011) satellite-tracked three whales from the WNP to the ENP (Mate *et al.* 2011; IWC 2012a; IWC 2012b). Finally, photographic matches between the WNP and ENP, including resightings between Sakhalin and Vancouver Island and Laguna San Ignacio, have further confirmed use of areas in the ENP by whales identified in the WNP (Urbán *et al.* 2012; Weller *et al.* 2012). Despite this level of mixing, significant mtDNA and nuclear genetic differences between whales in the WNP and ENP have been found (Lang *et al.* 2011b).

Observations of gray whales identified in the WNP migrating to areas off the coast of North America raise concern about placing the WNP population at potential risk of incurring mortality incidental to the ENP gray whale hunt proposed by the Makah Indian Tribe off northern Washington, USA (see IWC 2012a; IWC 2012b). Given the ongoing concern about conservation of the WNP population, in 2011 the Scientific Committee of the IWC emphasized the need to estimate the probability of a western gray whale being killed during aboriginal gray whale hunts (IWC 2012a). Additionally, NOAA is required by NEPA to prepare an Environmental Impact Statement (EIS) pertaining to the Makah's waiver request. The EIS will need to include an analysis of the likelihood of a western gray whale being killed during the proposed Makah gray whale hunt.

Moore summarized the work that he and Weller (SWFSC) have done to estimate the probability that a WNP whale might be taken during the proposed gray whale hunt (Moore and Weller 2013). Four alternative models were evaluated; these models made different assumptions about the proportion of WNP whales that would be available for the hunt or utilized different types of data to inform the probability of a WNP whale being taken. The probability of striking at least one WNP whale over the course of five years was estimated to range from 0.034 – 0.058 across different scenarios of the preferred model, with upper 95% CI estimates ranging from 0.107 –

0.170. This result may be compared to an estimate of PBR. If the recovery factor for calculating PBR is set to 0.1, and discounting the estimate for the proportion of the population that may be migrating through U.S. waters and the proportion of time (months out of a year) they are in U.S waters, then the 5-year PBR estimate is between 0.1 and 0.6 animals, depending on different assumptions about the amount of mixing between the WNP and ENP. Thus, if a WNP whale were to be struck during the 5-year period, PBR would be exceeded.

6. Status of Gray Whale Stocks as Defined by, MMPA, ESA and IUCN

At the request of the TF, Stone (NWR) provided a review of the status of ENP, WNP and PCFG gray whales under the MMPA, ESA, and the International Union for Conservation of Nature (IUCN) redlist.

(1) ENP – The ENP stock is not considered *"strategic/depleted"* under the MMPA and is listed as "*Least Concern*" by the IUCN. Gray whales in the ENP were delisted from the ESA in 1994. Although there have been two petitions (2001 and 2010) to relist the ENP stock under the ESA, both petitions were denied.

(2) WNP – The WNP stock is considered "*strategic/depleted*" under the MMPA and is redlisted as "*Critically Endangered*" by the IUCN. WNP whales are considered "*Endangered*" under the ESA, although there is no stand-alone SAR for WNP whales. Given that ENP whales were delisted in 1994, gray whales in the WNP would be considered a Distinct Population Segment (DPS) under the ESA. Use of the DPS terminology was not common at the time of the delisting and thus the listing documents do not describe the WNP as a DPS.

(3) PCFG - The PCFG does not have a formal status under the MMPA, IUCN nor ESA.

In addition to the above, the TF discussed the status of gray whale stocks as defined by the IWC. Under the IWC implementation review (IR) process, the IWC considers all plausible hypotheses of stock structure, and then determines which hypotheses have high or medium plausibility. Those stock hypotheses with high or medium plausibility are used to evaluate the management variants proposed by hunters. In the case of gray whales, the IWC traditionally considered only the hypothesis of a single ENP stock. New information presented to the IWC in 2010 (Frasier *et al.* 2011) suggesting that the PCFG could be a separate stock resulted in the IWC evaluating a two-stock hypothesis. Members of the TF reminded the group that the IWC does not have to decide if there are one or two gray whale stocks, but only if it is plausible that there is one stock and if it is plausible that there are two stocks (or three stocks). The objective of the IWC is to make sure that the stock or stocks are robust to the proposed hunt under all plausible scenarios. Thus, the IWC process is currently considering both stock hypotheses (1-stock and 2-stock). Future work by the IWC may need to incorporate a third stock (i.e., WNP) but for now the calculation of the probability of a WNP whale being killed during the Makah hunt (see section 5 above) is a stand-alone calculation.

7. Overview of Evidence Used in Recently Defined Population Stocks

Stone provided an overview of the lines of evidence used by NMFS to delineate stocks as inferred from the text of each SAR. It became clear during discussion of the summary that many of the SARs do not explicitly lay out the lines of evidence and justifications for originally delineating a stock but instead only present recent information. The killer whale SARs, for example, do not describe the acoustics data and other lines of evidence that were originally used to identify the stocks. There was general agreement that an updated summary, in spreadsheet form, would be useful as it could capture the history and provide a long-term record of how each stock was delineated, but this would not be a trivial task. In the end, the TF concurred that agency practices for delineating stocks were not based on a set standard but were more variable and fact-specific so as to use the best available information.

8. Review of Stock Definition Cases Relevant to the Pacific Coast Feeding Group

The TF reviewed several examples of stock delineations for other species exhibiting some similar characteristics to the PCFG. Similar characteristics included: (1) use of mtDNA as the sole genetic marker necessary for stock structure determination and (2) mixing with individuals from other stocks during parts of the year.

8.1 Atlantic harbor porpoises

Rosel (SEFSC) presented an overview of stock structure in Atlantic harbor porpoises (*Phocoena phocoena*) with a focus on the Gulf of Maine/Bay of Fundy stock. A single stock was designated in U.S. waters of the Northwest Atlantic based on published literature of Gaskin (1984) who hypothesized four populations in the Northwest Atlantic (three in Canadian waters and one in U.S. waters). While following Gaskin (1984), the first SAR for U.S. Gulf of Maine/Bay of Fundy harbor porpoises stated "*Presently there is insufficient evidence to accept or reject this hypothesis*" (Blaylock *et al*. 1995). In subsequent years, mtDNA evidence supported four stocks in the Northwest Atlantic, including the Gulf of Maine stock, but nuclear microsatellite data did not (Rosel *et al.* 1999). Organopollutant levels (Westgate *et al.* 1997, Westgate and Tolley 1999) and life history characteristics (Read and Hohn 1995) also differed between the Gulf of Maine/Bay of Fundy and other populations in the Northwest Atlantic. The weight of evidence supported delineation of the Gulf of Maine/Bay of Fundy stock and the lack of nDNA differentiation between this stock and others in the Northwest Atlantic was taken to indicate female philopatry coupled with male-mediated gene flow. Microsatellite data indicated that porpoises from the Gulf of Maine/Bay of Fundy probably overlap in winter in the mid-Atlantic with porpoises from other regions of the Northwest Atlantic (Hiltunen 2006), but this is outside the breeding season.

8.2 Alaska harbor seals

Taylor summarized the history of recognizing stocks of harbor seals in Alaska. Harbor seals (*Phoca vitulina*) are continuously distributed throughout Alaskan waters, but mtDNA indicates that genetic differentiation among sampled sites increases with increasing geographic distance (O'Corry-Crowe *et al.* 2003). The continuous distribution implies that there will be movement of animals across stock boundaries drawn on a map, but if no stock boundaries are designated, there is the risk of local depletion and loss of portions of the species' range. The first SARs for Alaska harbor seals comprised three stocks- Bering Sea, Gulf of Alaska and Southeast Alaska (Hill and DeMaster 1998). In 2011, the three stocks were changed to twelve (Allen and Angliss 2012). MtDNA, satellite telemetry, trend and distributional data were used to delineate these 12 stocks. At that time, nDNA data were not available and mtDNA analyses were considered sufficient to meet the criteria of demographic independence under the GAMMS guidelines.

8.3 Humpback whales

Lang presented a review of humpback whale (*Megaptera novaeangliae*) stocks, with a focus on the North Atlantic. There are multiple humpback whale feeding grounds in the Northwest Atlantic, but individuals from these different feeding grounds share one breeding ground in the

West Indies. Humpback whales throughout the Northwest Atlantic were originally classified as a single stock (Waring *et al.* 1999). However, genetic studies have revealed small but significant differences in mtDNA between animals sampled on different feeding grounds (Palsbøll *et al.* 2001) and photo-identification studies have documented strong site fidelity of individuals to the Gulf of Maine feeding area (Clapham *et al.* 1993). The 2000 SAR recognized whales utilizing the Gulf of Maine feeding area as a separate stock (Waring *et al.* 2000). Although this SAR covers only Gulf of Maine whales, individuals from other feeding areas have been identified in U.S. mid-Atlantic waters (Barco *et al.* 2002).

The stock structure of humpback whales in the Pacific is complex (Baker *et al.* 2008; Calambokidis *et al.* 2008) and differs from the western North Atlantic with respect to the “interbreed when mature” criteria. That is, humpback whales from different feeding grounds in the NW Atlantic have the opportunity to interbreed with each other in a single breeding area, while in the North Pacific not all animals have the opportunity to interbreed with each other because there are multiple breeding areas. There is some similarity between North Pacific humpbacks and those in the central and eastern North Atlantic, in that whales on the Norway and Iceland feeding areas may breed in different areas (Palsbøll *et al.* 1997; Stevick *et al.* 1998; Wenzel *et al.* 2009). Three humpback whale stocks are currently recognized in the North Pacific, based on three feeding areas (Allen and Angliss 2012; Carretta *et al.* 2013). The SAR for the Central North Pacific stock includes calculations of PBR for three different feeding areas (Allen and Angliss 2012), as is done for the PCFG in the current SAR (Carretta *et al*. 2013).

9. Review of Gray Whale Genetic Research on Population Structure

Lang provided a chronological summary of genetic research performed on North Pacific gray whales. Steeves *et al*. (2001) used mtDNA control region sequence data to compare 16 samples collected in summer in Clayoquot Sound, British Columbia, representing the PCFG, to 41 samples collected elsewhere in the ENP. Some haplotypes were shared between the two groups and no significant differentiation was found between them. Additional genetic analysis utilizing an extended set of samples (n=45) collected from whales within the seasonal range of the PCFG indicated that the genetic diversity and the number of mtDNA haplotypes identified among these samples were inconsistent with measures that would be expected (based on simulations) if recruitment into the group were exclusively internal (Ramakrishnan *et al*. 2001). Alternative scenarios, such as limited dispersal of whales from other areas into the PCFG, were not explored. LeDuc *et al*. (2002) examined mtDNA control region differences between ENP and WNP gray whales. The ENP sample consisted primarily of stranded animals along the migratory route with some samples from Chukotka, Russia (no distinctions between PCFG and non-PCFG whales were made). The WNP samples were collected off the northeastern coast of Sakhalin Island, Russia. Seven of the 36 identified haplotypes were shared between the two regions and significant genetic differentiation was found. In addition, haplotypic diversity of the WNP sample was lower than that seen for the ENP samples.

Within the ENP, Goerlitz *et al*. (2003) made comparisons between two wintering lagoons and between females sampled in wintering lagoons and those sampled outside the lagoons (in Clayoquot Sound and along the migration route- *i.e.,* “non-lagoon females”). They found small but significant differences in mtDNA data between Laguna San Ignacio cows (females with calves) and non-lagoon females and between Laguna Ojo de Libre cows and non-lagoon females but not when cows from the two lagoons were compared. Alter *et al*. (2009) compared both mitochondrial and nuclear microsatellite markers across three wintering lagoons and found small but significant differences between only one of the three pairwise comparisons using the microsatellite data set only. Similar to Goerlitz *et al.* (2003), they did not find significant differentiation between Laguna San Ignacio and Laguna Ojo de Libre at mitochondrial or nuclear DNA.

More recently, Frasier *et al*. (2011) examined mtDNA differences between whales sampled in Clayoquot Sound, British Columbia (representing the PCFG) and a more carefully constructed data set of ENP whales from LeDuc *et al.* (2002) in which known PCFG whales were specifically removed. They found significant genetic differentiation between the two sample sets and high levels of haplotype diversity in the PCFG sample, comparable to samples thought to represent the larger ENP population. Using this dataset, Frasier *et al.* (2011) also performed a likelihood ratio test using Theta (Θ) as a proxy for effective population size to examine whether the two sample sets come from the same population. The likelihood ratio test indicated that Θ for the PCFG did not equal Θ for the ENP and the authors concluded that the two groups were demographically independent.

D'Intino *et al*. (2012) made a comparison of whales sampled off Vancouver Island and representing the PCFG to whales sampled at the calving lagoon at San Ignacio. Using 15 microsatellite loci, they found no evidence for population differentiation between these two areas and concluded that the two sampled groups come from the same interbreeding population and that maternally-directed site fidelity to different feeding areas leads to genetic differentiation at mtDNA among feeding areas. Lang *et al*. (2011a) expanded on this result and compared whales sighted over two or more years within the PCFG seasonal range to animals sampled on the feeding ground(s) north of the Aleutians using both mtDNA and nuclear microsatellite markers. Significant differentiation was seen for the mtDNA data but not the microsatellite data, supporting the conclusion of Frasier *et al.* (2011) that structure is present among different feeding areas and this structure may be directed by matrilineal fidelity[5] to feeding grounds. Of note, when all samples collected on the PCFG seasonal range (including those collected from animals seen in only one year) were utilized in the mtDNA analyses, no significant differences were detected in the comparison to samples collected from whales off Chukotka. When all samples collected on the PCFG seasonal range were compared to all samples collected north of the Aleutians, the mtDNA F_{ST} comparison detected a significant difference although the χ^2 test did not.

Finally, Lang *et al.* (2011b) re-examined differences between ENP and WNP gray whales, expanding on the previous study of LeDuc *et al.* (2002) by using larger sample sizes, better characterized sampling and both mtDNA and nuclear microsatellite data. Comparisons of whales sampled off Sakhalin Island with whales feeding north of the Aleutians (i.e., ENP whales) and with the PCFG demonstrated significant differentiation at both nuclear and mtDNA markers. The extent of mtDNA differentiation between ENP strata (PCFG and whales feeding north of the Aleutians) and Sakhalin Island was higher than that observed in comparisons within ENP strata. As with previous studies, significant differentiation among ENP feeding areas was not seen in the microsatellite data. The Sakhalin stratum again displayed reduced haplotype diversity compared to the ENP strata. The authors conclude that the mtDNA data support demographic

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[5] Matrilineal fidelity as used here means the learned behavior of a calf (male or female) returning to the feeding ground of its mother.

independence for ENP and WNP gray whales. However, in examining the microsatellite genotypes, Lang *et al.* (2011b) found two individuals biopsied at the Sakhalin feeding ground and off the coast of southern California. These matches, in combination with recent photo-identification and telemetry data (Mate *et al.* 2011; Urbán *et al*. 2012; Weller *et al.* 2012), suggest that some animals summering off Sakhalin overwinter in the ENP in at least some years. Given that recent records document gray whales in the waters off Japan and China during winter and spring (see review in Weller and Brownell 2012) these results suggest that population structure in gray whales may be more complex than previously believed, such that not all of the animals that feed off Sakhalin share a common wintering ground, or that some animals may switch between wintering grounds.

In discussion, TF members suggested some further avenues for exploration including examining whether any microsatellite loci were out of Hardy-Weinberg equilibrium (HWE) for the Sakhalin samples, which might be an indication of mixing of multiple breeding populations on that feeding ground. It was noted that at the 2012 IWC Scientific Committee meeting a paper evaluating the use of HWE tests to look at mixing of stocks was presented and it might be worthwhile to see if the approaches in this paper could be applied to the Sakhalin dataset (IWC 2012b). There was also discussion regarding what proportion of mixing would have to take place before it would be detected by a relatively weak test like HWE.

9.1 Genetic modeling of immigration rates

Lang presented an overview of recent work utilizing a simulation-based approach to evaluate the plausible level of immigration (i.e., a permanent change of feeding ground fidelity, used interchangeably with external recruitment) that might be occurring into the PCFG. While the empirical studies summarized above have shown significant differences in mtDNA between the PCFG and other ENP gray whale feeding areas, suggesting that matrilineal fidelity is important in structuring feeding ground use, other evidence (some from genetics, mostly from photo-id) suggests that some immigration into the PCFG may be occurring. Lang and Martien (2012) used simulations to examine how much immigration into the PCFG could occur to produce results consistent with the empirical genetic (mtDNA) analyses. The results suggested that the plausible range of immigration is >1 and <10 animals/year on top of a two-year pulse of immigration (of 20 animals each year in 2000 and 2001). Annual immigration of 4 animals (with the 2 year pulse of immigration) produced simulated results that were most consistent with the empirical data. If the PCFG had been founded more recently or the abundance of the PCFG is greater than used in the simulations, it is plausible that no annual immigration could be occurring (still assuming the occurrence of a 2-year pulse of immigration).

In discussion of these results, the TF noted several important caveats to the approach used by Lang and Martien (2012), including: (1) the results may be overly precise because so many model parameters are set, and (2) the simulated abundance trajectories do not match well with the mark-recapture estimates (Calambokidis *et al*. 2012) when immigration is 4 immigrants/yr or more. The simulated population trajectories assumed that the PCFG split from the larger ENP population in 1930. Task Force members thought that the 1930 split might be unrealistic, as oceanographic conditions during the Little Ice Age (and earlier) would have limited access to the northern feeding ground(s) and thus may have caused some gray whales to utilize more southern waters for feeding. Lang commented that there were plans to model a split of the PCFG from the larger ENP in the Little Ice Age, but that this work is not yet complete. She also noted that there were many possible histories and it would be difficult to encompass all of them.

10. Discussion of Makah Documents Concerning the Pacific Coast Feeding Group

Weller introduced three documents drafted by or on behalf of the Makah Indian Tribe regarding the PCFG. These documents were provided to the TF in advance of the meeting for review and consideration. In combination, these three documents provided important summary information on the PCFG, including reviews of what is known about the history of the PCFG and summaries of the current status of the group.

The 2011 Makah document (Makah 2011) was drafted by the Tribe and their attorneys and provided to the Pacific and Alaska SRGs as a background paper to help inform their respective reviews of the draft 2012 gray whale SAR (NMFS 2012). This document provides the Makah perspective on whether the PCFG should be recognized as a stock and was therefore deemed important for the TF to review and consider. Information provided in Scordino *et al*. (2011) is largely the same as that presented in the Makah 2011 document.

The 2012 Makah document (Makah 2012) contains comments from the Makah Tribe and their attorneys on the 2012 draft gray whale SAR (NMFS 2012). This document was considered important for the TF to review. In response to the Tribe's request for government-to-government consultation, the SWFSC met with representatives from the Makah Tribe and their attorneys in person to review comments provided in the 2012 document. These comments, where appropriate, were incorporated as changes to the draft text of the SAR (NMFS 2012).

10.1 Discussion of genetics sections of Makah documents

In discussion of these documents, the TF agreed that it was most important to focus on the Makah comments and perspective regarding genetics research on the PCFG. Rosel agreed to lead the TF through the genetics sections of the Makah documents that called into question the strength of the genetic data presented with respect to demographic independence of the PCFG. These points were summarized as: (1) the samples used to represent the overall ENP stock may not be a random sample of the entire stock but could come from different and unknown feeding grounds. This calls into question what the PCFG is being compared to in the genetic analyses, (2) sample sizes from many locations are small relative to overall population size (i.e., relative to the size of the larger ENP population) and to the total level of genetic diversity and that this could cause misleading results, (3) many population comparisons of gray whales have yielded significant but low-level differences in haplotype frequencies; if this is considered sufficient evidence to classify the PCFG as a stock then every group of gray whales utilizing a particular feeding area should be considered a stock, and (4) the genetics results do not support reproductive isolation of the PCFG.

The first two points were related to sampling effects. In discussion, some members of the TF noted that it is not necessarily the sample size that is potentially problematic but rather if related animals are grouped together and multiple biopsies are taken from that "group" then the effective sample size is much smaller. It was further noted that small sample sizes may add variability, but it would only be a problem if there were additional (unrecognized) structure in the samples. From a genetic standpoint, many analyses rely on haplotype frequencies, but if a good sample relative to the genetic diversity of the group is not obtained then the genetic diversity may not be well characterized, especially if there are many rare haplotypes. Since haplotype frequency data also go into analyses for F_{ST} and Chi-square, then poor frequency estimates due to small sample size could affect the accuracy of the genetic differentiation results as well. Lang noted that there is some evidence from North Atlantic humpbacks that the migration to the West Indies is segregated according to feeding ground origin (Stevick *et al.* 2003).

The TF noted, however, that the recent PCFG genetic analyses show high diversity indicating that sampled animals have different haplotypes and are thus not related (maternally). The TF asked if the question at hand is whether gray whales have feeding aggregations or whether the group that migrates north of the Aleutians is different from the group that does not migrate north of the Aleutians. Lang noted that the original intent of the project was to compare samples collected from different feeding areas north of the Aleutians to the area used by the PCFG but in the end sample sizes were insufficient for areas other than Chukotka. Nevertheless, although there could be multiple feeding aggregations north of the Aleutians, one of the comparisons conducted by Lang *et al.* (2011a) used only samples collected off Chukotka to try to avoid including unrecognized structure.

The TF recognized the continuing need for additional data to be collected, but for the purposes of the workshop the focus was whether the lines of evidence from existing genetic analyses are strong enough to counter lines of evidence that put the demographic independence of the PCFG into question. The primary question in the short-term is what can be done with the information that is currently available.

The TF noted that Frasier *et al.* (2011) compared animals from the PCFG with a sample set primarily derived from stranded animals along the U.S. west coast during migration. They agreed that these samples might not be a random representation of the larger ENP, as was also pointed out in the Makah documents.

Overall, the TF felt it was important to recognize that the current research questions being addressed center around feeding-ground-based groups of animals. The genetics work has already shown that when the PCFG is compared to a sample set from northern feeding area (Chukotka) animals or to the Sakhalin animals (also a feeding area) differences have been found (Lang *et al.* 2011b). That is, the PCFG has been shown to be different from two other well-characterized feeding grounds.

While interpretation of the currently available genetic results as relevant to the PCFG has lead to debate amongst different groups, the TF concurred that it represents the best available science. In discussion, some members of the TF agreed that although more progress on this issue could be made over the next few years if resources were available for more intensive sampling, they did not think that the current interpretation of results would change much. That is, even if 1% of the 19,000 or so animals going through Unimak Pass were sampled, a mtDNA difference with the PCFG (as already observed) would remain. So far the PCFG has been compared to samples from feeding areas and from the migratory route and both comparisons detected a genetic difference. It was agreed that the critical issue for additional research to address was better determining the levels of internal versus external recruitment in the PCFG.

At this point the TF returned to discussing the remaining points raised by the Makah documents. The third point was that since multiple genetic comparisons have found low but significant differences, every group of gray whales should be considered a stock. The TF concurred and noted that there is nothing wrong with incrementally adding stocks as new evidence is uncovered, and that decisions have to be made based on the best available science.

The final point discussed was that the genetics results do not support reproductive isolation of the PCFG. The TF agreed in general that the pattern and timing of migration provide ample opportunity for breeding between PCFG whales and other ENP whales. Little is known about gray whale social and mating systems, however, and presently unrecognized mechanisms facilitating selective breeding could exist. If a form of selective breeding does exist, then it could be a long time before nDNA differences appear. A suggested approach to resolving this question is to look at the relatedness of animals in the PCFG. Despite this, the TF agreed that it is most likely that PCFG animals are interbreeding with animals coming from other areas.

11. Research Recommendations

The TF agreed that the following set of recommendations represent key research needs that could help provide additional insight regarding if the PCFG should be recognized as a population stock under the MMPA and GAMMS guidelines.

Given the limited photo-identification and biopsy effort north of 52°N but knowing that at least some observations of PCFG whales in northern feeding areas (e.g., Kodiak and Barrow, Alaska) have been recorded, the TF highlighted the importance of expanding the spatial and temporal coverage of the photo-identification and biopsy effort. In addition, the TF also recommended that further satellite tagging of known PCFG whales be conducted to better delineate habitat use and define the summer/fall feeding area boundaries.

The TF noted that PCFG animals might more regularly interact (compared to non-PCFG whales) with crab pots given their extended residency in coastal waters. Therefore, the TF recommended that the existing photo-identification time series be used to examine scarring patterns of PCFG whales to better understand the incidence of interactions with fishing gear.

Since much of the photo-identification sighting effort occurs in August and later, when many calves are likely to already be weaned and thereby more difficult to identify as a calf (versus a yearling), the TF recommended that the existing PCFG photo-identification time series be examined following a protocol developed by Bradford *et al*. (2011). This photo-based method uses barnacle and pigmentation characteristics on young gray whales to reliably distinguish calves of the year from yearlings.

Knowing that several lines of evidence demonstrate a relationship between minimum tenure and the probability of photographically capturing animals in the 42°N-52N° PCFG area, the TF recommended that the existing PCFG photo-identification time series be examined to see if moms/calves demonstrate higher degrees of fidelity than other whales.

Although photo-identification studies of the PCFG by Calambokidis and colleagues have been ongoing for over a decade, a relatively high number of "new" animals (not previously sighted in the area) are identified each year and subsequently show consistent return to the area (Calambokidis *et al*. 2012). These "new" animals could represent calves born into the group (i.e., internal recruitment) and not identified in their first year, or they could represent animals that traditionally feed in northern areas but now show fidelity to the seasonal range of the PCFG (i.e., external recruits). To better address this question, the TF recommended that relatedness analysis, in which microsatellite genotypes are used to identify animals that represent putative mother-offspring pairs, be used to assess the proportion of internal recruitment occurring within the PCFG. A sufficient understanding of recruitment to make a stock definition determination could potentially be achieved with a concerted effort to sample known mothers and recruits and determine their relatedness.

Related to the recommendation above, some TF members felt that it was plausible that the pulse of immigration into the PCFG could be larger than what the genetic simulations have modeled. If so, then the estimates of annual immigration into the PCFG could be lower than that estimated in the genetic simulations. With this in mind, the TF recommended that the genetic simulations should try pulses of 30 animals and see if that is consistent with the empirical genetic data.

12. Structured Decision-Making Process

At the request of the TF, Bettridge provided an overview of the FEMAT-style structured decision-making process[6]. In some NMFS status reviews, Biological Review Teams (BRTs) formed pursuant to the ESA have adopted formal methods to express plausibility for use in guiding its analysis of DPSs and in assessing the risks to the population(s). These formal methods are important in a setting where quantitative measures of uncertainty derived from the empirical data are unavailable. This point allocation method is often referred to as the "FEMAT" method because it is a variation of a method used by scientific teams evaluating options under the Northwest Forest Plan (Forest Ecosystem Management Assessment Team). In this approach, for example, each expert is asked to distribute plausibility points among the choices/scenarios for a given decision, reflecting his or her opinion of how likely that choice or option correctly reflected the population status. If the expert is certain of a particular option, or feels it is the only plausible scenario, he or she could assign all points to that option. An expert with less certainty about which option best reflected reality or best reflected the population's status could split the points among two or more options. This method has been used in all status review updates for anadromous Pacific salmonids since 1999, as well as in reviews of Southern Resident killer whales, West Coast rockfishes, Pacific herring (*Clupea pallasii*), Pacific groundfish, North American green sturgeon (*Acipenser medirostris*), black abalone (*Haliotis cracherodii*), Hawaii false killer whale (*Pseudorca crassidens*), and humpback whales.

In the humpback whale status review, BRT members distributed 100 likelihood points among the defined scenarios or options, reflecting their expert opinion of the relative likelihood that the status of a specific DPS falls into each of three risk categories. Then the team discussed how they had allocated points and subsequently had a chance to revise their scores. Scorer identity was known.

In the Hawaii false killer whale status review, BRT members distributed 10 points between the arguments for and against each factor. Team members agreed to view resulting scores with names associated to facilitate discussion and assure that linguistic uncertainty was not responsible for any disparate votes. The BRT discussed the scores and, in some cases, adjusted scores when prior articulation of the arguments had been unclear.

After presentation of the structured decision-making approach, Bettridge asked the TF the following questions: (1) Does the TF want to use this approach? (2) If so, how many points will each member allocate among scenarios? (3) Does the TF wish to disclose names, or keep scores anonymous? (4) Does the TF wish to allow for rescoring after discussion? The TF members agreed to employ the structured decision-making approach, allocating 100 points per person. The

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[6] The TF agreed that Bettridge, as leader of the decision-making process, should refrain from allocating points on the decision questions.

group agreed to disclose names with scores for the purposes of internal discussion and possible rescoring but to retain anonymity in the final report.

The TF further agreed that they needed to carefully formulate the questions to be addressed and clearly understand what it means to put likelihood points in one category or another so as to provide the necessary advice for management-related issues such as: (1) how future NMFS stock assessment reports will be drafted with regard to gray whale stock structure in the North Pacific and (2) how to interpret any new information in the context of the Makah Indian Tribe MMPA waiver request to resume hunting gray whales off Washington State, USA.

Some TF members with experience using this approach in other situations found that when one or a few members allocated points very differently it was often due to misunderstanding of the question or what the answers implied. Therefore, it was agreed that the questions and the categories of answers should be as clear as possible to make the process both efficient and transparent.

12.1 Question formulation

In keeping with the objectives stated above for developing questions, the TF dedicated significant time during day 2 of the workshop agreeing on questions to be considered during the decision-making process. A key objective of this exercise was to focus on existing lines of evidence to help create the questions while at the same time being mindful of the existing definitions of the terms (e.g., demographic independence, interbreed when mature, functioning element of the ecosystem) contained in the MMPA and GAMMS guidelines. For instance, a simple example of this might be; "*evidence of demographic independence is when the number of internal recruits is greater than the number of external recruits*". In general, this philosophy of creating questions was adopted by the TF and maintained during its deliberations.

After considerable work, the TF agreed to 11 questions. Overnight, TF members privately completed their point allocations for each of the questions. Point allocations were tallied and ready for discussion on the final day of the workshop. Allocating points in this manner allowed individual TF members to express their level of certainty on each of the questions, such that placement of all points in a single category indicated relative certainty in the lines of evidence discussed during the workshop. The TF agreed to view resulting scores with names associated to facilitate discussion and assure that linguistic uncertainty was not responsible for any disparate votes. The TF discussed the scores and, in some cases, members adjusted them when prior articulation of the lines of evidence had been unclear. The final 11 questions and likelihood point allocations for each of the TF members (anonymous, labeled A – G), as well as the proportional distribution of points overall, are provided below.

Question 1.	Overall	A	B	C	D	E	F	G
	Does the ecosystem occupied by the PCFG when they are feeding differ from the ecosystems occupied by other ENP gray whales?							
Strongly Agree	53	100	0	80	100	90	0	0
Somewhat Agree	47	0	100	20	0	10	100	100
Neutral	0	0	0	0	0	0	0	0
Somewhat Disagree	0	0	0	0	0	0	0	0
Strongly Disagree	0	0	0	0	0	0	0	0

Question 2.	Overall	A	B	C	D	E	F	G
	If gray whales in the ENP continued to be managed as a single stock, would the future abundance of PCFG gray whales be maintained above 60% of their current abundance if annual HCM in the PCFG was 5?							
Strongly Agree	38	0	95	0	0	20	50	100
Somewhat Agree	23	20	5	5	0	80	50	0
Neutral	25	50	0	25	100	0	0	0
Somewhat Disagree	14	30	0	70	0	0	0	0
Strongly Disagree	0	0	0	0	0	0	0	0

Question 3.	Overall	A	B	C	D	E	F	G
	If gray whales in the ENP continued to be managed as a single stock, would the future abundance of PCFG gray whales be maintained above 60% of their current abundance if annual HCM in the PCFG was 10?							
Strongly Agree	10	0	50	0	0	0	0	20
Somewhat Agree	24	10	50	0	0	25	30	50
Neutral	21	40	0	0	0	25	50	30
Somewhat Disagree	17	40	0	10	0	50	20	0
Strongly Disagree	29	10	0	90	100	0	0	0

Question 4.	Overall	A	B	C	D	E	F	G
	If gray whales in the ENP continued to be managed as a single stock, would the future abundance of PCFG gray whales be maintained above 60% of their current abundance if annual HCM in the PCFG was 20?							
Strongly Agree	0	0	0	0	0	0	0	0
Somewhat Agree	4	0	25	0	0	0	0	0
Neutral	7	0	50	0	0	0	0	0
Somewhat Disagree	22	10	25	0	0	50	50	20
Strongly Disagree	67	90	0	100	100	50	50	80

Question 5.	Overall	A	B	C	D	E	F	G
	Given the lack of significant differences found in nuclear markers between PCFG whales and other eastern Pacific whales, how would you allot points to:							
There is complete random mating within the eastern NP	63	70	70	70	50	80	60	40
There could be some non-random mating within PCFG whales that is either too recent or at too low a level to be detected given current sample sizes and marker numbers	37	30	30	30	50	20	40	60
PCFG whales breed primarily with each other	0	0	0	0	0	0	0	0

Question 6.	Overall	A	B	C	D	E	F	G
	Based on the genetic data and simulations, how would you allot points to:							
Nearly all recruitment into the PCFG area results from external recruitment (immigration)	0	0	0	0	0	0	0	NA
Most recruitment into the PCFG area results from external recruitment	21	20	30	20	0	20	33	NA
Recruitment is about equal between internal (births) and external (immigration) recruitment	56	60	50	60	100	30	34	NA
Most recruitment into the PCFG area results from internal recruitment	24	20	20	20	0	50	33	NA

Question 7.	Overall	A	B	C	D	E	F	G
	Based on the photo-identification data, how would you allot points to:							
Nearly all recruitment into the PCFG area results from external recruitment (immigration)	0	0	0	0	0	0	0	0
Most recruitment into the PCFG area results from external recruitment	38	30	55	50	0	30	50	50
Recruitment is about equal between internal (births) and external (immigration) recruitment	48	40	35	35	100	50	35	40
Most recruitment into the PCFG area results from internal recruitment	14	30	10	15	0	20	15	10
Nearly all recruitment into the PCFG area results from internal recruitment	0	0	0	0	0	0	0	0

Question 8.	Overall	A	B	C	D	E	F	G
	Do the genetic and photo-identification data indicate that the PCFG is a demographically independent population?							
Strongly Agree	0	0	0	0	0	0	0	0
Somewhat Agree	35	25	10	80	100	30	0	0
Neutral	21	50	30	10	0	40	20	0
Somewhat Disagree	25	25	50	10	0	30	40	20
Strongly Disagree	19	0	10	0	0	0	40	80

Question 9.	Overall	A	B	C	D	E	F	G
	Given all lines of evidence, is the PCFG a "population stock" under the agency's interpretation of the MMPA?							
Strongly Agree	14	0	0	0	100	0	0	0
Somewhat Agree	22	25	10	80	0	30	10	0
Neutral	21	50	30	10	0	40	20	0
Somewhat Disagree	24	25	50	10	0	30	35	20
Strongly Disagree	18	0	10	0	0	0	35	80

Question 10.	Overall	A	B	C	D	E	F	G
	Given that some whales identified in the WNP migrate through U.S. waters to Mexico, should a separate SAR be developed for the WNP?							
Yes	79	100	70	100	100	50	80	50
No	21	0	30	0	0	50	20	50

Question 11.	Overall	A	B	C	D	E	F	G
	Given the differences found in mtDNA and nDNA between Sakhalin Island (WNP) and ENP gray whales, is there a "population stock" within the WNP under the agency's interpretation of the MMPA?							
Strongly Agree	100	100	100	100	100	100	100	100
Somewhat Agree	0	0	0	0	0	0	0	0
Neutral	0	0	0	0	0	0	0	0
Somewhat Disagree	0	0	0	0	0	0	0	0
Strongly Disagree	0	0	0	0	0	0	0	0

12.2 Question outcomes and discussion

The outcomes of each question above are discussed below and follow the convention of using "percentage of total points" to describe the results. For example, in Question 1 the "strongly agree" category was allotted 53% of the total available TF points (370 points allotted/700 total points = 53%).

Question 1

The TF expressed general agreement, by allocating 100% of the their combined points to the categories "somewhat agree" (47%) and "strongly agree" (53%) that PCFG whales seasonally feed in a unique ecosystem that differs from other gray whale feeding areas in the Pacific. Therefore, the TF concurred that it is reasonable to consider that if the PCFG no longer existed and the region was not reoccupied via immigration, summer feeding gray whales would no longer be a functioning element of the coastal Pacific Northwest ecosystem. Although such a circumstance is plausible, keeping all other things equal (e.g., habitat, prey availability), the current lines of evidence from photo-identification studies suggest it is unlikely that the level of annual immigration into the PCFG in the past decade would cease. Thus, the likelihood of gray whales not being found in the PCFG area seems low. However, the time it might take for "recolonization" of the PCFG via immigration is undetermined and thereby puts into question whether this scenario would meet the MMPA objectives of maintaining stocks not only for ecological purposes but also for aesthetic, recreational and economic reasons.

Questions 2, 3 and 4
These three questions were meant to address the MMPA objective of maintaining population stocks as significant functioning elements in the ecosystem of which they are part, and that population stocks should not be permitted to decline below OSP. GAMMS II state that where mortality is greater than a PBR level calculated from the abundance for the region where human caused mortality (HCM) occurs, serious consideration should be given to identifying an appropriate management unit in the region. While estimates of PBR and HCM for a putative PCFG stock have been generated (Carretta *et al*. 2013), there is uncertainty about both estimates, especially with respect to: (1) whether HCM (e.g., ship strikes and fisheries bycatch) for whales in the PCFG area is indeed higher than for whales that migrate through the area, and (2) where HCM actually occurs. In response to these questions, the TF expressed increasing concern about the ability of the PCFG to be maintained above 60%[7] of its current abundance once HCM exceeded 5 whales per year.

The point allocation in Question 2 indicates that the TF overall tended to agree that the future abundance of PCFG gray whales would be maintained above 60% of their current abundance if annual HCM in the PCFG was 5. However, the relatively equal distribution of likelihood points in all categories except "strongly agree" indicates a high level of uncertainty among the TF.

For Question 3, points were allocated more broadly across categories, indicating a higher level of uncertainty among TF members as to whether the PCFG could sustain levels of HCM at 10 whales per year.

There was increased consensus among the TF for Question 4 in that none of them responded "strongly agree". Overall, the TF concurred that it somewhat (22%) or strongly disagreed (67%) that the future abundance of PCFG gray whales would be maintained above 60% of their current abundance if annual HCM in the PCFG was 20.

Question 5
The TF found no evidence to suggest that PCFG whales breed primarily with each other. While there was general agreement (63%) that the lack of significant differences found in nuclear DNA markers between PCFG whales and other ENP whales suggests random interbreeding among all ENP whales, the allotment of 37% of the total points to the intermediate category suggests TF members thought it was possible that some breeding segregation may exist based on migratory timing (see Lang *et al*. 2011) but there is no direct evidence presently available to support or further test this theory.

Question 6
The TF found no evidence in the results from genetics studies to suggest that nearly all recruitment into the PCFG area results from external recruitment (immigration). Based on the genetic data and simulations discussed during the workshop, the highest average TF response (56%) indicates that TF members believe recruitment is most likely about equal between internal (births) and external (immigration) recruitment. That being said, the remaining 45% of the total points were split between most recruitment into the PCFG area resulting from either internal or

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[7] The management goal of the MMPA is to prevent populations from "depletion". NMFS considers a population depleted if it fall below its Maximum Net Productivity Level (MNPL). For marine mammals, this level is thought to be between 50% and 85% of carrying capacity and is more likely to be in the lower portion of that range (Taylor and DeMaster 1993). Therefore, populations are considered depleted by the U.S. government if they are directly estimated to be below their MNPL, or if they are estimated to be below 50%-70% of a historic population size which it thought to represent carrying capacity (Gerrodette and DeMaster 1990).

external recruitment, indicating some overall uncertainty among members regarding the presently available lines of evidence about recruitment in the PCFG. It should be noted that one member of the TF refrained from assigning any points to this question, so these results represent 6 of 7 TF members actively involved in the point assignment process.

Question 7
Based on the photo-identification data, the TF found no evidence to suggest that nearly all recruitment was either external or internal, but rather some combination of the two. As with the genetics evidence, the highest average TF response (48%) indicates that the TF felt recruitment from internal (births) and external (immigration) sources are comparable. That being said, 38% of the total points were allocated to most recruitment into the PCFG area resulting from external recruitment. Therefore, a majority of the total points were allocated to either recruitment being about equal between internal (births) and external (immigration) recruitment (48%) or most recruitment into the PCFG area results from external recruitment (38%). As was also true with the genetic lines of evidence, these results from the TF suggest a fairly high level of uncertainty regarding recruitment into the PCFG.

Question 8
Based on the genetic and photo-identification data, the TF did not strongly agree that the PCFG is a demographically independent population. Although the highest average TF response (35%) was “somewhat agree” that the PCFG is a demographically independent population, the combined categories of “somewhat disagree” and “strongly disagree” elicited 44% of the total points allocated. Overall, these results from the TF suggest a high level of uncertainty regarding recruitment in the PCFG.

Question 9
Given all lines of evidence, the point allocation of the TF reflects broad uncertainty as to whether the PCFG should be regarded as a population stock under the MMPA and GAMMS guidelines. Perhaps more than all of the other questions considered, Question 9 reflects the highest degree of uncertainty. For instance, the “strongly agree” (14%) and somewhat agree (22%) categories are almost perfectly counter-balanced by the “somewhat disagree”(24%) and “strongly disagree” (18%) categories. An additional level of uncertainty is indicated by the “neutral” category (21%). Given these results, it seems clear that TF was unable to reach a definitive response with respect to the PCFG being a population stock. That is, members of the TF ranged in their opinions from strongly agree to strongly disagree as to whether the PCFG should be considered a separate stock.

Given that this question represents the primary purpose of the workshop, the following two sections provide insight into the deliberations of the TF with regard to arguments for and against the PCFG being a demographically independent unit.

❖ *Arguments for the PCFG being a demographically independent unit*

The return of individual whales to specific feeding areas for as long as the PCFG has been studied (30+ years) strongly suggests that site fidelity is key to maintaining gray whales as a functioning element of this ecosystem. There was agreement that this ecosystem differs from other feeding ecosystems occupied by gray whales. Gray whales are unique among the great whales in being found in only a single ocean basin. Within this ocean basin the PCFG is the only feeding group that does not rely on the dynamics of a sub-arctic ecosystem. As such, the PCFG deserves the protections afforded by being an MMPA stock because the ecosystem role of these animals is unique and also because it provides gray whales, as a species, the flexibility they may need given potential challenges in a changing sub-arctic ecosystem.

Although there is evidence of recruitment from other feeding aggregations, there is also evidence of direct internal recruitment because calves have been shown to return to the PCFG area and reside there. Furthermore, because photographic efforts take place after most claves would be weaned, the recruits into the population not first seen as calves are actually of unknown origin and cannot be definitively assigned as external recruits.

PCFG whales show a low but significant level of genetic differentiation at the mtDNA control region when compared to samples collected in Chukotka [representative of the ENP population and sampled at a single feeding location in the Bering Sea], and when compared to a set of samples collected primarily from animals that stranded along the west coast of the U.S. [representative of a broader sampling of the ENP population]. The significant differences found when the mtDNA haplotype data from the PCFG is compared with that of groups representing the larger ENP population provide indirect evidence of internal recruitment and matrilineally-directed site fidelity to feeding grounds. The level of differentiation is on par with levels identified among humpback whales feeding in different areas of the western North Atlantic (Palsbøll *et al*. 2001) as well as humpback whales using different breeding grounds in the Southern Hemisphere (Rosenbaum *et al*. 2009), suggesting that the PCFG exhibits demographic independence similar to what has been inferred for other large whales. Within the western North Atlantic, humpback whales feeding in the Gulf of Maine are managed as a separate stock despite the fact that they share a common breeding ground with humpbacks feeding in other areas. Although evidence for nuclear DNA differentiation between PCFG whales and other areas has not been found, nuclear genetic differentiation has not always been required for stock delimitation. Pacific harbor seal stocks were delimited on mtDNA differentiation alone (nuclear data were not available at the time), while the Gulf of Maine/Bay of Fundy stock of harbor porpoises was delimited based on significant differentiation at mtDNA, contaminant loads, and life history differences, and despite a lack of differentiation at nuclear markers.

❖ *Arguments against the PCFG being a demographically independent unit*

The evidence that external recruitment is not a rare event is quite strong. The genetic data have numerous rare haplotypes that are not consistent with a small, closed population. Indeed, simulations are not consistent with a closed population. A sizable number of individuals seen in the main feeding season are identified as transients, which is consistent with an on-going level of the main ENP population investigating this new habitat but then moving on. Further, when all samples collected in summer in the PCFG area are used there is not a significant difference found in mtDNA frequencies compared to all samples collected north of the Aleutian Islands. The number of recruits into the PCFG has been estimated, through genetic data, to be 4 to as high as 8 individuals per year. Photo-identification data suggest similarly high numbers of non-calf recruits per year (8-11). These numbers exceed the estimated number of internal recruits and, given that PCFG numbers appear to be relatively stable, an addition of 4 or more external recruits per year cannot be considered trivial. These external recruitment rates suggest the PCFG is not demographically independent from the larger ENP population.

Furthermore, unlike other large whale populations, the annual coastal migration of the vast majority of ENP gray whales brings most individuals into contact with the habitat used by the PCFG. Should there be increased removals from this area, the continual visitation to this area by a large number of gray whales would make it likely that external recruitment would increase to fill any voids. The apparent pulse recruitment in 1999-2000 when conditions in the sub-arctic feeding areas resulted in a large mortality event shows that gray whales can adapt to a new habitat when conditions dictate. Using data collected since 2002 (post-pulse recruitment event), an average of 29.3 new whales have been identified in summer in the area used by the PCFG, with 18.5 animals that are not seen in later years and 10.8 whales that are seen in later years. Given that an average of 18.5 new whales (at least, as this does not account for new whales not photographed) visit the PCFG area each summer but do not return, this suggests that something on the order of 10% of the whales that occur in the PCFG area each summer are transients that otherwise feed north of the Aleutians, and serve as a substantial and continuous source of potential recruitment into the PCFG.

To date, there is no evidence for nDNA differentiation between Chukotka and PCFG whales based on 8 microsatellite loci or between the PCFG and one Mexican calving lagoon based on 15 loci. These results may be interpreted as female directed site fidelity to the PCFG area coupled with random mating between PCFG and ENP whales on the breeding ground. Lack of nuclear differentiation diminishes support for demographic independence.

All lines of evidence (photo-identification and genetics) are consistent with ongoing external recruitment that could be at a magnitude that is not trivial to the persistence of the feeding aggregation (more than a percent or two per year). Uncertainty in the number of recruits per year and exactly who those recruits are (PCFG calves misidentified as recruits, true recruits of adults, temporary immigrants who do not stay more than a few years and may not even be contributing to the gene pool) creates significant uncertainty as to whether internal recruitment exceeds external recruitment. Given the high level of mtDNA haplotypic diversity, the precision of F_{ST} estimates is also uncertain. Taken together, the available evidence is weak for concluding the PCFG is demographically independent.

Question 10
Given that some whales identified in the WNP have been observed to migrate through U.S. waters to Mexico, in combination with the 1994 amendments to the MMPA requiring that SARs be published for all stocks of marine mammals in U.S. waters, the TF agreed to a high degree (79%) that a separate SAR should be developed in the future for the WNP stock of gray whales.

Question 11
Based on the differences found in mtDNA and nDNA between Sakhalin Island (WNP) and ENP gray whales, the TF unanimously (100%) agreed that it qualifies as a population stock under the MMPA and GAMMS guidelines.

13. Concluding Remarks

The implications of new data pertinent to stock structure, including considerable information related to the PCFG and WNP gray whales, were thoroughly reviewed during the workshop. Evaluating the new findings relevant to the status of the PCFG proved particularly complex. After review of results from photo-identification, genetics, tagging, and other studies within the context of the GAMMS guidelines there remains a substantial level of uncertainty in the strength of the lines of evidence supporting demographic independence of the PCFG. Consequently, the TF was unable to provide definitive advice as to whether the PCFG is a population stock under the MMPA and the GAMMS guidelines. Members of the TF ranged in their opinions from strongly agreeing to strongly disagreeing about whether the PCFG should be recognized as a separate stock.

In the case of WNP gray whales, the work of the TF was more straightforward. The mitochondrial DNA and nuclear DNA genetic differentiation found between the WNP and ENP stocks provided convincing evidence that resulted in the TF providing unambiguous advice that the WNP stock should be recognized as a population stock pursuant to the GAMMS guidelines and the MMPA.

Additional research may narrow the uncertainty associated with the question of whether the PCFG should be recognized as a population stock. To work towards this objective, the TF recommended further investigation of recruitment into the PCFG. Presently, both the photo-identification and genetics data indicate that the levels of internal versus external recruitment are comparable, but these are not quantified well enough to determine if the population dynamics of the PCFG are more a consequence of births and deaths within the group (internal dynamics) rather than related to immigration and/or emigration (external dynamics). The TF offered a number of research recommendations, using the existing photo-identification and genetics datasets, that could provide increased resolution on the issue of recruitment and, in turn, the question of stock identification.

While the need for additional data collection was apparent, especially with regard to recruitment into the PCFG, the purpose of the workshop was for the TF to determine whether the *existing* best available science was sufficient to advise that the PCFG be recognized as a population stock under the language of the MMPA and GAMMS guidelines. Therefore, the advice of the TF offered in this report should be viewed as a contemporary “snapshot” taken from an emerging and ever-changing body of knowledge regarding the PCFG.

The TF emphasizes that the PCFG is relatively small in number and utilizes a largely different ecosystem from that of the main ENP stock. While the status of the PCFG as a population stock has yet to be resolved, continued research on these whales should be undertaken with particular attention dedicated to collecting data relevant to the question of stock identification.

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16. Appendix 1 – Workshop Agenda

GRAY WHALE STOCK IDENTIFICATION WORKSHOP AGENDA

Southwest Fisheries Science Center
La Jolla, California
31 July-2 August 2012

Day 1 (31 July 2012)

8:30-8:45
1. Introductory Items
1.1 Convenor's opening remarks (Ballance)
1.2 Arrangements for the meeting (Henry)
1.3 Appointment of chair, task force and rapporteurs
1.4 Adoption of agenda
1.5 Documents available

8:45-9:15
2. Workshop Objectives
2.1 Provide scientific advice on gray whale stock structure (Weller)
2.2 Workshop relationship to stock assessment reports (Carretta/Bettridge)
    2.2.1 Confirm current stock structure
    2.2.2 Assess new information on putative or prospective stocks
    2.2.3 Provide advice on necessary changes to stock structure
2.3 Workshop relationship to Makah waiver request (Darm/Stone)
    2.3.1 History
    2.3.2 Key considerations
    2.3.3 Current status of waiver request
  2.3.4 Need to know information

9:15-10:30
3. Working Group on Stock Identification (Bettridge and Moore)
3.1 Overview of MMPA language and GAMMS guidelines pertaining to stock definition (Moore)
    3.1.1 Existing GAMMS language
    3.1.2 Proposed GAMMS revisions from the GAMMS III workshop
3.2 Overview of recent history pertaining to NMFS interpretation of "interbreed when mature" (Bettridge/Beale)
  3.2.1 Draft GAMMS II language pertaining to "interbreed when mature"
  3.2.2 Status of current legal analysis of NMFS proposed definition
3.3 Additional relevant history concerning definition of "population" for marine mammals (e.g., Taylor 1997, excerpts from Eagle *et al.* 2008) (Moore/ Taylor)

BREAK 10:30-10:45

10:45-12:00
3.4 Current status of gray whale SAR development (Bettridge)
3.5 Discuss key concepts: interbreed when mature, population, demographic independence, functioning element of ecosystem
3.6 Proposed TF voting protocol and process: examples from FEMAT and the ESA (humpback whale BRT, false killer whale BRT) (Bettridge)

3.7. Proposed questions to be voted on by the Task Force

12:00-12:45
4. Working Group on Other Information (Weller and Brownell)
4.1 Overview of gray whale "population stocks" (Lang)
  4.1.1 Eastern North Pacific Stock
  4.1.2 Western North Pacific Stock
    4.1.2.1 Genetic lines of evidence as being a stock
    4.1.2.2 Movements of whales between the WNP and ENP
4.2 Brief overview of the Pacific Coast Feeding Group (PCFG) putative stock (Lang)
    4.2.1 History
  4.2.2 Range
  4.2.3 Abundance
  4.2.4 Diet
  4.2.5 Movements (tagging, photo-ID)
  4.2.6 Incidental Take (Carretta)
  4.2.7 Emerging issues and areas of uncertainty
    4.2.7.1 Probability of a WNP Being Taken by the Makah (Moore)
4.3 Status of the ENP, WNP and PCFG as stocks (NMFS/MMPA/ESA/IWC) (Stone)
4.4 Proposed questions to be voted on by the Task Force

LUNCH 12:45-1:30

13:30-14:15
5. Working Group on Genetic Population Structure (Taylor and Rosel)
5.1 Broad overview of evidence used in recently defined stocks (Stone)
5.2 Review of stock definition cases relevant to the PCFG case
  5.2.1 Atlantic harbor porpoises (Rosel)
  5.2.2 Alaska harbor seals (Taylor)
    5.2.3 Humpback whales (Lang)

14:15-15:00
5.3 Review of gray whale genetic research relating to population structure (Lang)
  5.3.1 Summary of early work (LeDuc, Ramakrishnan, Alter breeding lagoon)
  5.3.2 Summary of recent work
    5.3.2.1 Frasier and D'Intino
    5.3.2.2 Lang – empirical genetics
    5.3.2.3 Lang – modeling genetics
5.4 Proposed questions to be voted on by the Task Force

BREAK 15:00-15:30

15:30-17:00

6. Discussion of Documents Drafted by the Makah Tribe and Other General Matters (Task Force)
6.1 Makah Tribe documents (Weller)
  6.1.1 Introduce GWLJ33: "Is the Pacific feeding group of gray whales a "population stock" within the meaning of the Marine Mammal Protection Act?"
  6.1.2 Introduce GWLJ32: "Comments on Draft 2012 Stock Assessment Report for eastern North Pacific stock of gray whales"
  6.1.3 Introduce GWLJ34: "What is the PCFG? A review of available information"
  6.1.4 Discuss genetics sections of Makah Tribe document GWLJ33 (Taylor/Rosel)
6.2 General discussion of Day 1 information

Day 2 (1 August 2012)

9:00-10:30
7. Working Group on Population Abundance and Trends (Laake and Wade)
7.1 Photo-identification and population dynamics of the PCFG (Laake)
    7.1.1 Definition of PCFG whales based on timing/area
    7.1.2 Movements of know PCFG whales (photo-identification and telemetry)
    7.1.3 Abundance/survival estimates
    7.1.4 Trends (Wade)
    7.1.5 Recruitment
    7.1.6 PCFG Trend/OSP (Moore)
    7.1.7 Discuss photo-identification and telemetry sections of Makah Tribe document GWLJ33 (Laake/Wade)
7.2 Proposed questions to be voted on by the Task Force

BREAK 10:30-11:00

11:00-12:30
8. Review and Agree on Workshop Questions for Voting

LUNCH 12:30-13:30

13:30-15:30
9. Description of Vote Procedure (Bettridge)
10. TF Voting on Workshop Questions (TF Only)

Overnight
11. Compile and Tally Votes (Lang/Henry)

Day 3 (2 August 2012)

9:00-12:00
12. Review of Vote Outcomes (Lang/Henry)
13. Discussion of Vote Outcomes
14. Revision of Questions for voting if Necessary
15. Revote if Necessary

LUNCH 12:00-13:30

13:30-16:30
16. Review of Revote Results if Necessary (Lang/Henry)
17. Other Business
18. Workplan for Workshop Report Completion
19. Adjourn

17. Appendix 2 - Workshop Document List

GWLJ01

Moore, J. E., and Merrick, R., eds. *Guidelines for Assessing Marine Mammal Stocks: Report of the GAMMS III Workshop, February 15 – 18, 2011, La Jolla, California*. Dept. of Commerce, NOAA Technical Memorandum NMFS-OPR-47.

GWLJ02

Andrews, K. R., Karczmarski, L., AU, W. W. L., Rickards, S. H., Vanderlip, C. A., Bowen, B. W., Grau, E. G., and Toonen, R. J. (2010), Rolling stones and stable homes: social structure, habitat diversity and population genetics of the Hawaiian spinner dolphin (*Stenella longirostris*). Molecular Ecology **19**: 732–748.

GWLJ03

Chivers, S. J., Dizon, A. E., Gearin, P. J., and Robertson, K. M. 2002. Small-scale population structure of eastern North Pacific harbour porpoises (*Phocoena phocoena*) indicated by molecular genetic analyses. Journal of Cetacean Research and Management **4**: 111–122.

GWLJ04

Courbis, S. S. 2011. Population Structure of Island-Associated Pantropical Spotted Dolphins (*Stenella attenuata*) in Hawaiian Waters. PhD Thesis, Portland State University, Oregon.

GWLJ05

Taylor, B. L. 2005. Identifying Units to Conserve. In: J. E. Reynolds III, W. F. Perrin, R. R. Reeves, S. Montgomery, and T. J. Ragen, eds. *Marine Mammal Research: Conservation beyond Crisis*. The John Hopkins University Press, Baltimore, MD.

GWLJ06

Carretta, J. V., Oleson, E., Weller, D. W., Lang, A. R., Forney, K. A., Baker, J., Hanson, B., Martien, K. Muto, M. M., Lowry, M. S., Barlow, J., Lynch, D., Carswell, L., Brownell Jr., R. L., Mattila, D. K., and Hill, M. C. *In press*. DRAFT: Gray whale (*Eschrichtius robustus*): Eastern North Pacific Stock and Pacific Coast Feeding Group. In: U.S. Pacific Marine Mammal Stock Assessments: 2012. U.S. Department of Commerce, NOAA Technical Memorandum, NMFS-SWFSC-XXX.

GWLJ07

Lang, A. R. 2010. The population genetics of gray whales (*Eschrichtius robustus*) in the North Pacific. PhD Thesis, University of California, San Diego, California.

GWLJ08

N/A

GWLJ09

Pyenson N. D., and Lindberg, D. R. 2011. What Happened to Gray Whales during the Pleistocene? The Ecological Impact of Sea-Level Change on Benthic Feeding Areas in the North Pacific Ocean. PLoS ONE **6**: e21295. doi:10.1371/journal.pone.0021295.

GWLJ10

Spalding, M. D., Fox, H. E., Allen, G. R., Davidson, N., Ferdana, Z. A., Finlayson, M. A. X., Halpern, B. S., Jorge, M. A., Lombana, A., Lourie, S. A., Martin, K. D., McManus, E., Molnar, J., Recchia, C. A., and Robertson, J. 2007. Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. BioScience **57**: 573-583.

GWLJ11

Calambokidis, J., Laake, J. L., and Klimek, A. 2010. Abundance and population structure of seasonal gray whales in the Pacific Northwest, 1998-2008. Paper SC/62/BRG32 presented to the IWC Scientific Committee.

GWLJ12

N/A

GWLJ13

Oleson, E. M., Boggs, C. H., Forney, K. A., Hanson, M. B., Kobayashi, D. R., Taylor, B. L., Wade, P. M. and Ylitalo, G. M. 2010. Status review of Hawaiian insular false killer whales (*Pseudorca crassidens*) under the Endangered Species Act. U. S. Dept Commerce, NOAA Technical Memorandum NOAA-TM-NMFS-PIFSC-22.

GWLJ14

NMFS. 2005. Revisions to Guidelines for Assessing Marine Mammal Stocks. 24 pp. Available at: *http://www.nmfs.noaa.gov/pr/pdfs/sars/gamms2005.pdf*.

GWLJ15

Eagle, T. C., Cadrin, S. X., Caldwell, M. E., Methot, R. D., Nammack, M. F. 2008. Conservation Units of Managed Fish, Threatened or Endangered Species, and Marine Mammals Report of a Workshop: February 14-16, 2006 Silver Spring, Maryland. U. S. Dept of Commerce, NOAA Technical Memorandum NMFS-OPR-37.

GWLJ 16

Taylor, B. L. 1997. Defining "Population" to Meet Management Objectives for Marine Mammals. Molecular Genetics of Marine Mammals **3:** 49-65.

GWLJ17

DRAFT Status Review of the Humpback Whale under the Endangered Species Act (confidential)

GWLJ18

Lang, A. R., Weller, D. W., LeDuc, R., Burdin, A. M., Pease, V. L., Litovka, D., Burkanov, V., and Brownell Jr., R. L. 2011. Genetic analysis of stock structure and movements of gray whales in the eastern and western North Pacific. Paper SC/63/BRG32 presented to the IWC Scientific Committee.

GWLJ19

Lang, A. R., Taylor, B. L., Calambokidis, J. C., Pease, V. L., Klimek, A., Scordino, J. Robertson, K. M., Litovka, D., Burkanov, V., Gearin, P., George, J. C., and Mate, B. 2011. Assessment of stock structure among gray whales utilizing feeding grounds in the Eastern North Pacific. Paper SC/M11/AWMP4 presented to IWC Scientific Committee.

GWLJ20

Lang, A. R. and Martien, K. K. 2012. Update on the use of a simulation-based approach to evaluate plausible levels of recruitment into the Pacific Coast Feeding Group of gray whales. Paper SC/64/AWMP4 presented to IWC Scientific Committee.

GWLJ 21

Alter, S. E., Rynes, E., and Palumbi, S. R. 2007. DNA evidence for historic population size and past ecosystem impacts of gray whales. Proceedings of the National Academy of Sciences **104**: 15162-15167.

GWLJ22

Alter, S. E., Ramirez, S. F., Nigenda, S., Ramirez, J. U., Bracho, L. R., and Palumbi, S. R. 2009. Mitochondrial and nuclear genetic variation across calving lagoons in eastern North Pacific gray whales (*Eschrichtius robustus*). Journal of Heredity **100**: 34-46.

GWLJ23

Alter, S. E., Newsome, S. D., and Palumbi, S. R. 2012. Pre-whaling genetic diversity and population ecology in eastern Pacific gray whales: insights from ancient DNA and stable isotopes. PLoS ONE **7**:e35039. doi: 10.1371/journal.pone.0035039.

GWLJ24

D'Intino, A. M., Darling, J. D., Urbán-Raminez, J., and Frasier, T. R. 2012. Substructuring of mitochondrial, but not nuclear, markers in the "southern feeding group" of eastern North Pacific gray whales. Paper SC/64/AWMP2 presented to IWC Scientific Committee.

GWLJ25

Frasier, T. R., Koroscil, S. M., White, B. N., & Darling, J. D. 2011. Assessment of population substructure in relation to summer feeding ground use in the eastern North Pacific gray whale. Endangered Species Research **14**: 39-48.

GWLJ 26

Goerlitz, D. S., Urbán, J., Rojas-Bracho, L., Belson, M., and Schaeff, C. M. 2003. Mitochondrial DNA variation among Eastern North Pacific gray whales (*Eschrichtius robustus*) on winter breeding grounds in Baja California. Canadian Journal of Zoology, 81: 1965-1972.

GWLJ27

Lang, A. R., Weller, D. W., LeDuc, R. G., and Burdin, A M. 2010. Delineating Patterns of Male Reproductive Success in the Western Gray Whale (*Eschrichtius robustus*) Population. Paper SC/62/BRG10 presented to IWC Scientific Committee.

GWLJ28

LeDuc, R. G., Weller, D. W., Hyde, J., Burdin, A. M., Rosel, P. E., Brownell Jr., R. L., Würsig, B., and Dizon, A. E. 2002. Genetic differences between western and eastern North Pacific gray whales (*Eschrichtius robustus*). Journal of Cetacean Research and Management **4**: 1-6.

GWLJ29

Ramakrishnan, U., & Taylor, B. L. (2001). Can gray whale management units be assessed using mitochondrial DNA? Journal of Cetacean Research and Management **3:** 13-18.

GWLJ30

Ramakrishnan, U., LeDuc, R. G., Darling, J., Taylor, B. L., Gearin, P., Gosho, M., Calambokidis, J., Brownell Jr., R. L., Hyde, J., and Steeves, T. E. 2001. Are the southern feeding group of Eastern Pacific gray whales a maternal genetic isolate? Report of the International Whaling Commission SC53/SD8.

GWLJ31

Steeves, T. E., Darling, J. D., Rosel, P. E., Schaeff, C. M., and Fleischer, R. C. 2001. Preliminary analysis of mitochondrial DNA variation in a southern feeding group of eastern North Pacific gray whales. Conservation Genetics **2**: 379-384.

GWLJ32

Makah 2012. Comments on Draft 2012 Stock Assessment Report for the Eastern North Pacific Stock of Gray Whales (Revised 11/1/2011) - Submitted by the Makah Indian Tribe on January 17, 2012

GWLJ33

Makah 2011. Is the Pacific Coast Feeding Group of Gray Whales a "Population Stock" within the Meaning of the Marine Mammal Protection Act? A Preliminary Analysis by the Makah Indian Tribe, October 5, 2011. PCFG Stock Status Memo from Makah Indian Tribe 10-5-2011; PSRG-2011-B13.

GWLJ34

Scordino, J., Bickham, J., Brandon, J., and Ammajian, A. 2011. What is the PCFG? A review of available information. Paper SC/63/AWMP1 presented to IWC Scientific Committee.

GWLJ 35

Brandon, J. R., Scordino, J., Butterworth, D. S., Donovan, G. P., and Punt, A. E. 2012. Towards the Selection of a Final Set of Trials for the 2012 ENP Gray Whale Implementation Review. Paper SC/64/AWMP11 presented to IWC Scientific Committee.

GWLJ 36

Ford, J. K., Durban, J. W., Ellis, G. M., Towers, J. R., Pilkington, J. F., Barrett-Lennard, L. G., and Andrews, R. D. 2012. New insights into the northward migration route of gray whales between Vancouver Island, British Columbia, and southeastern Alaska. Marine Mammal Science. doi: 10.1111/j.1748-7692.2012.00572.x

GWLJ37

Gosho, M., Gearin, P., Jenkinson, R., Laake, J., Mazzuca, L., Kubiak, D., Calambokidis, J., Megill, W., Gisborne, B., Goley, D., Tombach, C., Darling, J., and Deecke, V. 2011. Movements and diet of gray whales (*Eschrichtius robustus*) off Kodiak Island, Alaska, 2002-2005. Paper SC/M11/AWMP2 presented to IWC Scientific Committee.

GWLJ38

Mate, B., Bradford, A., Tsidulko, G., Vertyankin, V., and Ilyashenko, V. 2011. Late-Feeding Season Movements of a Western North Pacific Gray Whale off Sakhalin Island, Russia and Subsequent Migration into the Eastern North Pacific. Paper SC/63/BRG23 presented to IWC Scientific Committee.

GWLJ39

Punt, A. E. 2012. Revised ENP Gray Whale Trials and Initial Conditioning Results. Paper SC/63/AWMP presented to IWC Scientific Committee.

GWLJ40

Baird, R. W., Stacey, P. J., Duffus, D. A., and Langelier, K. M. 2002. An evaluation of gray whale (*Eschrichtius robustus*) mortality incidental to fishing operations in British Columbia, Canada. Journal of Cetacean Research Management **4**: 289–296.

GWLJ41

Conner, L., Stelle, L. L., Najera-Hillman, E., Megill, W., Calambokidis, J., and Klimek, A. 2011. Using Photo ID to Examine Injuries in Eastern Pacific Gray Whales (*Eschrichtius robustus*). Poster presentation, 20th Biennial Conference on the Biology of Marine Mammals, Tampa, Florida.

GWLJ42

International Whaling Commission. 2011. Report of the 2011 AWMP Workshop with a focus on eastern gray whales. Paper SC/63/Report 2 presented to the IWC Scientific Committee.

GWLJ43

International Whaling Commission. 2012. Report of the AWMP Workshop focussing on the PCFG gray whale Implementation Review. Paper SC/64/Report 3 presented to the IWC Scientific Committee.

GWLJ44

International Whaling Commission. 2012. Report of the Scientific Committee, Panama City, Panama, 11-23 June 2012. Paper IWC/64/Report 1, Revision 1.

GWLJ45

International Whaling Commission. 2012. Annex E: Report of the Scientific Committee: International Whaling Commission, Panama City, 2012. Paper IWC/64/Report 1 Annex E.

GWLJ46

O'Corry-Crowe, G. M., Martien, K. K., and Taylor, B. L. 2003. The analysis of population genetic structure in Alaskan harbor seals, *Phoca vitulina*, as a framework for the identification of management stocks. Southwest Fisheries Science Center Administrative Report LJ-03-08.

GWLJ47

Mate, B., Lagerquist, B., and Irvine, L. 2010. Feeding habitats, migration, and winter reproductive range movements derived from satellite-monitored radio tags on eastern North Pacific gray whales. Paper SC/62/BRG21 presented to IWC Scientific Committee.

GWLJ48

Weinrich, M. T., and Clapham, P. J. 2002. Population identity of humpback whales (*Megaptera novaeangliae*) in the waters of the US mid-Atlantic states. Journal of Cetacean Research and Management, **4**: 135-141.

GWLJ49

Palsboll, P. J., Clapham, P. J., Mattila, D. K., Larsen, F., Sears, R., Siegismund, H. R., Sigurjónsson, J. Vasquez, O., and Arctander, P. 1995. Distribution of mtDNA haplotypes in North Atlantic humpback whales: the influence of behaviour on population structure. Marine Ecology Progress Series **116**: 1-10.

GWLJ50

Palsboll, P. J., Allen, J. , Andersen, T. H. , Berube, M., Clapham, P. J., Federsen, T. P., Friday, N., Hammond, P.S., Jorgensen, H., Katona, S., Larsen, A. H., Larsen, F., Lien, J., Mattila, D. K., Nygaard, F. B., Robbins, J., Sears, R., Sigurjónsson, J., Smith, T., Sponer, R., Stevick, P., Oien, N., and Vikingsson, G. 2001. Stock structure and composition of the North Atlantic humpback whale, *Megaptera novaeangliae*. Paper SC/53/NAH11presented to IWC Scientific Committee.

GWLJ51

Waring, G. T., Josephson, E., Maze-Foley, K., Rosel, P. E., eds. 2012. U.S. Atlantic and Gulf of Mexico Marine Mammal Stock Assessments – 2011. NOAA Technical Memorandum NMFS-NE-221.

GWLJ52

Calambokidis, J., Falcone, E. A., Quinn, T. J., Burdin, A. M. Clapham, P. J., Ford, J. K. B., Gabriele, C. M., LeDuc, R., Mattila, D., Rojas-Bracho, L. Straley, J. M., Taylor, B. L., Urbán-R, J. Weller, D. Witteveen, B. H., Yamaguchi, M., Bendlin, A., Camacho, D., Flynn, K., Havron, A., Huggins, J., and Maloney, N. 2008. SPLASH: Structure of populations, levels of abundance and status of humpback whales in the North Pacific. Final report for Contract

AB133F-03-RP-00078 prepared by Cascadia Research for the U.S. Department of Commerce.

GWLJ53

Baker, C. S., Steel, D., Calambokidis, J., Barlow, J., Burdin, A. M., Clapham, P. J., Falcone, E., Ford, J. K. B., Gabriele, C. M., Gozález-Peral, U., LeDuc, R., Mattila, D., Quinn, T. J., Rojas-Bracho, L., Straley, J. M., Taylor, B. L., Urbán-R, J., Vant, M., Wade, P. R., Weller, D., Witteveen, B. H., Wynne, K., and Yamaguchi, M. 2008. geneSPLASH: An initial, ocean-wide survey of mitochondrial (mt) DNA diversity and population structure among humpback whales in the North Pacific. Final report for Contract 2006-0093-008 to the National Fish and Wildlife Foundation.

GWLJ54

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GWLJ55

Weller, D. W., Klimek, A., Bradford, A. L., Calambokidis, J., Lang, A. R., Gisborne, B., Burdin, A. M., Szaniszlo, W., Urbán, J., Gómez-Gallardo Unzueta, A., Swartz, S., and Brownell Jr., R. L. 2012. Movements of gray whales between the western and eastern North Pacific. Endangered Species Research **18**: 193–199.

GWLJ56

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GWLJ57

Table by Stone on MMP, ESA, IUCN listing status

GWLJ58

Table by Stone on SAR stock listings

International Convention
for the
Regulation of Whaling, 1946

Schedule

As amended by the Commission at the 67th Meeting

Florianópolis, Brazil, September 2018

INTERNATIONAL
WHALING COMMISSION

International Convention
for the
Regulation of Whaling, 1946
Schedule

EXPLANATORY NOTES

The Schedule printed on the following pages contains the amendments made by the Commission at its 67th Meeting in September 2018. The amendments, which are shown in ***italic bold*** type, come into effect on 29 December 2018.
In Tables 1, 2 and 3 unclassified stocks are indicated by a dash. Other positions in the Tables have been filled with a dot to aid legibility.
Numbered footnotes are integral parts of the Schedule formally adopted by the Commission. Other footnotes are editorial.
The Commission was informed in June 1992 by the ambassador in London that the membership of the Union of Soviet Socialist Republics in the International Convention for the Regulation of Whaling from 1948 is continued by the Russian Federation.
The Commission recorded at its 39th (1987) meeting the fact that references to names of native inhabitants in Schedule paragraph 13(*b*)(4) would be for geographical purposes alone, so as not to be in contravention of Article V.2(c) of the Convention (*Rep. int. Whal. Commn* 38:21).

I. INTERPRETATION

1. The following expressions have the meanings respectively assigned to them, that is to say:

A. Baleen whales

"baleen whale" means any whale which has baleen or whale bone in the mouth, i.e. any whale other than a toothed whale.

"blue whale" (*Balaenoptera musculus*) means any whale known as blue whale, Sibbald's rorqual, or sulphur bottom, and including pygmy blue whale.

"bowhead whale" (*Balaena mysticetus*) means any whale known as bowhead, Arctic right whale, great polar whale, Greenland right whale, Greenland whale.

"Bryde's whale" (*Balaenoptera edeni*, *B. brydei*) means any whale known as Bryde's whale.

"fin whale" (*Balaenoptera physalus*) means any whale known as common finback, common rorqual, fin whale, herring whale, or true fin whale.

"gray whale" (*Eschrichtius robustus*) means any whale known as gray whale, California gray, devil fish, hard head, mussel digger, gray back, or rip sack.

"humpback whale" (*Megaptera novaeangliae*) means any whale known as bunch, humpback, humpback whale, humpbacked whale, hump whale or hunchbacked whale.

"minke whale" (*Balaenoptera acutorostrata*, *B. bonaerensis*) means any whale known as lesser rorqual, little piked whale, minke whale, pike-headed whale or sharp headed finner.

"pygmy right whale" (*Caperea marginata*) means any whale known as southern pygmy right whale or pygmy right whale.

"right whale" (*Eubalaena glacialis*, *E. australis*) means any whale known as Atlantic right whale, Arctic right whale, Biscayan right whale, Nordkaper, North Atlantic right whale, North Cape whale, Pacific right whale, or southern right whale.

"sei whale" (*Balaenoptera borealis*) means any whale known as sei whale, Rudolphi's rorqual, pollack whale, or coalfish whale.

B. Toothed whales

"toothed whale" means any whale which has teeth in the jaws.

"beaked whale" means any whale belonging to the genus Mesoplodon, or any whale known as Cuvier's beaked whale (*Ziphius cavirostris*), or Shepherd's beaked whale (*Tasmacetus shepherdi*).

"bottlenose whale" means any whale known as Baird's beaked whale (*Berardius bairdii*), Arnoux's whale (*Berardius arnuxii*), southern bottlenose whale (*Hyperoodon planifrons*), or northern bottlenose whale (*Hyperoodon ampullatus*).

"killer whale" (*Orcinus orca*) means any whale known as killer whale or orca.

"pilot whale" means any whale known as long-finned pilot whale (*Globicephala melaena*) or short-finned pilot whale (*G. macrorhynchus*).

"sperm whale" (*Physeter macrocephalus*) means any whale known as sperm whale, spermacet whale, cachalot or pot whale.

C. General

"strike" means to penetrate with a weapon used for whaling.

"land" means to retrieve to a factory ship, land station, or other place where a whale can be treated.

"take" means to flag, buoy or make fast to a whale catcher.

"lose" means to either strike or take but not to land.

"dauhval" means any unclaimed dead whale found floating.

"lactating whale" means (a) with respect to baleen whales - a female which has any milk present in a mammary gland, (b) with respect to sperm whales - a female which has milk present in a mammary gland the maximum thickness (depth) of which is 10cm or more. This measurement shall be at the mid ventral point of the mammary gland perpendicular to the body axis, and shall be logged to the nearest centimetre; that is to say, any gland between 9.5cm and 10.5cm shall be logged as 10cm. The measurement of any gland which falls on an exact 0.5 centimetre shall be logged at the next 0.5 centimetre, e.g. 10.5cm shall be logged as 11.0cm.

However, notwithstanding these criteria, a whale shall not be considered a lactating whale if scientific (histological or other biological) evidence is presented to the appropriate national authority establishing that the whale could not at that point in its physical cycle have had a calf dependent on it for milk.

"small-type whaling" means catching operations using powered vessels with mounted harpoon guns hunting exclusively for minke, bottlenose, beaked, pilot or killer whales.

II. SEASONS

Factory Ship Operations

2. (a) It is forbidden to use a factory ship or whale catcher attached thereto for the purpose of taking or treating baleen whales except minke whales, in any waters south of 40° South Latitude except during the period from 12th December to 7th April following, both days inclusive.
   (b) It is forbidden to use a factory ship or whale catcher attached thereto for the purpose of taking or treating sperm or minke whales, except as permitted by the Contracting Governments in accordance with sub-paragraphs (*c*) and (*d*) of this paragraph, and paragraph 5.
   (c) Each Contracting Government shall declare for all factory ships and whale catchers attached thereto under its jurisdiction, an open season or seasons not to exceed eight months out of any period of twelve months during which the taking or killing of sperm whales by whale catchers may be permitted; provided that a separate open season may be declared for each factory ship and the whale catchers attached thereto.
   (d) Each Contracting Government shall declare for all factory ships and whale catchers attached thereto under its jurisdiction one continuous open season not to exceed six months out of any period of twelve months during which the taking or killing of minke whales by the whale catchers may be permitted provided that:
      (1) a separate open season may be declared for each factory ship and the whale catchers attached thereto;
      (2) the open season need not necessarily include the whole or any part of the period declared for other baleen whales pursuant to sub-paragraph (a) of this paragraph.
3. It is forbidden to use a factory ship which has been used during a season in any waters south of 40° South Latitude for the purpose of treating baleen whales, except minke whales, in any other area except the North Pacific Ocean and its dependent waters north of the Equator for the same purpose within a period of one year from the termination of that season; provided that catch limits in the North Pacific Ocean and dependent waters are established as provided in paragraphs 12 and 16 of this Schedule and provided that this paragraph shall not apply to a ship which has been used during the season solely for freezing or salting the meat and entrails of whales intended for human food or feeding animals.

Land Station Operations

4. (a) It is forbidden to use a whale catcher attached to a land station for the purpose of killing or attempting to kill baleen and sperm whales except as permitted by the Contracting Government in accordance with sub-paragraphs (*b*), (*c*) and (*d*) of this paragraph.
   (b) Each Contracting Government shall declare for all land stations under its jurisdiction, and whale catchers attached to such land stations, one open season during which the taking or killing of baleen whales, except minke whales, by the whale catchers shall be permitted. Such open season shall be for a period of not more than six consecutive months in any period of twelve months and shall apply to all land stations under the jurisdiction of the Contracting Government; provided that a separate open season may be declared for any land station used for the taking or treating of baleen whales, except minke whales, which is more than 1,000 miles from the nearest land station used for the taking or treating of baleen whales, except minke whales, under the jurisdiction of the same Contracting Government.
   (c) Each Contracting Government shall declare for all land stations under its jurisdiction and for whale catchers attached to such land stations, one open season not to exceed eight continuous months in any one period of twelve months, during which the taking or killing of sperm whales by the whale catchers shall be permitted; provided that a separate open season may be declared for any land station used for the taking or treating of sperm whales which is more than 1,000 miles from the nearest land station used for the taking or treating of sperm whales under the jurisdiction of the same Contracting Government.
   (d) Each Contracting Government shall declare for all land stations under its jurisdiction and for whale catchers attached to such land stations one open season not to exceed six continuous months in any period of twelve months during which the taking or killing of minke whales by the whale catchers shall be permitted (such period not being necessarily concurrent with the period declared for other baleen whales, as provided for in sub-paragraph (*b*) of this paragraph); provided that a separate open season may be declared for any land station used for the taking or treating of minke whales which is more than 1,000 miles from the nearest land station used for the taking or treating of minke whales under the jurisdiction of the same Contracting Government.

   Except that a separate open season may be declared for any land station used for the taking or treating of minke whales which is located in an area having oceanographic conditions clearly distinguishable from those of the area in which are located the other land stations used for the taking or treating of minke whales under the jurisdiction of the same Contracting Government; but the declaration of a separate open season by virtue of the provisions of this sub-paragraph shall not cause thereby the period of time covering the open seasons declared by the same Contracting Government to exceed nine continuous months of any twelve months.

(e) The prohibitions contained in this paragraph shall apply to all land stations as defined in Article II of the Whaling Convention of 1946.

Other Operations

5. Each Contracting Government shall declare for all whale catchers under its jurisdiction not operating in conjunction with a factory ship or land station one continuous open season~~s~~ not to exceed six months out of any period of twelve months during which the taking or killing of minke whales by such whale catchers may be permitted. Notwithstanding this paragraph one continuous open season not to exceed nine months may be implemented so far as Greenland is concerned. ***This paragraph shall not apply to aboriginal subsistence whaling under paragraphs 13(b)(3)(ii) and 13(b)(3)(iii).***

III. CAPTURE

6. The killing for commercial purposes of whales, except minke whales using the cold grenade harpoon shall be forbidden from the beginning of the 1980/81 pelagic and 1981 coastal seasons. The killing for commercial purposes of minke whales using the cold grenade harpoon shall be forbidden from the beginning of the 1982/83 pelagic and the 1983 coastal seasons.*

7. (a) In accordance with Article V(1)(*c*) of the Convention, commercial whaling, whether by pelagic operations or from land stations, is prohibited in a region designated as the Indian Ocean Sanctuary. This comprises the waters of the Northern Hemisphere from the coast of Africa to 100°E, including the Red and Arabian Seas and the Gulf of Oman; and the waters of the Southern Hemisphere in the sector from 20°E to 130°E, with the Southern boundary set at 55°S. This prohibition applies irrespective of such catch limits for baleen or toothed whales as may from time to time be determined by the Commission. This prohibition shall be reviewed by the Commission at its Annual Meeting in 2002.☼

(b) In accordance with Article V(1)(*c*) of the Convention, commercial whaling, whether by pelagic operations or from land stations, is prohibited in a region designated as the Southern Ocean Sanctuary. This Sanctuary comprises the waters of the Southern Hemisphere southwards of the following line: starting from 40 degrees S, 50 degrees W; thence due east to 20 degrees E; thence due south to 55 degrees S; thence due east to 130 degrees E; thence due north to 40 degrees S; thence due east to 130 degrees W; thence due south to 60 degrees S; thence due east to 50 degrees W; thence due north to the point of beginning. This prohibition applies irrespective of the conservation status of baleen and toothed whale stocks in this Sanctuary, as may from time to time be determined by the Commission. However, this prohibition shall be reviewed ten years after its initial adoption and at succeeding ten year intervals, and could be revised at such times by the Commission. Nothing in this sub-paragraph is intended to prejudice the special legal and political status of Antarctica.**+

Area Limits for Factory Ships

8. It is forbidden to use a factory ship or whale catcher attached thereto, for the purpose of taking or treating baleen whales, except minke whales, in any of the following areas:
   (a) in the waters north of 66°N, except that from 150°E eastwards as far as 140°W, the taking or killing of baleen whales by a factory ship or whale catcher shall be permitted between 66°N and 72°N;
   (b) in the Atlantic Ocean and its dependent waters north of 40°S;
   (c) in the Pacific Ocean and its dependent waters east of 150°W between 40°S and 35°N;
   (d) in the Pacific Ocean and its dependent waters west of 150°W between 40°S and 20°N;
   (e) in the Indian Ocean and its dependent waters north of 40°S.

Classification of Areas and Divisions

9. (a) *Classification of Areas*
   Areas relating to Southern Hemisphere baleen whales except Bryde's whales are those waters between the ice-edge and the Equator and between the meridians of longitude listed in Table 1.

   (b) *Classification of Divisions*
   Divisions relating to Southern Hemisphere sperm whales are those waters between the ice-edge and the Equator and between the meridians of longitude listed in Table 3.

   (c) *Geographical boundaries in the North Atlantic*
   The geographical boundaries for the fin, minke and sei whale stocks in the North Atlantic are:

FIN WHALE STOCKS
NOVA SCOTIA
South and West of a line through:
47°N 54°W, 46°N 54°30'W,
46°N 42°W, 20°N 42°W.

NEWFOUNDLAND-LABRADOR
West of a line through:
75°N 73°30'W, 69°N 59°W, 61°N 59°W,
52°20'N 42°W, 46°N 42°W and
North of a line through:
46°N 42°W, 46°N 54°30'W, 47°N 54°W.

WEST GREENLAND
East of a line through:
75°N 73°30'W, 69°N 59°W,
61°N 59°W, 52°20'N 42°W,
and West of a line through
52°20'N 42°W, 59°N 42°W,
59°N 44°W, Kap Farvel.

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*The Governments of Brazil, Iceland, Japan, Norway and the Union of Soviet Socialist Republics lodged objections to the second sentence of paragraph 6 within the prescribed period. For all other Contracting Governments this sentence came into force on 8 March 1982. Norway withdrew its objection on 9 July 1985 and Brazil on 8 January 1992. Iceland withdrew from the Convention with effect from 30 June 1992. The objections of Japan and the Russian Federation not having been withdrawn, this sentence is not binding upon these governments.

☼At its 54th Annual Meeting in 2002, the Commission agreed to continue this prohibition but did not discuss whether or not it should set a time when it should be reviewed again.

**The Government of Japan lodged an objection within the prescribed period to paragraph 7(*b*) to the extent that it applies to the Antarctic minke whale stocks. The Government of the Russian Federation also lodged an objection to paragraph 7(*b*) within the prescribed period but withdrew it on 26 October 1994. For all Contracting Governments except Japan paragraph 7(*b*) came into force on 6 December 1994.

[+] Paragraph 7(*b*) contains a provision for review of the Southern Ocean Sanctuary "ten years after its initial adoption". Paragraph 7(*b*) was adopted at the 46th (1994) Annual Meeting. The first review was completed in 2004, and the second in 2016.

EAST GREENLAND-ICELAND
East of a line through:
Kap Farvel (South Greenland),
59°N 44°W, 59°N 42°W, 20°N 42°W,
and West of a line through:
20°N 18°W, 60°N 18°W, 68°N 3°E,
74°N 3°E, and South of 74°N.

NORTH NORWAY
North and East of a line through:
74°N 22°W, 74°N 3°E, 68°N 3°E,
67°N 0°, 67°N 14°E.

WEST NORWAY-FAROE ISLANDS
South of a line through:
67°N 14°E, 67°N 0°, 60°N 18°W,
and North of a line through:
61°N 16°W, 61°N 0°, Thyborøn
(Western entrance to Limfjorden, Denmark).

SPAIN-PORTUGAL-BRITISH ISLES
South of a line through:
Thyborøn (Denmark), 61°N 0°, 61°N 16°W,
and East of a line through:
63°N 11°W, 60°N 18°W, 22°N 18°W.

MINKE WHALE STOCKS
CANADIAN EAST COAST
West of a line through:
75°N 73°30’W, 69°N 59°W, 61°N 59°W,
52°20’N 42°W, 20°N 42°W.

CENTRAL
East of a line through:
Kap Farvel (South Greenland),
59°N 44°W, 59°N 42°W, 20°N 42°W,
and West of a line through:
20°N 18°W, 60°N 18°W, 68°N 3°E,
74°N 3°E, and South of 74°N.

WEST GREENLAND
East of a line through:
75°N 73°30’W, 69°N 59°W, 61°N 59°W,
52°20’N 42°W, and
West of a line through:
52°20’N 42°W, 59°N 42°W,
59°N 44°W, Kap Farvel.

NORTHEASTERN
East of a line through:
20°N 18°W, 60°N 18°W, 68°N 3°E, 74°N 3°E,
and North of a line through:
74°N 3°E, 74°N 22°W.

SEI WHALE STOCKS
NOVA SCOTIA
South and West of a line through:
47°N 54°W, 46°N 54°30’W, 46°N 42°W,
20°N 42°W.

ICELAND-DENMARK STRAIT
East of a line through:
Kap Farvel (South Greenland),
59°N 44°W, 59°N 42°W, 20°N 42°W,
and West of a line through:
20°N 18°W, 60°N 18°W, 68°N 3°E,
74°N 3°E, and South of 74°N.

EASTERN
East of a line through:
20°N 18°W, 60°N 18°W, 68°N 3°E, 74°N 3°E,
and North of a line through:
74°N 3°E, 74°N 22°W.

(d) *Geographical boundaries in the North Pacific*

The geographical boundaries for the sperm, Bryde’s and minke whale stocks in the North Pacific are:

SPERM WHALE STOCKS
WESTERN DIVISION
West of a line from the ice-edge south along the 180° meridian of longitude to 180°, 50°N, then east along the 50°N parallel of latitude to 160°W, 50°N, then south along the 160°W meridian of longitude to 160°W, 40°N, then east along the 40°N parallel of latitude to 150°W, 40°N, then south along the 150°W meridian of longitude to the Equator.

EASTERN DIVISION
East of the line described above.

BRYDE’S WHALE STOCKS
EAST CHINA SEA
West of the Ryukyu Island chain.

EASTERN
East of 160°W (excluding the Peruvian stock area).

WESTERN
West of 160°W (excluding the East China Sea stock area).

MINKE WHALE STOCKS
SEA OF JAPAN-YELLOW SEA-EAST CHINA SEA
West of a line through the Philippine Islands, Taiwan, Ryukyu Islands, Kyushu, Honshu, Hokkaido and Sakhalin Island, north of the Equator.

OKHOTSK SEA-WEST PACIFIC
East of the Sea of Japan-Yellow Sea- East China Sea stock and west of 180°, north of the Equator.

REMAINDER
East of the Okhotsk Sea-West Pacific stock, north of the Equator.

(e) *Geographical boundaries for Bryde’s whale stocks in the Southern Hemisphere*

SOUTHERN INDIAN OCEAN
20°E to 130°E,
South of the Equator.

SOLOMON ISLANDS
150°E to 170°E,
20°S to the Equator.

PERUVIAN
110°W to the South American coast,
10°S to 10°N.

EASTERN SOUTH PACIFIC
150°W to 70°W,
South of the Equator (excluding the Peruvian stock area).

WESTERN SOUTH PACIFIC
130°E to 150°W,
South of the Equator (excluding the Solomon Islands stock area).

SOUTH ATLANTIC
70°W to 20°E,
South of the Equator (excluding the South African inshore stock area).

SOUTH AFRICAN INSHORE
South African coast west of 27°E and out to the 200 metre isobath.

Classification of Stocks

10. All stocks of whales shall be classified in one of three categories according to the advice of the Scientific Committee as follows:
    (a) A Sustained Management Stock (SMS) is a stock which is not more than 10 per cent of Maximum Sustainable Yield (hereinafter referred to as MSY) stock level below MSY stock level, and not more than 20 per cent above that level; MSY being determined on the basis of the number of whales.

    When a stock has remained at a stable level for a considerable period under a regime of approximately constant catches, it shall be classified as a Sustained Management Stock in the absence of any positive evidence that it should be otherwise classified.

    Commercial whaling shall be permitted on Sustained Management Stocks according to the advice of the Scientific Committee. These stocks are listed in Tables 1, 2 and 3 of this Schedule.

    For stocks at or above the MSY stock level, the permitted catch shall not exceed 90 per cent of the MSY. For stocks between the MSY stock level and 10 per cent below that level, the permitted catch shall not exceed the number of whales obtained by taking 90 per cent of the MSY and reducing that number by 10 per cent for every 1 per cent by which the stock falls short of the MSY stock level.

    (b) An Initial Management Stock (IMS) is a stock more than 20 per cent of MSY stock level above MSY stock level. Commercial whaling shall be permitted on Initial Management Stocks according to the advice of the Scientific Committee as to measures necessary to bring the stocks to the MSY stock level and then optimum level in an efficient manner and without risk of reducing them below this level. The permitted catch for such stocks will not be more than 90 per cent of MSY as far as this is known, or, where it will be more appropriate, catching effort shall be limited to that which will take 90 per cent of MSY in a stock at MSY stock level.

    In the absence of any positive evidence that a continuing higher percentage will not reduce the stock below the MSY stock level no more than 5 per cent of the estimated initial exploitable stock shall be taken in any one year. Exploitation should not commence until an estimate of stock size has been obtained which is satisfactory in the view of the Scientific Committee. Stocks classified as Initial Management Stock are listed in Tables 1, 2 and 3 of this Schedule.

    (c) A Protection Stock (PS) is a stock which is below 10 per cent of MSY stock level below MSY stock level.

    There shall be no commercial whaling on Protection Stocks. Stocks so classified are listed in Tables 1, 2 and 3 of this Schedule.

    (d) Notwithstanding the other provisions of paragraph 10 there shall be a moratorium on the taking, killing or treating of whales, except minke whales, by factory ships or whale catchers attached to factory ships. This moratorium applies to sperm whales, killer whales and baleen whales, except minke whales.

    (e) Notwithstanding the other provisions of paragraph 10, catch limits for the killing for commercial purposes of whales from all stocks for the 1986 coastal and the 1985/86 pelagic seasons and thereafter shall be zero. This provision will be kept under review, based upon the best scientific advice, and by 1990 at the latest the Commission will undertake a comprehensive assessment of the effects of this decision on whale stocks and consider modification of this provision and the establishment of other catch limits.*•#

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*The Governments of Japan, Norway, Peru and the Union of Soviet Socialist Republics lodged objection to paragraph 10(*e*) within the prescribed period. For all other Contracting Governments this paragraph came into force on 3 February 1983. Peru withdrew its objection on 22 July 1983. The Government of Japan withdrew its objections with effect from 1 May 1987 with respect to commercial pelagic whaling; from 1 October 1987 with respect to commercial coastal whaling for minke and Bryde's whales; and from 1 April 1988 with respect to commercial coastal sperm whaling. The objections of Norway and the Russian Federation not having been withdrawn, the paragraph is not binding upon these Governments.

•Iceland's instrument of adherence to the International Convention for the Regulation of Whaling and the Protocol to the Convention deposited on 10 October 2002 states that Iceland 'adheres to the aforesaid Convention and Protocol with a reservation with respect to paragraph 10(*e*) of the Schedule attached to the Convention'. The instrument further states the following:

> 'Notwithstanding this, the Government of Iceland will not authorise whaling for commercial purposes by Icelandic vessels before 2006 and, thereafter, will not authorise such whaling while progress is being made in negotiations within the IWC on the RMS. This does not apply, however, in case of the so-called moratorium on whaling for commercial purposes, contained in paragraph 10(*e*) of the Schedule not being lifted within a reasonable time after the completion of the RMS. Under no circumstances will whaling for commercial purposes be authorised without a sound scientific basis and an effective management and enforcement scheme.'

#The Governments of Argentina, Australia, Brazil, Chile, Finland, France, Germany, Italy, Mexico, Monaco, the Netherlands, New Zealand, Peru, San Marino, Spain, Sweden, UK and the USA have lodged objections to Iceland's reservation to paragraph 10(*e*).

Table 1

BALEEN WHALE STOCK CLASSIFICATIONS AND CATCH LIMITS[+] (excluding Bryde's whales).

		SEI		MINKE		FIN		BLUE		RIGHT, BOWHEAD, HUMPBACK		PYGMY RIGHT		GRAY	
		Classi-fication	Catch limit	Classi-fication	Catch limit	Classi-fication	Catch limit	Classi-fication	Catch limit	Classi-fication	Catch limit	Classi-fication	Catch limit	Classi-fication	Catch limit
SOUTHERN HEMISPHERE-***2018/2019 and 2019/2020*** pelagic season and ***2019 and 2020*** coastal season															
Area															.
I	120°W-60°W	PS	0	-	0	PS	0	PS	0	PS	0	PS	0	.	.
II	60°W- 0°	PS	0	-	0	PS	0	PS	0	PS	0	PS	0	.	.
III	0°- 70°E	PS	0	-	0	PS	0	PS	0	PS	0	PS	0	.	.
IV	70°E-130°E	PS	0	-	0	PS	0	PS	0	PS	0	PS	0	.	.
V	130°E- 170°W	PS	0	-	0	PS	0	PS	0	PS	0	PS	0	.	.
VI	170°W-120°W	PS	0	-	0	PS	0	PS	0	PS	0	PS	0	.	.
Total catch not to exceed:							0		0		0		0		
NORTHERN HEMISPHERE-***2019 and 2020*** season															
ARCTIC		.	.	.	.	.	.	.	.	.	.	PS	0	.	.
NORTH PACIFIC															
Whole region		PS	0	.	.	PS	0	PS	0	PS	0	PS	0	.	.
Okhotsk Sea-West Pacific Stock		.	.	-	0	.	.	.	.	.	.	.	.	.	.
Sea of Japan-Yellow Sea-East China Sea Stock		.	.	PS	0	.	.	.	.	.	.	.	.	.	.
Remainder		.	.	IMS	0	.	.	.	.	.	.	.	.	.	.
Eastern Stock		.	.	.	.	.	.	.	.	.	.	.	.	SMS	.[1]
Western Stock		.	.	.	.	.	.	.	.	.	.	.	.	PS	0
NORTH ATLANTIC															
Whole region		.	.	.	.	.	.	PS	0	PS	0	PS	0	.	.
West Greenland Stock		.	.	PS	0	-	19[2]	.	.	.	.	.	.	.	.
Newfoundland-Labrador Stock		.	.	.	.	-	0	.	.	.	.	.	.	.	.
Canadian East Coast Stock		.	.	-	0	.	.	.	.	.	.	.	.	.	.
Nova Scotia Stock		PS	0	.	.	PS	0	.	.	.	.	.	.	.	.
Central Stock		.	.	-	.	.	.	.	.	.	.	.	.	.	.
East Greenland-Iceland Stock		.	.	.	.	SMS	0	.	.	.	.	.	.	.	.
Iceland-Denmark Strait Stock		-	0	.	.	.	.	.	.	.	.	.	.	.	.
Spain-Portugal-British Isles Stock		.	.	.	.	-	0	.	.	.	.	.	.	.	.
Northeastern Stock		.	.	PS*	0	.	.	.	.	.	.	.	.	.	.
West Norway-Faroe Islands Stock		.	.	.	.	PS	0	.	.	.	.	.	.	.	.
North Norway Stock		.	.	.	.	-	0	.	.	.	.	.	.	.	.
Eastern Stock		-	0	.	.	.	.	.	.	.	.	.	.	.	.
NORTHERN INDIAN OCEAN		.	.	IMS	0	.	.	PS	0	PS	0	PS	0	.	.

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[1] Available to be taken by aborigines or a Contracting Government on behalf of aborigines pursuant to paragraph 13*(b)*2.

[2] Available to be struck by aborigines pursuant to paragraph 13*(b)*3. Catch limit for each of the years ***2019, 2020, 2021, 2022, 2023, 2024 and 2025***.

[+] The catch limits of zero introduced into Table 1 as editorial amendments as a result of the coming into effect of paragraph 10*(e)* are not binding upon the governments of the countries which lodged and have not withdrawn objections to the said paragraph.

*The Government of Norway presented objection to the classification of the Northeastern Atlantic stock of minke whales as a Protection Stock within the prescribed period. This classification came into force on 30 January 1986 but is not binding on the Government of Norway.

Table 2

Bryde's whale stock classifications and catch limits.[+]

	Classification	Catch limit
SOUTHERN HEMISPHERE-***2018/2019 and 2019/2020*** pelagic season and ***2019 and 2020*** coastal season		
South Atlantic Stock	-	0
Southern Indian Ocean Stock	IMS	0
South African Inshore Stock	-	0
Solomon Islands Stock	IMS	0
Western South Pacific Stock	IMS	0
Eastern South Pacific Stock	IMS	0
Peruvian Stock	-	0
NORTH PACIFIC-***2019 and 2020*** season		
Eastern Stock	IMS	0
Western Stock	IMS	0
East China Sea Stock	PS	0
NORTH ATLANTIC-***2019 and 2020*** season	IMS	0
NORTHERN INDIAN OCEAN-***2019 and 2020*** season	-	0

[+] The catch limits of zero introduced in Table 2 as editorial amendments as a result of the coming into effect of paragraph 10*(e)* are not binding upon the governments of the countries which lodged and have not withdrawn objections to the said paragraph.

Table 3

Toothed whale stock classifications and catch limits.[+]

SOUTHERN HEMISPHERE-***2018/2019 and 2019/2020*** pelagic season and ***2019 and 2020*** coastal season

		SPERM	
Division	Longitudes	Classification	Catch limit
1	60°W-30°W	-	0
2	30°W-20°E	-	0
3	20°E-60°E	-	0
4	60°E-90°E	-	0
5	90°-130°E	-	0
6	130°E-160°E	-	0
7	160°E-170°W	-	0
8	170°W-100°W	-	0
9	100°W-60°W	-	0
NORTHERN HEMISPHERE-***2019 and 2020*** season			
NORTH PACIFIC			
Western Division		PS	0[1]
Eastern Division		-	0
NORTH ATLANTIC		-	0
NORTHERN INDIAN OCEAN		-	0
		BOTTLENOSE	
NORTH ATLANTIC		PS	0

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[1] No whales may be taken from this stock until catch limits including any limitations on size and sex are established by the Commission.

[+] The catch limits of zero introduced in Table 3 as editorial amendments as a result of the coming into effect of paragraph 10*(e)* are not binding upon the governments of the countries which lodged and have not withdrawn objections to the said paragraph.

Baleen Whale Catch Limits

11. The number of baleen whales taken in the Southern Hemisphere in the ***2018/2019 and 2019/2020*** pelagic season and the ***2019 and 2020*** coastal season shall not exceed the limits shown in Tables 1 and 2.

12. The number of baleen whales taken in the North Pacific Ocean and dependent waters in ***2019 and 2020*** and in the North Atlantic Ocean in ***2019 and 2020*** shall not exceed the limits shown in Tables 1 and 2.

13. (a) Notwithstanding the provisions of paragraph 10, catch limits for aboriginal subsistence whaling to satisfy aboriginal subsistence need for the 1984 whaling season and each whaling season thereafter shall be established in accordance with the following principles:

(1) For stocks at or above MSY level, aboriginal subsistence catches shall be permitted so long as total removals do not exceed 90 per cent of MSY.

(2) For stocks below the MSY level but above a certain minimum level, aboriginal subsistence catches shall be permitted so long as they are set at levels which will allow whale stocks to move to the MSY level.[1]

(3) The above provisions will be kept under review, based upon the best scientific advice, and by 1990 at the latest the Commission will undertake a comprehensive assessment of the effects of these provisions on whale stocks and consider modification.

(4) For aboriginal whaling conducted under subparagraphs (*b*)(1), (*b*)(2), and (*b*)(3) of this paragraph, it is forbidden to strike, take or kill calves or any whale accompanied by a calf. For aboriginal whaling conducted under subparagraphs (*b*)(4) of this paragraph, it is forbidden to strike, take or kill suckling calves or female whales accompanied by calves.

(5) All aboriginal whaling shall be conducted under national legislation that accords with this paragraph.

(6) Commencing in 2026, and provided the appropriate Strike Limit Algorithm has been developed by then, strike/catch limits (including any carry forward provisions) for each stock identified in sub-paragraph 13(b) shall be extended every six years, provided: (a) the Scientific Committee advises in 2024, and every six years thereafter, that such limits will not harm that stock; (b) the Commission does not receive a request from an ASW country relying on the stock ('relevant ASW country'), for a change in the relevant catch limits based on need; and (c) the Commission determines that the relevant ASW country has complied with the approved timeline and that the information provided represents a status quo continuation of the hunt.

(7) The provisions for each stock identified in sub-paragraph 13(b), especially the provisions for carryover, shall be reviewed by the Commission in light of the advice of the Scientific Committee.

(b) Catch limits for aboriginal subsistence whaling are as follows:

(1) The taking of bowhead whales from the Bering-Chukchi-Beaufort Seas stock by aborigines is permitted, but only when the meat and products of such whales are to be used exclusively for local consumption by the aborigines and further provided that:

(i) For the years ~~2013, 2014, 2015, 2016, 2017 and 2018~~ ***2019, 2020, 2021, 2022, 2023, 2024 and 2025***, the number of bowhead whales landed shall not exceed ~~336~~ ***392***. For each of these years the number of bowhead whales struck shall not exceed 67, except that any unused portion of a strike quota from ~~any year (including 15 unused strikes from the 2008–2012 quota)~~ ***the three prior quota blocks*** shall be carried forward and added to the strike quotas of ~~any~~ subsequent years, provided that no more than ~~15~~ ~~strikes~~ ***50 percent of the annual strike limit*** shall be added to the strike quota for any one year.

~~(ii) This provision shall be reviewed annually by the Commission in light of the advice of the Scientific Committee.~~

(2) The taking of gray whales from the Eastern stock in the North Pacific is permitted, but only by aborigines or a Contracting Government on behalf of aborigines, and then only when the meat and products of such whales are to be used exclusively for local consumption by the aborigines.

(i) For the years ~~2013, 2014, 2015, 2016, 2017 and 2018~~ ***2019, 2020, 2021, 2022, 2023, 2024 and 2025***, the number of gray whales ***landed*** ~~taken~~ ~~in accordance with this sub-paragraph~~ shall not exceed ~~744~~ ***980***, provided that the number of gray whales ***struck*** ~~taken~~ in any one of the years ~~2013, 2014, 2015,~~ ~~2016, 2017 and 2018~~ ***2019, 2020, 2021, 2022, 2023, 2024 and 2025*** shall not exceed 140, ***except that any unused portion of a strike quota from the prior quota block shall be carried forward and added to the strike quotas of subsequent years, provided that no more than 50 percent of the annual strike limit shall be added to the strike quota for any one year***.

~~(ii) This provision shall be reviewed annually by the Commission in light of the advice of the Scientific Committee.~~

(3) The taking by aborigines of minke whales from the West Greenland and Central stocks ***from the East Greenland hunt*** and fin whales from the West Greenland stock and bowhead whales from the West Greenland feeding aggregation and humpback whales from the West Greenland feeding aggregation is permitted and then only when the meat and products are to be used exclusively for local consumption.

(i) The number of fin whales struck from the West Greenland stock ~~in accordance with this subparagraph~~ shall not exceed 19 in each of the years ~~2015, 2016, 2017 and 2018~~ ***2019, 2020, 2021, 2022, 2023, 2024 and 2025, except that any unused portion of a strike quota from the prior quota block under a Strike Limit Algorithm management advice shall be carried forward and added to the strike quotas of subsequent years, provided that no more than 50 percent of the annual strike limit shall be added to the strike quota for any one year***.

(ii) The number of minke whales struck from the Central stock ~~in accordance with this sub-paragraph~~ shall not exceed ~~12~~ ***20*** in each of the years ~~2015, 2016, 2017 and 2018~~ ***2019, 2020, 2021, 2022, 2023, 2024 and 2025,*** except that any unused portion of ~~the~~ ***a*** strike quota ~~for each year~~ shall be carried forward ~~from that year~~ and added to the ***strike*** quota***s*** of ~~any~~ subsequent years, provided that no more than 3 ***strikes*** shall be added to the ***strike*** quota for any one year. ***Commencing in 2020, and provided a Strike Limit Algorithm for this stock has been developed by then, any unused portion of a strike quota from the prior quota block under a Strike Limit Algorithm management advice shall be carried forward and added to the strike quotas of subsequent years, provided that no more than 50 percent of the annual strike limit shall be added to the strike quota for any one year.***

(iii) The number of minke whales struck from the West Greenland stock shall not exceed 164 in each of the years ~~2015, 2016, 2017 and 2018~~ ***2019, 2020, 2021, 2022, 2023, 2024 and 2025,*** except that any unused portion of ~~the~~ ***a strike*** quota ~~for each year~~ ***from the prior quota block under a Strike Limit Algorithm management advice*** shall be carried forward ~~from that year~~ and added to the strike quota**s** of ~~any of the~~ subsequent years, provided that no more than ~~15 strikes~~ ***50 percent of the annual strike limit*** shall be added to the strike quota for any one year. ~~This provision will be reviewed if new scientific data become available within the 4 year period and if necessary amended on basis of the advice of the Scientific Committee.~~

(iv) The number of bowhead whales struck off West Greenland ~~in accordance with this sub-paragraph~~ shall not exceed 2 in each of the years ~~2015, 2016, 2017 and 2018~~ ***2019, 2020, 2021, 2022, 2023, 2024 and 2025,*** except that any unused portion of ~~the~~ ***a strike*** quota ~~for each year~~ ***from the prior quota block under a Strike Limit Algorithm management advice*** shall be carried forward ~~from that year~~ and added to the ***strike*** quota**s** of ~~any~~ subsequent years, provided that no more than ~~2 strikes~~ ***50 percent of the annual strike limit*** shall be added to the ***strike*** quota for any one year. ~~This provision will be reviewed if new scientific data become available within the 4 year period and if necessary amended on basis of the advice of the Scientific Committee.~~

(v) The number of humpback whales struck off West Greenland ~~in accordance with this sub-paragraph~~ shall not exceed 10 in each of the years ~~2015, 2016, 2017 and 2018~~ ***2019, 2020, 2021, 2022, 2023, 2024 and 2025,*** except that any unused portion of ~~the~~ ***a strike*** quota ~~for each year~~ ***from the three prior quota blocks under a Strike Limit Algorithm management advice*** shall be carried forward ~~from that year~~ and added to the strike quota**s** of ~~any of the~~ subsequent years, provided that no more than ~~2 strikes~~ ***50 percent of the annual strike limit*** shall be added to the strike quota for any one year. ~~This provision will be reviewed if new scientific data become available within the remaining quota period and if necessary amended on basis of the advice of the Scientific Committee.~~

(4) For the seasons ~~2013-2018~~ ***2019-2025*** the number of humpback whales to be taken by the Bequians of St. Vincent and The Grenadines shall not exceed ~~24~~ ***28***. The meat and products of such whales are to be used exclusively for local consumption in St. Vincent and The Grenadines.

14. It is forbidden to take or kill suckling calves or female whales accompanied by calves.

Baleen Whale Size Limits

15. (a) It is forbidden to take or kill any sei or Bryde's whales below 40 feet (12.2 metres) in length except that sei and Bryde's whales of not less than 35 feet (10.7 metres) may be taken for delivery to land stations, provided that the meat of such whales is to be used for local consumption as human or animal food.

(b) It is forbidden to take or kill any fin whales below 57 feet (17.4 metres) in length in the Southern Hemisphere, and it is forbidden to take or kill fin whales below 55 feet (16.8 metres) in the Northern Hemisphere; except that fin whales of not less than 55 feet (16.8 metres) may be taken in the Southern Hemisphere for delivery to land stations and fin whales of not less than 50 feet (15.2 metres) may be taken in the Northern Hemisphere for delivery to land stations, provided that, in each case the meat of such whales is to be used for local consumption as human or animal food. ***This paragraph shall not apply to aboriginal subsistence whaling under paragraph 13(b)(3)(i).***

Sperm Whale Catch Limits

16. Catch limits for sperm whales of both sexes shall be set at zero in the Southern Hemisphere for the 1981/82 pelagic season and 1982 coastal seasons and following seasons, and at zero in the Northern Hemisphere for the 1982 and following coastal seasons; except that the catch limits for the 1982 coastal season and following seasons in the Western Division of the North Pacific shall remain undetermined and subject to decision by the Commission following special or annual meetings of the Scientific Committee. These limits shall remain in force until such time as the Commission, on the basis of the scientific information which will be reviewed annually, decides otherwise in accordance with the procedures followed at that time by the Commission.
17. It is forbidden to take or kill suckling calves or female whales accompanied by calves.

Sperm Whale Size Limits

18. (a) It is forbidden to take or kill any sperm whales below 30 feet (9.2 metres) in length except in the North Atlantic Ocean where it is forbidden to take or kill any sperm whales below 35 feet (10.7 metres).
    (b) It is forbidden to take or kill any sperm whale over 45 feet (13.7 metres) in length in the Southern Hemisphere north of 40° South Latitude during the months of October to January inclusive.
    (c) It is forbidden to take or kill any sperm whale over 45 feet (13.7 metres) in length in the North Pacific Ocean and dependent waters south of 40° North Latitude during the months of March to June inclusive.

IV. TREATMENT

19. (a) It is forbidden to use a factory ship or a land station for the purpose of treating any whales which are classified as Protection Stocks in paragraph 10 or are taken in contravention of paragraphs 2, 3, 4, 5, 6, 7, 8, 11, 12, 14, 16 and 17 of this Schedule, whether or not taken by whale catchers under the jurisdiction of a Contracting Government.
    (b) All other whales taken, except minke whales, shall be delivered to the factory ship or land station and all parts of such whales shall be processed by boiling or otherwise, except the internal organs, whale bone and flippers of all whales, the meat of sperm whales and parts of whales intended for human food or feeding animals. A Contracting Government may in less developed regions exceptionally permit treating of whales without use of land stations, provided that such whales are fully utilised in accordance with this paragraph.
    (c) Complete treatment of the carcases of "dauhval" and of whales used as fenders will not be required in cases where the meat or bone of such whales is in bad condition.
20. (a) The taking of whales for treatment by a factory ship shall be so regulated or restricted by the master or person in charge of the factory ship that no whale carcase (except of a whale used as a fender, which shall be processed as soon as is reasonably practicable) shall remain in the sea for a longer period than thirty-three hours from the time of killing to the time when it is hauled up for treatment.
    (b) Whales taken by all whale catchers, whether for factory ships or land stations, shall be clearly marked so as to identify the catcher and to indicate the order of catching.

V. SUPERVISION AND CONTROL

21. (a) There shall be maintained on each factory ship at least two inspectors of whaling for the purpose of maintaining twenty-four hour inspection provided that at least one such inspector shall be maintained on each catcher functioning as a factory ship. These inspectors shall be appointed and paid by the Government having jurisdiction over the factory ship; provided that inspectors need not be appointed to ships which, apart from the storage of products, are used during the season solely for freezing or salting the meat and entrails of whales intended for human food or feeding animals.
    (b) Adequate inspection shall be maintained at each land station. The inspectors serving at each land station shall be appointed and paid by the Government having jurisdiction over the land station.
    (c) There shall be received such observers as the member countries may arrange to place on factory ships and land stations or groups of land stations of other member countries. The observers shall be appointed by the Commission acting through its Secretary and paid by the Government nominating them.

22. Gunners and crews of factory ships, land stations, and whale catchers, shall be engaged on such terms that their remuneration shall depend to a considerable extent upon such factors as the species, size and yield of whales and not merely upon the number of the whales taken. No bonus or other remuneration shall be paid to the gunners or crews of whale catchers in respect of the taking of lactating whales.

23. Whales must be measured when at rest on deck or platform after the hauling out wire and grasping device have been released, by means of a tape-measure made of a non-stretching material. The zero end of the tape- measure shall be attached to a spike or stable device to be positioned on the deck or platform abreast of one end of the whale. Alternatively the spike may be stuck into the tail fluke abreast of the apex of the notch. The tape-measure shall be held taut in a straight line parallel to the deck and the whale's body, and other than in exceptional circumstances along the whale's back,

and read abreast of the other end of the whale. The ends of the whale for measurement purposes shall be the tip of the upper jaw, or in sperm whales the most forward part of the head, and the apex of the notch between the tail flukes.

Measurements shall be logged to the nearest foot or 0.1 metre. That is to say, any whale between 75 feet 6 inches and 76 feet 6 inches shall be logged as 76 feet, and any whale between 76 feet 6 inches and 77 feet 6 inches shall be logged as 77 feet. Similarly, any whale between 10.15 metres and 10.25 metres shall be logged as 10.2 metres, and any whale between 10.25 metres and 10.35 metres shall be logged as 10.3 metres. The measurement of any whale which falls on an exact half foot or 0.05 metre shall be logged at the next half foot or 0.05 metre, e.g. 76 feet 6 inches precisely shall be logged as 77 feet and 10.25 metres precisely shall be logged as 10.3 metres.

VI. INFORMATION REQUIRED

24. (a) All whale catchers operating in conjunction with a factory ship shall report by radio to the factory ship:
    (1) the time when each whale is taken
    (2) its species, and
    (3) its marking effected pursuant to paragraph 20(b).

    (b) The information specified in sub-paragraph (a) of this paragraph shall be entered immediately by a factory ship in a permanent record which shall be available at all times for examination by the whaling inspectors; and in addition there shall be entered in such permanent record the following information as soon as it becomes available:
    (1) time of hauling up for treatment
    (2) length, measured pursuant to paragraph 23
    (3) sex
    (4) if female, whether lactating
    (5) length and sex of foetus, if present, and
    (6) a full explanation of each infraction.

    (c) A record similar to that described in sub-paragraph (b) of this paragraph shall be maintained by land stations, and all of the information mentioned in the said sub-paragraph shall be entered therein as soon as available.

    (d) A record similar to that described in sub-paragraph (b) of this paragraph shall be maintained by "small-type whaling" operations conducted from shore or by pelagic fleets, and all of this information mentioned in the said sub-paragraph shall be entered therein as soon as available.

25. (a) All Contracting Governments shall report to the Commission for all whale catchers operating in conjunction with factory ships and land stations the following information:
    (1) methods used to kill each whale, other than a harpoon, and in particular compressed air;
    (2) number of whales struck but lost.

    (b) A record similar to that described in sub-paragraph (a) of this paragraph shall be maintained by vessels engaged in "small-type whaling" operations and by native peoples taking species listed in paragraph 1, and all the information mentioned in the said sub-paragraph shall be entered therein as soon as available, and forwarded by Contracting Governments to the Commission.

26. (a) Notification shall be given in accordance with the provisions of Article VII of the Convention, within two days after the end of each calendar week, of data on the number of baleen whales by species taken in any waters south of 40° South Latitude by all factory ships or whale catchers attached thereto under the jurisdiction of each Contracting Government, provided that when the number of each of these species taken is deemed by the Secretary to the International Whaling Commission to have reached 85 per cent of whatever total catch limit is imposed by the Commission notification shall be given as aforesaid at the end of each day of data on the number of each of these species taken.

    (a) If it appears that the maximum catches of whales permitted by paragraph 11 may be reached before 7 April of any year, the Secretary to the International Whaling Commission shall determine, on the basis of the data provided, the date on which the maximum catch of each of these species shall be deemed to have been reached and shall notify the master of each factory ship and each Contracting Government of that date not less than four days in advance thereof. The taking or attempting to take baleen whales, so notified, by factory ships or whale catchers attached thereto shall be illegal in any waters south of 40° South Latitude after midnight of the date so determined.

    (b) Notification shall be given in accordance with the provisions of Article VII of the Convention of each factory ship intending to engage in whaling operations in any waters south of 40° South Latitude.

27. Notification shall be given in accordance with the provisions of Article VII of the Convention with regard to all factory ships and catcher ships of the following statistical information:
    (a) concerning the number of whales of each species taken, the number thereof lost, and the number treated at each factory ship or land station, and
    (b) as to the aggregate amounts of oil of each grade and quantities of meal, fertiliser (guano), and other products derived from them, together with
    (c) particulars with respect to each whale treated in the factory ship, land station or "small-type whaling" operations as to the date and approximate latitude and longitude of taking, the species and sex of the whale, its length and, if it contains a foetus, the length and sex, if ascertainable, of the foetus.

    The data referred to in (a) and (c) above shall be verified at the time of the tally and there shall also be notification to the Commission of any information which may be collected or obtained concerning the calving grounds and migration of whales.

28. (a) Notification shall be given in accordance with the provisions of Article VII of the Convention with regard to all factory ships and catcher ships of the following statistical information:
    - (1) the name and gross tonnage of each factory ship,
    - (2) for each catcher ship attached to a factory ship or land station:
        - (i) the dates on which each is commissioned and ceases whaling for the season,
        - (ii) the number of days on which each is at sea on the whaling grounds each season,
        - (iii) the gross tonnage, horsepower, length and other characteristics of each; vessels used only as tow boats should be specified.
    - (3) A list of the land stations which were in operation during the period concerned, and the number of miles searched per day by aircraft, if any.

    (b) The information required under paragraph (a)(2)(ii) should also be recorded together with the following information, in the log book format shown in Appendix A, and forwarded to the Commission:
    - (1) where possible the time spent each day on different components of the catching operation,
    - (2) any modifications of the measures in paragraphs (a)(2)(i)-(iii) or (b)(1) or data from other suitable indicators of fishing effort for "small-type whaling" operations.

29. (a) Where possible all factory ships and land stations shall collect from each whale taken and report on:
    - (1) both ovaries or the combined weight of both testes,
    - (2) at least one ear plug, or one tooth (preferably first mandibular).

    (b) Where possible similar collections to those described in sub-paragraph (a) of this paragraph shall be undertaken and reported by "small-type whaling" operations conducted from shore or by pelagic fleets.

    (c) All specimens collected under sub-paragraphs (a) and (b) shall be properly labelled with platform or other identification number of the whale and be appropriately preserved.

    (d) Contracting Governments shall arrange for the analysis as soon as possible of the tissue samples and specimens collected under sub-paragraphs (a) and (b) and report to the Commission on the results of such analyses.

30. A Contracting Government shall provide the Secretary to the International Whaling Commission with proposed scientific permits before they are issued and in sufficient time to allow the Scientific Committee to review and comment on them. The proposed permits should specify:
    - (a) objectives of the research;
    - (b) number, sex, size and stock of the animals to be taken;
    - (c) opportunities for participation in the research by scientists of other nations; and
    - (d) possible effect on conservation of stock.

    Proposed permits shall be reviewed and commented on by the Scientific Committee at Annual Meetings when possible. When permits would be granted prior to the next Annual Meeting, the Secretary shall send the proposed permits to members of the Scientific Committee by mail for their comment and review. Preliminary results of any research resulting from the permits should be made available at the next Annual Meeting of the Scientific Committee.

31. A Contracting Government shall transmit to the Commission copies of all its official laws and regulations relating to whales and whaling and changes in such laws and regulations.

INTERNATIONAL CONVENTION FOR THE REGULATION OF WHALING, 1946
SCHEDULE APPENDIX A

TITLE PAGE
(one logbook per catcher per season)

Catcher name…………………………………………… Year built…………………………………………

Attached to expedition/land station ………………………………………………………………………

Season…………………………………………………

Overall length…………………………………………… Wooden/steel hull………………………………

Gross tonnage……………………………………………

Type of engine..………………………………………… H.P. ………………………………………………

Maximum speed………………………………………… Average searching speed…………………………

Asdic set, make and model no.………………………………………………………………………………

Date of installation………………………………………

Make and size of cannon………………………………………………………………………………………

Type of first harpoon used……………………………… Explosive/electric/non-explosive

Type of killer harpoon used…………………………………………………………………………………

Length and type of forerunner………………………………………………………………………………

Type of whaleline………………………………………………………………………………………………

Height of barrel above sea level…………………………

Speedboat used, Yes/No

Name of Captain………………………………………………………………………………………………

Number of years experience……………………………

Name of gunner………………………………………………………………………………………………

Number of years experience……………………………

Number of crew…………………………………………

INTERNATIONAL CONVENTION FOR THE REGULATION OF WHALING, 1946

DAILY RECORD SHEET TABLE 1

Date .... Catcher name .... Sheet No.............

Searching: Time started (or resumed) searching
*Time whales seen or reported to catcher
Whale species
Number seen and no. of groups
Position found
Name of catcher that found whales
Chasing: Time started chasing (or confirmed whales)
Time whale shot or chasing discontinued
Asdic used (Yes/No)
Handling: Time whale flagged or alongside for towing
Serial No. of catch
Towing: Time started picking up
Time finished picking up or started towing
Date and time delivered to factory

Resting: Time stopped (for drifting or resting)
Time finished drifting/resting
Time ceased operations

WEATHER CONDITIONS

Time	Sea state	Wind force and direction	Visibility

Total searching time..............................
Total chasing time ....
A) with asdic ....
B) without asdic ....
Total handling time ....
Total towing time
Total resting time ....
Other time (e.g. bunkering, in port) ....

Whales Seen (No. and No. of schools)

Blue...
Fin...
Humpback.......................................
Right..
Sei..
Signed...
Bryde's
Minke
Sperm ....
Others (specify)
....
....

*Time whales reported to catcher means the time when the catcher is told of the position of a school, and starts to move towards it to chase it.

SCHEDULE APPENDIX A

SCHOOLING REPORT TABLE 2

To be completed by pelagic expedition or coastal station for each sperm whale school chased. A separate form to be used each day.

Name of expedition or coastal station

Date Noon position of factory ship

Time School Found

Total Number of Whales in School

Number of Takeable Whales in School

Number of Whales Caught from School by each Catcher

Name of Catcher

Name of Catcher

Name of Catcher ....

Name of Catcher

Total Number Caught from School

Remarks:

Explanatory Notes

A. Fill in one column for each school chased with number of whales caught by each catcher taking part in the chase; if catchers chase the school but do not catch from it, enter O; for catchers in fleet which do not chase that school enter X.

B. A school on this form means a group of whales which are sufficiently close together that a catcher having completed handling one whale can start chasing another whale almost immediately without spending time searching. A solitary whale should be entered as a school of 1 whale.

C. A takeable whale is a whale of a size or kind which the catchers would take if possible. It does not necessarily include all whales above legal size, e.g. if catchers are concentrating on large whales only these would be counted as takeable.

D. Information about catchers from other expeditions or companies operating on the same school should be recorded under Remarks.

MONITORING IN 2019
BY THE RUSSIAN FEDERATION AND THE UNITED STATES
OF THE ABORIGINAL SUBSISTENCE QUOTA
FOR GRAY WHALES SET BY
THE INTERNATIONAL WHALING COMMISSION

The International Whaling Commission (IWC) at its Meeting in September 2018 set a seven-year block quota of 980 gray whales landed, based on a joint proposal by the Russian Federation and the United States (which was incorporated into the Schedule to the International Convention for the Regulation of Whaling, Article 13(b)(2)). . In addition, for each of the years 2019 through 2025, the IWC limited the number of gray whales that may be struck to 140, except that any unused portion of a strike quota from the prior quota block may be carried forward, provided that no more than 50 percent of the annual strike limit may be added to the strike quota for any one year. At the end of the 2018 harvest, there were zero strikes available for carry-forward, so the strike quota for 2019 is 140.

So that the 2019 quota of gray whale strikes is not exceeded, subject to domestic legal requirements, the Makah Indian Tribe may strike no more than five gray whales, and the Russian Natives may strike no more than 135 gray whales. Each side will ensure that the numbers specified in this paragraph for its Native group are not exceeded. Each side will consider any strikes or landings in excess of the specified numbers in discussing monitoring of the quota for 2020.

The U.S. side plans to inform the Russian side immediately upon learning if the Makah Indian Tribe has struck or landed a gray whale. The Russian side plans to inform the U.S. side once a month of the number of gray whales struck or landed by its Natives in the preceding month. In September-October, 2019, either side may initiate discussions on the transfer of unused strikes from one Native group to the other. During the last quarter of 2019, the two sides plan to confer on monitoring of the 2020 quota.

Dated 28 November 2018 Dated 7 December 2018

Ryan J. Wulff

Irina B. Fominykh
IWC Commissioner
Russian Federation

Ryan Wulff
Acting IWC Commissioner
United States of America

ADDENDUM TO MONITORING IN 2017
BY THE RUSSIAN FEDERATION AND THE UNITED STATES
OF THE ABORIGINAL QUOTA FOR GRAY WHALES SET BY
THE INTERNATIONAL WHALING COMMISSION

The above-captioned Monitoring in 2017 agreement provides for potential transfers of the unused takes of gray whales from the Makah Indian Tribe to the Russian Natives. Due to domestic legal obligations, the Makah Indian Tribe has been unable to harvest gray whales. This addendum formalizes the transfer a total of 8 unused takes of gray whales from 2016 and 2017 from the Makah Indian Tribe to the Russian Natives.

Dated Декабрь 21, 2017

Irina B. Fominykh
IWC Commissioner
Russian Federation

Dated December 20, 2017

Ryan Wulff
Acting IWC Commissioner
United States of America

ADDENDUM TO MONITORING IN 2016 BY THE RUSSIAN FEDERATION AND THE UNITED STATES OF THE ABORIGINAL QUOTA FOR GRAY WHALES SET BY THE INTERNATIONAL WHALING COMMISSION

The above-captioned Monitoring in 2016 agreement provides for potential transfers of the unused takes of gray whales from the Makah Indian Tribe to the Russian Natives. Due to domestic legal obligations, the Makah Indian Tribe has been unable to harvest gray whales. This addendum formalizes the transfer of 12 unused takes of gray whales from 2013-2015 from the Makah Indian Tribe to the Russian Natives.

Dated 9. 03. 2016

Dated 2 - 29 - 2016

Irina B. Fominykh
IWC Commissioner
Russian Federation

Russell F. Smith III
IWC Commissioner
United States of America

ADDENDUM TO MONITORING IN 2012 BY THE RUSSIAN FEDERATION AND THE UNITED STATES OF THE ABORIGINAL QUOTA FOR GRAY WHALES SET BY THE INTERNATIONAL WHALING COMMISSION

The International Whaling Commission (IWC) at its Annual Meeting in June 2007, set a five-year block quota of 620 gray whales, with an annual cap of 140 animals taken, based on a joint proposal by the Russian Federation and the United States. The IWC regulation does not address the number of allowed strikes. The requested quota and accompanying documentation assumed an average annual harvest of 120 whales by the Chutkotka people and an average annual harvest of four whales by the Makah Indian Tribe.

So that the 2012 quota of gray whales is not exceeded, subject to domestic legal requirements the Makah Indian Tribe may take no more than five gray whales, and the Russian Natives may take no more than 135 gray whales. Each side will ensure that the numbers specified in this paragraph for its Native are not exceeded. Each side will consider any landings in excess of the specified numbers in excess of the specified numbers in discussing monitoring of the quota for 2013.

During the remainder of 2012, either side may initiate discussions on the transfer of unused takes from one Native group to the other. In February 2012, discussions were initiated to transfer the unused takes of gray whales from the Makah Indian Tribe to the Russian Natives. Due to domestic legal obligations, the Makah Indian Tribe have been unable to harvest gray whales. This agreement formalizes the transfer of 20 unused takes of gray whales from the Makah Indian Tribe to the Russian Natives.

Dated 6 july 2012

Valentin Ilyashenko
IWC Commissioner
Russian Federation

Dated 6 July 2012

Doug DeMaster
Douglas DeMaster
IWC Commissioner
United States of America

ADDENDUM to MONOITORING IN 2007 BY THE RUSSIAN FEDERATION AND THE UNITED STATES OF THE ABORIGINAL SUBSISTENCE QUOTA FOR GRAY WHALES SET BY THE INTERNATIONAL WHALING COMMISSION

The International Whaling Commission (IWC) at its Annual Meeting in May 2002 set a five-year block quota of 620 gray whales, with an annual cap of 140 animals taken, based on a joint proposal by the Russian Federation and the United States. The IWC regulation does not address the number of allowed strikes. The requested quota and accompanying documentation assumed an average annual harvest of 120 whales by the Chukotka people and an average annual harvest of four whales by the Makah Indian Tribe.

So that the 2007 quota of gray whales is not exceeded, subject to domestic legal requirements the Makah Indian Tribe may take no more than five gray whales, and the Russian Natives may take no more than 135 gray whales. Each side will ensure that the numbers specified in this paragraph for its Native group are not exceeded. Each side will consider any landings in excess of the specified numbers in discussing monitoring of the quota for 2008.

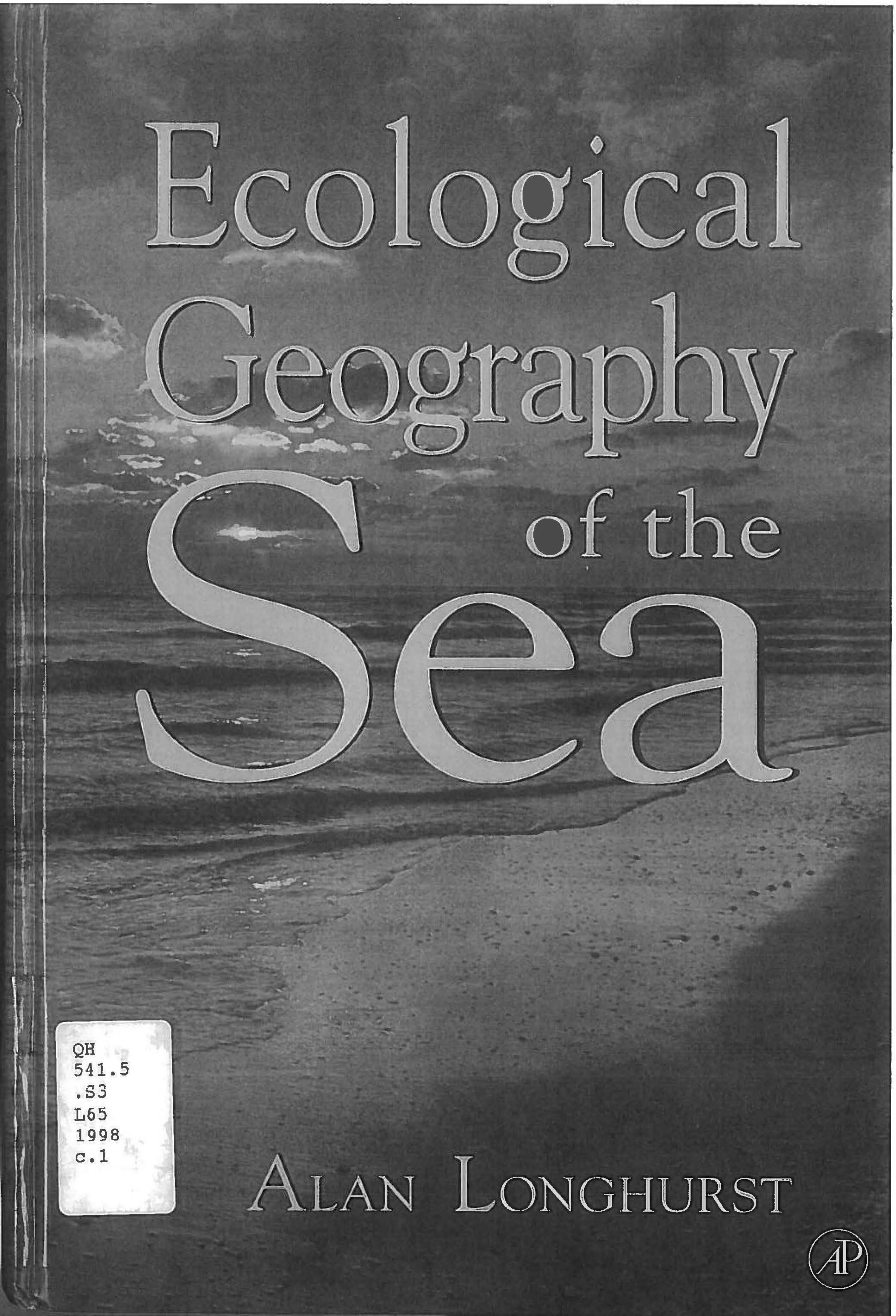
During the remainder of 2007, either side may initiate discussions on the transfer of unused takes from one Native group to the other. In February 2007, discussions were initiated to transfer the unused takes of gray whales from the Makah Indian Tribe to the Russian Natives. Due to domestic legal obligations, the Makah Indian Tribe have been unable to harvest gray whales. This agreement formalizes the transfer of 20 unused takes of gray whales from the Makah Indian Tribe to the Russian Natives.

Dated 20. 05. 2007

Dated 20 May, 2007

Valentin Ilyashenko
IWC Commissioner
Russian Federation

William T. Hogarth
William T. Hogarth
IWC Commissioner
United States of America



Ecological Geography of the Sea

ALAN LONGHURST

Cover photograph: © Jim Brandenburg, Minden Pictures

This book is printed on acid-free paper. ♾

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gated there) in summer along the route of juvenile salmon, spawned in rivers to the south but bound for offshore feeding grounds to the north. Their trip takes 1 or 2 months, during which time considerable growth as well as locomotion is accomplished by the young fish.

Synopsis

The permanent halocline caps winter mixing and entrainment of nitrate from below, so the spring–summer bloom is thought to be supported by nitrate entrained during this period by topographic coastal processes (Fig. 9.15). Chlorophyll consistently tracks primary production rate and nitrate-based production is assumed to dominate during the whole productive period.

California Current Province (CALC)

Extent of the Province

The CALC province comprises the California Current from the bifurcation of the eastwards flow of the North Pacific Current south to the convergent front which lies southwest off the tip of Baja California at the root of the NEC. The California Front is the seaward limit, though this front is progressively less well defined toward the south. For this reason, the canonical boundary of the California Current is often set at 1000 km offshore, a definition I use where necessary.

Continental Shelf Topography and Tidal and Shelf-Edge Fronts

The continental shelf is narrow, with the 200-m isobath occurring as little as 10 km from the shore in southern California (or even closer, where Scripps Canyon runs into the beach) to a distance of about 75 km off Oregon and Washington. A continental borderland with deep (approx 200 m) basins, shallow banks, and islands occupies the bight (including the Santa Barbara Basin) south of Point Conception (34.5°N). Tidal fronts have not been described, but the entire coastal boundary province is populated by upwelling fronts and fronts associated with meanders of the coastal jet and their associated cyclonic eddies.

Defining Characteristics of Regional Oceanography

The California Current is the most intensively investigated of the eastern boundary currents, especially because of the results from the long time series (1950–present) of the California Cooperative Fisheries Investigations (CalCOFI) managed jointly by federal, state, and university research groups. Much of what follows is drawn from reports, atlases, and research papers arising from CalCOFI.

The California Current takes its source in the divergence of the west wind drift water of the North Pacific Current as this approaches the American continent within what Favorite *et al.* (1976) term the dilution zone, where precipitation greatly exceed evaporation. The eastward flow diverges northwards into the eastern limb of the Alaska gyre and southwards into the California Current as a cool, low-salinity, high-nutrient water mass entraining biota with the flow.

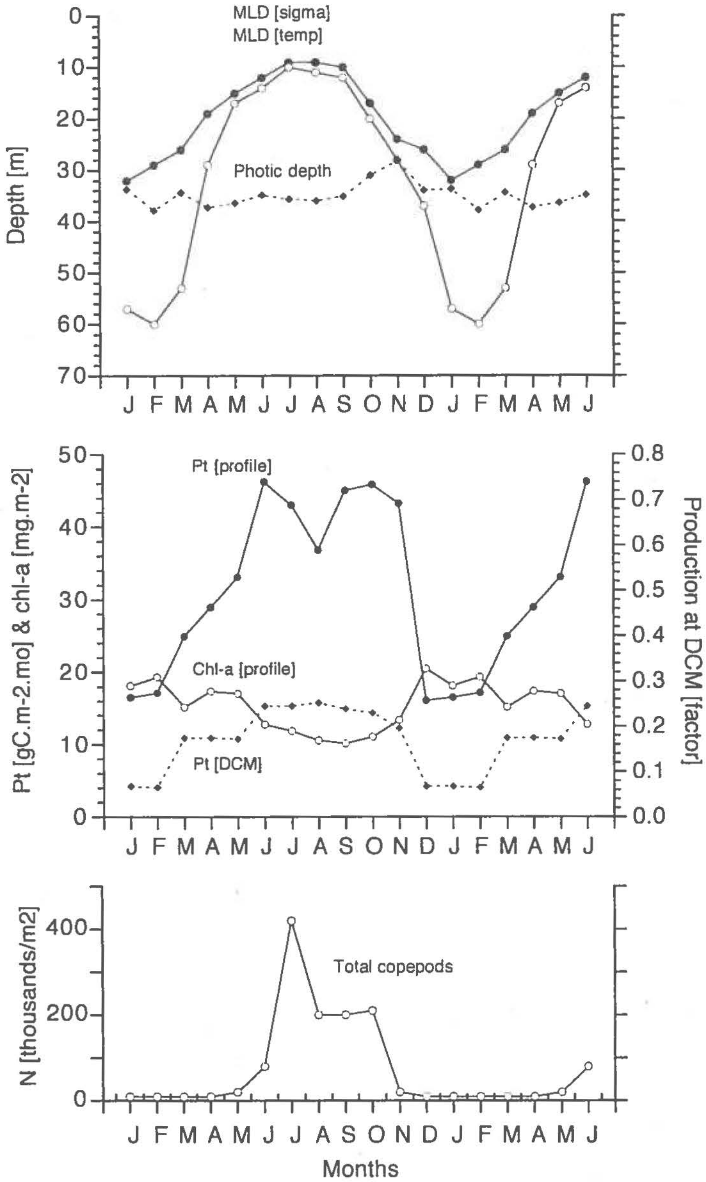

FIGURE 9.16 CALC: characteristic seasonal cycles of monthly averaged mixed layer and photic depths, chlorophyll at the surface, and rate of primary production, both depth-integrated and at the DCM. Data sources are discussed in Chapter 1.

The following account of the California Current describes the normal condition, when the trade wind regime is fully developed; during ENSO events, when trade wind stress is relaxed in the western Pacific, El Niño conditions prevail in the eastern boundary currents of the Pacific (see Chapter 6). The characteristics of the province derive from the conjunction between the southward geostrophic current, the coastal boundary, and an alternating wind

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regime—equatorward upwelling winds in summer and poleward downwelling winds in winter.

The offshore California Current is a shallow, complex southerly flow of cool, low-salinity water extending about 1500 km seawards off central California but progressively closer to the coast toward the south: 850 km off Cape Mendocino and 500 km off Cape San Lazaro. The main core of the current occurs 200–400 km offshore, where southward wind stress is greatest, especially at 30–45°N and during summer. The zone of maximum wind stress coincides with zero wind-stress curl, which is anticyclonic (convergent) to the west of this line and cyclonic (divergence) to the east (Bakun and Nelson, 1991). A separate and narrower maximum flow occurs within 100–150 km of the coast as the inshore California Current, which partially reverses with the seasons.

The southward flow of the offshore current includes mesoscale eddies and meanders 120–150 km in dimension; these are anticyclonic on the seaward side and cyclonic on the landward side of the flow. Among the mesoscale features of the offshore current are intense jets and plumes originating at the coast, which entrain upwelled water and advect it far offshore (Burkov and Pavlova, 1980; Mooers and Robinson, 1984). At about 1500 km from the coast, mesoscale eddying gives way to flow to the south, which is less complex and slower. This transition is often marked by a salinity front which is continuous with the Subarctic Front and is often termed the California Front.

Upwelling at the coast is forced by coastal winds, modified by their response to blocking of the zonal westerlies by the coastal mountain chain. Thus, the coastal wind regime is not uniform: A local maximum of cyclonic curl is associated with the Southern California Bight, and a lobe of anticyclonic curl frequently reaches the coast at Punta Baja, where longshore equatorward wind stress is maximal. Off Oregon and Washington wind-stress curl is variable, with frequent brief episodes of anticyclonic curl related to storm tracks (Bakun and Nelson, 1991) which are reflected in event-scale variability of circulation within the coastal boundary province.

It remains critical to understanding circulation in this province, however, to distinguish the flow of the coastal current from the low-salinity velocity core of the offshore California Current. Equatorward transport in the separate coastal velocity core may be interrupted by discontinuous northward flow beginning seasonally in August–October. In early winter (November–January) continuous poleward flow occurs from the Mexican border almost to Cape Mendocino, with this continuity breaking down in February and March with the development of frequent cyclonic eddies between Point Conception and Cape Mendocino. In March or April the summer pattern of eddying southward flow becomes fully established. (Wyllie, 1966). When reversal of coastal flow is most strongly developed during early spring, the poleward current lies closest to the coast.

When transport is integrated over 200 or 500 m, the northward counterflow below the inshore California Current is continuous. Therefore, especially during spring and early summer, there is a shear zone between coastal poleward and offshore equatorward flow about 100–125 km offshore. Geostrophy requires that a pycnocline ridge (marked at the surface by a divergent front) should occur along this line of zero flow to compensate a depression in the sea surface, and this has consequences for the supply of nutrients to the photic layer. There is also, especially off Oregon, an upwelling front that occurs 5–15 km offshore during the summer coastal upwelling season which is forced by cross-shelf circulation over the very narrow continental shelf (Peterson *et al.*, 1979).

The southward flow of the coastal current in summer is a meandering jet with persistent eddies and cool filaments that may extend 200 km offshore and originate at prominent capes. Some of these topographically locked eddies, especially those at the Straits of Juan de Fuca, at Hecata Bank, and at Capes Blanco and Mendocino, often form cold filaments that may extend several hundred kilometers offshore, having a dipole termination, representing the development of a pair of counterrotating eddies. The actual development of these features is associated with variability of coastal winds. Upwelling winds normally occur for periods of 1–3 weeks, with relaxation periods of 2 or 3 days, and individual cold filaments may transport water from more than a single upwelling event (Lagerloef, 1992; Traganza *et al.*, 1981).

Coastal upwelling cells in the Southern California Bight are small and localized east of Point Conception, at Point Dume and in the bight lying between La Jolla and San Clemente; they are effective only 25–30 km from the coast. These cells, in the Southern California Bight, exhibit simultaneous upwelling (marked by dense sea fog and increased sales of wet suits in the beach towns of surfers' paradise) several times each summer, forced by events in the local wind field (Dorman and Palmer, 1981). Along the coast of Baja California, coastal upwelling cells occur during summer at Punta Eugenia, Punta Abreojos, Cape San Lazaro, and Punta Tosca.

Biological Response and Regional Ecology

The effects of wind-stress curl on nutrient dynamics are similar in each of the four principal eastern boundary currents (Bakun and Nelson, 1991). Though the paradigm of eastern boundary current nutrient dynamics is usually described simply as "coastal upwelling," the reality is far more complex and a variety of enrichment processes occur: (i) coastal upwelling cells, due to Ekman divergence at the coast, usually of small dimension and often topographically locked; (ii) continued upwelling in offshore-trending filaments of cool coastally upwelled water; (iii) upwelling in cyclonic eddies shed from meanders of the coastal current; (iv) and upwelling in the offshore divergent front at the shear zone between inshore poleward and offshore equatorward flows.

Of these, the offshore divergent front may be the most difficult feature to identify and is likely to be represented by a weak coastwise field of high chlorophyll but connected in various ways with the offshore-trending chlorophyll fields arising from eddies and filaments. It is often associated with the location of an offshore zooplankton biomass maximum.

Seasonal variation in algal growth within cyclonic eddies can be associated with seasonal variation in Ekman suction (Robinson *et al.*, 1993). However, in the offshore California Current, nutrient input appears to be principally advective in the cool, low-salinity, high-nutrient core of the southward flow. Both off California (especially at 35–42°N) and off northern Oregon–British Columbia (46–48°N and beyond), a winter bloom occurs which is unrelated to the effects of coastal upwelling plumes and filaments. Here, from October to March, chlo-

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rophyll values >1.5 mg chl m^{-3} occur over wide areas as far as 300 km from the coast. Between these two regions, chlorophyll values offshore are generally lower even at this season, and a "blue hole" region (covering several degrees of latitude) is persistent offshore, centered at about the Columbia River.

Because the processes leading to upwelling are not uniform throughout the coastal area, it is useful to review the processes that are characteristic of four compartments: Oregon–British Columbia, Point Conception to Cape Mendocino, the Southern California Bight, and the Baja California coast.

- *Oregon–British Columbia (42–48°N):* Winter storms are strong and frequent and seasonal current reversal occurs regularly; primary production is strongly seasonal. Upwelling occurs in summer at a coastwise front about 10 km offshore as well as at the coast itself, and response to wind events typically results after 4 or 5 days in the development of an upwelling cell, whose seawards front moves progressively offshore during development and returns shorewards during subsequent relaxation of upwelling. During this process, mean offshore flow is restricted to the surface 20–30 m (Brink, 1983; Smith, 1981). Upwelling occurs in persistent, topographically locked gyres during summer (e.g., at Juan de Fuca). During both summer and winter, frequent cold tongues of upwelled water on the scale of hundreds of kilometers extend westwards from the continent across and beyond the relatively broad continental shelf. Relatively high levels of nutrients occur throughout this region offshore, entrained toward the south from the subarctic zone.
- *Point Conception to Cape Mendocino (33–41°N):* Upwelling is strongest here but primary production is markedly seasonal. CZCS images show persistent offshore meanders, shed eddies (anticyclonic to the north and cyclonic to the south) and offshore cool filaments entraining coastally upwelled water. These most frequently occur in summer and south of Cape Mendocino, Point Arena, and Point Sur. Upwelling also occurs at the shallow banks off Point Reyes.
- *Southern California Bight (32 to 33°N):* The upwelling plume from Point Conception is frequently observed in summer, curving to the south around the outer limb of the eddy which occupies this bight. This plume has consistently lower surface chlorophyll values than those north of Point Conception or off Baja California. Off Southern California, the winter wind regime is established only relatively briefly, though (because the bight is wholly occupied by a quasi-permanent cyclonic eddy) poleward flow along the coast is more continuous here than elsewhere. Upwelling occurs as small coastal cells in summer (Point Dume and Del Mar) and at offshore islands and banks during all seasons. The inshore flow around the southern limb of the eddy may be marked as a chlorophyll feature.
- *Baja California (22–31°N):* The coastal wind regime is weaker but apparently favorable for upwelling year-round, though some seasonality in upwelling is evident in the chlorophyll field. Upwelling cells south of prominent capes are persistent: Cape Colonet, Punta Baja, Cape San Quintin, Punta Eugenia, Punta Abreojos, and Cape Falso all may generate such cells. The seasonal CZCS pigment fields (e.g., Thomas *et al.,* 1994) suggest that jets and filaments of upwelled water pass farther offshore from coastal upwelling cells from late summer (August) through early winter (November) and that south of Cape San

Lazaro even coastal upwelling ceases in autumn and winter (September–January).

Because of the large number of published studies of the California Current, in reviewing this province it is easier to concentrate on the individual processes rather than to see the whole. For instance, it is easy to lose sight of the fact that there is a seasonal cycle in the depth of the pycnocline that obtains over the whole area of the province (summer, 20–25 m; winter, ~75 m). At all seasons, if one ignores the effects of mesoscale features, the thermocline slopes downwards to the west, offshore, as it must. In upwelling cells, the density profile may be relatively featureless but wherever a significant mixed layer exists, a DCM occurs on the density gradient, usually with the depth of primary production a few meters shoaler. The offshore region has a seasonal cycle typical of subtropical oceans: Primary production rate and chlorophyll accumulation begin as soon as the mixed layer begins to deepen in the autumn. As noted previously, in the offshore areas chlorophyll values peak in midwinter, and primary production rate slows again with the shoaling of the thermocline in spring. Analysis of chlorophyll fields, integrated for the whole province, shows that this process—not summer upwelling at the coast—dominates the seasonal cycle. This observation recalls earlier suggestions that between-year variability in biological properties was forced primarily by changes in the advection of nutrients from the source of the California Current rather than by variation in the nutrients brought to the surface by coastal upwelling (Chelton, 1982).

Coastal upwelling is, nevertheless, a special case which merits special attention. The upwelling cells generate diatom–copepod assemblages of remarkably low diversity: In repeated net tows in one assemblage such as a few kilometers off Baja California (25°N), I could find no more than 29 species of zooplankton (and no more than 20 in any one haul), or about one-quarter the number taken 25 km farther offshore and examined with equivalent attention. Large, filter-feeding copepods, especially *C. pacificus* (which you will find described as *C. helgolandicus* in much of the Californian literature), at 115 ind m^{-3} comprised 77% of zooplankton dry weight at the coast. The seasonal ontogenetic migrations of this species cause the deep basins on the continental shelf to trap large concentrations of overwintering stage 5 copepodites; early in the winter these aggregate near the bottom, but the layers progressively shoal as oxygen concentration in the bottom water progressively declines, eventually forcing them over the sill depth of the basin (Osgood and Checkly, 1997). Compare this situation with that of *C. finmarchicus* in the deep basins of the Scotia Shelf in the Northwest Atlantic Shelves Province.

A few large species of diatoms (*Coscinodiscus, Nitzschia,* and *Tripodonesis*) formed 81% of algal cell volume. However, these rich diatom crops are also utilized by a very unusual organism—a bright red, swimming galatheid crab, *Pleuroncodes planipes*. These (in their pelagic phase) crowd into the surface layer off Baja California where they tail-flip up to the surface and then parachute down again with outstretched legs, filtering actively with their maxillipeds; this is a remarkable sight against the rich olive-green upwelled water. These crabs (at one per 3 m^3, each capable of clearing diatoms from 3 or 4 $liters^{-1}$ hr^{-1}) may comprise 90% of the total zooplankton/nekton biomass in nter (September–

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upwelling cells and contribute 85% of all zooplankton/nekton grazing pressure. *Pleuroncodes* is directly preyed on, and a preferred food of, yellowfin tuna in the same region, so this is a remarkably direct link from diatoms to your table.

How copepods exploit upwelling cells off Oregon has been most elegantly described by Peterson *et al.* (1979), who were able to use the three-dimensional differential distribution of the five abundant species to clarify the details of water movement during upwelling. Over a very narrow continental shelf (100 m is 10 km from the coast) the pycnocline lies at 20–50 m, sloping up toward the beach: in an upwelling episode the pycnocline intersects the surface 5–10 km seawards and nitrate-replete deep water is brought to the surface. Within this system each copepod has a narrowly defined and specialized distribution, in which it is maintained by details of the circulation pattern and its reproductive behavior: *Acartia clausii* is restricted to the upper 5–10 m and within 5 km of the shore; *Acartia longiremis* occurs 10 km offshore and similarly near the surface; *Pseudocalanus* occurs out to 15 km from shore but also only within the pycnocline at 10–20 m; *Oithona similis* occurs at similar depths but not in the first 10 km offshore; and *C. pacificus* has wider ranges for both depth and distance offshore. In fact, off California the endemic *Calanus* has a life history like that of *Calanoides* elsewhere; during winter and other periods when upwelling is not active, it descends to 400–600 m as a population of copepodite 5's and remains dormant in the oxygen minimum layer which underlies the coastal California Current.

I have already discussed some of the consequences for the ecology of this province of an ENSO event in Chapter 6. Because the El Niño phenomenon was first described in relation to the Peruvian coastal region I shall reserve for the HUMB province a general account of the processes involved. Much of what appears in that section is relevant in general terms to the California Current.

Synopsis

Archived data does not capture details of upwelling cells, so the winter deepening of the mixed layer below the photic zone represents the seasonality of the California Current generally (Fig. 9.16). Offshore, an autumn–spring progressive increase in primary production rate is accompanied only initially by accumulation of chlorophyll. Herbivore abundance appears to be a negative correlate of chlorophyll biomass.

Central American Coastal Province (CAMR)

Extent of the Province

The Central American Coastal Province (CAMR) extends from the tip of Baja California at Cape San Lucas in Mexico to the Gulf of Guayaquil in Ecuador. For convenience, it also includes the long, narrow epicontinental sea of the Gulf of California which lies behind the peninsula of Baja California.

Continental Shelf Topography and Tidal and Shelf-Edge Fronts

The west coast of America is an active continental margin in the geological sense, so the continental shelf is narrow, usually a few tens of kilometers wide.

Biomass Yields and Geography of Large Marine Ecosystems

Edited by Kenneth Sherman
and Lewis M. Alexander

f Science

AAAS Selected Symposium **111**

There are 3 modes of transmission of AVHRR data. The High Resolution Picture Transmission (HRPT) mode broadcasts full-resolution data in real-time. As the satellite passes over a receiving station equipped with a tracking antenna, data can be received. There are currently 23 non-NOAA HRPT stations in the U.S. and 55 in other countries (NOAA, 1985). In Global Area Coverage (GAC) mode, every orbit is processed on board the satellite to a reduced resolution (nominally 4 km), recorded, and eventually dumped and archived by NOAA/NESDIS. In Local Area Coverage (LAC) mode, up to 10% of each orbit is recorded at full resolution and later dumped and stored by NOAA/NESDIS. NOAA/NESDIS can search by time and place to check data availability and deliver data to users. It is possible to request of NOAA/NESDIS that certain locations be recorded. It is also currently possible to receive GAC and LAC data shortly after dumping as they are uplinked from NOAA receiving stations to the NOAA central processing facility. This is done by listening to a geostationary satellite communications network. Table 14.2 summarizes products available from NOAA/NESDIS (see also Kidwell, 1985).

The operational nature of the Polar Orbiter program means that data coverage and data availability is more regular than for the CZCS. Orbits were regularly recorded, except for documented periods of data outage. Like the CZCS, however, the digital scenes are in the form of sensed radiances, and require further processing to produce full-resolution, earth-located geophysical measurements which can be directly incorporated into scientific analysis. The system described in Brown and Evans (1982) is one example of the many extant. At least three systems are available commercially. Basic processing steps are similar to the CZCS. The existence of HRPT mode has fostered a number of smaller collections of local data. HRPT stations usually have some local processing capability, spawning, in turn, aggregations of regional geophysical data.

CASE STUDY: THE WEST COAST TIME SERIES

Introduction

One example of a planned effort to create, utilize, and distribute useful satellite data in the context of LME study is the West Coast Time Series at NASA/JPL. This data set is being created to provide the repeated, synoptic, high-resolution data necessary to observe the high degree of temporal and spatial variability in the California

Table 14.2. CZCS and AVHRR products available through NOAA/NESDIS. Adapted from NOAA/NESDIS (1985).

Sensor	Format	Product
CZCS	Tape and Film	Level 1 radiances
	Tape and Film	Level 2 derived products
AVHRR	Tape	LAC Level 1b radiances
	Tape	GAC Level 1b radiances
	Film	LAC images
	Tape and Film	Polar projection - daily mosaics
	Tape	SST observations, analyses
	Tape	23 km resolution sampled global data

Current System, the eastern boundary current along the North American west coast. To the degree that the oceanographic issues of the California Current are representative of those in other LMEs, the relationship between the data set and its utilization by the scientific community is an instructive example of the possibilities of active use of satellite data in oceanography.

Rationale

The California Current System has been extensively studied by field programs. Foremost among these is the CalCOFI (California Cooperative Fisheries Investigations) sampling program (Reid et al., 1958; MacCall, 1986). Studies based on this long-term (35-year) data set have shown the importance of large-scale variability in the physics and biology of this economically important ecosystem. For example, interannual changes in the southward flow (Bernal and McGowan, 1981; Chelton et al., 1982) seem to be responsible for changes in zooplankton biomass. The large-scale spatial distribution of zooplankton appears to be related to upwelling (Chelton, 1982). Within such a system, biological interactions such as competition and predation may not be dominant in determination of the distributions of organisms because of the effects of variable physical processes (McGowan, 1974).

Regional studies in the California Current System have focused on a variety of physical and biological processes. For example, OPUS (Organization of Persistent Upwelling Structures) concentrated on the upwelling center near Point Conception, California (Jones et al., 1983); OPTOMA (Ocean Prediction through Observation, Modeling, and Analysis) examined the effects of mesoscale variability off Northern California (e.g., Mooers and Robinson, 1984); U.S. CODE (Coastal Ocean Dynamics Experiment) studied the wind-driven circulation off Point Arena, California (CODE Group, 1983); and Canadian CODE studied the interaction of physical and biological processes on the shelf off Vancouver Island (e.g., Freeland et al., 1984). In addition to these large, intensive field studies, there have been several long series of less extensive measurements (e.g., Eppley et al., 1979 in the Southern California Bight). There have also been numerous single expeditions to various regions in the California Current (e.g., Simpson et al., 1984; Denman et al., 1986).

Time series of CZCS and AVHRR data have been used for studying many mesoscale phenomena in the California Current. Kelly (1983) studied coastal dynamics using AVHRR; Laurs et al. (1984) applied CZCS imagery to fisheries studies; Ikeda and Emery (1984) used an AVHRR time series to describe and model meanders; Rienecker et al. (1985) tracked a jet using AVHRR imagery; Abbott and Zion (1985) studied the kinematics of an upwelling event using CZCS and AVHRR imagery; Emery et al. (1986) computed advective surface velocities from an AVHRR time series. Real-time satellite data can be used to guide ships to active areas of interest, which may include fronts, for fishery applications (Montgomery, 1981), or specific features for research (Denman et al., 1986).

Questions relating to the characterization of large-scale processes in the California Current System LME were listed by the West Coast Time Series Advisory Group (WCTSAG) (WCTSAG, 1985). The science issues are addressable directly using a synoptic multiyear time series of satellite data, in some cases with concurrent in situ measurements. Some of the issues were: further definition of the relationship between physical processes such as longshore transport, or wind stress, and their biological manifestations in phytoplankton and zooplankton distributions, productivity fluctuations, and fishery implications; refinement of satellite productivity estimates; the effect of phytoplankton variability on recruitment success of fish; estimates of cross-shore transport of materials, heat, and momentum; coupling between large-scale, mesoscale, and small-scale events; derivation of seasonal statistics of variability; study of the role of seasonal forcing in maintenance of observed features; the importance, characteristic time/space scales, and factors controlling the distribution of persistent features such as eddies and jets; the longshore coherence and phase relationships of variability within the current system and these relationships between the current system and other ocean areas; coherence between SST and pigment signals; and derivation of flow fields from SST and pigment isolines.

Studies of smaller regional processes are perhaps more common because processes that dominate these areas are better sampled by ships. In the California Current, time series of satellite images on this scale have been very useful (e.g., Kelly, 1983; Abbott and Zion, 1983). Certainly each region will have its local features of interest that merit study. WCTSAG (1985) named some general questions addressable with satellite data: the relative importance of mechanisms causing upwelling; the "life history" of upwelling centers and mesoscale eddies; decorrelation length and time scales for mesoscale variability and development of ship sampling strategies for these scales; the degree to which eddies are ecosystems separate from the surrounding ocean; and the use of SST and pigment images to estimate phytoplankton growth rates.

In summary, there is a very active research program studying the California Current System. This research is a mixture of intensive regional studies, medium-term, less extensive studies, and very long, large-scale studies. These lists show that long time series of satellite data have application to quantitative statistical analyses and qualitative descriptions of variability at these scales.

Since 1979, the west coast of North America has been one of the best-sampled in the world in regard to CZCS and AVHRR data. There is a comprehensive Level 1 archive of over 800 CZCS passes and over 4000 AVHRR passes at the Scripps Institution of Oceanography Satellite Oceanography Facility (SSOF). These passes cover the west coast and are received in real-time by the SSOF tracking antenna. Paradoxically, West Coast oceanographers lacked adequate access to the necessary CZCS and AVHRR data. The small number of academic sites with data processing systems were rightly focused on research issues and could not process the data in bulk. Acquisition and maintenance of such systems by many new investigators was not economically feasible.

Strategy

The West Coast Time Series (WCTS) was created to alleviate this problem. All available data from SSOF will be distributed as a comprehensive, consistently processed, documented time series of earth-gridded, geophysical pigment and SST quantities. The extent of the WCTS study area is bounded by 20°N, 55°N, 140°W, and 105°W for the period 1979-1986.

WCTS data are processed as follows. Data are acquired by copying the SSOF tapes. Each tape contains one "swath," the area visible to the satellite while in range of the receiving antenna. Browse images are created to assess cloud cover (neither sensor can see through clouds) and areal coverage (different swaths see slightly different areas of the earth). Swaths are divided into 5 x 5 "tiles" (Figure 14.2). Totally cloudy tiles are identified and excluded from further processing. Remaining tiles are processed to the geophysical quantities and separate cloud masks are created (procedure of Kelly 1985 for nighttime AVHRR swaths, albedo-based thresholds for other data). The tiles are mosaicked (Figure 14.3) at reduced resolution (nominally 7 km) to provide a single image for the entire swath. There are 35 possible non-land tiles in the study grid; on the average about half are useful.

The WCTS is coordinated with another NASA project to ensure that once created, the data are available to the community. Browse,

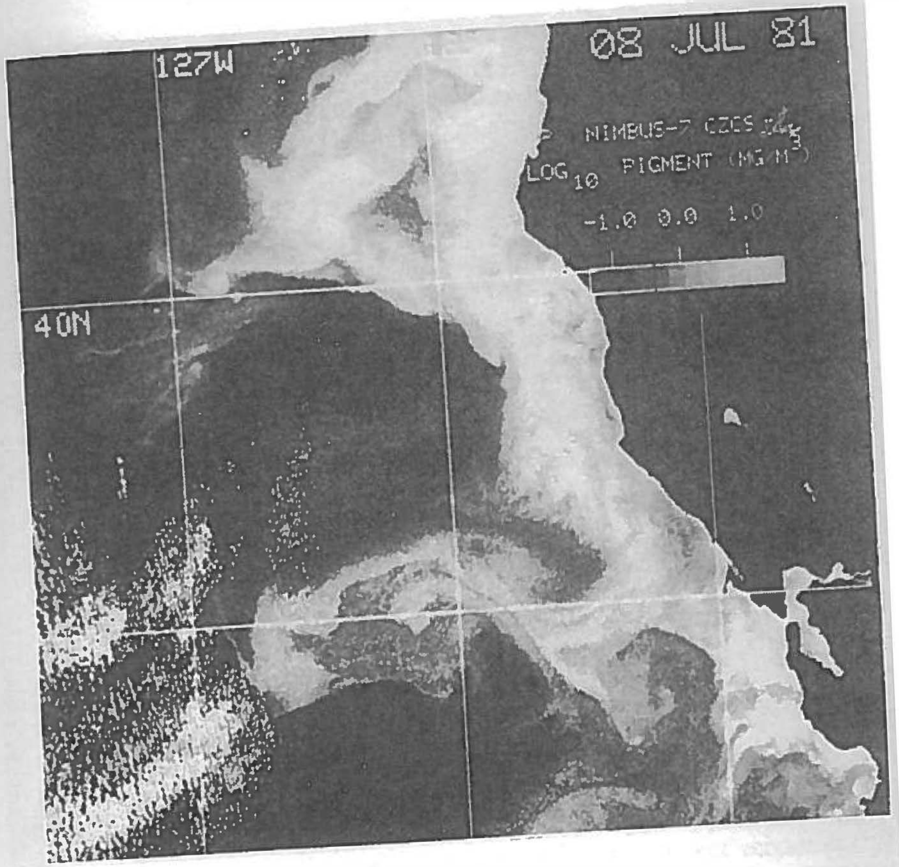
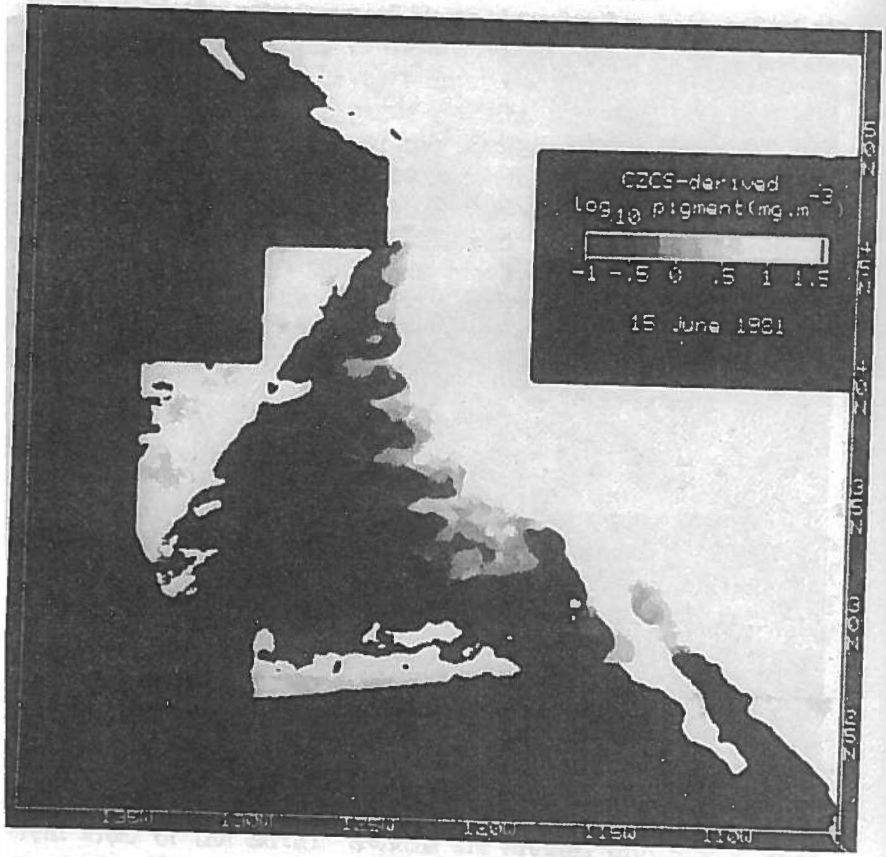


Figure 14.2. CZCS image off Central California, 8 July 1981. Mesoscale features such as eddies and jets are visible.



gure 14.3. CZCS mosaic image for the West Coast Time ries study area, 15 July 1981.

tile and mosaic products will be archived and distributed by the NASA Ocean Data System (NODS). Data can be searched by specifying space and time windows. Data can be ordered from a user's terminal for electronic or mail shipping to the user's site. Data access from NODS is described in NASA (1986b).

Results

Research based on WCTS products is at an early stage but shows promise. Abbott and Zion (unpublished data) have produced monthly means of pigment for the period 1979-1982 and noted the expected northward progression and southward retreat of phytoplankton blooming with the advance of the year. Abbott (1986) used WCTS imagery to map the length, orientation, and "root" of jets in the California Current System. Balch (1986) and Collins et al. (1986) have incorporated imagery into development of models of productivity based on satellite data. Denman and Abbott (1986) reported on decorrelation times of CZCS-derived pigment patterns. It is expected that data utilization will continue.

Summary

Several factors converged to promote the development of the WCTS. There was much data available as Level 1 tapes. The WCTS study area already was being researched, including investigations of interannual variability. There was already a realization that satellite data was a necessary tool for studying certain classes of problems. The scientific community was willing to codify a rationale for the project and to generate specific requirements. Also, separating the production work from research sites was accepted, with the proviso that scientific oversight of the project be maintained. Algorithms were at a stage of development to permit acceptable (though still improvable) data to be produced. Finally, improvements in price/performance ratios for computers made the project economically tractable. This experience may illuminate one set of conditions amenable to the development of effective utilization of satellite data.

STUDIES IN OTHER REGIONS

Satellite data have been used in many other areas of the world. The following brief survey shows that satellite methods have been applied to many diverse ecosystems.

plankton and prey fish. In some cases the proximity of land serves to delineate the region, as in the case of semi-enclosed seas, in which oceanographic properties are influenced greatly by the nearby terrestrial areas and the limited communication of the waters to other marine regions.

The concept of LMEs is undoubtedly sound from a biological standpoint, but it may be difficult to apply the idea of an LME to problems of fisheries management. According to customary international law and the Convention on the Law of the Sea (CLS) (United Nations, 1983) coastal states have sovereign rights over resources within 200 nm of their coastal baselines. This Exclusive Economic Zone (EEZ), defined and described in Articles 55-75 of the CLS, is, in effect, a management region, which in many cases does not coincide with the biological region, the LME.

THE PACIFIC OCEAN

As the world's largest ocean, the Pacific measures 15,500 km from Bering Strait to Cape Adare, Antarctica, and 17,200 km from Panama to Mindanao (Fairbridge, 1966). With those boundaries and dimensions it is one of only three oceans; the Atlantic and the Indian Oceans are the others. However, many oceanographers and geographers prefer to include the Arctic and the Antarctic (or Southern), on the basis of their distinguishing oceanographic characteristics.

There have been a number of schemes for subdividing the Pacific proposed over the past 100 or so years. One suggests that the Pacific be divided into northern, southern and intertropical sections, while others employ the more conventional north, south, east, and west subdivisions. Frequently, the term "Central Pacific" is employed also. The northern, southern, and intertropical division is logical when ocean currents are considered. In the North Pacific the clockwise gyre of Kuroshio, North Pacific, California, and North Equatorial Currents is dominant, while a counterclockwise gyre (Peru, South Equatorial, East Australia, and Antarctic Circumpolar Currents) prevails in the Southern Pacific. In the Equatorial Pacific there is a distinct pattern of currents, with the North and South Equatorial Currents flowing from east to west and the Equatorial Counter Current flowing in the opposite direction.

On the basis of water masses, large three-dimensional bodies of water with distinctive temperature-salinity relationships, five regions can be identified: Subarctic Water, Western North Pacific Water, Eastern North Pacific Water, Western South Pacific Water, and Eastern South Pacific Water. Along the west coast of the mainland United States there is a Transition Zone where Subarctic and Eastern North Pacific waters mix.

When more conventional sub-regions are discussed it can be seen that in the Eastern Pacific, both North and South, the coastlines of the North and South American continents are generally smooth, with only the Gulf of California qualifying as a semi-enclosed sea. There are few oceanic islands: the Galapagos, Clipperton, Easter Island, Sala y Gomez, the Juan Fernandez group, and a few others. In the Central Pacific, both North and South, the Polynesian islands, which form a large triangle with the apexes at Easter Island, the Hawaiian Islands, and New Zealand, are prominent. The Western Pacific is characterized by many island groups and a number of marginal, semi-enclosed seas. The presence of numerous island nations, some entitled to claim archipelagic nation status according to the Convention on the Law of the Sea, and the semi-enclosed seas in which jurisdictional claims overlap makes the Western Pacific a region fraught with management problems and potential political conflicts. In the Northwest Pacific the littoral states are in general at a much higher level of economic development than the small island nations of the Southwest Pacific. In general, however, countries in both regions view fishery resources as important.

PACIFIC LMEs

Figure 15.1 depicts 23 LMEs; no attempt has been made to delineate them precisely, since the current state of knowledge of distributions of the various species comprising the ecosystems is still general rather than specific. However, it is possible to classify the LMEs in some meaningful ways, despite an inability to draw exact boundaries.

Some are almost oceanwide in extent; the Eastern and Western Insular Pacific LMEs each cover a very large expanse of Pacific Ocean. Other LMEs are more or less delineated by the ocean currents in which the organisms thrive. The Humboldt, Kuroshio, and Oyashio Currents are good examples. Still others are delineated by the reasonably well-defined boundaries of semi-enclosed seas, such as the Sea of Japan, the East China Sea, the South China Sea Basin, and the Sea of Okhotsk. Another very large category of LMEs consists of those which could be termed "open seas." Examples are the Gulf of Alaska, the Western Isthmus, the Coral Sea, and New Zealand Seas.

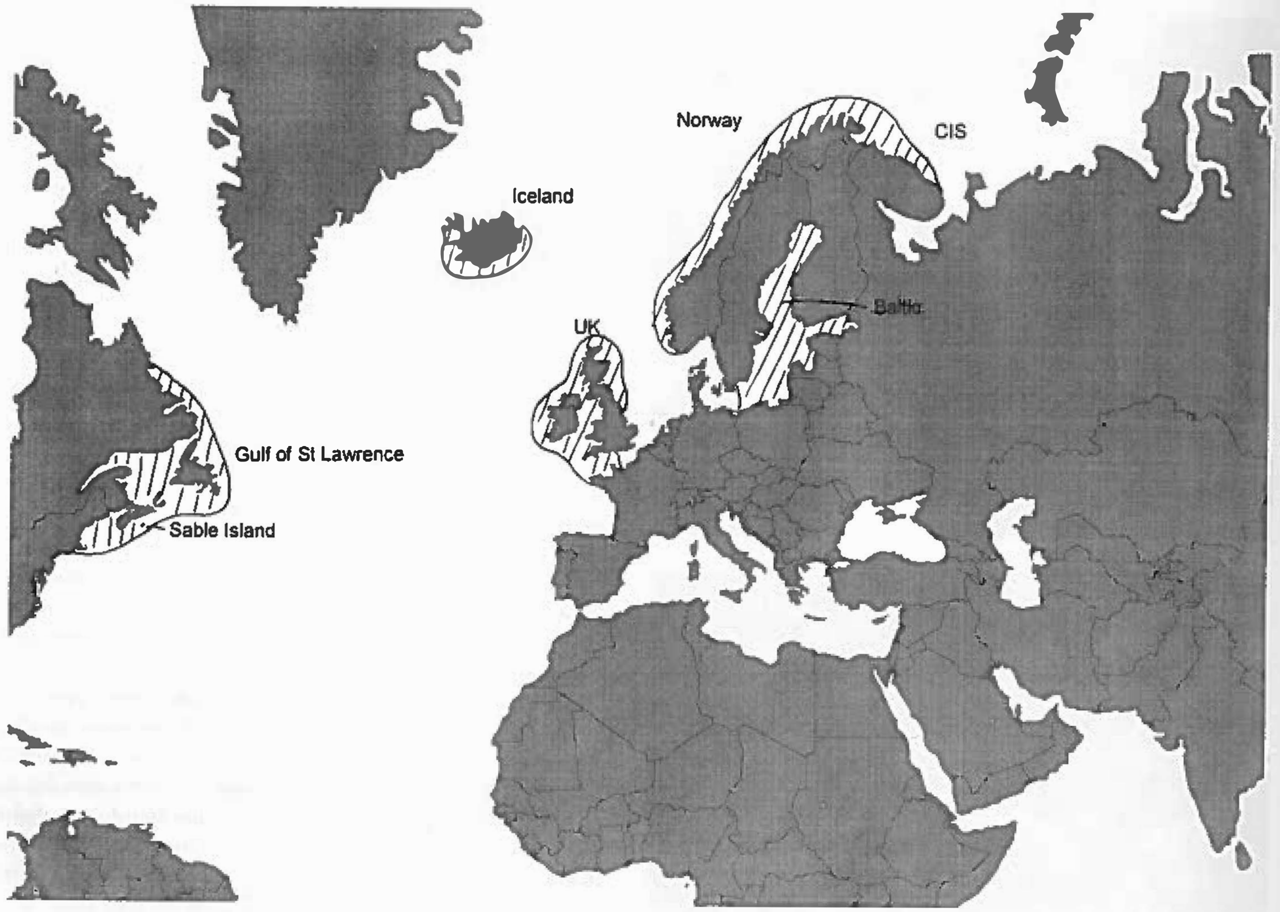


Figure 2 *Map showing the geographic distribution of the gray seal.*

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Gray Whale

Eschrichtius robustus

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The family Eschrichtiidae includes a single known genus and species, the gray whale, which now is found only in the North Pacific and Pacific Arctic Oceans (though it once lived in the North Atlantic until the 17th or early 18th century). Grays are by far the most coastal of all the great whales, and inhabit primarily inshore or shallow, offshore continental-shelf waters. They tend to be nomadic, highly migratory, and are tolerant of climatic extremes. Each year, they make the longest migration of any whale (up to 15,000–20,000 km round trip) largely without FEEDING, traveling along nearshore routes between a summer feeding zone of high productivity in Arctic or subarctic waters and a winter breeding zone in temperate or subtropical southern waters. Unlike other mysticetes, the gray is primarily a bottom feeder and influences the topography of the seabed in the Arctic (from sucking its prey out of the sediments). It is the only whale to bear its young in warm, shallow, coastal areas and lagoons.

There are two populations. The western North Pacific population (or Korean-Okhotsk) migrates along the coast of Asia. It was hunted to the verge of extirpation and is extremely rare. Another much larger, eastern North Pacific population (or California-Chukchi) migrates along the coast of North America and eastern Siberia (Fig. 1). It too was severely overexploited in the latter half of the 19th and early 20th centuries, but, following protection from commercial WHALING, has increased to about 26,600 (in 1999). The resilient eastern North Pacific gray whale is the only cetacean population that, following severe depletion, has sufficiently recovered under protection from commercial whaling to be removed from the list of endangered species. The western Pacific population, however, remains listed as critically endangered.

An active but gentle species, as long as they are not molested, the gray whale had a reputation for ferocity among the old whalers, who dubbed it "devilfish" for its habit of crashing into and staving in boats when harpooned or in defense of its young. Despite it being the trickiest and most dangerous prey, early whalemen developed a special affection for grays and found them to be the most interesting and intelligent of all the great whales. Grays seemed to learn quickly the dangers from whaling and performed a remarkable array of evasive maneuvers. They were admired for their fierce protection of their young and habit of giving assistance or "standing by" an injured companion, often reaching self-sacrificing measures. When attacked, they showed a power of resistance and tenacity of life that distinguished them from all other cetaceans. Today, many people have come to value gray whales more highly as a living resource than as one to slaughter, and they have become a WHALE-WATCHING phenomenon. Their coastal habits make them the most accessible of all the mysticetes and they can be seen most easily, often from shore. Gray whales are unusually sportive; breaching, spy-hopping, LOBTAILING, and mating extravaganzas are essential elements of their migratory and breeding-grounds repertoires. Their willingness to allow whale watchers to stroke them is an added attraction, and grays are now known as "friendly" whales.

I. Systematics

A. Evolutionary History and Classification

No fossils of a direct gray whale ancestor have been found. The family Eschrichtiidae is known only from the Recent and from a single Pleistocene specimen about 50,000–120,000 years old found in California, and a less certain one from Alaska. A long-held theory proposed that gray whales could have evolved from the Cetotheridae, an extinct family of whales dating back some 38 million years, and could be their closest living relatives. Due to the lack of any fossil remains linking the modern gray whale to the far more ancient cetothere, some challenge that view and are unwilling to link them to any of the known early whales. A highly distinctive species, the gray whale has been placed in its own family: Eschrichtiidae (Ellerman and Moirrison-Scott, 1951) (=Rhachianectidae, Weber, 1904).

Most experts have considered the gray whale to be more closely related to the rorquals (Balaenopteridae) than to the right

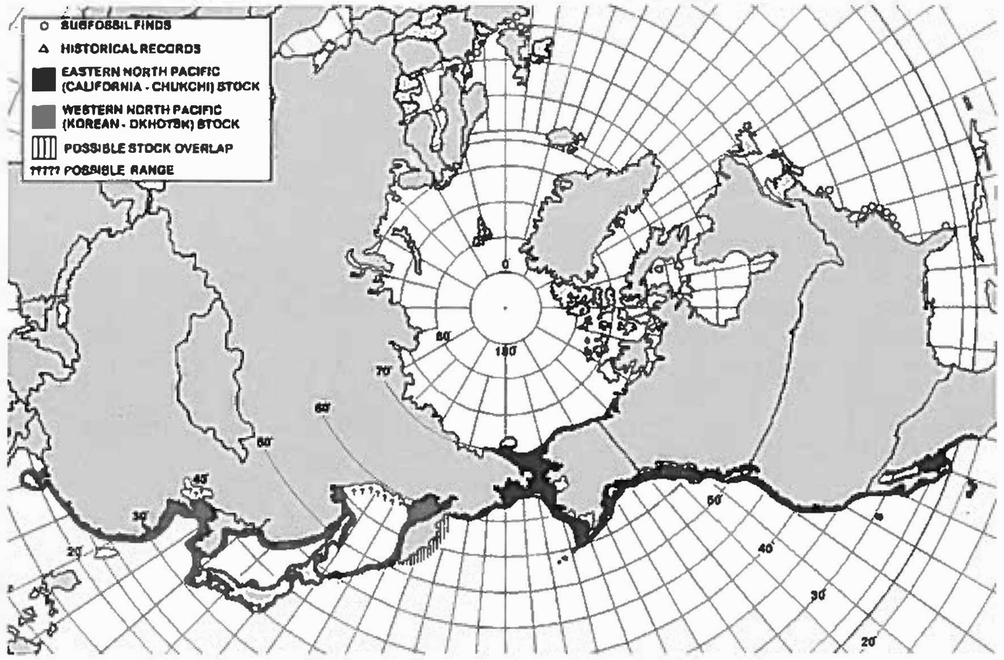

Figure 1 *Known distribution, historic and current, of the gray whale. The eastern North Pacific population (black) has recovered from depletion. The western North Pacific population (gray) remains critically endangered. The Atlantic gray whale is extinct and is known from subfossil finds (circles).*

whales (Balaenidae). Others have given it an intermediate position between the two. However, for the four modern families of baleen whales commonly recognized (Balaenopteridae: rorquals, or fin whales; Balaenidae: bowhead and right whales; Eschrichtiidae: the gray whale; and Neobalaenidae: the pygmy right whale), the pattern of phylogenetic relationships at the base of baleen whale divergence is unresolved. With respect to gray whales, analyses of their position within the Mysticeti conflict. Molecular studies position gray whales within the balaenopterids, while analyses based on morphology and including fossil and extant taxa differ in suggesting grays are linked with the balaenids and the pygmy right whale. Moreover, some biologists place the gray whale as a subfamily of Balaenopteridae.

B. Names

The gray whale has many English names, first applied by 19th century whalers. *Scrag* was used by old whalers on the Pacific coast of North America because they identified it with a whale called a scrag that was taken in the Atlantic Ocean in the 17th and 18th centuries. *Devil fish* and *hard head* were derived from the often violent reaction of the grays that commonly smashed boats with their heads and flukes when harpooned. *Mud digger* and *mussel digger* referred to the bottom feeding of the whales. *Gray* and *gray back* characterized its color. *Okhotsk* and *Korean* denoted the western population's feeding and presumed breeding grounds, and *Chukchi* and *California*, the feeding and breeding grounds for the eastern population (also the whaling grounds).

As for its scientific name, the generic name *Eschrichtius* (Gray, 1865) was given to honor a 19th century Danish zoologist, Daniel Eschricht; and the specific name *robustus* (Lilljeborg, 1861) is from the Latin for "oaken" or "strong." The gray whale first became known to science not through observations of living animals but through the discovery of subfossil skeletal remains from Europe where it had long been extinct. Conspecificity cannot be proven by purely anatomical data, but the SKELETON of the gray is distinctive and no anatomical difference has been found between extinct Atlantic and extant Pacific populations (or between the eastern and western populations of the Pacific) that would justify separating them on the basis of species, or even subspecies. Thus, the odd situation exists where the remains from the extinct Atlantic population serve as the type specimen for in the Pacific Ocean (=*Eschrichtius gibbosus* Erxleben, 1777).

II. Description

The gray whale is a robust, slow-moving whale with a flexible body, more slender than the right whales and more stocky than most rorquals (Fig. 2). This species is readily identified by the mottled gray color of the skin with numerous lighter patches scattered all over the body (although color may vary from gray-brown to slate-black). Grays have more external PARASITES and epizoites than any other cetacean. The barnacle, *Cryptolepas rhachianecti*, thought to be host specific, has been found on beluga whales (*Delphinapterus leucas*). As larvae, BARNACLES are free swimming but soon settle onto calves and adults alike, eventually forming large colonies that are deeply embedded in the skin. Grays also host three species of WHALE LICE (they are cyamids, not insects) that feed on skin and damaged tissue: *Cyamus scammoni* and *Cyamus kessleri* occur only on grays, whereas *Cyamus ceti* also lives on other whales (Fig. 3). The lice cling by the thousands in areas of reduced water flow, such as around barnacle clusters, blowholes, and folds of skin, and swarm into wounds. In the breeding lagoons, schools of topsmelt (*Atherinops affinis*) symbiotically clean lice and sloughing skin from the whales. Much of the whale's mottled appearance comes from the parasites or scars from previous infestations and abrasions. By photographing the skin pigmentation patterns on the backs and sides, it is possible to identify individual animals, which is important to the study of gray whales.

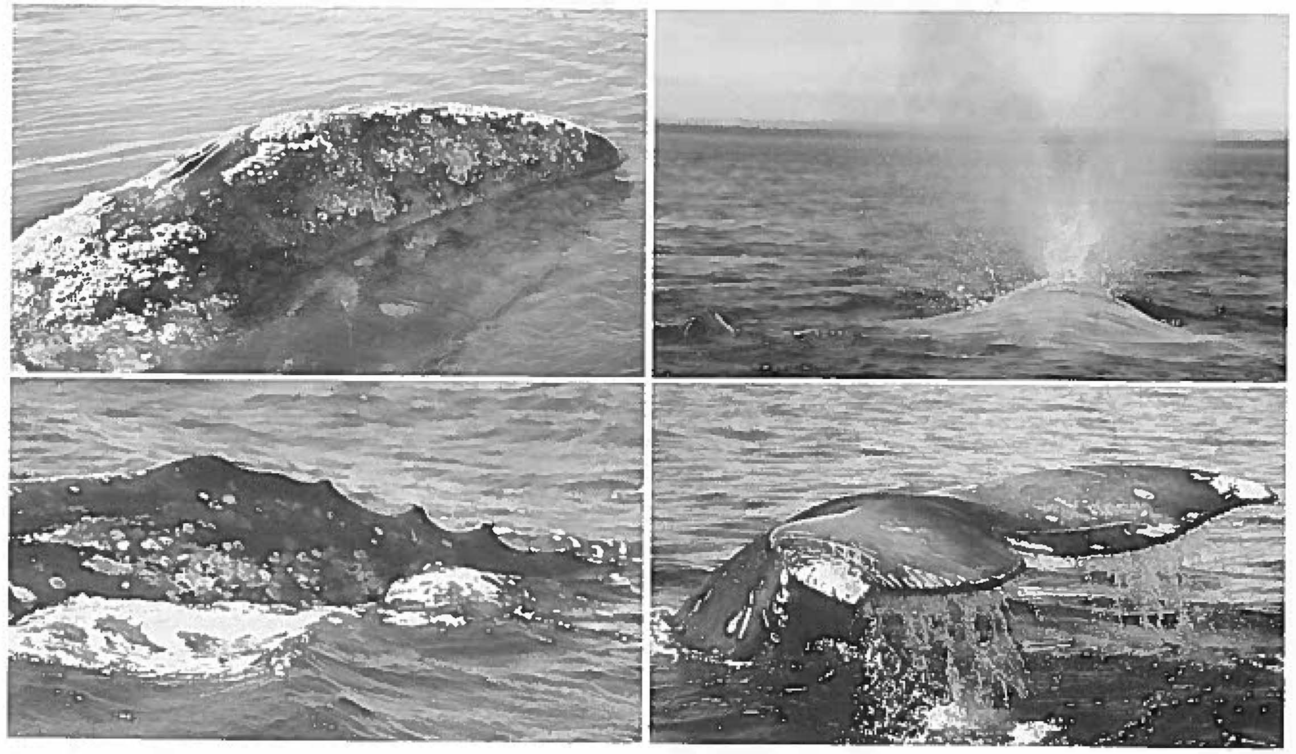

Figure 2 *The narrow head of the gray whale is usually covered with patches of barnacles and whale lice (top left). The blow is heart-shaped and 3–4 m high (top right). Instead of a dorsal fin, grays have a low hump followed by a series of bumps (bottom left). The flukes are over 3 m wide, frequently bear scars from the teeth of killer whales, and are often lifted before a deep dive (bottom right).*

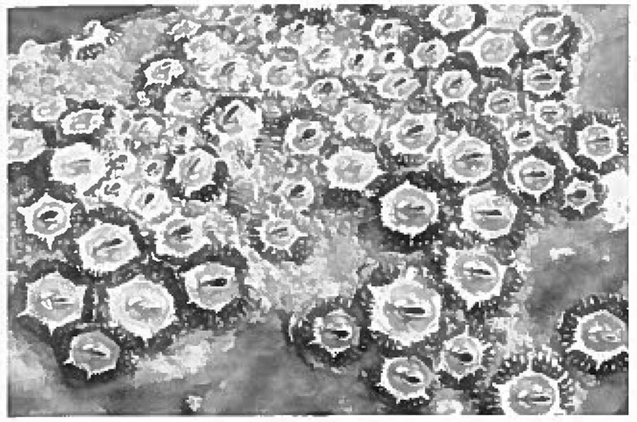

Figure 3 *Dense clusters of barnacles surrounded by whale lice develop shortly after birth. Barnacles leave white scars on the whale's skin, which slowly repigments over time.*

The gray whale's relatively short, narrow head is triangular (in top view) and moderately curved downward (in side view) (Fig. 4). It is encrusted with patches of barnacles and associated whale lice, particularly on top. Widely spaced bristles sprout from small dimples on the upper and lower jaw (no other whale has so many hairs); these short bristles, linked with sensory cells, are extra noticeable on calves. The skull comprises only about 20% of the total skeletal length. A unique feature is the presence of paired occipital tuberosities on the posterior part of the skull. Small eyes, with eyelids, are located just behind the corners of the mouth. Directly above them, on top of the head, is a pair of blowholes (nostrils). Barely visible, the ear opening is a tiny hole just behind the eye. The narrow upper jaw has 130 to 180 baleen plates hanging down on each side, separated in the front of the snout. A gray's BALEEN is the shortest (5–40 cm), thickest, and coarsest of all mysticetes and is cream-white to pale yellow. The lower jaw is broad, with a keel-like protuberance in front, and slightly arched. On the throat there are two to seven (commonly three) short, deep creases that stretch open and allow the mouth to expand a little during feeding, but they do not extend beyond the throat region and are insignificant compared with the many long ventral grooves found in balaenopterids.

Gray whales lack a dorsal fin but have a low hump followed by a series of 8–14 small bumps (knuckles) along the top of the tail stock. The ventral part of the body is smooth, without any longitudinal grooves. The paddle-shaped flippers are up to 200 cm long. Tail flukes are over 3 m wide on adults, with smooth trailing edges and a deep median notch. The flippers and flukes are often marred with tooth scars from killer whales (*Orcinus orca*). Unique to this species is a cyst-like structure (10–25 cm in diameter) beneath a swelling on the ventral surface of the tail stock, which may be similar to sebaceous glands of land mammals, or function as a track-laying scent gland, although its exact function

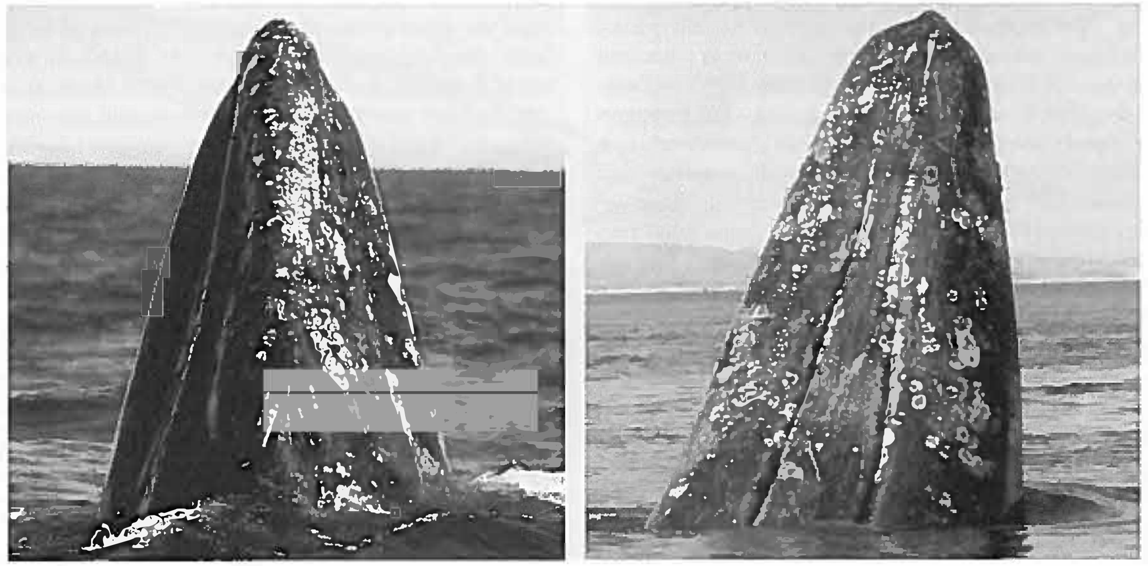

Figure 4 *Gray whales commonly spyhop, lifting the head vertically above the water. The head is narrow and triangular when viewed from the top (left), and they have from two to seven short creases on the throat (right), rather than the long, ventral throat grooves found in balaenopterids.*

is unknown. Grays, which survive in extremely cold water for about half of the year during the feeding season, are insulated with a layer of BLUBBER averaging 15 cm thick beneath the skin and can tolerate a great drop in their skin surface temperature to only a degree or so above that of the surrounding water.

Newborn grays (calves) average 4.6 to 4.9 m long and weigh about 920 kg. The sex ratio is parity at all ages. They reach puberty at anywhere from 6 to 12 years of age (average is 8), at a mean length of 11.7 m in females (called cows) and 11.1 m in males (called bulls). Adults weigh 16,000 to 45,000 kg and stop growing at about 40 years, when the average female is 14.1 m long and the average male is 13.0 m. The largest female recorded was 15 m, and the largest male 14.6 m long. Although adult females are slightly bigger than males, there is no significant difference in their appearance (the distance from the genital slit to the anus is wider in males). The maximum, as well as average, life span is unknown (age is calculated from growth layers in the waxy ear plugs that fill the auditory canal). One large female was estimated to have been 75–80 years old when she was killed and she was pregnant.

III. Ecology and Behavior

A. Social Organization

The gray whale is not a highly social species. Individuals may associate with many conspecifics, but they do not appear to form stable pairs or groups and come together for only part of the year during migration and on the winter breeding range. The only persistent social bond known is between a mother and a calf, which disappears at weaning. Now and then, short-term associations lasting several days or weeks are reported, but their significance is still a mystery to us. Very little research into the social organization of the gray whale has been done. It is possible that they communicate even over large distances, sending and receiving acoustic signals. No territoriality, dominance, or overt aggression toward conspecifics has been reported.

On the summer feeding grounds, grays are usually widely spaced, solitary (commonly pregnant females), or in pairs, and less often in small groups of 3–5, although many may be in proximity in the patchily distributed food-rich areas. Larger aggregations in tens or even hundreds can occur in a particularly rich feeding area but are likely related to a mutually available mass of food rather than to social cohesion or interaction (these aggregations fluctuate constantly). Occasionally, some grays stop feeding to form groups of 30–40 or 100–400 animals that engage in bouts of social activity (lasting 1–4 days) reminiscent of courting and mating; however, their function is unknown. During migration, singles, pairs, and trios are most common but grays sometimes form transient groups of up to 16 individuals.

On the winter breeding grounds, large aggregations of mothers with young and courting/mating whales are common, but are in constant flux (1000 or more will crowd into the largest breeding lagoon). Initially, mothers with neonates have little interaction with other mothers and calves, although many are concentrated in the nursery areas of the breeding grounds. When calves are 2–3 months old, however, they often form highly interactive social groups. In these encounters, mothers and young cavort en masse, rolling about on top of each other, rubbing and touching from head to flukes, and often emitting huge bursts of underwater air bubbles. Groups last from a few minutes to over 3 hr and involve up to 40 individuals at a time, with many others coming and going, and may play a role in the social development of the calf.

Overall, there is a low degree of cooperation among gray whales, except limited examples of joint defense against killer whale attacks and assistance or support behavior, mainly for the aid of the young and especially in the calving areas. This is evidenced by adults coming to the aid of a mother whose calf is in trouble. Standing by (whales in a pair or group assisting, supporting, or staying with an injured companion) also occurs occasionally among adults in times of distress.

B. Feeding

Gray whales do almost all of their feeding during summer and fall when they are in higher latitudes, where they forage on the ocean floor in shallow waters over continental shelves (4–120 m deep). They are adapted to exploit the tremendous seasonal abundance of food that results as the Arctic pack ice (sea ice that is unattached to land) retreats in spring, exposing the sea to the polar summer's continuous daylight, which triggers an enormous bloom of microorganisms in the water down to the sea floor. Unlike other baleen whales, the gray is mainly a bottom feeder and sucks small invertebrates and crustaceans out of the sand and mud. Their distribution in the feeding grounds coincides with the concentrations of these bottom-dwelling prey. As the summer advances and the edge of the pack ice recedes and uncovers more of the feeding grounds, the whales move. They feed heavily from about May through October, gaining enough stores of fat to sustain them during fasting or greatly reduced intake of food during the rest of the year, when the polar feeding grounds are ice covered and they migrate south to warm winter breeding grounds.

During about 5 months of intensive feeding in Arctic waters, an adult will consume roughly 170,000 kg of food. By the time the grays return to the feeding grounds (5 to 6 months later) they will have lost up to 30% of their body weight and must single-mindedly forage to replenish their fat reserves. The highest energy costs during migration are incurred by pregnant or lactating cows. For cows, the cost of reproduction includes the ENERGETIC requirements for gestation (producing a calf) and lactation (nursing young until weaning), which is far greater. During summer and fall, pregnant cows put on 25–30% more weight than other gray whales (exclusive of fetus).

An extraordinary aspect of the gray whale's feeding ecology is its apparent dietary flexibility. Over 80 species of prey have been identified, reflecting its opportunistic approach to foraging. On the summer feeding grounds, grays primarily consume benthic gammaridean amphipods (shrimp-like crustaceans that live on or buried in the sediment). Amphipods from four families account for about 90% of the food, but depending on the feeding area, 1 of 7 species is usually dominant. Four are from the family Ampeliscidae (*Ampelisca macrocephala*, *A. eschrichti*, *Byblis gaimardi*, *Haploops* sp.). They are tube builders that live in dense colonies or "tube mats" in the upper few centimeters of sea floor sediments. Overall, the amphipod *A. macrocephala* (up to 33 mm long) is probably the most commonly taken species (and occurs in concentrations as high as 23,780/m^2 in the Chirikov Basin in the Bering Sea). The other three species are from separate families: Haustoriidae (*Pontoporia femorata*), Lysianassidae (*Anonyx nugax*), and Atylidae (*Atylus bruggeni*), which are mobile scavenging amphipods that rove freely over the seafloor in search of prey. In some areas, polychaete tube worms (*Travisia forbesi*) are their main food. Planktonic prey items eaten in the peripheral feeding areas south of the main feeding grounds occur in swarms or schools and include mysids, crab larvae, red crab, mobile amphipods, herring eggs and larvae, squid, megalops, and bait fish. Some plant material also occurs in their stomachs.

To bottom feed, grays roll to one side, bringing the head parallel with the seabed, sweep the side of the mouth close over the bottom a few centimeters above it, and open the jaws slightly to suck sediment containing prey into the mouth (which has flexible lips) (Fig. 5). Water, sand, and mud are strained through the comb-like baleen, leaving the food trapped on its inner margin. The suction might be created by retracting the large, strongly muscled tongue (weighing 1400 kg). The grays move slowly along the bottom, sucking up infauna in pulses, and surface with clouds of sediment (called mud plumes) streaming from the mouth. Mud plumes mark the meandering path of the feeding whales. Seabirds feed on prey brought to the surface in the plumes.

Grays impact their feeding grounds more than any other cetacean. Bottom feeding leaves mouth-sized depressions or "feeding pits" in the sea floor, from which the top layers of sediment are removed. Foraging is a major source of physical disturbance to the benthic community and plays an important role in the rate of turnover of the epibenthos. In some areas of the Arctic, over 40% of the seafloor is pock-marked with feeding pits. It is thought that by clearing space in the bottom, whales open areas for recolonization, succession, and maturing of the prey community, thus promoting the growth and diversity of life on the seafloor. Periods of nonuse are presumed to correspond to rapid recovery of the habitat. However, if the resource is overutilized and the area is stripped, it could be a one-way street leading to the permanent loss of amphipod communities and changing feeding patterns. In this way, graywhales are an integral part of the coastal community and participate in a dynamic feedback loop, termed "niche construction," whereby their feeding activities function to shape their ecological niche through alteration of the benthos.

In addition to bottom feeding, grays also occasionally feed by surface skimming and engulfing planktonic prey out of the

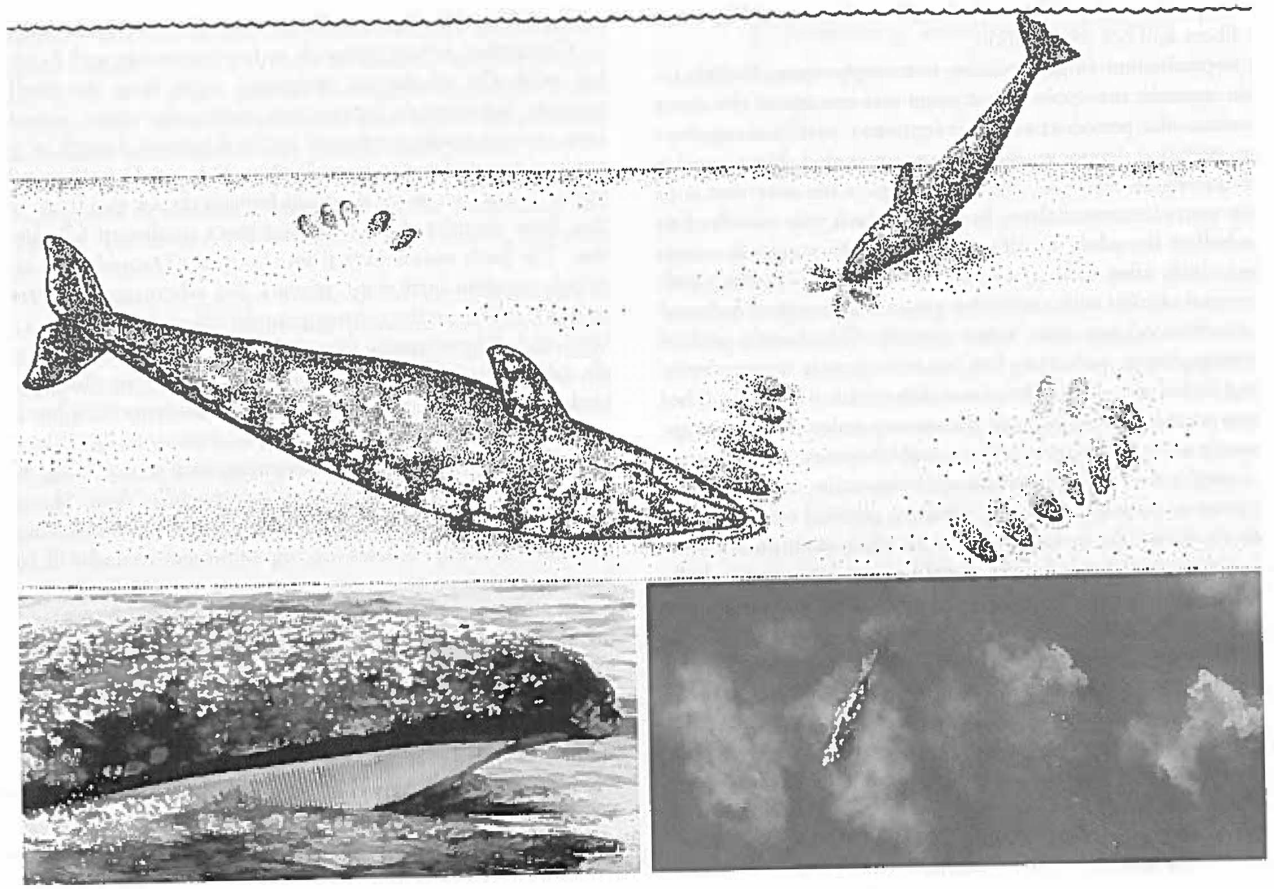

Figure 5 *A bottom feeding gray whale swims on one side to suck prey from the seafloor, creating mouth-sized depressions or feeding pits (top). The cream-white baleen plates are the coarsest, shortest, and fewest of any mysticete (bottom left). Sieving prey-laden sediments through the baleen creates billowing mud plumes (bottom right).*

water column. Zooplankton are only known to be utilized outside of the principle feeding grounds, in peripheral feeding areas throughout the migratory range. Instead of traveling the entire distance to the feeding grounds, some whales spend the summer feeding along the coast in other parts of their range. Also, whales destined for the summer grounds sometimes stop to feed periodically on the way if the opportunity arises. The importance of peripheral feeding areas is unclear. With three modes of feeding (benthic suction, engulfing, and skimming) the gray has perhaps a greater range of foraging techniques than any other of the great whales.

C. Reproduction

Gray whales are thought to have a promiscuous mating system: males and females do not form long-term pair associations and both sexes may copulate with several partners during the same breeding season. Because multiple inseminations can occur, it is proposed that *sperm competition* may be taking place in gray whale fertilization (sperm from two or more males compete to fertilize the ovum within a female). Adult males have relatively large testes weight (averaging 38 kg in mating season) to body weight ratios and presumably produce large quantities of sperm. In this mating strategy, copulating males attempt to dilute or displace the sperm of other males to increase the likelihood of being the male to fertilize the female. Their fibroelastic penis reaches 170 cm in length and is erected by muscle fibers and not vasodilation.

Reproduction in gray whales is strongly seasonal. The female reproductive cycle lasts 2 years and consists of the onset of estros (the period of sexual receptivity), ovulation, conception, gestation, lactation, and an anestros period. Most females bear young in alternate years, although some may rest 2 or more years between calves. In general, each year one-third to one-half of the adult females are birthing (they are not receptive to bulls after calving) and the remainder are mating, with a reversal of roles each successive year. Cows continue to breed at an advanced age. Bulls mate annually. They have a peak of spermatogenetic activity in late autumn or early winter, correlating with the time females come into estrus. Some sexual behavior on the feeding grounds and among males occurs that apparently serves nonreproductive social purposes.

Lengthy courting (precopulatory) behavior is part of the mating process, evidently requiring sufficient physical contact by the bulls to arouse the cows, but detailed information on the constituents of courtship is not yet available. Copulation occurs belly to belly. Pairs or trios of whales sometimes court and mate quite gently together. More often (or perhaps just more readily visible), there is a high level of activity, marked by whales rolling, touching, splashing, and cavorting energetically, at which times bulls with extended penises can be seen (Fig. 6). While some nudging and pushing may take place to get close to a cow, bulls do not appear to fight to keep others away. Bulls outnumber available cows by as much as two to one, leading to the belief of a ménage à trois mating group by early naturalists. In fact, although trios are common, so are pairs and groups of various sizes that can blossom into a giant free for all involving as many as 20 consorting adults at a time. The large groups constantly fluctuate, with some participants departing while others join in as if stimulated by the sexual activity of the initial core group.

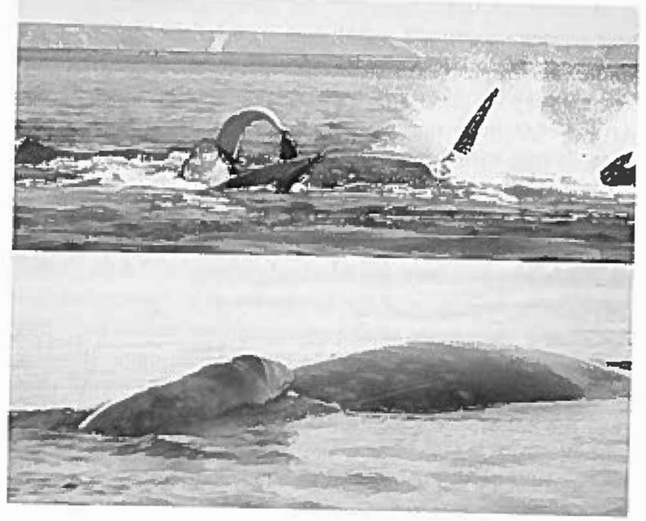

Figure 6 *Gray whales mate with multiple partners, often in large, energetic courting groups (top). Newborn calves have more uniformly dark skin and are supported on their mothers' backs for their first few breaths (bottom).*

Conception occurs primarily in late November and December while the whales are migrating south from the feeding grounds, but some do not conceive until in the winter assembly area, or even on the northward spring migration. Length of gestation is disputed, but is generally thought to last 11 to 13 months, which means that newly pregnant females do not give birth until they have completed the following year's southward fall migration. The birth season lasts from about late December to early March (median birth date: January 27), when most near-term cows are in or near the calving grounds, although some calves are born during the migration from California south. Cows bear a single calf, unattended, and provide sole parental care. Reports of births cite head-first deliveries, with the cow supporting her calf at the surface for the first few breaths of air. Initially, its movements are uncoordinated, but swimming soon steadies (Fig. 6).

A mother's bond with her calf is especially close. She displays an unusual degree of affection, often gently stroking it with her flippers. Mothers are highly protective and will fight fiercely to defend their young from danger. While in the lagoons and on migration, calves stay close to and almost touching their mothers. They drink about 189 liters of rich milk (about 53% fat and 6% protein) each day and grow rapidly, reaching 8.7 m when weaned. The calf remains dependent on its mother until it is weaned in the summer feeding area, at about 7–8 months of age, and perhaps 1 or 2 months longer, when they have solid food in their stomachs but remain with their mother. It is thought that calves begin to forage during the latter stages of nursing and thus may gain some experience while still with the mother. After the calves are weaned, around August, cows are anestrous for 3 to 4 months. Then in November to December a new mating period begins.

D. Sensory Perception

1. Acoustics Once reported to be almost silent, it is now known that gray whales are soniferous both day and night. They create a variety of phonations that sound like rasps, croaks, snorts, moans, groans, grunts, pops, roars, quick series of clicks, belches, and metallic knocks and bongs. These low-frequency broadband signals range from about 100 Hz to 4 kHz, but may go up to 12 kHz. The most prevalent sounds for whales feeding in the Arctic and those in the breeding lagoons are pulsive signals, usually emitted in bursts, that sound like a series of metallic knocks (broadband pulses, from about 100 Hz to 2 kHz). Tonal moans are the most common phonation from migrating whales. Some behaviors may also serve an acoustic function. Grays expel huge bursts of air bubbles underwater (explosive exhalations). These emissions are often released in profusion from the blowholes in social settings. Occasionally, large quantities of air are released from the sides of the mouth as the whale swims by, producing a spectacular display of bubbles. The functions are still obscure, but the joint effect of the acoustic and visual components could create a potent short-range communication signal. Other behaviors that may have an acoustic function include percussive jaw claps, head slaps, backslaps, BREACHING, flipper slapping, and LOBTAILING.

Gray whales are not known to echolocate by means of high-frequency click trains as odontocetes do. However, some low-frequency click-like sounds resembling ECHOLOCATION (which enables a whale to detect objects by listening to the reflected echo of its own sound pulses) have been recorded. These sounds are very tentatively proposed as evidence for primitive echolocation aptitudes that may serve a long-distance function limited to large targets (such as whales) or to detecting broad topographical or oceanic features useful for orientation and navigation. The theory of echolocation in gray whales, however, is as yet unsubstantiated.

Whalers have long stood in awe of the gray's sensitivity to sound. Even the water disturbance by an oar may put a whale to flight. The relatively low upper limit of the frequency range of their vocalizations suggests that they may hear well into the low sonic or infrasonic regions (below the range of human hearing, frequencies lower than 18 Hz). The use of mostly low-frequency sounds is thought to be an adaptive strategy whereby gray whales circumvent the high levels of natural background noise prevalent in their coastal environment by producing sounds that are generally at frequencies below it. Unfortunately, much of the man-made noise in the ocean also occurs in the lower frequency range and has a high level of output, which could interfere with or mask the gray whale's sounds or possibly damage their hearing. Gray whales appear to try to get around some man-made noise by increasing their call types, calling rates, and the loudness of calls to enhance signal transmission and reception.

2. Other Sensory Perception Gray whales can see moderately well both in air and water, but color VISION is probably weak. The position of the eyes suggests that they have stereoscopic vision forward and downward permitting efficient estimation of distance. The eyes are adapted for heightened sensitivity to dim light and for improving contrast and resolution underwater. Grays have retained some sense of smell but are micronosmic at best. In water, the nares are almost always closed (but whales may smell the air as they breathe). The sense of touch is well developed. Some taste buds occur at the back of the tongue, and the possibility of chemoreception through taste has been conjectured.

E. Sleep

It is not known if gray whales sleep. Whales on migration have not been observed to stop to rest for long periods of time. One exception is mothers and calves, which stop to nurse and rest during the north migration. In polar regions during summer when daylight is continuous, most gray whales remain active continually, usually foraging or moving between feeding areas, although occasionally a few resting animals are seen. It is speculated that grays, like some delphinids, may rest one hemisphere of the brain at a time (presumably essential to a voluntary breather). In the breeding grounds, there are more obvious indications that grays sleep, particularly near-term pregnant females and those with neonates. They rest, barely awash, floating at or just beneath the surface, with head and flukes hanging down, for up to an hour, and raise the head to breathe periodically in a slow rhythmic pattern.

F. Swimming, Breathing, and Diving

Overall, gray whales are relatively slow but steady swimmers on migration, although speeds vary from the beginning to the end of the route and there are periods of wandering, resting, milling, feeding, and breeding activity in addition to directed travel along the way. They make the southward trip from the feeding to the breeding grounds in an average of 55 days, swimming at about 7–9 km/hr, and cover a distance of about 144–185 km/day. On the north migration, grays move at a slower speed, averaging 4.5 km/hr (88–127 km/day), and may socialize and feed more, which effectively slows their diurnal rate of migration. Mothers and calves travel up to 96 km/day. Speed of directed travel is about the same as that of other whales, but mothers and calves pause to rest and nurse along the migration. When pursued, grays may reach about 13 km/hr but can only maintain this pace for a few hours. Speed under duress can surge to 16 km/hr, at least for short bursts (avoiding predators). Interestingly, gray whales are very efficient swimmers. They travel mostly at speeds that minimize their energy expenditure and maximize their range, and swim at depths that minimize total drag, important factors in successfully covering the long migratory distances they travel.

Gray whales usually are not exceptionally long or deep divers. The pattern of BREATHING between dives can vary greatly for different activities, with grays averaging only 3% of the time at the surface. When migrating, whales typically remain submerged during traveling–dives for 3 to 5 min during which they may travel 300 m. They surface to blow three to five times at intervals of 15 to 30 sec during a series of short, shallow, surface dives showing only a small portion of the back. The bushy spout is 3 to 4 m high (Fig. 2). Following the terminal blow in a series, traveling whales typically lift their flukes into the air (fluke up) to begin the next traveling dive. During prolonged dives, they may remain submerged 7 to 10 min (or longer) and travel 500 m or more before resurfacing to breathe. Usually, the longer the dive, the greater the number of blows, as the need to reoxygenate the system is greater. Their maximum known dive depth is 170 m.

Breathing and DIVING BEHAVIOR on the feeding and breeding grounds is more variable than on migration. When foraging on summer feeding grounds in shallow coastal waters of 50–60 m, grays dive to the bottom by submerging almost vertically and lifting their flukes above water, and stay under for 5 to 8 min while swimming very slowly. In the breeding lagoons, about 50% of the dives are less than 1 min and 99% are less than 6 min, whereas dives longer than 12 min are associated with resting animals. Mothers, for example, typically float at or slightly below the surface for periods of up to an hour and then submerge for 5 to 10 min, or up to 26 min. When evading detection, grays often surface cautiously, exposing only the blowholes, exhale quietly without a visible blow, and sink silently beneath the surface (called snorkeling).

The species is active at the surface; spyhopping (raising the head vertically out of the water), breaching (leaping vigorously into the air), and other aerial behaviors (head stands with tails in the air, flipper slaps on the surface, etc.) are commonly performed by adults and older calves, especially on the breeding grounds (Fig. 7, also Fig. 4). Throughout their range, grays often appear to "play" and surf in or near the breakers and shallow water along shore. Some grays regularly rub themselves on beaches and sandbars on the breeding grounds and on the rubbing beaches off Vancouver Island. They also rub on pebble beaches and rocks in the Arctic, leaving behind shed barnacles. Some enter brackish water in fjords, coastal lagoons, and the mouths of rivers and emerge cleaned of barnacles and lice. Gray whales are noted to frequent places so shallow that they appear to be lying on the bottom. Occasionally during the ebb tide, some are stranded (apparently unharmed) until the incoming tide refloats them.

G. Friendly Whale Behavior

Gray whales exhibit a sense of curiosity that appears early in life as calves investigate and "play" with floating objects such as balls of kelp and small logs. The whales, including mothers and calves, frequently approach whale-watching skiffs, particularly on the breeding grounds. Behaviors include stationing alongside the skiffs, rubbing against them, bumping, lifting, and blowing bubbles beneath the boats, and allowing the passengers to pet and stroke them (Fig. 8). This activity is popularly termed "friendly" behavior. In the lagoons, these curious grays seem to be initially attracted to the sounds made by the motors of the skiffs, which fall within the same frequency range as gray whale vocalizations. Since the first encounter with a friendly whale at the calving lagoons in the 1970s, friendly whales have become commonplace there and are also encountered to a lesser degree along the migratory route and even in the Bering Sea.

H. Predators and Mortality

Killer whales are the only predator of gray whales (besides humans), although several species of sharks, including the great white shark (*Carcharodon carcharias*) and tiger shark (*Galacocerdo cuvier*), scavenge on carcasses and might kill a small number of calves. Pods of killer whales cooperatively pursue grays, especially calves and juveniles, and seem to attack by repeatedly ramming along their sides, grasping the flukes and flippers to immobilize and drown them, and trying to open their mouths to bite into the tongue. Killer whales have frequently been reported feeding on the tongues of gray whales and then leaving the carcasses as carrion. Sometimes grays turn on their back and slash out with a powerful tail to ward off the swift wolf-like packs of killer whales. Oddly, if cornered, they may go into "shock," floating motionless at the surface, stomach up, while killer whales bite at the tongue and flippers. Rake-mark scars from teeth are often seen on living whales, indicating that many successfully ward off an attack. Some attacks may also represent practice or play by killer whales. A reduced risk of PREDATION from killer whales (more abundant at high latitudes in colder coastal seas) might be a primary benefit to females leaving polar waters to give birth in the subtropics. However, predation pressure does not appear to be a significant determinant in the gray whale's social organization.

Figure 7 *Gray whales breach frequently while migrating and on their winter breeding grounds. One animal was observed to breach 40 consecutive times.*

Figure 8 *A "friendly" gray whale cow and calf allow whale watchers to pet them (note the tip of the mother's lower jaw in the foreground).*

Other known causes of gray whale mortality include ship collisions, ENTANGLEMENT in fishing gear (particularly gill nets) and man-made debris, and whaling (legal aboriginal takes and poaching). Also, calves are sometimes severely struck by whales involved in courting/mating groups, which could result in accidental fatalities. No infectious diseases have been reported. Internal parasites occur but are not known to cause death. In 1999, 2000, and 2001 an unexplained, severe deterioration was seen in the physical condition and health status of some individuals in both eastern and western populations (gray whales were unusually thin, or emaciated). In the eastern population, mortality was unusually high, and some whales appeared to have died from starvation.

IV. Distribution, Migration, and Status

A. North Atlantic Population(s) (Extinct)

The gray whale once existed on both sides of the North Atlantic. Complete and partial skeletons of grays that are subfossils (not yet mineralized) have been found on the east coast of the United States (from New Jersey to Florida) and in the eastern Atlantic from the Baltic coast of Sweden, the Netherlands, Belgium, and the Channel coast of England, the most recent dated from about 1650 A.D. (see Fig. 1). In the western Atlantic, the gray whale is thought to have migrated all along the Atlantic seaboard from Florida to Canada. The youngest North American specimen is from colonial times about 1675 A.D., whereas the oldest are around 10,000 years old. The European gray whale may have disappeared around 500 A.D., but there is a credible record for Iceland in the early 17th century. Evidently, based on written accounts, the last few gray whales in the Atlantic were exterminated by the late 17th or early 18th century, apparently by early Basque, Icelandic, and Yankee whalers. The disappearance of grays from both sides of the Atlantic coincides with the development of WHALING, supporting the idea that overhunting in Europe, Iceland, and North America was responsible for, or at least contributed to, its demise.

B. Western North Pacific Population
(or Korean-Okhotsk)

1. Distribution and Migration Historic records suggest that the western North Pacific population of gray whales formerly occupied summer feeding grounds in the Okhotsk Sea as far north as Penzhinskaya Bay and south to Akademii and Sakhalinskiy Gulfs on the west and the Kikhchik River on the east (see Fig. 1). In autumn, the whales migrated south along the coast of eastern Asia from the Tatarskiy Strait to South Korea (passing Ulsan from late November to late January) to winter breeding grounds suspected to be along the coast of Guangdong Province and around nearby Hainan Island in southern China. The southern-most record was from the east coast of Hainan Island. The long-held belief that the western grays spent the winter on the south coast of Korea was unfounded. It was proposed that an additional migration corridor led down the east coast of Japan to winter breeding grounds in the Seto Inland Sea (where calving occurred) in southern Japan, but this is largely unsubstantiated. In spring, it is assumed that the whales undertook a reverse migration, passing back through the Sea of Japan to reach their summer feeding habitat in the Okhotsk Sea.

Today, the number of gray whales inhabiting the above region is severely reduced. Currently their only known summer–fall feeding ground is off the northeastern coast of Sakhalin Island, Russia. The winter calving and mating grounds are unknown, but may be in coastal waters of the South China Sea.

2. Exploitation and Population Status The western North Pacific gray whale was considered to be extirpated, or nearly so, during the 20th century but is known to survive today as a tiny remnant population. It is one of the most endangered and little-known whale populations in the world. This group was hunted intensely during the past three centuries, but its decline can be largely attributed to modern commercial whaling off Russia, Korea, and Japan between 1890 and 1960. Preexploitation abundance is unknown. Whaling pressure from the Japanese hand-harpoon fishery was underway by the 16th century. Japanese whalers continued to take grays in the 17th, 18th, and 19th centuries. A branch of the population speculated to have bred in the Seto Inland Sea of Japan was gone by 1900. Beginning in the 1840s, American and European whalers took grays in the Okhotsk Sea and western North Pacific until the early 20th century. The last major whaling period occurred between 1910 and 1933, when about 1400 whales were harvested by Japanese and Korean whalers. The fishery dwindled as the whales ran out, and many authorities thought the population was exterminated. However, catch records for 67 whales taken from the Korean coast from 1948 to 1966 indicated that some western grays remained. From 1967 to 1975, a few were continuously caught. Sightings along the coast of Korea, Japan, China, and Russia after that were rare.

During the 1990s, a small number of gray whales were found feeding during summer and fall in the Okhotsk Sea, mostly along northeastern Sakhalin Island (in Russian waters north of Japan), emphasizing its importance as a feeding ground. The population size of western gray whales was estimated to be about 100 individuals in 1999 and less than 100 in 2001. The World Conservation Union listed this population as critically endangered in 2000. Some believe it is likely that the population is below a critical size sufficient for recovery and may soon become extinct; others suggest that it may be increasing slowly. There are no data from the population's southern range off China, North Korea, South Korea, or Japan, and research is needed. It is generally agreed that the western and eastern gray whales are discrete geographical populations. Recent genetic work has documented pronounced differences between them (implying negligible levels of gene flow) and indicates that the eastern and western gray whales can be genetically differentiated at the population level.

C. Eastern North Pacific Population
(or California-Chukchi)

1. Distribution and Migration From the end of May through September, most of the eastern North Pacific population is on its summer feeding grounds in the shallow, continental shelf waters of the Bering Sea and Chukchi Sea (between Alaska and Siberia), the Beaufort Sea (east to 130°W), and the east Siberian Sea (west to 178°30′E) (Fig. 1). The range reaches its northern limit at 69°N at the edge of the zone of close pack ice (to Wrangel Island in some years). Access to the vast feeding ground is controlled by the seasonal formation, disintegration, and drift of ice (for 5–6 months it is ice covered). Gray whales are widely dispersed throughout much of the region, but the major feeding areas where they occur in greatest ABUNDANCE are the northcentral and northwestern Bering Sea, as well as the western and southwestern Chukchi Sea. Although many of the feeding areas have not been studied, those that have are underlain by dense, infaunal amphipod communities. A highly preferred habitat is the Chirikov Basin (between St. Lawrence Island and Bering Strait). It contains one of the largest and most productive amphipod beds in the world and extends over 40,000 km^2. Apparently, whales do not forage in the coastal waters on the eastern side of the Bering and Chukchi Seas, which is consistent with the lack of benthic amphipod infauna in that portion of the continental shelf. As a rule, grays are distributed in shallow waters near shore and rarely go beyond 50 km offshore, although they also aggregate on shallow flats a great distance from shore (up to 180 km). The habitat utilized averages 38 to 40 m in depth, and from 1% to 7% ice cover, but can be as great as 30%. The grays are constantly moving; their DISTRIBUTION varies yearly, and even monthly, as a result of constant ranging between feeding areas. Their foraging areas also support the largest number of bottom-feeding marine mammals in the world, including walruses (*Odobenus rosmarus*), bearded seals (*Erignathus barbatus*), and sea otters (*Enhydra lutris*).

The departure of grays from the northern feeding grounds in late summer and fall is cued primarily by shortening photoperiods and ultimately necessitated by advancing ice formation over feeding areas as the Arctic summer draws to a close. Some turn southward as early as mid-August and begin the long migration extending 7500–10,000 km to the breeding grounds, depending on where they are on the feeding range. Starting in September, grays leave the Beaufort and east Siberian Seas and converge into the Chukchi Sea. In October and November, whales move south out of the Chukchi Sea into the Bering Sea. Then, whales travel southeast and exit the Bering Sea via Unimak Pass, Alaska (in the Aleutian Islands), the easternmost prominent corridor between the Bering Sea and the North Pacific Ocean. Some pass through as early as October, others as late as January, but 90% leave from mid-November to late December. Females in late pregnancy go first, followed by other adults and immature females, and then immature males.

Once through Unimak Pass, the whales travel along the coast of North America down to central California. The migration is spread out all along the coast of Canada and the United States. The main body of the population arrives in central California by mid-January and takes about 6 weeks to pass. Beyond Point Conception, California, the majority take a more offshore route across the southern California Bight, through the Channel Islands, and reencounter the coast in northern Baja California. When the last of the southward migrants reach central California in February, they begin to overlap with the first of the northward migrants returning to the feeding grounds.

From January to early March (through May for some cows and calves), most of the population is in the winter assembly area, which extends from about central California (Point Conception) southward along the west coast of the Baja California Peninsula and continues around Cape San Lucas to the southeastern shore of the Gulf of California off Sonora and Sinaloa, Mexico. Historically, a few continued on to Guadalupe Island, whereas others reached the Revillagigedo Islands. Although a few calves are born off California, most are born along the open coast and in the calving lagoons and bays of Baja California and mainland Mexico. The principal calving areas (with 85% of the calves) are Scammon's Lagoon (Laguna Ojo de Liebre), Black Warrior Lagoon (Laguna Guerrero Negro), San Ignacio Lagoon (Laguna San Ignacio), and the Magdalena Bay complex (from Boca de las Animas to Bahía Almejas), all on the outer coast of the Baja California Peninsula. A few calves are also born on the mainland coast of Mexico at Yavaros in Sonora, and Bahía Reforma in Sinaloa.

The breeding lagoons penetrate far into desert regions through narrow entrances marked by lines of whitewater over barrier sand bars. Except for mothers and calves, however, the vast majority of gray whales in Baja California are outside the lagoons and estuaries in Bahía Sebastián Vizcaíno and Bahía de Ballenas and along the coastline, milling, courting, and wandering along the coast. Courting whales in general do not remain in the lagoons for extended periods. Rather, they are constantly passing and repassing into and out of them, and roving to other areas of the winter assembly grounds, leading to a high turnover of courting whales and subadults in the lagoons. The activity of the grays continues unabated day and night. Cows with newborns seek the quiet, inner reaches of the lagoons early in the season, away from harassment by courting whales concentrated in the areas around the lagoon entrances and outside along the outer coast, where much rolling, splashing, and sexual play can be seen. However, cows with calves also move into the ocean (often at night) and then return during darkness in morning hours, and some visit other lagoons within a season. As the consorting adults start their north migration, the mothers and calves essentially abandon the inner lagoon nurseries and occupy the area near the lagoon entrances. Some cows return to the same lagoon in successive years to hear their young, whereas others rear calves in various lagoons in different years.

The spring migration north to the Arctic feeding grounds begins in mid-February. It retraces the route of the fall migration, but is not as concentrated or as fast. Newly pregnant females migrate first, returning soonest to the Arctic to feed in preparation for the high energetic cost of gestation and lactation. They are followed by anestrous females, adult males, and then immatures. Last to migrate are the mothers and calves; they remain in the breeding area 1–1.5 months longer than most grays while the calves strengthen and grow. The first journey to the Arctic is a time of particular danger for the calves, which are occasional targets of killer whales. Cows and calves tend to travel extremely close to shore (90% are within 200 m) and are mostly alone or in pairs. Northbound whales funnel into the Bering Sea through Unimak Pass from March through June.

The north migration culminates in the dispersal of gray whales throughout their Arctic feeding grounds, which is extended in time and closely related to the ice condition (spring melt). The earliest arrivals generally reach St. Lawrence Island by May as ice recedes north or when leads or polynyas (a large area of water in pack ice that remains open throughout the year) are extensive. The main core of the population usually arrives in the Bering Strait by the end of May, where they are distributed along the cracks of ice throughout areas free of pack ice. One part of the population moves southward along the Asiatic coast and another passes through the Bering Strait into the Chukchi Sea where the whales split off in two directions: east toward the Alaska Peninsula and west toward the Chukotka Peninsula. Another smaller route possibly runs toward the Asian coast, along the Aleutian and Commander Islands. By June, grays are common in the northern Bering Sea in ice-free years, and through the Bering Strait into the southern Chukchi Sea during summer and autumn, as well as into the northeastern Chukchi and Beaufort Seas. By August and September, the ice has retreated north an average of 480 km into the Chukchi Sea. Their eastern distribution in the Beaufort Sea is limited by pack ice, as is their western distribution in the Chukchi and east Siberian Seas.

The vast majority of gray whales go to the northern feeding grounds; however, a small but perhaps increasing number do not migrate the entire distance and spend the summer feeding along the coast from Baja California to British Columbia. These whales (called seasonal residents) join the southbound migrants again in early winter. Areas where they have been observed out of season in Mexico include Bahía San Quintin and Cabo San Lorenzo, on the Pacific coast of Baja California, and Bahía de Los Angeles in the Gulf of California.

2. Exploitation and Population Status Native peoples of North America and Siberia have taken gray whales from the eastern North Pacific population for thousands of years, and a few groups continue to hunt them today. The impact of aboriginal whaling was relatively slight, however, compared to the wholesale slaughter of this population by the first American and European commercial whalers to hunt them in the Pacific. In 1846, they discovered the winter breeding grounds of the gray whale, and commercial harvests began soon thereafter in the lagoons of Baja California, then along the migration route, and spread to the feeding grounds in the Bering Sea. From 1846 to 1874, it is estimated that a minimum of 11,390 grays (not including calves) were taken. From its inception, the relentless 19th century whaling, mainly by American whalers, devastated the population. The hunt in the breeding range was largely concentrated on the cows and calves that were easily killed in the crowded lagoons and bays. Because most of the cows carried fetuses, or would have been impregnated, or had calves that were killed or died of starvation, the reproductive capacity of the population was reduced greatly. By 1900, the once abundant population was thought to be nearly extinct, and whaling all but stopped due to lack of quarry. The attention of the whalers turned to other species, allowing the gray (perhaps a few thousand remained) a brief respite before the advent of modern whaling.

With the introduction of floating factory ships on the west coast of North America in 1905, the hunting of gray whales resumed. A few were taken off Baja California and California in 1919, but mostly between 1925 and 1929. About 48 were taken annually in the Bering Sea from 1933 to 1946. All together, at least 1153 were taken from the remnant population, mainly by Norwegian, Russian, Japanese, and United States vessels. Only fear of EXTINCTION led to their official protection in 1946, except for an aboriginal harvest of about 160 whales each year that have been taken legally by Siberian Eskimos, and also a few by Alaskan natives. Since receiving protection, and the end of research harvests of about 316 grays in the 1960s, the population has increased steadily (by 2.5% per year). Based on the most recent survey (in 1997–1998), the eastern North Pacific population was estimated to be 26,600, possibly exceeding the 1846 preexploitation abundance, which most experts place at between 15,000 and 24,000. There have been indications, however, that the population is approaching, or possibly exceeding, its carrying capacity and may have become food limited (large decreases in amphipod biomass have been linked to increased predator pressure from gray whales and to detrimental effects of global warming in the Arctic). If this is correct, we can expect the gray whale population to level off or even decline.

V. Conservation and Management

A. Legal Protection

Gray whales received partial protection from commercial whaling in 1931 under the Convention for the Regulation of Whaling (which was largely ineffectual). The major whaling nations, Japan and the former Soviet Union, were not signatories to this agreement. They continued to take grays until 1946, when they joined 15 other countries and ratified the International Convention for the Regulation of Whaling, which established the INTERNATIONAL WHALING COMMISSION (IWC). The IWC was intended to provide for the proper conservation of whale stocks and thus make possible the orderly development of the whaling industry. Although it failed in its primary mission, one of its first actions was to officially halt commercial whaling for gray whales in 1946, while allowing native subsistence harvests and scientific collections. Nevertheless, there were violations of the agreement by member nations of IWC, as well as pirate whaling (whaling that is practiced by fleets that acted beyond any national jurisdiction). In 2000, Russian scientists revealed that "literally at every sighting" this prohibited species was illegally killed by the former Soviet Union from 1961 to 1979, and whaling statistics were falsified.

Gray whales were listed as endangered under the U.S. Endangered Species Conservation Act in 1969. Further protection was given by the Marine Mammal Protection Act of 1972 and the U.S. Endangered Species Act of 1973. Under the protection afforded by these and other measures, the eastern population of gray whales recovered. In 1994, it was removed from the List of Endangered and Threatened Wildlife and Plants (under the U.S. Endangered Species Act) when the population numbered 21,000. The population was also downlisted in the World Conservation Union's "1996 IUCN Red List of

Threatened Animals," from "endangered" to "lower risk: conservation dependent." However, changes to the listing of the eastern North Pacific gray whale had no bearing on the status of the western North Pacific gray whale population, which is still critically endangered.

There is no allowable commercial take of any gray whales. The IWC quota for the years 1998–2002 of 140 eastern grays annually (with an overall total of 620 in five seasons) is in response to the catch requested by the Russian Federation for its native people. It also includes an annual quota of five whales requested by the United States to satisfy the Makah Indian tribe's tradition of whaling in Washington state. No grays have been allocated to Alaskan native hunters since 1991. Further protection for eastern gray whales was given by Mexico in 1972 when two of the principal breeding lagoons, Black Warrior Lagoon and Scammon's Lagoon, were declared the world's first whale sanctuaries. The same status was extended to San Ignacio Lagoon in 1979. All lie within the Vizcaíno Desert Biosphere Reserve, Mexico's largest refuge, and entrance into the lagoons is regulated. Currently, not only is it illegal to hunt gray whales, it is also illegal to harm, harass, or even cause behavioral changes without special permits.

B. Concerns

Recently there has been a major shift in the physical environment of the Arctic region with wide-ranging effects on the biota, which may have a deleterious impact on gray whales. Over the past 20 to 30 years, there has been a trend of decreasing sea ice concurrent with increased sea surface temperatures due to global warming. Primary productivity has decreased an estimated 30–40% since 1976. Major declines of marine mammal, fish, and bird populations have occurred in the Arctic's Bering Sea. Although the effects of climate warming on grays are unknown, there are indications that the depression in primary production may lead to reductions in the benthic prey communities on which they feed. Increased predation from the growing population of whales themselves also appears to be stressing the amphipod populations. The eastern North Pacific gray whales may be expanding their summer range in search of additional feeding grounds. Moreover, it is hypothesized that the increase in gray whale mortality in 1999 and 2000 included some whales that were starving. A substantial reduction in food resources, through anthropogenic or natural causes, could have long-term effects on the future health, growth, and stability of the gray whale population.

The region of the Okhotsk Sea around Shakalin Island holds large reserves of oil and gas and is currently being developed jointly by Russian, Japanese, and U.S. companies; oil drilling and production activities plus increased shipping and aircraft traffic may cause physical habitat damage or disturb or displace the highly endangered western Pacific population of gray whales on their only known feeding ground.

Gray whales are intimately related to the coastal habitats in which they have evolved, and it is the dynamic nature of coastal regions that has shaped their unique life history and behavior. It is also precisely their coastal habits that place them in direct conflict with humans. It is not enough to stop overharvesting the whales, we must also protect their critical habitat and allow them living space. They cannot avoid exposure to our intensive coastal development, POLLUTION, vessel traffic, military activities, noise, and industrial activities associated with increased exploration and development of continental shelf, oil, and gas resources over virtually their entire range. Additional concerns include disturbance from ecotourism along migration routes and within the calving grounds, entanglement in fishing gear (particularly gill nets), ship strikes, pollution from salt extraction facilities in Mexico's gray whale refuges, and commercial developments in the breeding area of Magdalena Bay, Mexico. In a world where the human population is expected to double in the next century, the pervasive effects of the population explosion will lead to additional regional and global environmental problems and further approbation of living space and resources that the gray whale requires to sustain itself.

See Also the Following Articles

Diving Physiology ▪ Endangered Species and Populations ▪ Migration and Movement Patterns ▪ Reproductive Behaviors

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Offshore Distances of Gray Whales Migrating Along the Oregon and Washington Coasts, 1990

Abstract

Aerial surveys were conducted during January and March, 1990, to determine the width of the gray whale (*Eschrichtius robustus*) southbound and northbound migration corridors along Oregon and Washington. Migrating gray whales occurred significantly farther offshore during the southbound migration compared to the northbound migration. Also, whales occurred significantly farther offshore Washington than Oregon during both migration periods, which we attribute to a portion the whales following a more direct offshore route between approximately the Columbia River mouth and central Vancouver Island rather than a longer nearshore route past Cape Flattery. When compared with previous studies, the migration corridor along the coasts of Oregon and Washington appears to be both seasonally and annually elastic, and in some locations expanding as far offshore as 43 km. These results question the feasibility of conducting accurate shore-based gray whale censuses along these coasts because of the high proportion of whales traveling beyond a shore-based observer's range of view. These results also suggest that the migration corridor is sufficiently wide, especially during the southbound migration, that it might overlap potential offshore oil development areas on the continental shelf.

Introduction

Nearly the entire population of approximately 21,000 (Breiwick et al. 1988) gray whales (*Eschrichtius robustus*) passes through the waters off Oregon and Washington twice yearly while migrating between winter calving lagoons in Mexico and summer feeding grounds in the Bering and Chukchi seas (Wolman 1985). The southbound migration generally peaks off Oregon and Washington during December and January with approximately 90% passing Yaquina Head, Oregon, between December 19 and January 23 (Herzing and Mate 1984). The first phase of the northbound migration peaks in mid-March, typically followed 7 to 9 weeks later by a second (cow/calf) phase (Herzing and Mate 1984).

Migrating gray whales generally travel close to shore, remaining within 3 km throughout most of the route (Hessing 1981, Braham 1984, Rugh 1984, Herzing and Mate 1984, Brueggeman et al. 1987, Breiwick et al. 1988). For instance, land-based observations by Herzing and Mate (1984) indicated that nearly all southbound and northbound (first phase) migrants passed within 5 km of Yaquina Head, Oregon, from 1978-1981. However, gray whales have been observed traveling through the Channel Islands 80-200 km from the southern California mainland (Rice 1965, Rice and Wolman 1971, Leatherwood 1974, Kent et al. 1980, Jones and Swartz 1987) following a more direct route past the California Bight. Also, Poole (1984) observed that the first phase of northbound migrators in California traveled a straight-line route past Estero Bay while the second cow/calf phase followed the longer coastal corridor inside the bay. Furthermore, in the 1960s, Wilke and Fiscus (1961) and Pike (1962) observed numerous gray whales migrating 8 to 28 km offshore of the Columbia River mouth and the Washington outer coast, and Pike (1962) reported a single sighting of 3 whales 37 km west of Cape Flattery.

In 1989-1990, we conducted aerial surveys for marine fauna (marine mammals, seabirds, and sea turtles) occurring within 185 km of the Oregon and Washington coasts as part of an impact assessment of potential offshore oil development. One objective of the study was to determine the breadth of the gray whale migration corridor along Oregon and Washington relative to the 1990 southbound and first wave of the northbound migration periods to identify where the corridor might overlap with potential oil development areas. This paper reports the results of this investigation.

Study Area and Methods

Aerial surveys were conducted during 3-12 January (southbound gray whale migration) and 11-16

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March (first phase northbound), 1990, along 32 east-west oriented transect lines located between Cape Flattery, Washington, and the Oregon/California border. Spacing between transect lines varied to ensure coverage of areas where marine mammals and seabirds are known to concentrate (bays, river mouths, oceanic banks, etc.), but averaged approximately 22 km. Transect line lengths also varied with 75% of them extending from the coast to the 1,000-m isobath (50-75 km offshore) and 25% extending from the coast to 185 km offshore. This variation in line lengths were established to limit survey effort in typically less productive offshore waters.

Surveys were flown in a 300-series DeHavilland Twin Otter aircraft equipped with bubble windows providing forward and downward visibility. The marine mammal survey team consisted of two observers (one located on each side of the aircraft) and a data recorder. Surveys were flown at a 60-m altitude and a 185 km/hr ground speed.

Statistical comparisons between migration periods and between states (Oregon and Washington) were made using Student's t-test (Zar 1974). Centers and directions of migration corridors were approximated using linear regression (Neter and Wasserman 1974). Data were log-normal transformed before analysis.

Results

A total of 44 groups of 85 gray whales were observed during the January 1990 survey of the southbound migration and 68 groups of 124 whales during the March 1990 survey of the first wave of the northbound migration. Nearly 66% of the southbound migrating groups were >10 km from shore compared to 24% of the northbound groups (Figure 1). Gray whales occurred significantly ($t = 4.78$, $p < 0.0001$) farther from shore during the southward migration ($\bar{x} = 14.3$ km ± 8.2 SD) relative to the northward ($\bar{x} = 8.0$ km ± 3.9 SD).

Gray whales occurred significantly ($t = 3.10$, $p < 0.007$) farther offshore Washington ($\bar{x} = 18.5$ km ± 11.9 SD) than Oregon ($\bar{x} = 9.2$ km ± 4.2 SD) when data from both migration periods were combined. This difference was especially apparent during the southbound migration when Washington observations ($\bar{x} = 25.2$ km + 13.2 SD) were on average over 13 km farther offshore than Oregon observations ($\bar{x}$ = 11.9 km + 3.9 SD; $t = 2.81$, $p < 0.025$). Differences during the northbound migration period were less significant ($t = 2.21$, $p < 0.059$) although Washington sightings ($\bar{x} = 11.8$ km + 5.4 SD) still averaged over 4 km farther offshore than Oregon sightings ($\bar{x} = 7.5$ km + 3.4 SD). The farthest offshore distance during the southbound migration off Washington was 43 km (5 groups) and off Oregon 23 km (2 groups). During the northbound migration the farthest offshore sightings were 20 km off Washington (1 group) and 19 km off Oregon (1 group).

The linear regression analysis showed that the center of both the southbound ($r^2 = 0.0003$) and northbound ($r^2 = 0.033$) corridors did not change in respect to latitude off Oregon, while off Washington the distance whales traveled from shore increased dramatically with increasing latitude during both migration periods (southbound, $r^2 = 0.803$; northbound, $r^2 = 0.636$) (Figure 2).

All whales observed on full-effort (2 observers at full attention) transects migrating past Washington were >5 km offshore. Eight whales, however, were incidently observed migrating within 5 km of the Washington coast during transit flights. Although gray whales were generally found closer to shore along the Oregon coast, only 16% of these whales were observed within 5 km.

Discussion

Although gray whale migration patterns are relatively predictable with respect to timing and location, the extent of the migration corridor may change annually. Our observations off Oregon (only 16% of all whales passing within 5 km of shore) are in contrast with Herzing and Mate's (1984) shore-based observations of nearly all southbound and first phase northbound migrants passing within 5 km of Yaquina Head, Oregon, suggesting a change in the offshore distribution has occurred since their study ended in 1981. Past studies have also suggested that the width or location of the migration corridors may fluctuate over time. For instance, Hubbs (1959) and Rice and Wolman (1971) suggested that the few whales observed along traditional migration routes off California in the late 1800s and early 1900s (Townsend 1887, Andrews 1914, Howell and Huey 1930) was due to animals traveling farther offshore to avoid shore-based whaling pressure rather than an overall population decline.

That gray whales migrate within 5 km past Cape Flattery can not be refuted based on

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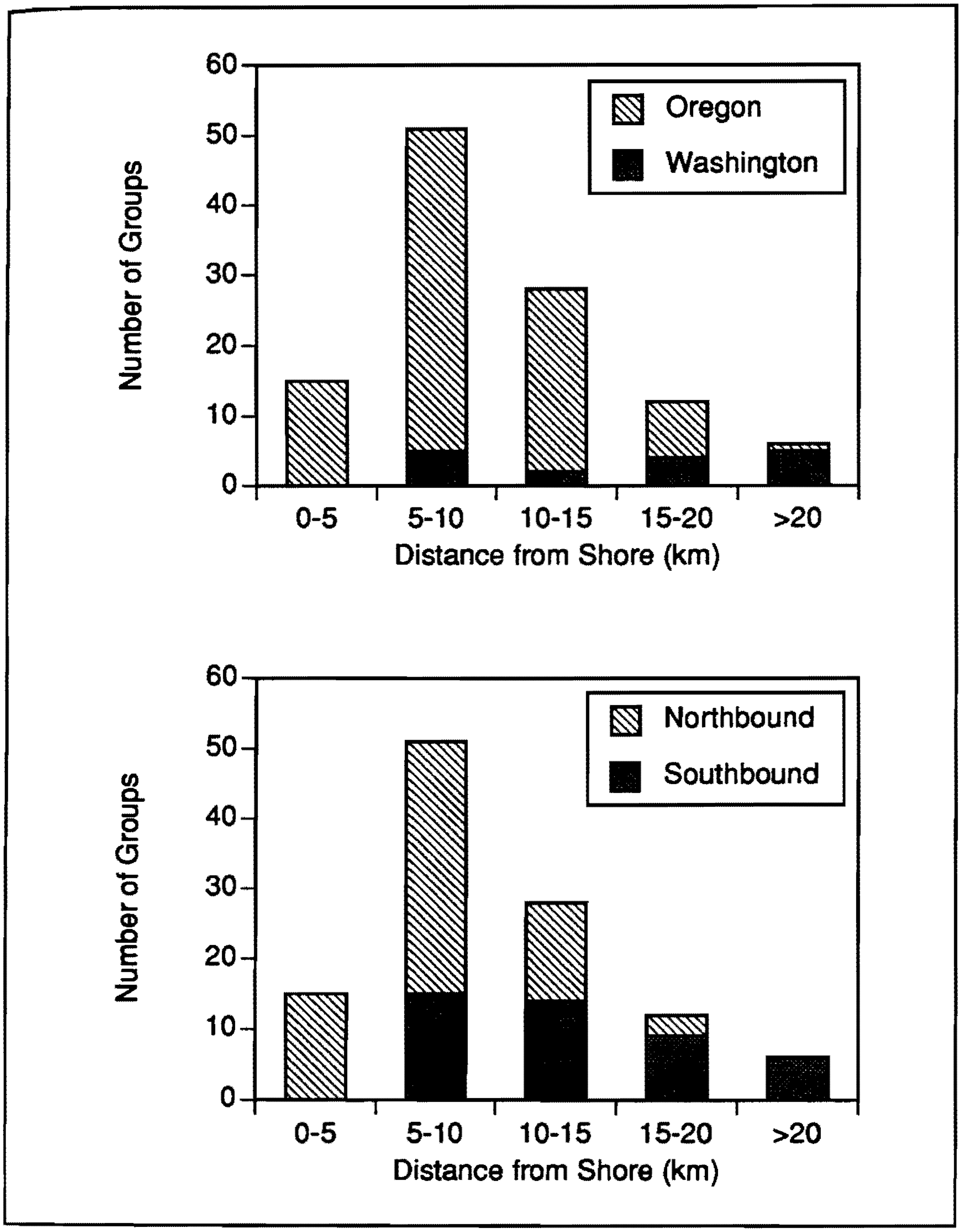

Figure 1. Distances from shore of migrating gray whales comparing between Oregon and Washington, and between the southbound and first phase of the northbound migrations, 1990.

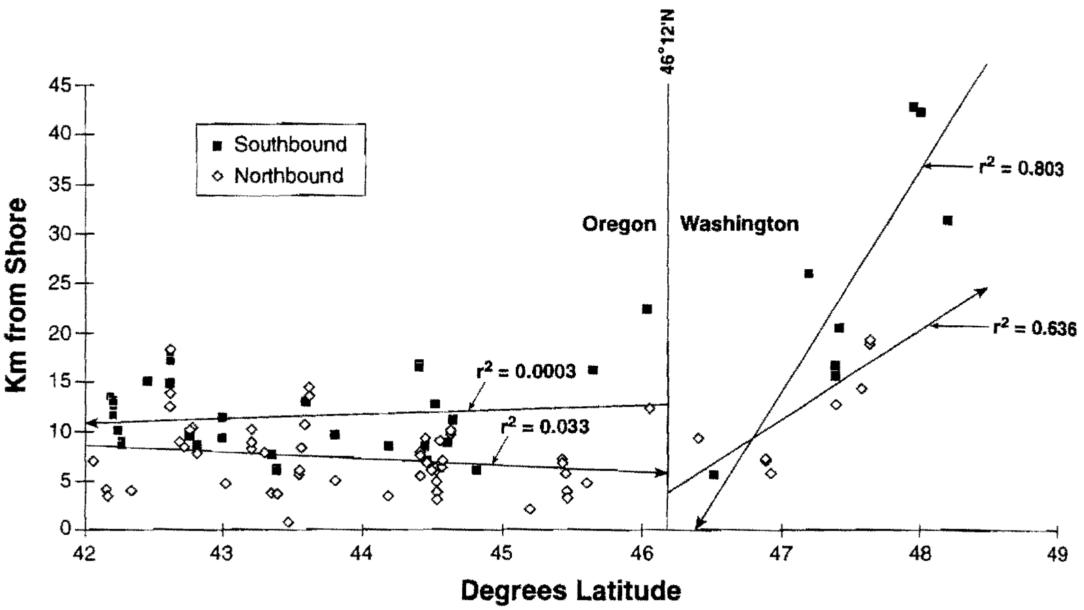

Figure 2. Distribution and mean directions of travel for gray whales migrating along the coasts of Oregon and Washington, 1990.

observations by Pike (1962) and Hatler and Darling (1974). However, our sightings of whales traveling 5-43 km offshore of Washington coupled with observations by Wilke and Fiscus (1961) and Pike (1962) of whales traveling 9-37 km off Washington support the occurrence of either a single, very broad corridor or an alternate offshore route. We suggest that the some portion of the population take a more direct route to and from the central coast of Vancouver Island thereby avoiding the longer coastal route past Cape Flattery. Previous researchers in California have noted migrating whales following more direct routes past coastal indentations such as the California Bight (Rice 1965, Rice and Wolman 1971, Leatherwood 1974, Kent et al. 1980, Jones and Swartz 1987) and Estero Bay (Poole 1984). The Washington offshore route also allows whales to cross the deep (250-650 m) Juan de Fuca submarine canyon at its narrowest point (a pattern reported by Brueggeman et al. [1987] in the southeastern Gulf of Alaska), and the whales are able to travel in relatively shallow (100-150 m) water off the north coast of Washington as the continental shelf (water <200 m deep) here extends nearly 75 km from shore.

Our study also supports previous observations (Pike 1962, Braham 1984, Brueggeman et al. 1987) that the southbound migration in general occurs farther offshore than the northbound, and further suggests that the southbound migration corridor, in particular, could overlap potential offshore oil development areas.

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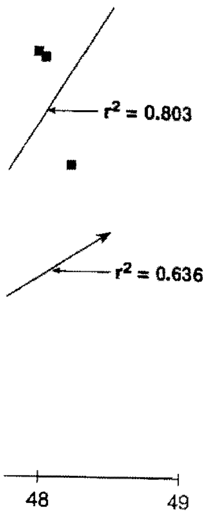

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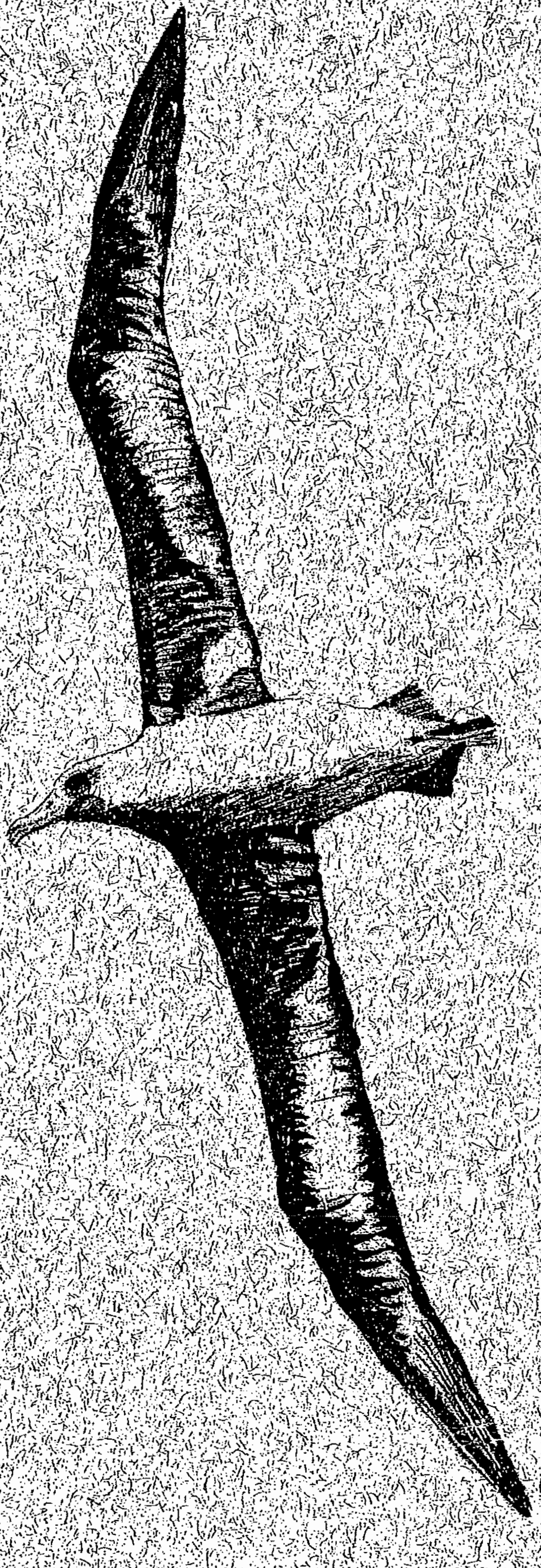
FINAL REPORT

OCS STUDY
MMS 91-0093

OREGON and WASHINGTON Marine Mammal and Seabird Surveys

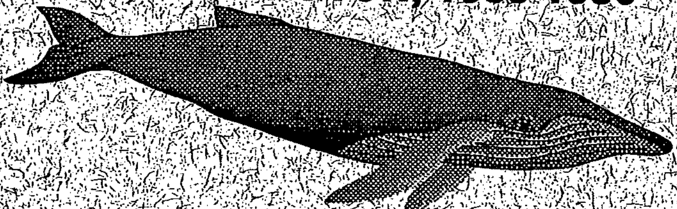


May 1992

Prepared for:
Pacific OCS Region
Minerals Management Service
U.S. Department of the Interior
Los Angeles, California

CHAPTER I

CETACEAN DISTRIBUTION AND ABUNDANCE OFF OREGON AND WASHINGTON, 1989-1990



OCS STUDY
MMS 91-0093

OREGON AND WASHINGTON MARINE MAMMAL AND SEABIRD SURVEYS

FINAL REPORT

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Program Manager and Editor

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and

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Portland, Oregon

Prepared for
Pacific OCS Region
Minerals Management Service
U.S. Department of the Interior
Los Angeles, California
Contract #14-12-0001-30426

May 1992

REPORT ORGANIZATION AND ACKNOWLEDGEMENTS

This draft report, entitled Oregon and Washington Marine Mammal and Seabird Surveys, was prepared for the Minerals Management Service (MMS) under contract No. 14-12-0001-30426 by Ebasco Environmental and Ecological Consulting, Inc. The report is divided into three chapters addressing cetaceans, pinnipeds, and seabirds. Too little information was obtained on sea otters and sea turtles to prepare separate chapters, so information on these species was incorporated into the cetacean chapter. Each chapter is a "stand-alone" document" that includes an Abstract, Introduction, Methods and Materials, Results, Discussion, and Literature Cited section. This format was followed so that the chapters could be more easily modified for publication in the scientific journals. In addition, this format gives MMS the option of distributing the chapters as separate reports rather than one large volume.

We thank D. Lewis, D. Claridge, R. Rowlett, B. Troutman, M. Pierson, and D. Jaques for their assistance in the field. K. Short did a thorough job of compiling and analyzing the oceanographic data presented in this report. We are also grateful for the technical assistance provided by L. Russell, D. Volsen, D. Lehtinen, K. Winnick, C. Johnson-Dean, S. Gooljar, and, most especially, J. Vulk. T. Drummer, D. DeMaster, D. Palka, and A. York provided helpful advice on statistical analyses which was greatly appreciated. R. Lowe, P. Sekora, and U. Wilson of the U.S. Fish and Wildlife Service, and P. Crawford of the National Park Service were helpful in securing permits and coordinating logistics.

Empire Airways supplied the aircrafts for these surveys and their pilots ensured safe and successful flights. We are also grateful to E. Nunnally and W. Karp of the National Marine Fisheries Service for allowing us to piggyback on their Pacific whiting research cruise and to

the Captain and crew of the NOAA-Ship *Miller Freeman* for making our stay aboard a pleasant one.

Our study plan was reviewed by K. Burnham, D. Chapman, D. DeMaster, D. Hood, G. Hunt, L. Jones, P. Sekora, and J. Weins. Finally, we are most grateful for the support provided by the project COTR, G. Reetz, and his staff with the Minerals Management Service, Pacific OCS Region.

CONTENTS

Access Number: 30426

STUDY TITLE: Oregon and Washington Marine Mammal and Seabird Surveys.

REPORT TITLE(S): (1) Information Synthesis and Hypothesis Formulation for Oregon and Washington Marine Mammal and Seabirds Surveys; (2) Cetacean Distribution and Abundance Off Oregon and Washington, 1989-1990; (3) Pinniped Distribution and Abundance Off Oregon and Washington, 1989-1990; (4) Seabirds of the Oregon and Washington OCS, 1989-1990.

CONTRACT NUMBER: 14-12-0001-30426.

SPONSORING OCS REGION: Pacific.

APPLICABLE PLANNING AREA: Oregon-Washington.

FISCAL YEARS OF PROJECT FUNDING: 1989-1992.

COMPLETION DATE OF REPORT: June 1992.

CUMULATIVE PROJECT COST: $1,637,472.

PROJECT MANAGER(S): J. J. Brueggeman.

AFFILIATION: Ebasco Environmental.

ADDRESS: 10900 NE 8th Street, Bellevue, WA 98004-4405.

PRINCIPAL INVESTIGATOR(S)*: G. A. Green, M. L. Bonnell, K. T. Briggs.

KEY WORDS: Oregon, Washington, marine mammals, seabirds, cetaceans, pinnipeds, sea turtles, sea otters, aerial survey, shipboard survey.

BACKGROUND: Information on the distribution, abundance, and habitat use patterns of marine mammals and seabirds off the coasts of Oregon and Washington was lacking. The study was intended to characterize the marine mammal and seabirds fauna of the Oregon and Washington coastal and offshore environments using aerial and shipboard survey techniques.

OBJECTIVES: (1) Review and analyze all available literature and databases to formulate hypotheses concerning marine mammal and seabird diversity, distribution, and abundance in the Oregon-Washington coastal and offshore areas; (2) To conduct field surveys over a 18-month period and test the developed hypotheses; (3) To prepare three reports (each addressing cetaceans, pinnipeds, and seabirds) showing the findings of the surveys and providing recommendations for future surveys.

DESCRIPTION: The information synthesis task was based the reviews of published and unpublished literature and the analysis of available databases from the North Pacific concerning the marine mammals and seabirds which inhabit the marine waters of Oregon and Washington. Hypotheses were developed from the information synthesis and tested by conducting aerial and shipboard surveys in the Oregon-Washington OCS. Field data were analyzed and conclusions drawn on the distribution, abundance, and habitat use patterns of Oregon and Washington marine mammals and seabirds.

SIGNIFICANT CONCLUSIONS: The cetacean faunal component was dominated by delphinids, especially Risso's and Pacific white-sided dolphins, which occurred primarily in slope and offshore waters. The nearshore waters were dominated by harbor porpoise and migrating gray whales, especially in the winter. The gray whale migration corridor and the distribution of harbor porpoises extended farther offshore than previously noted in the literature. Humpback whales use in the Oregon-Washington OCS was low and whales were photographically linked with the California feeding herd. Harbor seal and northern sea lion breeding populations appear stable or increasing and a northern elephant seal breeding haulout may become established in southern Oregon in the near future. The number of northern fur seals inhabiting the study area was estimated at between 1,200 animals in January and 7,000 in April. Seabirds were most densely concentrated in shelf waters and least so in offshore waters. Particularly high seabird use was recorded over the shelf-edge banks off central Oregon and the broad shelf area off northern Washington. Peak populations in Oregon and Washington reached into the millions of birds.

STUDY RESULTS: Aerial and shipboard surveys were conducted off the coasts of Oregon and Washington to determine the distribution, abundance, and habitat use patterns of cetaceans, pinnipeds, seabirds, sea otters, and sea turtles. Twelve surveys were conducted from a DeHavilland Twin Otter aircraft along 40,013 km of systematic trackline between April 1989 and September 1990. An additional aerial survey, targeting migrating gray whales, was conducted in May 1990 from a Cessna 337 aircraft along 2,555 km of systematic trackline. The shipboard survey was conducted from aboard the NOAA-Ship *Miller Freeman* during August 1989 from which 1,677 km of systematic effort was accomplished. Total survey effort accomplished, including systematic, coastal, and deadhead surveys, was 76,050 km. Additionally, over 10,000 aerial photographs were taken of seabird colonies and pinniped rookeries.

Fourteen species of cetaceans were observed during the study which included 381 *mysticetes* (6%) and 5,892 *odontocetes* (94%). Six species contributed 97% of the identified animals. Gray whales were found year-round in the study area, but were most common during the southbound (January) and first wave of the northbound (March) migrations. Eighty-seven percent of the migrants occurred >5 km from shore and 38% were >10 km from shore. Humpbacks first appeared off Oregon in May and Washington during July and were found in all depth zones (shelf, slope, and offshore), but most frequented the slope waters. Concentrations of these whales were found in Oregon along the southern edge of Heceta Bank and in Washington near Grays, Astoria, and Nitinat canyons. Humpbacks observed during June and September 1990 were photographed and matched with whales previously photographed in California and Mexico.

Risso's and Pacific white-sided dolphins, the most commonly observed cetaceans, were found year-round in the study area, but were most common during the spring and summer. Risso's dolphins were found almost exclusively in slope waters and none were observed offshore, while Pacific white-sides dolphins were found offshore in large groups during the spring. Seasonal changes in relative densities for both species indicated north-south movements between

California and the study area. Minimum population estimates (uncorrected for missed or submerged animals) for Risso's dolphins was about 7,700 for both spring and summer combined and for Pacific white-sided dolphins about 38,500 for spring only. Northern right whale dolphins were found in the study area during all seasons except winter. However, highest densities occurred in slope waters during the fall, especially during September 1990 when several large groups were observed off central Washington. Because data were clumped, population estimates were not calculated for northern right whale dolphins.

Harbor porpoise were found year-round in the study area with highest densities in the fall and winter, and lowest during the summer. Ninety-six percent of the harbor porpoise sightings occurred in shelf waters with 5-30% of the seasonal sightings occurring in waters 100-200 m deep. Our results show relatively high densities occurring from Cape Blanco to California and Hoh Head to the Columbia River. Minimum population estimates for the spring, summer, and fall seasons combined ranged between 3,858 animals for waters 0-100 m deep and 941 animals for waters 100-200 m deep. The pooled estimate for both depth classes was approximately 4,800 animals. Densities of Dall's porpoises were relatively consistent throughout the year. Dall's porpoise were also distributed across all three depth zones, although they did not inhabit waters <100 m deep. Distribution shifted seasonally from the outer shelf (100-200 m) in the summer and fall to offshore during the winter and spring. Seasonal densities were not significantly different and were pooled to provide a year-round minimum population estimate of 2,149 animals.

Five species of pinnipeds comprise the marine mammal fauna of Oregon and Washington. Pacific harbor seals used haulout sites clustered at about 50 general locations along the Oregon and Washington coasts. During the pupping season of 1990, 9,700 animals were counted in May and 7,700 animals in June; pups represented 13-19% of total numbers. At sea, 88% of harbor seal sightings were recorded over shelf waters (<200 m depth). Northern (Steller) sea lions have large rookeries off southern Oregon at the Rogue and Orford reefs; a few pups may also be born at Three Arch Rocks. In June 1990, a total of 3,400 animals were counted at the rookeries, including 745 pups. Distribution at sea was distinctly inshore with 89% of the sightings in shelf waters. In the summer, northern sea lions were predominantly in cold, upwelled waters off southern Oregon, over Heceta and Stonewall banks, and near the mouth of the Umpqua River. The greatest numbers of California sea lions occurred in the study area in the fall when migrating animals, mostly adult males, arrived from California. Fall counts ranged from 900 to 1,800 animals, with greatest numbers found at Shell Island off Cape Arago in southern Oregon. Northern elephant seals were seen on land only at Shell Island, which may be an incipient breeding colony; no pups were observed during our study. At sea, northern elephant seals were seen in approximately equal numbers in shelf, slope, and offshore waters. Northern fur seals were present off Oregon and Washington year-round, but found in substantial numbers only in January through May. They were 5-6 times more abundant in offshore waters than over the shelf or slope. Minimum estimates of the pelagic population increased from 1,200 animals in January to 7,000 in April. In January, 77% of the sightings were off the northern Washington coast, while in April, 77% of all sightings were off central and southern Oregon.

Forty-two species of seabirds were recorded in the Oregon-Washington OCS. Seabird populations were found to most densely concentrated over the continental shelf least so in offshore waters. During late spring through late summer, the shearwaters, storm-petrels, gulls, Common murres, and Cassin's Auklets numerically dominated the seabird fauna. All except the shearwaters nest in the study area. With fall migration, the importance of shearwaters and petrels declined, while the numbers of phalaropes, California Gulls, and fulmars increased. The latter, together with gulls, murres, auklets, and kittiwakes, constituted the major elements of the winter fauna. Although total population estimates have not been attempted in this study, there is no doubt that peak populations off Oregon and Washington reach into the millions of birds. Every area over the shelf harbored dense concentrations of birds during the year. However, a few stood out prominently. The major colony complexes were located in southern and northern Oregon and along the Olympic coast of Washington. Offshore of these sights, nesting birds foraged in dense aggregations within a 50-km radius. Petrels, shearwaters, and alcids heavily used the shelf-edge banks off central Oregon and northern Washington. The broad shelf area of northern Washington consistently harbored large populations of shearwaters, gulls, murres, and auklets.

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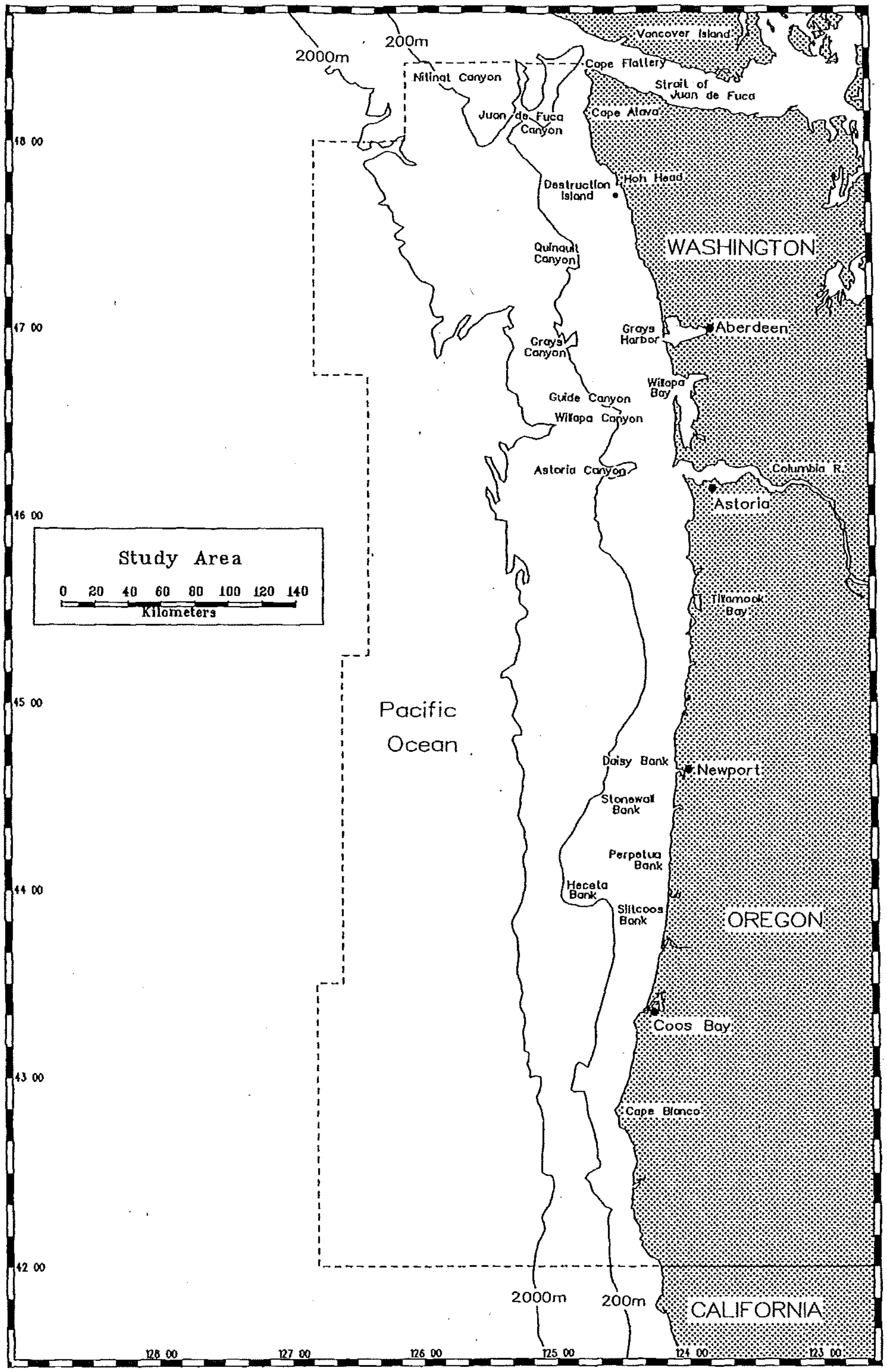
*Principal Investigator's affiliation may be different than Project Manager.



Map of the study area.

CHAPTER I

CETACEAN DISTRIBUTION AND ABUNDANCE OFF OREGON AND WASHINGTON, 1989-1990

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INTRODUCTION

Until recently, few studies have been conducted to characterize cetacean populations off the Oregon and Washington coasts. Prior to 1989, the resource agencies' or scientific community's understanding of cetacean use off Oregon and Washington was based on sightings made during pelagic fur seal investigations (Fiscus and Niggol 1965), data collected ancillary to other activities (Wahl 1977), whaling records (Rice 1978), or collections of stranding data and anecdotal observations (Scheffer and Slipp 1948). Detailed studies have been conducted for only a few nearshore species such as gray whales (*Eschrichtius robustus*) (Sumich 1984, Herzing and Mate 1984) and harbor porpoises (*Phocoena phocoena*) (Barlow 1988, Barlow *et al.* 1988, Kajimura *in press*, Calambokidis *et al. in prep.*). Funding resources, or inducements to provide these resources, have simply not been available to adequately characterize cetacean populations, especially in offshore waters.

In the 1970s, the U.S. Department of the Interior, Minerals Management Service (MMS), supported a series of oceanographic and marine ecology programs in California, including studies of the cetacean populations (Dohl *et al.* 1978, 1983), to gather information for the management of marine fauna and habitat during the exploration and development of potential offshore oil and gas reserves. In the late 1980s, MMS expanded these programs to Oregon and Washington in anticipation of potential offshore development. The study we report here, which began in 1988, was a part of these programs and represents the first comprehensive survey of Oregon/Washington marine fauna using replicate, quantitative sampling. The purpose of this study was to document and describe the cetacean, pinniped, sea otter (*Enhydra lutris*), seabird, and sea turtle use of the study area. This chapter addresses the cetacean studies, which were aimed at characterizing the cetacean population and interpreting its spatial and temporal distribution in relation to the physical environment. The sea otter and sea turtle results are also summarized in this chapter because sightings were too few to warrant preparing separate chapters. Our approach was guided by a series of hypotheses directed toward species-specific distributional questions that were developed from a database synthesis report prepared at the beginning of this study (Brueggeman 1989). Hypotheses were developed only for those species where prior information was available; consequently, data analysis for some species was not hypothesis-directed.

This paper comprises several sections addressing aspects of our results. First, we discuss the numbers, distribution, and habitat relationships in a species accounts format. We also estimate encounter rates and abundance for those species observed frequently enough to produce meaningful results and investigate interspecific relationships of cetaceans. Finally, our results are discussed at a community level by looking at patterns of species diversity and associations, as well as locations of major concentration areas.

STUDY AREA

The study was conducted in the coastal and offshore waters of Oregon and Washington extending to 185 km offshore (Fig. 1). The orientation of the Oregon-

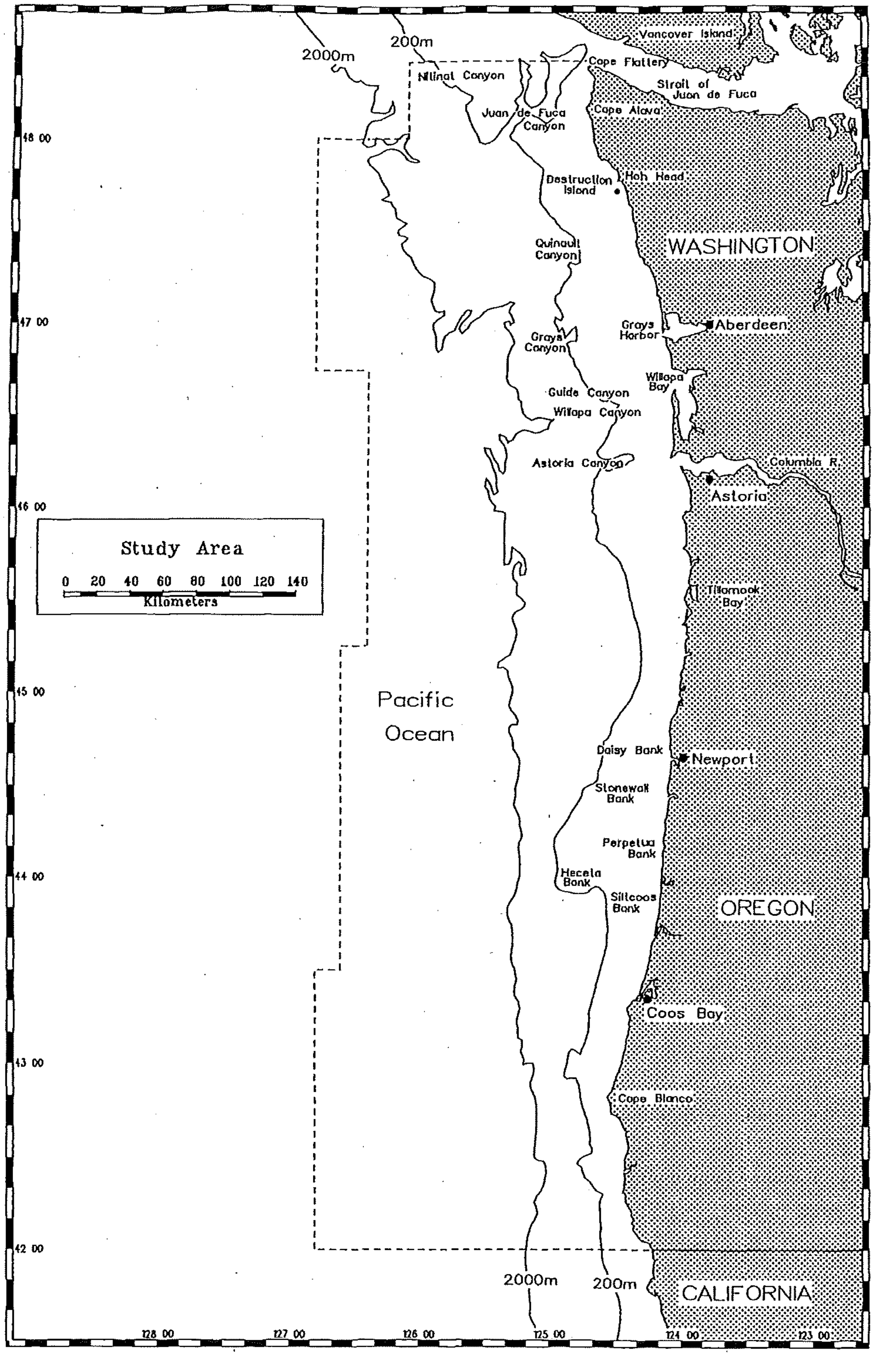

Fig. 1. Map of the study area showing place names and oceanographic features mentioned in the text.

Washington coastline is approximately north-south, unlike much of the California and British Columbia coasts. The continental shelf ranges in width from about 15 to 40 km, and exhibits topography that is relatively uniform compared to other coastal regions of North America. The shelf break occurs at approximately the 200-m isobath.

Although the shelf topography is relatively uniform, there are numerous geomorphologic features that influence the physical and biological processes. The continental shelf along Oregon is characterized by a series of oceanic banks, including Daisy, Stonewall, Perpetua, Heceta, and Siltcoos banks, and a major promontory, Cape Blanco. In contrast, the Washington shelf is furrowed by the Nitinat, Juan de Fuca, Quinault, Grays, Guide, Willapa, and Astoria submarine canyons. The 20- to 25-km-wide Strait of Juan de Fuca, separating Vancouver Island from mainland Washington, is a glacially excavated channel that is the primary avenue for vigorous estuarine exchange between the coastal ocean and the inland marine waters of Washington and British Columbia. The Columbia River discharges through a relatively narrow and deep river mouth that defines the coastal boundary between Washington and Oregon. Numerous small islands dot the coastal area of which Destruction Island off Washington is most prominent. Finally, two very large semi-enclosed bays, Grays Harbor and Willapa Bay, are on the southern Washington coast.

The physical oceanography of this area has been discussed in Landry and Hickey (1989) and shows that, compared to California, the shelf is relatively wide and tends to isolate the large-scale California Current and its infusion of nutrients from nearshore flows. Consequently, the nearshore biological productivity is primarily due to wind-driven coastal upwelling. The oceanography is also heavily influenced by freshwater infusion from the Columbia River, the largest river on the Pacific west coast. The Columbia River effluent amounts to approximately 60% of the freshwater entering the Pacific Ocean between San Francisco and the Strait of Juan de Fuca in winter, and more than 90% in spring, summer, and fall (Barnes *et al.* 1972). Coastal upwelling occurs most frequently in summer and fall, promoted by northerly and northwesterly winds. The upwelling season runs from April to October, with maximum intensity in July and August (Bakun 1973). Upwelling intensity is typically greatest along the southern Oregon coast (the Cape Blanco upwelling zone) and diminishes northward. However, it can occur anywhere along the Oregon-Washington coast under favorable winds.

Seasonal variations in the oceanography of the study area occur in response to solar heating and cooling, wind mixing, freshwater runoff, and coastal upwelling. During the 1989 to 1990 study, sea surface temperature (SST) analyses were conducted to identify pronounced or long-term anomalies in the physical environment that might constitute anomalous conditions for marine mammals. The database consisted of remotely sensed data (from aircraft and satellites) analyzed both by us and government agencies. SST characteristics for each year are summarized in Tables 1 and 2, which present values for waters off Oregon, Washington, and California. The SST data indicated that overall oceanography along the Oregon-Washington coast during 1989 to 1990 was normal. The SST anomaly patterns comprised an assortment of transitory positive and negative departures.

Table 1. West Coast sea surface temperature (SST) (°C) characteristics, 1989.

	OREGON - WASHINGTON		CALIFORNIA	
Month	$\bar{x}$ SSTs	Description	$\bar{x}$ SSTs	Description
1/89	7.5-9.5	near normal	9-11(N)[a]; 11-14(S)	near normal
2/89	7-9	1-2°C neg. anomaly from Grays Harbor to CA border	9-11(N); 12-15(S)	near normal
3/89	8-10	>1°C neg. anomaly 50-100 mi offshore; near normal nearshore	10-12(N); 13-15(S)	>1°C pos. anomaly off central and southern CA
4/89	11-12	1-2°C pos. anomaly	11-13(N); 14-16(S)	1-2°C pos. anomaly
5/89	12-13	1-2.5°C pos. anomaly	11-12(N); 13-17(S)	near normal N of San Francisco; 1-2°C pos. anomaly S of San Francisco
6/89	13-14	near normal off WA; >1°C pos. anomaly off OR	11-13(N); 14-18(S)	1°C neg. anomaly N of San Francisco; near normal S of San Francisco
7/89	14-16	>1°C pos. anomaly off Vancouver Is. and central OR; near normal elsewhere	11-13(N); 15-20(S)	>1°C neg. anomaly N of San Francisco; 1°C pos. anomaly S. CA Bight
8/89	13-16	>1°C neg. anomaly N of Columbia R.; near normal elsewhere	12-14(N); 15-21(S)	1-2.5°C neg. anomaly N of San Francisco; 1°C pos. anomaly S. CA Bight
9/89	12-15	1-3°C neg. anomaly	12-15(N); 15-21(S)	1-2.5°C neg. anomaly N of Pt. Arena; near normal elsewhere
10/89	12-14	>1°C neg. anomaly S of Columbia R.; near normal elsewhere	12-14(N); 15-19(S)	1-2.5°C neg. anomaly N of Pt. Arena; near normal elsewhere
11/89	10-12	near normal	11-14(N); 15-17(S)	>1°C neg. anomaly N of Cape Mendocino; near normal elsewhere
12/89	9-11	near normal	11-14(N); 15-17(S)	>1°C pos. anomaly offshore central CA and S. CA Bight; near normal elsewhere

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[a] N = northern half of California, S = southern half of California.

Table 2. West Coast sea surface temperature (SST) (°C) characteristics, 1990.

	OREGON - WASHINGTON		CALIFORNIA	
Month	$\bar{x}$ SSTs	Description	$\bar{x}$ SSTs	Description
1/90	8.5-10.5	near normal	10.5-13(N)[a]; 14-16(S)	near normal N of San Francisco; 1-2°C pos. anomaly S of San Francisco
2/90	7.5-9.5	near normal	9-11(N); 12-15(S)	near normal
3/90	8-10	near normal	10-11(N); 12-15(S)	near normal
4/90	10-11	>1°C pos. anomaly along WA and 50 mi off OR	11-12(N); 12-16(S)	1°C pos. anomaly 50 mi. off N. CA; >1°C pos. anomaly S of Monterey
5/90	11-12	>1°C pos. anomaly along N. OR; near normal elsewhere	10-12(N); 12-17(S)	1°C neg. anomaly N of San Francisco; near normal central CA; >2°C pos. anomaly S. CA Bight
6/90	13	near normal - WA; 1°C pos. anomaly - OR	12-14(N); 14-19(S)	1°C pos. anomaly 50 mi. offshore N half; near normal central CA; 1-2°C pos. anomaly S. CA Bight; 2-3°C pos. anomaly Baja
7/90	13-15	>1°C pos. anomaly S end Vancouver Is.; near normal elsewhere	12-15(N); 15-21(S)	>1°C neg. anomaly Cape Mendocina; near normal central CA; 1-2°C pos. anomaly S. CA Bight; 2-5°C pos. anomaly Baja
8/90	13-16	>1°C neg. anomaly S end Vancouver Is.; 1-2°C neg. anomaly OR-WA	12-16(N); 16-21(S)	1-2°C neg. anomaly Cape Mendocina; 1°C anomaly S of Monterey; 2-3°C pos. anomaly Baja
9/90	15-17	1-2°C pos. anomaly - WA; near normal - OR	14-17(N); 16-21(S)	1-2°C pos. anomaly; 2-4°C pos. anomaly Baja

[a] N = northern half of California, S = southern half of California.

Although the magnitude of these anomalies occasionally reached ±2-3°C, such fluctuations were not persistent or widespread. During this 2-year period, there were no apparent consistent or recurrent anomalous features.

A more detailed description of the oceanography of the study area, including oceanographic characteristics during each survey period, is provided in Addendum A.

METHODS AND MATERIALS

SURVEY DESIGN AND PROCEDURES

Twelve aerial surveys, one aerial survey targeting gray whales, and one shipboard survey were conducted between April 1989 and September 1990. A photo-identification survey of humpback whales (*Megaptera novaeangliae*) was also conducted in June and September 1990 in conjunction with aerial surveys to study their movement patterns.

Aerial Surveys

Aerial surveys were conducted along 32 east-west oriented transect lines, termed systematic tracklines (Fig. 2). Transects were equally spaced every 22 km from a random starting point, except for a few transects that were placed to intersect submarine canyons, banks, the Columbia River, and bay mouths—areas where we expected that marine fauna might concentrate. The pattern remained fixed over the study period to enable "pairing" of the data when analyzing changes in animal distribution and density (or encounter rate) over time (Burnham *et al.* 1980). Transect line lengths varied with 75% of the transects extending from the coast to the 1,000-m isobath and 25% extending from the coast to 185 km offshore. This stratification allocated 60% of the survey effort to shelf and slope waters where marine mammals are typically most common and the remaining 40% to offshore waters where, presumably, cetacean diversity and/or density is lower. Surveys generally began with the most northern transect lines and finished with the most southern ones.

Upon completion of the east-west transects, the entire length of the study area was surveyed from south to north in one of three ways: coastal surveys flown 0.5 km off the coast (targeting summering gray whales, pinnipeds, and seabirds); sawtooth surveys conducted over the outer continental shelf (targeting harbor porpoises and migrating gray whales); and sawtooth surveys over the continental slope (targeting schooling delphinids) (Fig. 2).

Surveys were flown in a 300-series DeHavilland Twin Otter aircraft modified for viewing marine mammals. The survey team consisted of two observers and a recorder. One observer was located on each side of the forward part of the fuselage where each viewed through bubble windows. One observer rotated with the recorder every 1.5 hr to reduce visual fatigue. Marine mammal observers were occasionally backed-up by a seabird observer

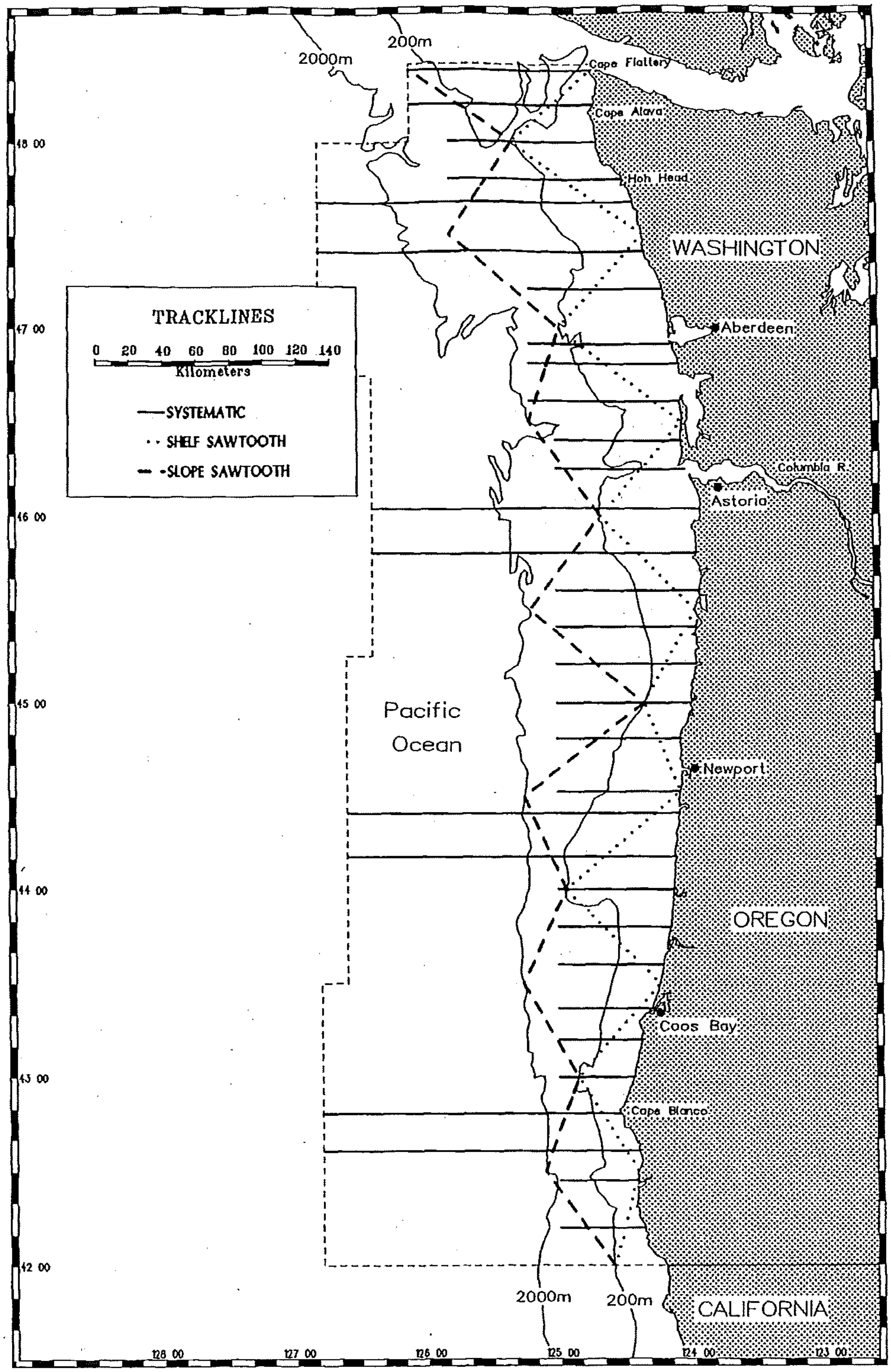

Fig. 2. Distribution pattern of systematic tracklines flown during aerial surveys.

seated in the rear of the aircraft. Seabird and marine mammals were concurrently surveyed from the aircraft. All marine mammal observers were experienced and had previously logged at least 800 hr of aerial survey effort. Surveys were flown at a 60-m altitude and a 185 km/hr ground speed. The low altitude permitted the simultaneous survey of seabirds and marine mammals. Surveys were terminated when sea states exceeded a Beaufort 4 (>30 km/hr wind speed) or visibility was below safe flying conditions. Previous research (Brueggeman *et al.* 1984, 1987; Au and Perryman 1985; Payne *et al.* 1986) has shown that cetacean detectibility from an aircraft is greatly reduced when sea states exceed a Beaufort 4.

An on-board Compaq Portable II computer was linked to the aircraft's Loran-C navigation system and radar altimeter, and to a Pyrometer PRT-5 radiation thermometer. The computer provided, both on-demand and at set intervals, a record of time, latitude, longitude, altitude, speed, bearing, and sea surface temperature. This information was automatically written at each entry to a hard drive, a floppy disk, and as a hard-copy printout. Using a data form, the recorder linked the computer records with sighting and weather information provided by the observers via an intercom system. For each marine mammal sighting, the observer related to the recorder the number of individuals, species, vertical angle (measured to the individual or center of group using a clinometer, and later used to calculate the perpendicular distance from the transect line), behavior, direction of travel, reaction to aircraft, and observer name and position. Weather information included Beaufort sea state, visibility, (Brueggeman *et al.* 1988) and glare, which was recorded at the beginning of each transect line and whenever conditions changed.

Gray Whale Aerial Survey

An additional aerial survey was conducted specifically for gray whales in May 1990 to better define the timing and distribution pattern of the cow/calf phase (Herzing and Mate 1984) of the spring migration. Two complete sawtooth surveys were conducted off the shelf and a single sawtooth survey within 9 km of shore. Observations were conducted from a Cessna 337 equipped with Loran-C navigation and flown at a 230-m altitude at 185 km/hr. Data collection procedures were identical to the other aerial surveys, except the data recorder, seated in the copilot seat, manually recorded all data onto a field form. Also, observations were made through large flat windows rather than bubble windows.

Vessel Survey

A vessel-based survey was conducted from the NOAA-Ship *Miller Freeman* in August 1989 to compare assessments of marine fauna distribution and abundance in shelf waters with the aerial platform. These surveys were conducted ancillary to a fishery study (NMFS, MF89-5).

Thirty-nine east-west transect lines, spaced 18.5 km apart and extending from the nearshore zone (55-m isobath) to just beyond the continental shelf edge (200-m isobath), were surveyed (Fig. 3). Observations were made from the flying bridge, 12 m above the

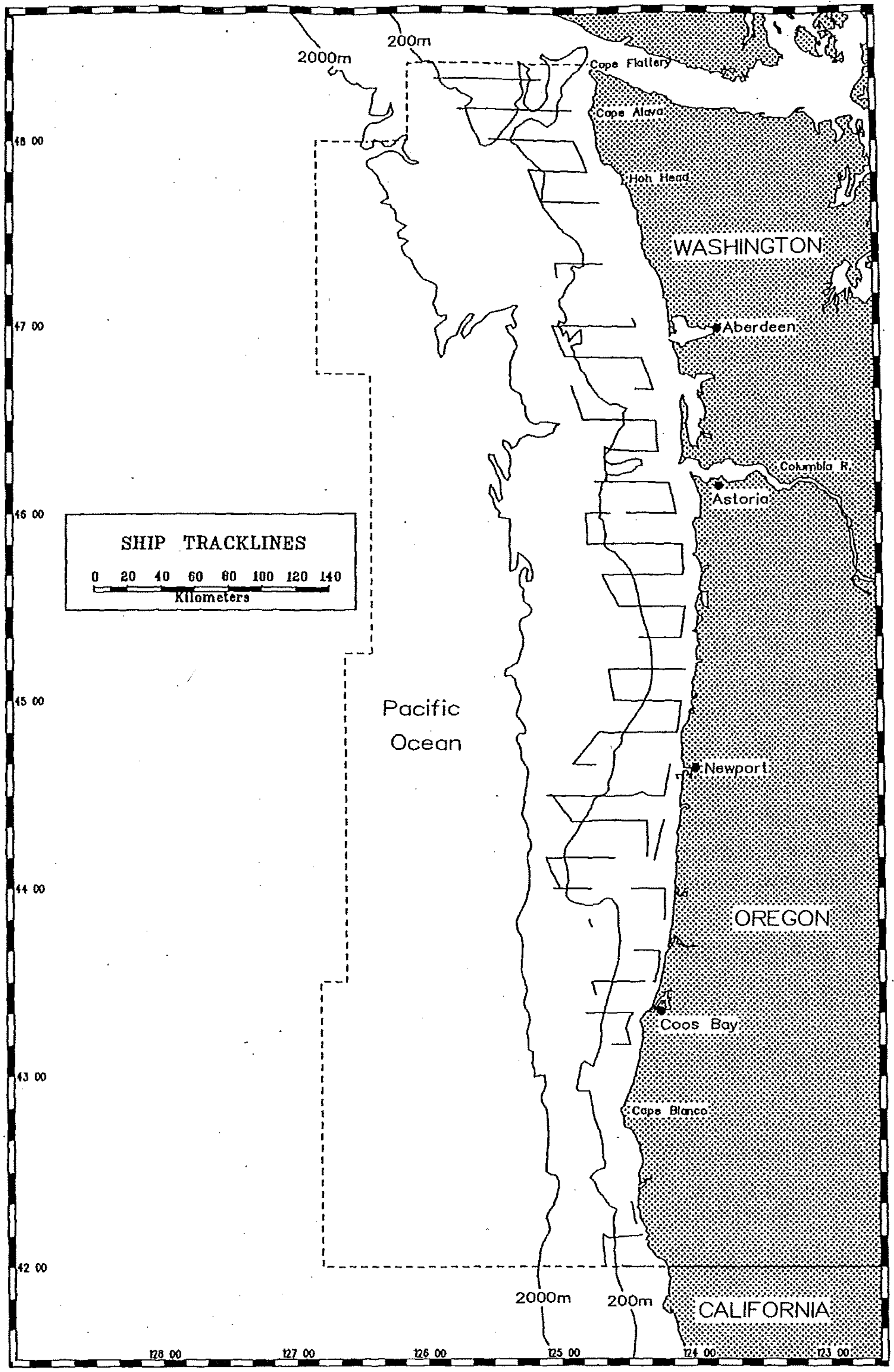

Fig. 3. Distribution pattern of systematic tracklines cruised during the shipboard surveys.

waterline. Surveys began off central California and ended off Vancouver Island, British Columbia; however, only data collected off Oregon and Washington are reported here. Data were recorded by the observer onto a field form, and position information was obtained from a Loran-C unit mounted on the flying bridge. One observer viewed an approximately 120° area centered at the ship's bow as the ship traveled along pre-established tracklines at 18 to 22 km/hr. The radial angle from the ship's bow (using a map compass) and the distance to an animal (using a horizon distance gauge with 230-m reticles) were measured for each sighting. The same sighting and environmental data recorded during the aerial surveys were recorded for the vessel survey, except where they were not relevant.

Photo-identification of Humpback Whales

During June and September 1990, a photo-identification survey was conducted to determine humpback whale movement patterns in the study area (and beyond) based on matching fluke photographs available from elsewhere in their range. Extensive catalogs of photographs have been developed for humpbacks that seasonally occur in the waters off Mexico, California, Hawaii, Alaska, British Columbia, Korea, and Japan. Humpback whale sightings made during June and September 1990 aerial surveys were provided to a vessel-based photographic crew directly by radio from the aircraft or by telephone after returning to an airfield. The vessel was a 6.7-m rigid-hull Novurania inflatable powered by a 200-hp outboard motor and equipped with Loran-C for navigating. Vessel range was limited for safety reasons to coastal waters within 75 km of shore and periods when surface winds were <11 km/hr. The photographic procedure followed the recommendations of Katona and Whitehead (1981), which involved photographing the fluke underside with a 35-mm camera equipped with a telephoto lens. The film was Ilford HP-5 pushed to 1600 ASA (Miles 1990). Film negatives were analyzed with a magnifying lupe, and the best photo of the fluke scars and pigmentation was selected to represent an individual whale. Photographic prints of animals were compared to fluke catalogs available from several sources to identify individual whales. Copies of prints were provided to the National Marine Mammal Laboratory (NMFS, Seattle, WA) for continuing analysis and archiving.

DATA ANALYSIS

The level of data analyses varied according to the survey type. Systematic, random, and sawtooth surveys were used to determine encounter rates, abundance, and habitat use patterns because both marine mammal observers were always on-duty (full-effort). Coastal surveys generally had only one marine mammal observer whose viewing conditions were inconsistent due to constantly changing altitudes and the presence of surf foam and direct sun glare. Marine mammal observers were generally not consistently viewing during deadhead (limited effort) transects but did make incidental sightings. Deadheads included flights flown between tracklines, during high-altitude transits to and from the survey area, during unacceptable survey conditions, and to confirm animal sightings. Because of inconsistency in viewing effort, coastal and deadhead survey observations were only used to describe cetacean distribution.

Encounter rates (number/1,000 km) were calculated for each species and compared by seasons, depth zone, and years to determine spatial and temporal changes in numbers. Encounter rates were calculated from all data collected on full-effort aerial surveys except under poor visibility conditions. The seasons used in the analysis were defined as spring (March to May), summer (June to August), fall (September to November), and winter (December to February). These "solar seasons" were selected to correspond to calendric periods used by Dohl *et al.* (1983) in order that comparisons could be made with their data. The depth zones corresponded to the continental shelf (0- to 200-m isobaths), slope (200- to 2,000-m isobaths) and offshore (>2,000-m isobath) regions. This stratification was used to define water-depth habitat associations by cetaceans.

Density and abundance were estimated for only those species (Risso's dolphin [*Grampus griseus*], Pacific white-sided dolphin [*Lagenorynchus obliquidens*], harbor porpoise, and Dall's porpoise [*Phocoenoides dalli*]) that had sample sizes sufficient to obtain reliable estimates. Density and abundance were estimated according to the line transect procedure (Burnham *et al.* 1980), except for harbor porpoises in which estimates were calculated using strip transect (Eberhardt *et al.* 1979). Line transect estimates were derived from program DISTANCE (Laake *et al.* 1991). The major steps involved in deriving the estimates are summarized below.

Density as derived from the line transect approach was calculated from the following expression:

$$1. \quad \hat{D}=\frac{nf(0)}{2L}$$

where n is the number of groups, L is the number of km of trackline observed under acceptable survey conditions, and $f(0)$ is the probability density function of the perpendicular distances, $f(x)$, evaluated at zero. Because dolphins and porpoises commonly occur in groups, it was more appropriate to treat the group, rather than the individual, as the observation. The $f(0)$ was calculated using the best-fitting estimator available in program DISTANCE (Fourier series, negative exponential, half-normal, Hazard). The tail of the sightability curve was truncated at the farthest perpendicular distances to reduce variability as recommended by Burnham *et al.* (1980). Variance of the density was calculated from the following equation:

$$2. \quad var(\hat{D})=\hat{D}^2[(cv(n))^2+(cv(f(0)))^2]$$

Where cv is the coefficient of variation of a given parameter.

A major assumption of the line transect procedure is that all animals on the trackline center are seen. To minimize violation of this assumption, bubble windows were used that provided downward visibility. However, the distortion in the bottom of the windows, speed and altitude of the aircraft, and physical difficulty in maintaining a downward head position made vigilance in observing the centerline difficult. The closest distance to the trackline that could be consistently covered, based on observer viewing angles, was 25 m. Consequently, the "centerline" was reset for each side of aircraft at 25 m, assuming a 50-m wide strip under the aircraft was not viewable. All perpendicular distance data were adjusted to account for the 25-m blindspot.

Density calculations only included data collected during full-effort surveys, by on-duty marine mammal observers, and in Beaufort sea state and visibility conditions when a given species could be effectively observed. Sighting rates were computed by species for each sea state and visibility condition. Sea state and visibility limitations were selected at the point the sighting rates began to substantially decline.

Abundance was estimated from the following formula:

$$3.\quad \hat{N}=\hat{D}A\bar{G}$$

where $\hat{N}$ is the abundance estimate, $\hat{D}$ the calculated density, A the area under consideration, and $\bar{G}$ the mean group size. The variance of mean group size was calculated using the equation:

$$4.\quad var(\bar{G})=\frac{\sum G_i^2-\frac{(\sum G_i)^2}{n}}{n(n-1)}$$

Finally, the variance of the abundance estimate ($\hat{N}$) was calculated by using:

$$5.\quad var(\hat{N})=A^2[\hat{D}^2 var(\bar{G})+\bar{G}^2 var(\hat{D})-var(\bar{G})var(\hat{D})]$$

with the coefficient of variation (*cv*) for the abundance estimate equalling:

$$6.\quad cv(\hat{N})=\frac{100\sqrt{var(\hat{N})}}{\hat{N}}$$

Abundance was estimated by depth zones where significant differences in animal densities occurred between depth zones, and then pooled into one value for the study area.

The line transect approach was used for estimating abundance of most cetaceans except harbor porpoises. Harbor porpoises at the surface were effectively counted within the 50-m seabird observation strip (combining both seabird observer and marine mammal observer sightings). Harbor porpoise abundance was calculated according to Method I of the strip transect procedure described by Estes and Gilbert (1978), with the variance of the estimated abundance calculated from Equation 5 above. This approach reduced the percentage of animals missed at the surface by the line-transect approach, which occurred because of the low survey altitude coupled with marine mammal observers spending significant time searching beyond the effective viewing distance (approximately 100 m) for harbor porpoise.

RESULTS

SURVEY EFFORT

Fourteen surveys were conducted in the study area between April 1989 and October 1990 (Table 3). Twelve aerial surveys were conducted across the entire study area, which included four surveys during spring, four during summer, three during fall, and one during winter. Replicate surveys were conducted in 1989 and 1990 for the May through September surveys. In addition, two surveys were conducted over the shelf, which included an aerial survey in the spring for gray whales and a vessel survey in summer. All surveys were generally scheduled to coincide with seasonal movement and use patterns of marine mammals and birds.

Survey effort in the study area totaled 76,050 km, which included 44,244 km of systematic, 27,925 km of deadhead, and 3,881 km of coastal survey effort (Table 3). Effort per survey averaged 5,850 km and ranged from 1,750 to 6,976 km. The 12 surveys represented 94% of the total effort compared to 4% for the gray whale survey and 2% for the vessel survey. Because of limited survey effort and coverage associated with the gray whale and vessel surveys, only data collected for the 12 aerial surveys along systematic tracklines was analyzed in detail.

A total of 40,012 km of full-effort survey was accomplished during the 12 aerial surveys with effort highest over the continental shelf (17,418 km), lowest offshore (7,350 km), and intermediate over the slope (15,244 km) (Table 4). Effort was also highest during the spring and summer survey periods (13,383 and 13,152 km, respectively), lowest during the winter (3,971 km), and intermediate during the fall (9,506 km).

SPECIES COMPOSITION AND TOTAL NUMBERS

Scheffer and Slipp (1948) and Mate (1981) listed 24 species of cetaceans off the Oregon and Washington coasts. We observed 14 species (two of which were identified only to genus) of cetaceans, which included 381 *mysticetes* (6%) and 5,892 *odontocetes* (94%) during all types of survey effort (Table 5). All species were observed in both states, except fin (*Balaenoptera physalus*) and Baird's beaked (*Berardius bairdii*) whales were observed only in Oregon, and a single *Kogia* was observed in Washington. Additionally, 208 cetaceans, mostly dolphins, were observed but not identified to the genus level. The most commonly observed species were Risso's dolphins (2,855), Pacific white-sided dolphins (1,377), northern right whale dolphins (*Lissodelphis borealis*) (661), harbor porpoises (559),

Table 3. Effort (km) accomplished during each of the 13 aerial and 1 shipboard survey periods by the various survey types in the Oregon/Washington study area, 1989-1990.

Survey	Date	Season	Survey Type			Total
			Systematic[a]	Coastal	Deadhead	
1	23-27 Apr 89	Spring	3,267	800	1,408	5,475
2	23 May - 1 Jun 89	Spring	2,761	684	3,298	6,743
3	18-28 Jun 89	Summer	3,302	514	2,722	6,538
4	25-29 Jul 89	Summer	4,180	34	1,074	5,288
5	16-20 Sep 89	Fall	2,904	538	2,210	5,652
6	13-18 Nov 89	Fall	3,272	754	1,564	5,590
7	3-12 Jan 90	Winter	3,971	0	1,552	5,523
8	11-16 Mar 90	Spring	4,181	0	1,657	5,838
9[b]	8-12 May 90	Spring	2,555	153	309	3,017
10	23-30 May 90	Spring	3,173	196	3,607	6,976
11	18-24 Jun 90	Summer	3,298	208	3,420	6,926
12	25 Jul - 3 Aug 90	Summer	2,372	0	2,508	4,880
13	26 Sep - 4 Oct 90	Fall	3,331	0	2,523	5,854
Ship	7-21 Aug 89	Summer	1,677	0	73	1,750
Total			44,244	3,881	27,925	76,050

[a] Includes systematic, sawtooth, and random surveys (see page 1-10 for definition of survey types).
[b] Gray whale survey.

Table 4. Kilometers of trackline flown during full-effort aerial surveys (excluding the May 1990 gray whale survey) for each season by the depth zones.

	Season				
Depth Zone	Spring	Summer	Fall	Winter	Total
Inner Shelf (0-100 m)	2,967	2,572	1,989	1,067	8,595
Outer Shelf (100-200 m)	2,956	2,832	1,951	1,084	8,823
Slope (200-2,000 m)	4,757	5,557	3,689	1,241	15,244
Offshore (>2,000 m)	2,703	2,191	1,877	579	7,350
Total	13,383	13,152	9,506	3,971	40,012

Table 5. Species composition and number of cetaceans observed off Oregon and Washington, April 1989 - September 1990.

Species	Oregon (49,035 km)[a] No.	Oregon (49,035 km)[a] Groups	Washington (27,015 km)[a] No.	Washington (27,015 km)[a] Groups	Total (76,050 km)[a] No.	Total (76,050 km)[a] Groups
Mysticetes						
Gray whale	225	150	57	51	282	201
Humpback whale	43	23	25	13	68	36
Fin whale	27	13	0	0	27	13
Minke whale	3	3	1	1	4	4
Subtotal	298	189	83	65	381	254
Odontocetes						
Risso's dolphin	2,233	105	622	57	2,855	162
Pacific white-sided dolphin	917	69	460	58	1,377	127
Northern right whale dolphin	221	18	440	49	661	67
Harbor porpoise	378	214	181	132	559	346
Dall's porpoise	222	92	119	58	341	150
Sperm whale	32	20	4	4	36	24
Killer whale	24	8	9	7	33	15
Baird's beaked whale	21	5	0	0	21	5
Mesoplodon sp.	1	1	7	1	8	2
Kogia sp.	0	0	1	1	1	1
Subtotal	4,049	532	1,843	367	5,892	899
Total	4,347	721	1,926	432	6,273	1,153

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[a] Total survey effort for all survey types.

Dall's porpoises (341), and gray whales (282); these species represented 97% of the identified animals. Fewer than 70 animals were encountered for each of the remaining eight species. Four species that were observed (gray, humpback, fin, and sperm [*Physeter macrocephalus*] whale) are federally listed as endangered.

Twelve species known to occur off Oregon and Washington occasionally or historically were not identified in this study:

Blue whale (*Balaenoptera musculus*)
Sei whale (*Balaenoptera borealis*)
Northern right whale (*Eubalaena glacialis*)
Stejneger's beaked whale (*Mesoplodon stejnegeri*)
Hubb's beaked whale (*Mesoplodon carlhubbsi*)
Cuvier's beaked whale (*Ziphius cavirostris*)
Pygmy sperm whale (*Kogia breviceps*)
Beluhka whale (*Delphinapterus leucas*)
False killer whale (*Pseudorca crassidens*)
Short-finned pilot whale (*Globicephala macrorhynchus*)
Striped dolphin (*Stenella coeruleoalba*)
Common dolphin (*Delphinus delphis*)

Cetaceans of the genus *Mesoplodon* and *Kogia* were sighted during this survey, but were not identified to species, and a single Cuvier's beaked whale was found stranded in southern Oregon.

SPECIES ACCOUNTS

In the following species accounts we provide the numbers, distribution, and, where data are sufficient, encounter rates and abundance estimates of all species observed during this study.

Gray Whale

Nearly the entire population of 21,000 (Breiwick *et al.* 1988) Pacific gray whales passes through the waters off Oregon and Washington twice yearly as it migrates between breeding lagoons in Mexico and summer feeding grounds in the Bering and Chukchi seas (Wolman 1985). The southbound migration generally peaks off Oregon and Washington during late December/early January (B. Mate, Oregon State University, Personal Communication), while the first wave of the northbound migration peaks in mid-March typically followed 7 to 9 weeks later by the second cow/calf wave (Herzing and Mate 1984). An unknown percentage of gray whales (Brueggeman 1989) summer along the Oregon and Washington coasts (Sumich 1984, Calambokidis *et al.* 1987). Aerial survey periods during this study were partly established to coincide with the migration peaks.

There were 201 groups totaling 282 gray whales recorded in the study area (Table 5). Most were observed during the spring (169) and winter (85), with only a few animals sighted during fall (15) and summer (13). Twenty-nine percent of the whales were observed during the January 1990 survey of the southbound migration and 44% during the first wave of the northbound migration (March 1990). Only 5 whales were observed during a special survey of the second northbound wave during early May 1990. The timing of the 1990 cow/calf migration appeared to be atypical throughout the migration route (M. Dahlheim, NOAA, NMML, Seattle, Personal Communication). The remaining whales were observed between April and November. No calves were observed during migration, although a cow/calf pair was observed at the mouth of the Siuslaw River in July 1989. All gray whales were observed on the shelf (Fig. 4).

Point location studies indicate that migrating gray whales generally travel within 3 to 5 km of shore throughout most of their route (Hessing 1981, Braham 1984, Rugh 1984, Herzing and Mate 1984, Brueggeman *et al.* 1987, Breiwick *et al.* 1988). However, information from Rugh (1984) and Brueggeman *et al.* (1987) suggests that the width of the migration corridor may change as the width of the 0 to 40-m depth zone changes. This depth band is relatively narrow off Oregon (4-5 km) and wide off Washington (17-28 km), thus providing the opportunity to test the null hypothesis: *The width of the gray whale migration corridor does not change in concert with varying widths of certain depth zones.* Our results show that only 13% of all whales observed on full-effort transects off Oregon and Washington were found within 5 km of shore (Fig. 5). The migration corridor extended relatively far offshore with 38% of the sightings occurring >10 km from shore. The widest margin of the corridor occurred from approximately the Columbia River through Washington where the shelf (and 40-m isobath) extends farther offshore (Fig. 4). In fact, the mean distance gray whales occurred offshore Washington was 18.5 km (SD = 11.9 km) compared to 9.2 km (SD = 4.2 km) for Oregon. The differences are significant ($t = 3.10$, $p < 0.007$) indicating the migration corridor does change in concert with changes in the width of the shallower isobaths. All of the migrating whales observed on full-effort transects were >5 km offshore of Washington, which is similar to observations by Wilke and Fiscus (1961) and Pike (1962) where numerous gray whales occurred 8 to 28 km offshore of the Columbia River and Washington. Although gray whales were found closer inshore along the Oregon coast, only 16% of these whales were observed within 5 km, which contrasts with Herzing and Mate's (1984) shore-based observations that nearly all of the southbound and first wave of the northbound migrants passed Yaquina Head, Oregon, within 5 km.

Braham (1984) and Brueggeman *et al.* (1987) provided information that the southbound migration, at least in Alaska, occurred farther offshore than the northbound migration. In testing the null hypothesis: *The gray whale migration corridor width is constant relative to migration period*, we found gray whales to migrate farther offshore of Oregon and Washington during the southbound migration than during the first wave of the northbound. Nearly 66% of the southbound migrating groups were >10 km offshore compared to 24% of the northbound groups (Fig. 5). The mean distance offshore that gray whales occurred during the southbound migration was 14.3 km (SD = 8.2 km) compared to

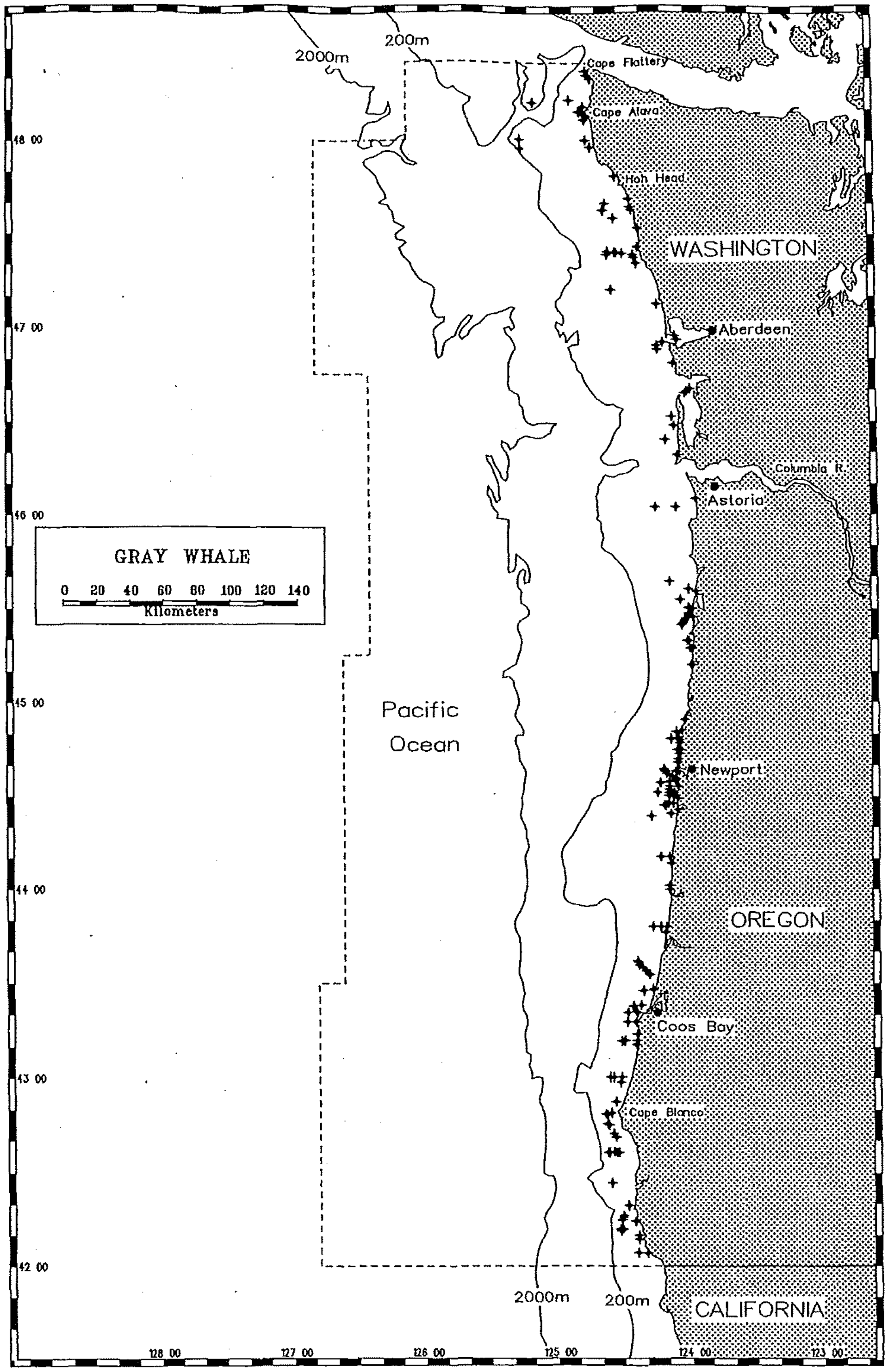

Fig. 4. Distribution plot of all gray whale sightings in the study area.

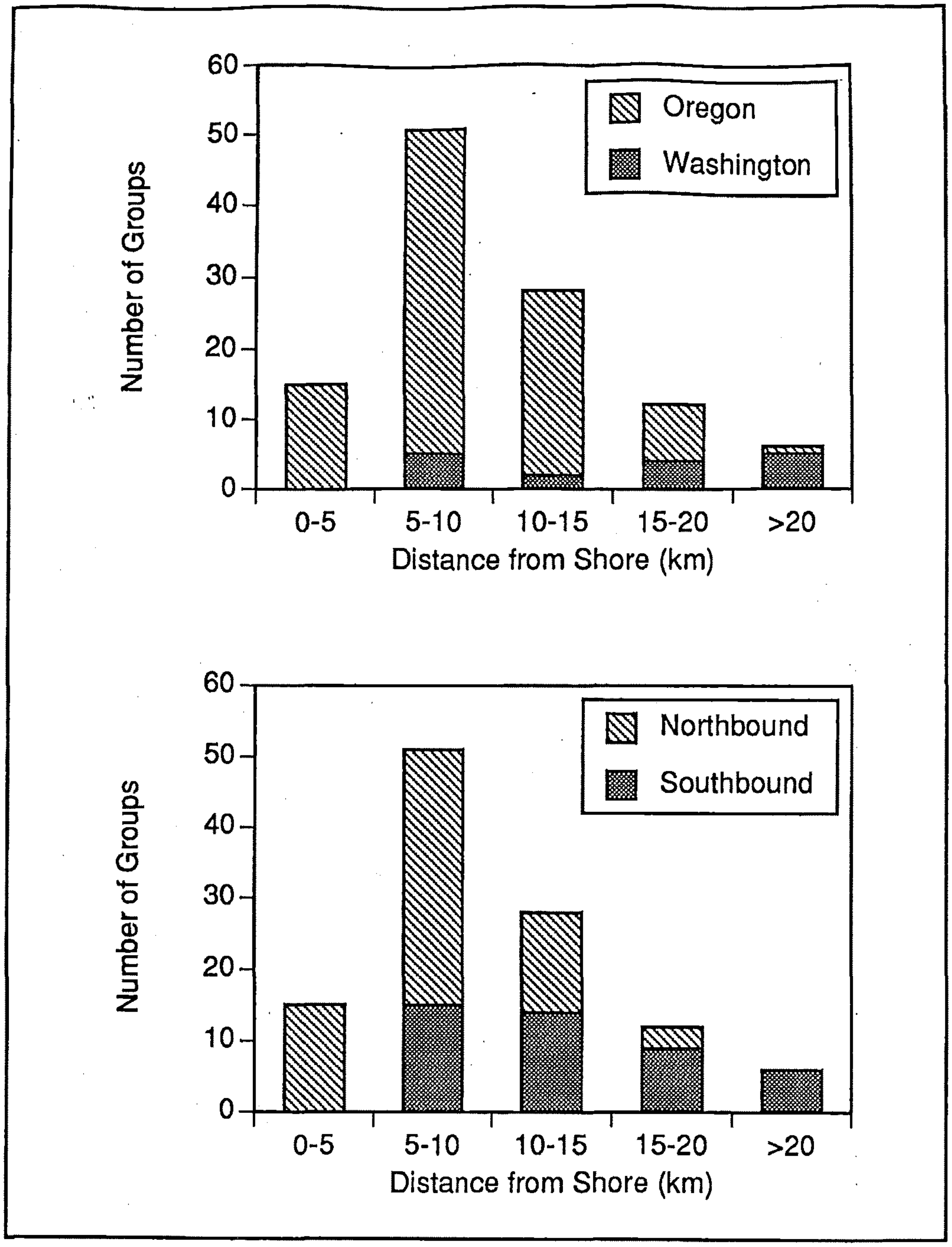

Fig. 5. Distance from shore of migrating gray whales comparing between states and the southbound and first wave of the northbound migrations.

8.0 km (SD = 3.9 km) for the northbound migration. The differences were significant ($t = 4.78$, $p < 0.0001$). The three farthest offshore sightings (>30 km) were southbound migrants (which included a group of three in the act of mating) that appeared to be taking a more direct route from Vancouver Island (a pattern reported by Rice and Wolman [1971] and Poole [1984] elsewhere) by crossing the Juan de Fuca submarine canyon at its most narrow point (a pattern reported by Brueggeman *et al.* [1987] in Alaska). Information reported by Pike (1962), Hatler and Darling (1974), and Hart (1977) suggests that the migration route between Washington and Vancouver Island is variable and wide with some animals crossing the strait to and from Cape Flattery while others follow a more direct offshore route.

Thirteen percent (26) of the sightings occurred during the non-migration period (mid-June to November) indicating a relatively strong presence of gray whales along the Oregon and Washington coasts during the summer and fall. Thirty-one percent of these sightings (over four surveys) were made in the vicinity of Yaquina Head (near Newport, Oregon), which falls within the stretch of Oregon coastline where Sumich (1984) found most of 1,200 sightings of summering gray whales. All our summer sightings, except one, occurred within bays or within 1 km of the coast, which roughly supports Sumich's (1984) observations that gray whales summering in the study area are nearly always within 0.5 km of the coast.

Humpback Whale

The North Pacific humpback whale population was severely depleted in this century by commercial whaling (Starks 1922; Scheffer and Slipp 1948; Pike and MacAskie 1969; Rice 1974, 1978; Tonnessen and Johnsen 1982; Reeves *et al.* 1985; Webb 1988). Approximately 28,000 humpbacks were killed in the North Pacific between 1905 and 1965, including almost 2,000 off Oregon and Washington (Rice 1978). Rice (1978) estimated that an original population of approximately 15,000 animals was reduced to approximately 850 by 1965. Present estimates for the North Pacific population vary between 1,200 and 2,100 (Baker *et al.* 1986, Darling and Morowitz 1986).

Major feeding aggregations of humpback whales occur in Alaska (Rice and Wolman 1982; Darling and Jurasz 1983; Baker *et al.* 1985, 1986; Reeves *et al.* 1985; vonZiegesar and Matkin 1985; Brueggeman *et al.* 1987, 1988) and California (Rice 1977; Calambokidis *et al.* 1988, 1989). Recent photo-identification studies have shown that California feeding aggregations winter off Mexico (Urban *et al.* 1987, Calambokidis *et al.* 1989, Balcomb *et al.* 1990) and most Alaska whales winter around the Hawaiian Islands (Darling and Jurasz 1983; Baker *et al.* 1985, 1986), although some slight interchange occurs between Hawaii and Mexico (Baker *et al.* 1986, Perry *et al.* 1988). DNA research by Baker *et al.* (1990) indicated a marked segregation of mitochondrial DNA halotypes between Alaska and California populations. Prior to this study, it was unknown whether Oregon and Washington humpbacks were associated with the California or Alaska feeding herds.

A total of 36 groups comprising 68 humpback whales was observed off Oregon and Washington between May and November (Table 5). No calves were encountered and the

Migration and Feeding of the Gray Whale (*Eschrichtius gibbosus*)[1]

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ABSTRACT

Observations of gray whales from the coasts of British Columbia, Washington, and Alaska are compared with published accounts in order to re-assess knowledge of migration and feeding of the American herd. Source of material is mainly from lighthouses and lightships.

The American herd of gray whales retains close contact with the shore during migration south of Alaska. Off Washington and British Columbia the northward migration begins in February, ends in May, and is at a peak during the first two weeks in April; the southward migration occurs in December and January, and is at a peak in late December. Northward migrants stop occasionally to rest or feed; southward migrants are travelling faster and appear not to stop to rest or feed during December and January. Gray whales seen off British Columbia, sometimes in inside protected waters, from June through October, probably remain in this area throughout the summer and fall months.

Available evidence suggests that gray whales retain contact with the coast while circumscribing the Gulf of Alaska, enter the Bering Sea through eastern passages of the Aleutian chain, and approach St. Lawrence Island by way of the shallow eastern part of the Bering Sea. Arriving off the coast of St. Lawrence Island in May and June the herd splits with some parts dispersing along the Koryak coast and some parts continuing northward as the ice retreats through Bering Strait. Gray whales feed in the waters of the Chukchi Sea along the Siberian and Alaskan coasts in July, August and September. Advance of the ice through Bering Strait in October initiates the southern migration for most of the herd. In summering areas, in northern latitudes, gray whales feed in shallow waters on benthic and near-benthic organisms, mostly amphipods.

There is no evidence to indicate that gray whales utilize ocean currents or follow the same routes as other baleen whales in their migrations. Visual contact with coastal landmarks appear to aid gray whales in successfully accomplishing the 5000-mile migration between summer feeding grounds in the Bering and Chukchi Seas and winter breeding grounds in Mexico.

Reconstruction of the migration from all available data shows that most of the American herd breeds and calves in January and February, migrates northward in March, April and May, feeds from June through October, and migrates southward in November and December.

INTRODUCTION

The gray whale (*Eschrichtius gibbosus*) is at present found only in the North Pacific Ocean and the adjacent Bering, Chukchi and Okhotsk Seas. It is represented by two herds. An American herd alternates between winter breeding grounds in the lagoons of Mexico and summer feeding grounds in the Bering and Chukchi Seas; an Asian herd alternates between winter breeding grounds along the south and west coasts of Korea and the Okhotsk Sea.

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Gray whales have been seriously reduced by excessive exploitation and, since 1937, their capture has been prohibited by international agreement. Consequently, the species has afforded neither opportunity nor an important practical need for careful biological study in recent years. Knowledge of the gray whale's migrations and distribution, however, are perhaps better known than that of any other stock of baleen whales, because of the species' predilection to shallow coastal waters for calving, migrating and feeding, and because of precision in the timing of its migrations.

This paper deals primarily with migrations of the American herd and secondarily with supplementary considerations of feeding and route-finding. Basic knowledge of the migrations, feeding areas and breeding areas of this herd was first described by Scammon (1874). Following a period of excessive exploitation during the last part of the 1800's the species was thought to be extinct on the American Coast. Its reappearance in recent years has led to renewed interest and several papers describing behaviour, migration, and population growth, have been published since 1954. Accumulated knowledge has not been sufficient to describe the entire migration route with certainty, however, and too few stomachs have been examined to confidently describe feeding habits of the species.

This paper describes observations of gray whales mostly during the northward migration along the coasts of Washington and British Columbia, and during their feeding period in the Bering and Chukchi Seas. These observations provide information which is used, in conjunction with published accounts, to re-assess the extent of knowledge on migration and feeding habits.

SOURCES OF INFORMATION AND ACKNOWLEDGMENTS

Observations are based chiefly upon the returns of log-book sight records from lightships and lighthouses along the coasts of Washington and British Columbia. Among these are included: Umatilla, Columbia River and Swiftsure Lightships; and Kains Island, Cape St. James, Langara, Amphitrite and Cape Beale Lighthouses (Fig. 1). The co-operation of personnel manning these light stations is gratefully acknowledged.

Dr Francis H. Fay, during the course of walrus studies in the vicinity of St. Lawrence Island, has kept notes on all whales observed. His permission to use these records and to examine and report on the stomach contents of two gray whales captured by the natives of this region is gratefully acknowledged. Mr T. H. Butler, Dr D. B. Quayle and Mr and Mrs Cyril J. Berkeley, of the Biological Station in Nanaimo, B.C., kindly identified the contents of these stomach samples.

Records of gray whales sighted by Department of Fisheries personnel, especially those from the C.G.S. *Laurier*, and by Mr W. F. Hausner of the tug *Neptune*, are greatefully acknowledged.

Supplementary observations by biologists and technicians aboard the M.V. *Pacific Ocean*, chartered for pelagic fur seal research from 1958 to 1961, are included.

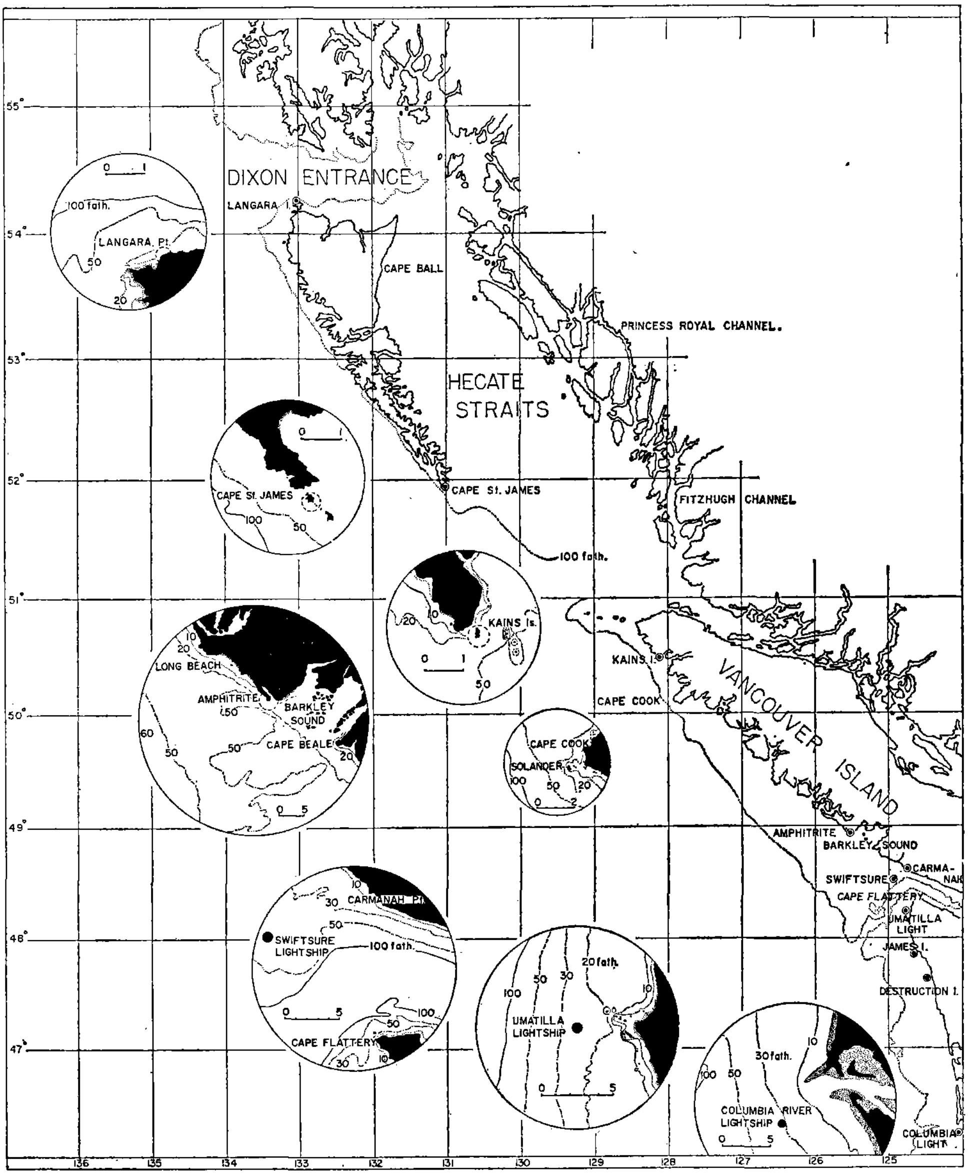

FIG. 1. Locations of gray whale observations along the coasts of Washington and British Columbia.

OBSERVATIONS OFF WASHINGTON

An estimated 500 to 1000 gray whales pass within sight of the Umatilla Lightship on their northward migration each year from March into May. This lightship is located 4½ miles[2] from shore near Latitude 48°10′N. Many whales pass by close to shore where their presence is difficult to detect against the surf breaking along the rocky coast and boiling over Umatilla reef. Many, however, pass by close to the lightship and sometimes remain in the vicinity for periods up to 4 hours. At these times their behaviour is variously described as "playing", "mating", "circling", "rolling" or "feeding". On several occasions the whales occupied their respite in rubbing themselves gainst the anchor chain.

In 1958 gray whales were seen from the Umatilla Lightship almost every day from March 16 to April 11; none was seen in May although sighting conditions were good. In 1959 gray whales were seen from this lightship almost every day from March 15 to May 14; the last northbound whale was seen on May 29. The peak of the migration at this latitude occurs during the first 2 weeks in April and is earlier in some years than in others. Few are seen at other times of the year. Six have been reported in December and 4 in January, mostly travelling southward.

Gray whales are seldom seen from the Columbia River Lightship during the northward migration. More are seen during the southward migration in December and January. Reports for these months include: 2 in late January, 1958; 2 in late January, 1959; 8 in early January, 1960; 5 in late December, 1960; and a school on January 11, 1960. Most northward migrants probably pass shoreward of this vessel which is stationed about 6 miles off. The *Pacific Ocean* encountered many gray whales 5 to 10 miles north of this lightship on March 12, 1958; at least 10 blows could be seen at any one time; all were within 6 miles of shore and most were close to the beach. During this same month, only 2 gray whales were reported from the Columbia River Lightship.

The *Pacific Ocean* conducted fur seal research off the coast of Washington in March, April and May, 1958 to 1960, inclusive. Waters up to 20 miles from shore were hunted intensively. Only once were gray whales seen more than 10 miles from shore; 2 adults and a calf were seen 20 miles off Cape Flattery on March 19, 1959. Gray whales were frequently encountered while the vessel lay at anchor or passed close to shore in transit to and from port; few were seen farther than 6 miles from shore; most appeared to be travelling within a mile of the coast where their presence was difficult to detect against the breaking surf. Important observations of gray whales from this vessel include: many between Gray's Harbor and Destruction Island from April 6 to 22, 1959; 20 to 30, 5 miles off Cape Flattery on March 27, 1958; and 50 between Destruction Island and Cape Flattery on March 27, 1960. While the vessel lay at anchor in shallow water off Raft River, Washington, whales could be heard blowing and splashing throughout the night of April 5–6, 1960.

The *Laurier* estimated 150 gray whales travelling close to shore between Destruction Island and Cape Flattery on April 1, 1958.

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[2] Distances in this paper are given in nautical miles. 1 nautical mile = 1.855 km; 1 knot = 1 nautical mile per hour.

TABLE I. Observations of gray whales off Washington, 1958–60.

Location and vessel	Date	Remarks
	1958	
5–10 mi north of Columbia River; *Pacific Ocean*	Mar. 12	At least 10 blows seen at any one time; mostly northbound
5 mi off Cape Flattery; *Pacific Ocean*	Mar. 27	20–30 northbound gray whales
Destruction Island to Cape Flattery; *Laurier*	Apr. 1	150; mostly gray whales; close to shore; all northbound
Umatilla Lightship	Mar. 16–Apr. 11	Estimated 500–1000; all northbound; seen almost every day
Umatilla Lightship	May	Visibility good, but no whales seen
Umatilla Lightship	Dec. 10–31	6 whales, thought to be grays, southbound
	1959	
Umatilla Lightship	Jan. 18–19	4 gray whales; southbound
Umatilla Lightship	Mar. 15 29	Gray whales almost every day; all northbound; mostly from March 28 to April 12
Umatilla Lightship	Dec. 16–17	7 or more gray whales; southbound
Umatilla Lightship	Dec. 25–28	5 unidentified whales; probably grays; southbound
Columbia River Lightship	Jan. 21	2 gray whales; southbound
Gray's Harbor to Destruction Island; *Pacific Ocean*	Apr. 6–22	Many northbound gray whales
20 mi off Cape Flattery; *Pacific Ocean*	Mar. 19	3 gray whales: 2 adults, 1 calf
	1960	
Columbia River Lightship	Jan. 1–5	8 southbound gray whales
Columbia River Lightship	Jan. 11	School of southbound gray whales
Columbia River Lightship	June 30	1 southbound gray whale
Columbia River Lightship	Dec. 28–30	2 gray whales circling vessel
Destruction Island to Cape Flattery; *Pacific Ocean*	Mar. 27	50 gray whales en route; some feeding near Destruction Island
Near Destruction Island; *Pacific Ocean*	Apr. 5	Few northbound gray whales travelling both inside and outside Destruction Island
Mouth of Raft River (Lat. 49°20′N); *Pacific Ocean*	Apr. 5–6	Many gray whales blowing throughout night; very active in shallow water

OBSERVATIONS OFF BRITISH COLUMBIA

After leaving the Washington coast at Cape Flattery, gray whales cross the Strait of Juan de Fuca in a general northerly direction before changing course westerly to follow the west coast of Vancouver Island. Gray whales are frequently seen by coastal vessels close to shore between Carmanah Point and Barkley Sound, but few are seen from the Swiftsure Lightship located 8 miles off the coast.

Off Cape Beale, which is located at the lower entrance to Barkley Sound, gray whales sometimes stop to play or feed during the northward migration in March and April. After rounding Cape Beale some may enter the Sound for a short distance and have been seen rubbing themselves against the rocks along Folger Island. Most of the herd proceeds directly across the 15-mile mouth of the Sound towards Amphitrite Point, following closely along the outer edges of a group of rocks lying part way across; a few enter narrow channels between these rocks. Most of the northward migrating whales pass Amphitrite Point shoreward of a buoy which lies about 1 mile off the light. Some have been seen rubbing themselves against the lines which moor this buoy.

The lightkeeper at Amphitrite Point, former whaler, reports that almost 1000 gray whales pass northward within sight of the lighthouse each spring, mostly in March and April, but in some years beginning in February and in other years ending in May. He has never seen them travelling southward.

During the course of fur seal hunting in 1958, gray whales were seen at the mouth of Barkley Sound and along Long Beach almost every day from March 14 to April 30. Some were seen moving back and forth along Long Beach as though feeding and some were seen rubbing themselves against Long Beach Rocks and Florencia Island, both of which lie about 1½ miles off the sandy beach. No gray whales are seen more than 2 miles from shore in this locality although fishing activity and ship traffic are fairly heavy during the migratory period.

Whalers from the Coal Harbour whaling station, while passing in and out of Quatsino Sound, report that gray whales are seen following closely along the shoreline but are never encountered on the whaling grounds which extend from 10 to 100 miles offshore. While rounding Cape Cook, gray whales pass inside Solander Island, a rock located 1 mile off Cape Cook.

When crossing the mouth of Quatsino Sound, some gray whales enter the Sound for a short distance before regaining the shore near Kains Island Light. Northbound gray whales pass this lighthouse mostly during the second and third week in April at which time approximately 5 per day are seen, travelling close to shore at a rate of about 4 knots.

The scarcity of sightings of gray whales on the southward run along the west coast of Vancouver Island in winter is chiefly a result of poor weather which discourages coastwise shipping and makes observation difficult. Only three noteworthy reports of southward migrants along this coast have yet appeared. A whaling captain, Mr Einar Jensen, reports a school of gray whales travelling southward off Long Beach in January, 1953. Another whaling captain, Mr Harold Sampson, saw gray whales travelling southward off the west coast of Vancouver Island, December 15 to 20, 1955. Eighty gray whales, all travelling southward, were sighted from the Kains Island Lighthouse during a period of exceptionally good weather from December 15 to January 4, 1955–56. Up to 21 whales per day were seen on and near December 17. Some of these whales entered the Sound for a short distance or tarried briefly near the rocks.

The route taken by gray whales on leaving the north end of Vancouver Island is not known. The few observations available suggest that the whales may become temporarily confused in crossing this broad 120-mile stretch of water between Vancouver Island and the Queen Charlotte Islands. On April 7, 1958, 8 gray whales were sighted from the *Pacific Ocean* 10 miles east of the Cape St. James Light. Two gray whales were sighted from the *Laurier* 5 miles east of Cape Ball in northern Hecate Strait on April 23, 1958. The outer coast of Cape St. James is largely obscured from view from the lighthouse. Consequently, few gray whales are seen from this station. The few which have been sighted at the time of the northward migration in April appeared to be travelling southward along the Hecate Strait shoreline to re-enter the Pacific by way of a narrow channel which isolates the island on which the lighthouse is located.

Few gray whales are seen along the uninhabited west coast of the Queen Charlotte Islands during the northward migration. Some are seen from the Langara Island Lighthouse which is located near the northwest tip of the Islands. This lighthouse is, however, poorly located for observing gray whales, which may pass some distance offshore in commencing the crossing of Dixon Entrance. More are seen at times other than spring months, suggesting that some gray whales may linger in the vicinity of Langara Island throughout the summer and fall feeding season. Southbound gray whales are seen here from September through January, but mostly in December. During summer and fall months, the direction of travel is variable.

Two reports by reliable observers show that gray whales occasionally enter inland passages in British Columbia during summer months. The *Laurier* reports one gray whale in Princess Royal Sound on August 1, 1958, and one in Fitz Hugh Sound on August 2, 1958.

No gray whales are reported by research vessels operating offshore of Vancouver Island and the Queen Charlotte Islands and westward into the Gulf of Alaska, suggesting that the whales continue to hug the coast closely except when crossing major waterways such as Dixon Entrance and Queen Charlotte Sound.

TABLE II. Observations of gray whales off British Columbia, 1958–60.

Location and vessel	Date	Remarks
	1957	
Langara Light	Dec. 20–28	Several whales near shore, probably grays

(Table II continued)

Location and vessel	Date	Remarks
	1958	
Langara Light	Feb. 2–30	Several southbound gray whales
Langara Light	Mar. 25–30	10 northbound gray whales and several more blows; mostly April 20–26
Langara Light	June 18, Aug. 20, Sep. 4	3 eastbound gray whales
Langara Light	October	Several gray whales travelling in various directions
Langara Light	Nov. 24	8 blows near shore; 1 gray whale breached
Langara Light	Dec. 2–Jan. 18/59	50+ southbound gray whales
Kains Island Light	Mar. 11–Apr. 12	150+northbound whales; mostly grays
Cape St. James Light	Apr. 12–25	12 gray whales
10 mi east of Cape St. James; *Pacific Ocean*	Apr. 7	8 westbound gray whales
5 mi east of Cape Ball; *Laurier*	Apr. 23	2 gray whales
Princess Royal and Fitz Hugh Sounds	Aug. 1–2	2 gray whales
Off Barkley Sound and Long Beach; *Hillier Queen*	Mar. 14–Apr. 30	Northbound gray whales seen almost every day; mostly April 10–12
2 mi off Pachena Point; *Pacific Ocean*	Mar. 20	10 northbound gray whales
1–2 mi off Amphitrite Point; *Howay*	Apr. 11	12 gray whales feeding
Swiftsure Lightship	Apr. 4–12	28 northbound whales; probably grays
	1959	
Langara Light	May 18	3 eastbound gray whales
Langara Light	Sep. 9	6 southbound gray whales
Langara Light	October, November, December	Many southbound whales, mostly grays; in groups of 4–6
Sydney Inlet; *Pacific Ocean*	June 2	2 gray whales near mouth of inlet
Dixon Entrance	June 20	2 eastbound gray whales
Kains Island Light	Mar. 2–Apr. 1	27 northbound whales, probably grays
Swiftsure Lightship	Apr. 23	3 gray whales
	1960	
Estevan Point to Cape Cook; *Laurier*	Mar. 10–20 Apr. 26	10 gray whales 4 gray whales
Off Long Beach; coastal vessels	Mar. 15–30	Many gray whales
Off Cape Beale; *Atlin Post*	Apr. 3	12 northbound gray whales
Langara Light	Aug. 31	Several gray whales going northwest
Langara Light	September	Many gray whales seen
Langara Light	Sep. 10	6 southbound gray whales; 1 being attacked by killer whales
Langara Light	December	Many southbound gray whales
Langara Light	Jan. 3	Several southbound gray whales

OBSERVATIONS OFF ALASKA

Dr F. H. Fay (personal communication) has kindly supplied the following information on gray whales he has observed in the vicinity of St. Lawrence Island, Alaska. Gray whales, sometimes singly and sometimes in pairs consisting of a mother and a calf, were seen travelling and feeding close to the western shores of St. Lawrence Island from May 11 through July, 1952, from June 4 to July 26, 1953, and from May 11 to June 19, 1954. More recent records from Gambell on the west coast of St. Lawrence Island show that gray whales usually arrive in this area about the middle of May. Dr Fay records the following early arrivals at Gambell: May 17, 1956; May 18, 1957; May 11, 1958; May 20, 1959; and May 21, 1961. Most are seen near the beginning of June but some remain as late as November. Dr Fay records one seen near Northeast Cape, on the west coast, on November 14, 1957, a stranded carcass at Northeast Cape about October 24, 1959, and a fresh stranded carcass near Gambell about October 24, 1959. Most, but not all, gray whales pass along the western shore of St. Lawrence Island on the northward migration; some split off from the main herd and pass northward along the eastern shores of the Island.

Reports from the tug *Neptune* describe whales sighted while running between St. Lawrence Island and Point Barrow in 1958 and 1959. In July, 1959, a school of gray whales followed the vessel into a lagoon located south of Northeast Cape on St. Lawrence Island. During the last two weeks in July, 1958, 8 to 10 whales could be seen blowing at any one time in waters of 8 to 22 fathoms between the Diomedes Islands and St. Lawrence Island. Farther north, in waters of 10 to 20 fathoms, many gray whales were seen feeding 8 to 15 miles from shore between Cape Prince of Wales and Icy Cape. At this time in July, 1958, many unidentified whales were seen from an aircraft flying between St. Lawrence Island and Nome. In August, 1958, a gray whale was observed feeding in water 5 fathoms deep north of Cape Prince of Wales. As this whale surfaced close to the vessel, mud was seen washing from its back.

Mr Karl Kenyon (personal communication) reports that he saw no gray whales while he was hunting walrus at Little Diomede Island in the Bering Straits from May 11 to June 14, 1958. He reports also that he saw no gray whales from Amchitka, located near the western end of the Aleutian Chain, during a year's stay on this island.

A specimen of baleen from a gray whale was taken from the beach on St. Matthew Island on August 4, 1954 (courtesy of Dr Robert Rausch). Gray whales have not previously been recorded from this locality.

MIGRATION ROUTE

The route followed by gray whales in migration between winter breeding and calving grounds in and about the lagoons of Mexico and feeding grounds in the Bering and Chukchi Seas has been the subject of much recent controversy mainly because of insufficient data. Original observations of gray whales off Washington, British Columbia and Alaska presented in this paper are combined, by areas, with selected published records of gray whales from the west coast of North America in the following summary which attemps to define the route and timing of the migration.

MEXICO

Gray whales are concentrated for breeding and calving in coastal areas from San Diego to Cabo San Lucas and the southern end of the Gulf of California, mostly from early January to the end of February; a few stragglers have been seen offshore in the region of Guadalupe and Clarion Islands; some are still present along the Mexico coast in March and April (Gilmore, 1960b). At Magdelena Bay the height of the southward migration is January 22, but early whale catches were made from January 4 to February 16 (Risting, 1928).

CALIFORNIA AND OREGON

The northward spring migration past San Diego begins in mid-February, is at a peak in March and April, and tapers off in early May (Gilmore, 1960b). Five gray whales, one of which was captured, were seen near Crescent City on July 21, 1926 (Howell and Huey, 1930).

Southward migrants arrive along the coast of Oregon and northern California in October and November (Scammon, 1874). Twelve to 15 were seen off southern Oregon in September, 1947 (Gilmore, 1960b).

The southward migration past San Diego occurs from December 25 to February 10, with stragglers passing 3 weeks earlier or later; late southbound migrants overlap early northbound migrants in late February (Gilmore, 1960a).

WASHINGTON AND BRITISH COLUMBIA

The northward spring migration in this locality begins usually in March, is at a peak from mid-March to mid-April, and ends in May.

Stragglers are occasionally seen at various coastal points from the Columbia River mouth to Dixon Entrance and in protected waters of British Columbia during the summer months.

Gray whales are occasionally seen near Dixon Entrance travelling in various directions during fall months; some of these are probably early southward migrants but most appear to linger here throughout the summer and fall.

During periods of good weather in winter many southward migrants pass close to shore in December and January, mostly in late December.

SOUTHEAST ALASKA AND KODIAK ISLAND

There are few records of gray whales from the Gulf of Alaska. One was taken by whalers operating from Baranov Island in southeast Alaska, 3 were taken by whalers off Kodiak, 2 of them in May, 1928 (Gilmore, 1960a). Eight were seen travelling westward along the south coast of Kodiak Island on May 11, 1957 (Wilke and Fiscus, 1961).

ALEUTIAN ISLANDS

No gray whales are seen by Japanese whalers operating north and south of the Aleutian Islands in spring and summer (Ichihara, 1958). The whaling station located at Akutan on Unimak Island recorded no gray whales taken (Kellogg, 1931). A dozen or so were seen passing through Unimak Pass in early June (Turner, 1886) and one was seen in the northern part of Unimak Pass on May 29, 1957 (Ichihara, 1958). No gray whales pass Amchitka in the western Aleutians (Mr Karl Kenyon, personal communication).

Bering Sea from Alaska Peninsula to St. Lawrence Island

There are no sight records of gray whales from this region although whalers are active in offshore waters north of the Aleutian Islands throughout late spring, summer, and early fall months. Only once, in July, 1958, have gray whales been seen from the Pribilof Islands (Gilmore, 1960a).

St. Lawrence Island to Bering Strait

Gray whales are well known to residents of St. Lawrence Island where they first appear each year in May (Dr F. H. Fay, personal communication).

Several recent reports show that gray whales, travelling and feeding, are abundant in this area during the summer months. One hundred seventy-two were counted off the northwest coast of the Island on August 2, 1955 (Ichihara, 1958). A school entered a lagoon on the east coast of the Island in July, 1959 (p. 823). Approximately 150 were seen off the east coast of the Island and a scattered few northward to Bering Strait in August, 1958 (Nasu, 1960). Many whales, possibly grays, were seen between the Island and Nome in late July, 1958 (p. 823).

Some gray whales are still found in Bering Strait in October (Nikulin, 1946). Strandings on St. Lawrence Island, mostly along the east coast, occur during fall months as late as November.

Chukchi Sea

The Chukchi Sea is closed by ice throughout the spring months and does not open until late June and early July (Maher, 1960). Gray whales are abundant near the arctic Alaska coast during summer months. Many (200+) were seen feeding in Kotzebue Sound on August 10 to 20, 1959, and 20 were seen scattered and moving southward north of Cape Prince of Wales on August 24, 1959 (Wilke and Fiscus, 1961). Eskimos see gray whales migrating northward past Cape Thompson during the first half of July each year (Fay, MS, 1961a). Many whales, some of which were definitely grays, were seen feeding off Kotzebue Sound in July, 1958 (p. 823).

Maher (1961) provides the following information: 9 gray whales were taken by Eskimos between Wainright and Point Barrow from July 18 to September 13, 1954 to 1959; 50 to 100, travelling southward, were seen from the beach at Wainwright on August 9 to 10, 1953; a few were seen passing Cape Sabine on August 3 to 5, 1959; gray whales are scarce at Point Barrow; gray whales are present near Point Barrow until mid-September, but some may begin moving southward in early August.

Gray whales are also abundant near the northern Siberian coast during early summer until ice restricts their movements. Seventy-eight were seen from a Japanese oceanographic vessel off the Siberian coast on July 27, 1958 (Nasu, 1960). Fifty-eight were taken by Japanese whalers off the Siberian coast in August, 1940 (Mizue, 1951).

KORYAK COAST

Gray whales arrive off this coast in May and early June; they no longer range southward to Kamchatka (Sleptsov, 1955). Thirty-one gray whales were taken by the "Vega" expedition between Cape Olyutorskii and Cape Navarin from July 27 to August 19, 1925 (Risting, 1928). A few were seen off the Gulf of Anadyr in August, 1958 (Nasu, 1960).

Two major gaps remain in our knowledge of the route followed by this population of gray whales. Knowledge of the route between British Columbia and feeding grounds in the Bering Sea during both northward and southward migrations remains speculative. Available evidence as to the most probable route taken will be discussed later.

Northward migrants pass San Diego from February (when others are still moving southward) into May, but mostly in March and April. The literature contains no information on the exact dates during which peak numbers pass by this point going north. Near Cape Flattery, some 1200 miles north, peak numbers pass during the first two weeks in April. The peak of the northward migration past San Diego is, therefore, probably within the first two weeks of March, assuming a rate of travel of 35 to 50 miles per day or 1.5 to 2.0 knots. From San Diego the whales appear to head directly across the Santa Catalina bight and are several miles from shore when passing La Jolla (Gilmore, 1960b). Farther north they travel close to shore, skirting headlands and usually cutting directly across the mouths of large bays.

The re-appearance of gray whales on the southward run off San Diego begins in early December and ends in late February; most whales pass during the middle two weeks in January (Gilmore, 1960b), at which time they are travelling in a narrow stream, little more than a mile wide, at an average rate of 4.6 knots, and seem to converge on the kelp beds off La Jolla (Wyrick, 1954). Similarly, at San Simeon, located on a coastal bight, pregnant females appear closer to shore during the "down" season as they seek bays and lagoons to bring forth their young (Townsend, 1886). Scammon (1874) states that they appear off the coast of Oregon and northern California during October and November and that both males and females keep near to shore during the southward passage. Observations off northern British Columbia show that, although gray whales appear during the fall months, the main herd of southward migrants does not pass until December and January, with maximum numbers passing in December. Off the north end of Vancouver Island they pass in greatest numbers near the end of December and off Washington in early January. The southward run from British Columbia to San Diego appears to take from 2 to 4 weeks at an average rate of about 50 to 100 miles per day or 2 to 4 knots.

The southward migrants proceeding towards the breeding grounds are more concentrated, pass by over a shorter period of time, and travel at a faster rate, than the northward migrants proceeding towards the feeding grounds (Fig. 2).

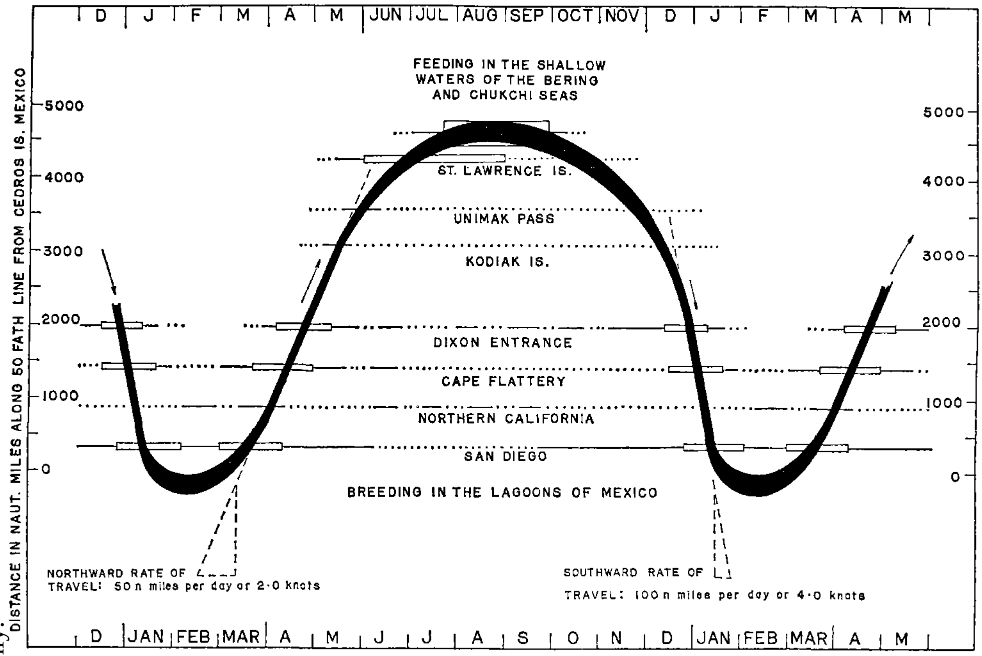

FIG. 2. Diagram summarizing the seasonal distribution of the American herd of gray whales. Relative abundance is indicated horizontally across the graph as follows: *open rectangles*—numerous; *solid line*—few records; *dotted line*—probable occurrence.

The route from Dixon Entrance to the Bering Sea is unknown except for a few observations of westbound whales from the south coast of Kodiak Island in May (Wilke and Fiscus, 1961) and north of Unimak Pass in late May and early June (Ichihara, 1958; Turner, 1886). None have been reported by oceanographic and fisheries research vessels operating offshore in the Gulf of Alaska and none have been reported by Japanese whalers operating north and south of the Aleutian Islands. The *Baikal Maru* operated from 48° to 54°N and 159° to 173°W from May 20 to October 3, 1953, and saw no gray whales (Sakiura and Ozaki, 1953). We consider that this evidence, although negative, is important in showing that gray whales do not cross the Gulf of Alaska on leaving British Columbia, but continue to follow the coastline northward and westward towards Unimak Pass. The coastal route is approximately 200 miles greater than a direct route across the Gulf, and would, therefore, not greatly prolong the journey.

Japanese whalers operating in the Bering Sea concentrate their hunting in areas which lie to the west of a line joining Unimak Pass and St. Lawrence Island, in waters outside the 50-metre contour (Fig. 3). Whaling is conducted from June to September, but no gray whales are seen. Gray whales have only once been reported from the Pribilof Islands, which also lie to the west of this line. Fiscus saw 3 or 4 gray whales off St. Paul Island on July 2, 1958 (Gilmore, 1960a). Gray whales have never been reported from the Aleutian Islands west of Unimak Pass. We consider that this evidence strongly favours a route which crosses the Bering Sea in its eastern part over the Alaskan continental shelf rather than in the western part as suggested by Gilmore (1955, 1960a, 1960b) At St. Lawrence Island gray whales first appear off the east coast in May, following the retreat of the pack ice. Whaling statistics show that they appear along the Koryak coast first in July (Risting, 1928) although the area is ice-free in June. The earlier arrival of gray whales off St. Lawrence Island suggests that the route followed is by way of the eastern rather than the western Bering Sea.

Fay (MS, 1961a), records 13 strandings of gray whales on St. Lawrence Island, where the species is occasionally hunted by the Eskimos, from 1955 to 1959. Most of these occurred in July and August; the latest stranding was in October. About two-thirds of the stranded whales were young animals less than 30 feet (9.2 m) in length, and 2 had been injured by killer whales. Three gray whales, each carrying crude harpoons of a type used by the natives of Cape Chaplin, stranded on St. Lawrence Island in September, 1961.

Three strandings on the Alaska mainland in 1959 are recorded by Fay (MS, 1961a). One stranded on September 4 at Scammon Bay, south of Norton Sound, where Eskimos report the species to be rare. Two stranded in August near Cape Thompson, 125 miles northwest of Kotzebue, where Eskimos report gray whales migrating northward during the first half of July each year.

A map showing the distribution of the American herd of gray whales is presented in Fig. 3. Arrows indicating the route past St. Lawrence Island represent probable routes taken by the main herd. Some whales pass northward along the east coast of the Island and, no doubt, some also pass southward along the west side.

The northward migration in June and July is impeded by the retreating pack ice which, in most years, provides a lead past the west coast of St. Lawrence Island in early June and through Bering Strait in July. Maher (1960) shows the approximate mean limits of the pack ice at about 300 miles north of Bering Straits in the Chukchi Sea in August and September. Ice re-appears in the Gulf of Anadyr and closes Bering Strait in October. It then moves rapidly southward until December when it completely closes the northern part of the Bering Sea from Cape Navarin to Nunivak Island.

Leads past St. Lawrence Island are closed in December or January. Assuming a rate of travel of 50 to 100 miles per day (2 to 4 knots) gray whales would cover the 2000-mile distance between St. Lawrence Island and Dixon Entrance via Unimak Pass in 3 to 6 weeks. Most gray whales pass northern British Columbia in December, which suggests, on the basis of the foregoing assumptions, that most of the herd leaves the Bering Sea early in November. A few southward migrants (which had probably left the Bering Sea in September and October) are seen off northern British Columbia in October and November.

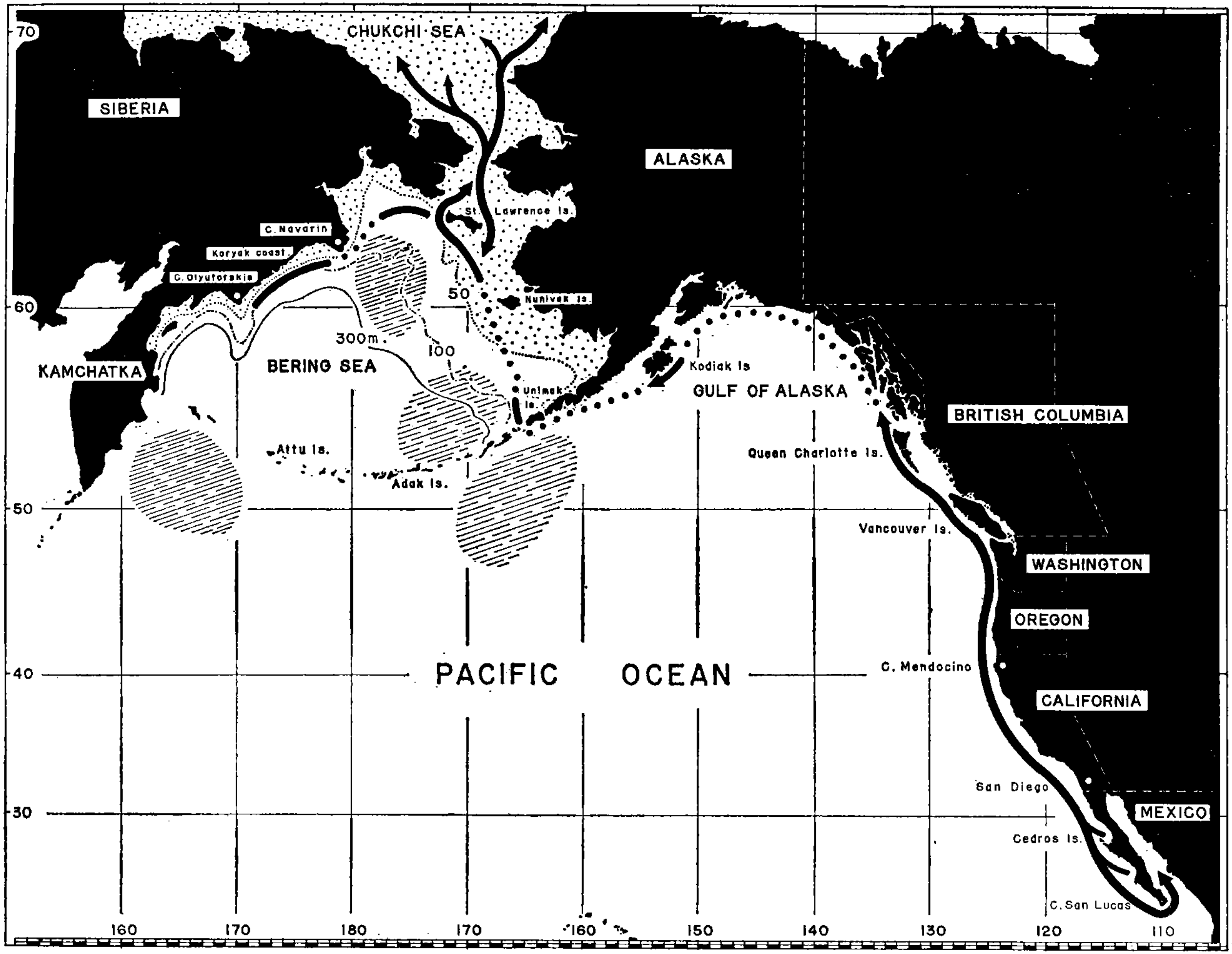

FIG. 3. Map showing the distribution of the American herd of gray whales. Solid lines: known routes; broken lines: probable routes; hatched areas: commercial whaling areas where gray whales are not seen.

TABLE III. Distances from Cedros Island, Mexico, along the migration route of gray whales.

Location	Distance in nautical miles	
	Point to point	Cumulative
Cedros Island	0	. . .
San Diego	300	300
Point Conception	240	540
Cape Mendocino	420	960
Cape Flattery	500	1460
Cape Scott	200	1660
Cape St. James	120	1780
Langara Island	180	1960
Unimak Pass	1600[a] (coastal)	3560
St. Lawrence Island	700[b] (direct)	4260
Koryak Coast, Siberian Coast or Point Barrow	400–600	4660–4860

[a]Direct distance across the Gulf of Alaska is approximately 1400 miles.

[b]Approximate distance along Aleutian Islands to St. Lawrence Island is 2000 miles via Attu and 1400 miles via Adak.

FEEDING

A sample from the stomach contents of 2 small gray whales taken near Gambell, west coast of St. Lawrence Island, were as follows:

(1) Taken June 9, 1954; sample size about 200 cc
Amphipods: several *Ampelisca macrocephala*; one *Anonyx nugax*
Polychaetes: several tubes of *Pectinaria* (sp.)
Gastropods: one moon-snail, family Photidae
Other: some sand and silt

(2) Taken May 29, 1958; sample size about 1 litre
Amphipods: about 90%; mostly *Ampelisca eschrichti*, few *Anonyx nugax*
Ascidians: remains of 2 compound, branched and globular ascidians
Decapods: 2 intact spider crabs, *Chionoecetes bairdi* and *Hyas coarctatus*
Lamellibranchs: remains of 3 small bivalves; one 7-mm shell of *Liocyma*, probably *L. fluctuosa*
Polychaetes: 2 pieces of shells from *Pectinaria*
Cumacea: remains of 1 unidentified specimen
Gastropods: a 9-mm shell of *Volutina*; part of an operculum
Other: some sand and a few bits of wood

Tomilin (1954) earlier described gray whales in arctic regions as feeding upon near-benthic amphipods and true benthic organisms, including polychaetes, hydroid polyps, the mollusc *Buccinum*, and others, in some cases mixed with tiny pebbles and silt.

Feeding behaviour of gray whales in shallow waters has been described by several authors. Scammon (1874) describes gray whales surfacing with head and lips besmeared with mud from soft bottoms. Wilke and Fiscus (1961) describe gray whales feeding in August in the Chukchi Sea, in waters of about 24 fathoms, making muddy blotches in the water as they surfaced, apparently having expelled the mud through the baleen. Tomilin (1954) describes the baleen plates of the gray whale according to the animal's ability to dig up and probably even plough up the silty benthic ground. Reports of the tug *Neptune* describe gray whales surfacing with mud washing from their backs as they fed in water 5 fathoms (9 m) deep north of Cape Prince of Wales in August. Seabirds have been seen following feeding gray whales and settling into the muddy spots where the whales had surfaced (Wilke and Fiscus, 1961).

Fay (MS, 1961a) describes the waters about St. Lawrence Island as an important summer feeding ground. Here gray whales feed usually in waters of 15 fathoms (27 m) or less and within 300 yards (270 m) of shore, creating muddy patches in the water as they surface. Photographs taken by Dr Fay show them feeding in the surf within 50 feet (15 m) of the beach (Fig. 4).

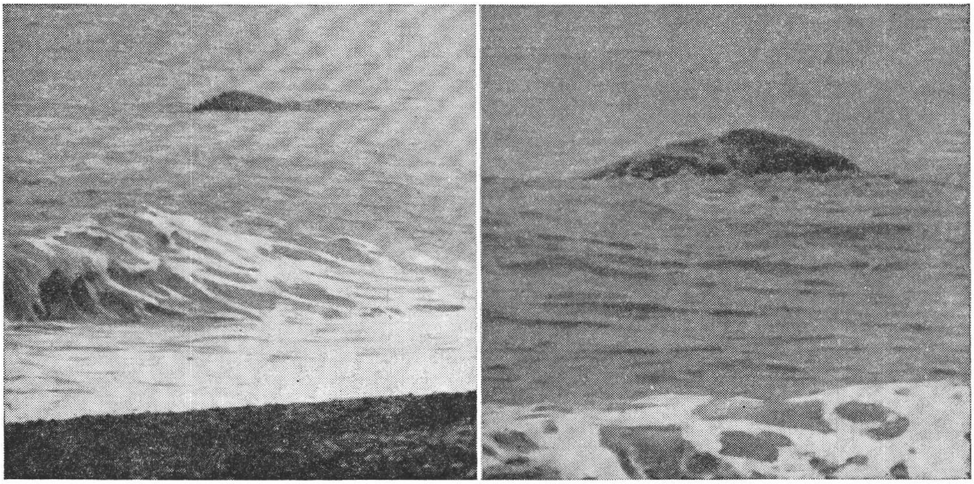

FIG. 4. Gray whales feeding close to shore off St. Lawrence Island, Alaska. (Photo by Dr F. H. Fay.)

Outside its arctic habitat, gray whales appear to feed little (Andrews, 1914; Townsend, 1886; Scammon, 1874). Scammon (1874) observed that stomachs of gray whales caught in the breeding lagoons were usually empty although some contained "sedge" or "sea-moss". He also describes mussels found in the mouths and among the baleen, but does not state the locality in which this occurred. Matthews (1932) describes sei, humpback and gray whales feeding on schools of the anomuran decapod *Pleuronocodes planipes* in Magdelena Bay, in 1926. Dr Carl L. Hubbs (personal communication) relates local testimony that "several barrels of sardines" were found in the stomach of a gray whale stranded near the north end of San Ignacio Lagoon in Mexico. Mizue (1951) reports that the anomuran decapod *Nephrops thomsoni* was found in the stomachs of 2 gray whales caught in the northern waters of the Yellow Sea in May 1922.

Two reports suggest that gray whales injest plant material incidentally during bottom forages while on migration. Andrews (1914) examined a number of stomachs of gray whales during the southward migration off North Korea and found only dark green water with bits of kelp, seaweed and a light gelatinous material he thought might be jelly-fish. The present author examined the stomachs of 10 gray whales taken under special permit by whale catchers off the west coast of Vancouver Island, near the mouth of Quatsino Sound, in April, 1953, during the northward migration. These stomachs contained a green liquid within which was suspended bits of plant material; the intestines contained variable quantities of thick mucous coloured from a dark cream to a yellow-green. Although these stomachs contained no animal material, the cream-coloured intestinal contents suggest animal material in an advanced stage of digestion and that the whales had probably been feeding. Mizue (1951) reports only green-coloured gastric juice in the stomachs of gray whales taken during the southward migration off Korea.

Observations off Washington and British Columbia during the northward migration in March and April show that gray whales occasionally tarry to feed en route. Behaviour which is described as feeding has been reported from several localities along the coast of Washington and Vancouver Island, but mostly from the Umatilla Lightship and along Long Beach. The depth of water at Umatilla is 20 to 25 fathoms (37–46 m) over a sandy bottom; the depth where whales feed along Long Beach is 5 to 10 fathoms (9–18 m) over a sandy bottom. The overall rate of progress north of San Diego appears to be slower during the northward run, probably as a result of frequent interruptions in the migration as the whales slow down or stop for the purpose of resting or feeding.

Dr Carl L. Hubbs (personal communication) cites instances of gray whales near La Jolla stopping sometimes for more than an hour, circling tightly, and otherwise behaving as though feeding, while most whales carry on without hestitation; in one specific instance gray whales behaved in this manner on the occasion of the spawning of squid off La Jolla, on January 21, 1954.

Howell and Huey (1930) report that a male gray whale, 39 feet or 11.9 m long, in company with 4 others, was taken by whale catchers off northern California in July, 1926. This whale had within its mouth and among its baleen a quantity of *Euphausia pacifica*.

DISCUSSION

Original observations described in this paper, when combined with recent publications on the species, show that gray whales follow the coastline closely when migrating between the breeding lagoons of Mexico and the northern part of British Columbia, and that they stop on occasion to rest and to feed. The northward migration is more protracted in time, proceeding at a slower rate than the southward migration. Information on the migration route north of British Columbia is scanty. Lack of offshore sightings in the Gulf of Alaska, combined with a few sightings along the coast, however, suggest that northward migrants continue to hug the coastline while circumscribing this area. Similar evidence along the Aleutian Chain and in the Bering Sea suggests that during the northward run, gray whales pass through Unimak Pass and/or Isanotski Strait and proceed directly towards the west coast of St. Lawrence Island. Off the west coast of St. Lawrence Island gray whales begin to disperse as they search for food. Some disperse westwards to feed off the Koryak coast and the Gulf of Anadyr; some proceed northward past St. Lawrence Island following the retreat of the ice through Bering Strait in July. The migration route splits again north of Bering Strait with some whales following the Siberian coast in a northwesterly direction and some continuing northward across the mouth of Kotzebue Sound to follow the Alaska coast northwesterly towards Point Barrow.

Open ice-free water permits feeding in the Chukchi Sea during July, August and September. From August to September, with the encroachment of ice through Bering Strait, gray whales proceed southward usually, past the east coast of St. Lawrence Island. They are next seen, travelling close to shore, along the coast of British Columbia, mostly in December and January. Some, probably those which fail to complete the migration to its limits in the Bering and Chukchi Seas, are present along the northern British Columbia coast as early as September, others spend the summer between northern California and southeastern Alaska.

The scarcity of reports of gray whales from whalers and from research vessels operating in oceanic regions off British Columbia, in the Gulf of Alaska, north and south of the Aleutian Islands, off Kamchatka, and over deep waters of the central and western parts of the Bering Sea is, in my opinion, convincing evidence that gray whales avoid these areas during migration and feeding. The absence of reports of gray whales in coastal regions such as Unimak Pass and the southeastern coast of Alaska, however, is not convincing evidence that gray whales avoid these localities. Experience has shown that gray whales travelling close to shore are difficult to see against the breaking surf by vessels which must keep well off shore along treacherous storm-lashed and rock-strewn coasts.

Existing knowledge of ocean currents and of whale migrations fails to support the theory (Gilmore, 1955, 1960a, 1960b) that gray whales follow ocean currents. Previous attempts to relate oceanic migrations of other whale species to ocean currents have been unsuccessful (Harmer, 1931; Townsend, 1935; Dawbin, 1956). With few exceptions, gray whales, wherever observed, have been travelling close to shore where large oceanic water masses lose their identity under the influence of topographical irregularities in the coastline, freshwater run-off, and climatic aberrations caused by proximity to land. One of several inconsistencies in Gimore's theory that gray whales are assisted in their migration by ocean currents is that the coastal Davidson Current flows northward along the North American coast to at least 48°N Latitude in November, December and January (Sverdrup *et al.*, 1946) at a time when migrating gray whales are travelling southward. Another inconsistency is that there is no appreciable surface current northward of the Strait of Juan de Fuca to Dixon Entrance in summer (Favorite, 1961) as gray whales migrate northward. The effects of local run-off, which can be traced several hundred miles offshore along the coasts of British Columbia and Washington (Favorite, 1961), show no evidence of deflecting gray whales in their migration.

In seeking environmental conditions associated with the distribution of gray whales, it would be more appropriate to consider the coastal climate and topography rather than the oceanic climate. A continuous temperate faunistic province stretches along the west coast of North America from the middle of lower California, along the coastal arch to the Aleutian Islands, and continues uninterrupted in the eastern Bering Sea as far north as the Bering Strait (Ekman, 1953). The Aleutian Trench and the basin of the western Bering Sea constitute faunistic barriers. Coastal waters of the Asian parts of the Bering Sea, the sea around Kamchatka, and the Okhotsk Sea are distinctly Arctic. The American side of the Bering Sea is, however, warmed by northward-flowing temperate water which is seldom less than 6°C even in July and August. Bottom topography of the Bering Sea features a wide continental shelf in its eastern parts. The 50-metre contour continues through Unimak Pass to outline a narrow band along the north side of the Alaska Peninsula, curving into Bristol Bay and continuing in a northwest direction to the west coast of St. Lawrence Island. Bering Strait and the Chukchi Sea are mostly less than 30 m in depth.

Ichihara (1958) admits doubt as to the true migration route of the gray whale in the Bering Sea, but draws inferences from the migrations of other baleen whales in this area as learned from marking experiments. There is, however, little reason to expect gray whales, which are known to hug the coastline closely during a large part of their migration, to conform to migration routes used by other whale species which are oceanic in their distribution; nor should we expect them to select feeding areas used by other whales. Hardy and Gunther (1935) and Nemoto (1959) have shown that oceanic species of baleen whales concentrate in feeding areas as an indirect result of the search for preferred foods. Euphausians are a preferred food of fin and humpback whales whose feeding apparatus is adapted to skimming these as they swarm near the surface, usually off the edge of the continental shelf or in areas of convergences. Only one euphausiid, *Thysanoessa raschii*, is abundantly distributed in cold shallow waters of the Gulf of Anadyr and the northern Bering, Chukchi and Okhotsk Seas. Fin and humpback whales may feed directly or indirectly on this species in shallow waters in the northern parts of the Bering Sea (Nemoto, 1959) where they are sometimes associated with gray whales, but mostly these whales concentrate along the edges of the shelf in deeper waters. The gray whale, however, is adapted to feeding on benthic or near-benthic organisms (Tomilin, 1954) which abound in cold shallow seas. It would neither be expected to distribute itself in the same manner as those whales which feed on epipelagic plankton, nor does evidence from stomachs and feeding behaviour indicate that it does.

There is no evidence available to show that gray whales ever cross broad expanses of ocean or stray far from land. Throughout the feeding migration south of the Bering Sea, they travel in a general northwesterly direction, keeping exposed ocean coasts of all major land masses, including large islands such as Vancouver Island, the Queen Charlotte Islands and Kodiak Island on the right side. When passing small islands such as Solander Island, where an unobstructed view of open ocean appears beyond, they pass on the inside; when passing large islands where an unobstructed view of open ocean does not appear, they pass on the seaward side.

The combination of senses providing clues to the migration route is not certain. Circumstantial evidence suggests that gray whales supplement their directional sense by means of visual clues provided by coastal landmarks. In this regard, Gilmore (1960a) remarks on the gray whale's habit of periodically thrusting its head out of the water, while subsequent movements suggest re-orientation, and on page 417 of his paper he illustrates this behaviour with the caption "gray whale spying out a boat". Scammon (1874, p. 32) illustrates similar behaviour of gray whales in the Arctic ice. While blowing, the gray whale barely exposes the eyes.

The distance (d) in nautical miles at which landmarks of various heights (h) in feet may be seen from the sea surface is described by the formula:

$$d = 1.2\sqrt{h}$$

According to this formula, landmarks 100, 500, 1000, 2000, 4000 and 8000 feet high are visible from approximate distances of 10, 25, 35, 50, 75 and 100 nautical miles, respectively (1 foot = 0.305 m). Although it is not certain that baleen whales in general and gray whales in particular are anatomically equipped to see great distances in air (some authorities generalize that the Mysticetes lack the power of accommodation and are myopic in aerial vision), their behaviour in following the coastline, except when by-passing wide openings in the coastline, suggests that they are utilizing landmarks for orientation. High mountains fringing the west coast of North America provide an almost continuous path for gray whales should they utilize these for directing their coastal courses between breeding and feeding areas. Specific mention has been made of one locality where gray whales appear temporarily to deviate from their route. This is the mouth of Queen Charlotte Sound, a gap of 120 miles between Cape Scott and Cape St. James. Mountains near the southern end of Queen Charlotte Islands range to heights of from 1500 to 2000 feet (460–610 m) and could not be seen from the sea surface at distances greater than 40 to 50 miles. Northbound whales appear to continue on a northwesterly course after leaving Vancouver Island; later, probably when within sight of these mountains, they appear to re-orientate in the direction of Cape St. James. Some may continue northward through Hecate Strait. Future studies in Queen Charlotte Sound are planned in order to learn how gray whales orient themselves in the absence of visible landmarks.

Navigational aids used by gray whales need not be completely innate since calves accompany their mothers on their first northward migration, and are thereby provided with the opportunity to learn the route.

SUMMARY AND CONCLUSIONS

The northward migration of gray whales along the coasts of Washington and British Columbia begins in February, ends in May, and is at a peak during the first two weeks in April. At the peak of the migration, gray whales are seen almost every day at several points between the Columbia River and Dixon Entrance, travelling close to shore except when by-passing wide indentations in the coastline at which time they travel from headland to headland. None are seen offshore. Occasional stops are made for resting and feeding.

Few southbound migrants are seen off Washington and British Columbia because of reduced visibility in winter months. The southward migration begins in late September and October, ends in late January, and is at a peak in late December. Gray whales continue to hug the coast on the southward run, but appear to be travelling at a faster rate and seldom stop to rest or feed.

Gray whales sometimes occur along the coast and in protected waters of British Columbia from June through September. At this time the direction of travel is not constant; these whales are probably summer residents in the area and are not migrating.

On their feeding grounds in the Bering and Chukchi Seas, gray whales feed on benthic and near-benthic organisms, mostly amphipods. They are, consequently, distributed over the shallow continental shelf in northern regions rather than in offshore oceanic areas where commercial species of baleen whales distribute themselves in search of favoured epipelagic plankton. When dispersing to feed, gray whales first appear off the west coast of St. Lawrence Island in May. The herd splits up in this region with part travelling westward towards the Koryak coast and part continuing northward through Bering Strait. The herd splits again in the Chukchi Sea with part travelling westward along the Siberian coast and part travelling northward along the Alaskan coast. Encroachment of the ice through Bering Strait in October probably initiates the southward migration which is directed mainly along the eastern side of St. Lawrence Island.

Available evidence suggests that northward migrants travel a coastal route until they reach the western tip of the Aleutian Peninsula where they enter the Bering Sea and continue northward within the 50-metre contour which outlines a broad pathway in the eastern Bering Sea. It is unlikely that they follow ocean currents, since throughout known parts of the migration they travel close to shore where ocean currents lose their identity under the influence of coastal configurations.

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LIFE HISTORY AND ECOLOGY OF THE GRAY WHALE (Eschrichtius robustus)

RICE AND WOLMAN

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FOREWORD

WHALES long remained among the world's least known mammals because their large size and oceanic habitat make them difficult to observe and collect. Individual whales cannot be observed repeatedly, therefore knowledge of most aspects of their life history must be deduced from data provided by examining large series of specimens. In the early decades of this century the expansion of the modern whaling industry with its efficient catcher boats and its mechanized shore stations and floating factory ships finally provided biologists the opportunity to undertake large-scale studies of whales. Concern for the future of whale stocks provided an incentive for government support of whale research. As a result, we have now learned more about the biology of the rorquals and the sperm whale than of most other species of wild mammals. Gray whale populations, however, had been depleted before this opportunity for research arose. Although field observations had provided a fairly detailed picture of the distribution, migration, and behavior of the gray whale, many important aspects of the species' biology—such as age and growth, reproduction, parasites, pathology, and population dynamics—remained virtually unknown.

Under the protection afforded by the 1946 International Convention for the Regulation of Whaling, the California gray whale stock has increased so much that a resumption of commercial exploitation has been considered. As the dearth of basic data on the biology of the species would handicap any efforts at rational regulation of the harvest, the Bureau of Commercial Fisheries in 1959 initiated a research program that included collecting small series of gray whales under Special Scientific Permits. Beginning in 1966, the number of animals taken annually was increased upon recommendation of the Scientific Committee of the International Whaling Commission, which has reviewed the work each year and provided much encouragement and advice. The data now available reveal the basic features of the ecology of the gray whale and provide a foundation for further studies on its population dynamics.

This study would not have been possible without the cooperation of the Del Monte Fishing Company and the Golden Gate Fishing Company of Richmond, California. John Caito and Charles Caito of Del Monte, and Robert Casebeer of Golden Gate placed the facilities and crews of their whaling stations and catcher boats at our disposal for collecting and examining specimens. Kenneth C. Balcomb III, James Ekberg, Bernard Lenheim, and Toshio Kasuya (Ocean Research Institute, University of Tokyo), assisted in the examination of whales at the whaling stations. Margaret Anderson, Lawrence Dickson, Susan D'Vincent, Ekberg, James Houk, Hiroshi Kajimura, Lenheim, Donald Ramsey, Jeffrey Rochin, James Rote, Catherine Short, and Robert Strawn manned the counting stations. Lenheim, Ramsey, and Ancel M. Johnson conducted the transect cruises of the catcher-boat *Allen Cody*. Balcomb, Kasuya, Thomas J. McIntyre, Masaharu Nishiwaki (Ocean Research Institute), Daniel Lluch B., and Joaquin Arvizu M. (both with the Instituto Nacional de Investigaciones Biologico Pesqueras, Mexico) assisted in the whale-marking cruises. Ford Wilke, Johnson, and Lenheim assisted in the aerial surveys. Francis H. Fay, Arctic Health Research Laboratory, U. S. Public Health Service, provided a sample of the stomach contents of a gray whale killed near St. Lawrence Island, Alaska. Earl L. Bousfield, National Museum of Canada, identified the amphipods, provided information on the habits of benthic invertebrates, and made suggestions concerning the feeding behavior of gray whales. The following individuals identified other stomach contents or parasites: Martin W. Johnson and Margaret D. Knight, Scripps Institution of Oceanography (crab larvae); Josephine F. L. Hart, British Columbia Provincial Museum (cumaceans); Frank Bernard (ascidians and holothurians) and Cyril Berkeley (polychaetes and salps), Pacific Biological Station, Fisheries Research Board of Canada; Yuk-maan Leung and John L. Mohr, University of Southern California (cyamids); Kenneth M. Neiland, Alaska Department of Fish and Game (acanthocephalans and campulid trematodes); Robert L. Rausch, Arctic Health Research Laboratory (cestodes and notocotylid trematodes); John T. Davey, Commonwealth Bureau of Helminthology (nematodes). Daniel F. Cowan, Michigan State University, examined a pathological liver specimen. The late Gordon C. Pike, Arctic Biological Station, Fisheries Research Board of Canada, made the baleen tracings and allowed us to see his unpublished manuscript on gray whales taken off British Columbia. Unless otherwise noted, individuals mentioned above are present or former employees of the Marine Mammal Biological Laboratory, Bureau of Commercial Fisheries.

CONTENTS

INTRODUCTION

IN February each year, pod after pod of gray whales departs from the tropical mangrove-fringed lagoons bordering Bahia Magdalena, from Laguna Ojo de Liebre in the heart of the Vizcaino Desert, and from other lagoons on the west coast of Baja California. Swimming slowly but steadily, they move northward along the coast; four months later the same whales may be surfacing and blowing among the ice floes of the Chukchi Sea. This migration is the longest performed by any mammal.

The gray whale, *Eschrichtius robustus* (Lilljeborg, 1861), is unique in other ways. It is the sole member of the family Eschrichtiidae and the most primitive surviving baleen whale. In structure it is remarkably similar to the extinct cetotheres, which were ancestral to all living baleen whales. The gray whale became extinct in the North Atlantic only a few centuries ago and is now a relict species confined to neritic waters of the North Pacific Ocean and adjacent waters of the Arctic Ocean (Fig. 1).

Because gray whales swim slowly and congregate in near-shore waters, they were easy prey to whalers. By the turn of the century, the species was almost extinct. Since 1946, the eastern Pacific stock has increased under the legal protection afforded by the International Convention for the Regulation of Whaling to the point that commercial utilization may again be advocated.

Gray whales are the only large whales that can regularly be observed in large numbers from shore. Their annual passage along the coast of California is one of the world's outstanding wildlife spectacles. Public interest in gray whales is increasing, and they have become an important tourist attraction in southern California. More than a million people visit Cabrillo National Monument on Point Loma, San Diego, each year to watch the migrating whales, and several sport-fishing companies in San Diego and San Pedro profitably operate "whale watching" cruises (Rice, 1961).

The abundance and accessibility of gray whales in their calving lagoons and along the coast is also attracting a growing number of experimental biologists, and there is cause for concern that, especially on the calving grounds, repeated harassment of gray whales

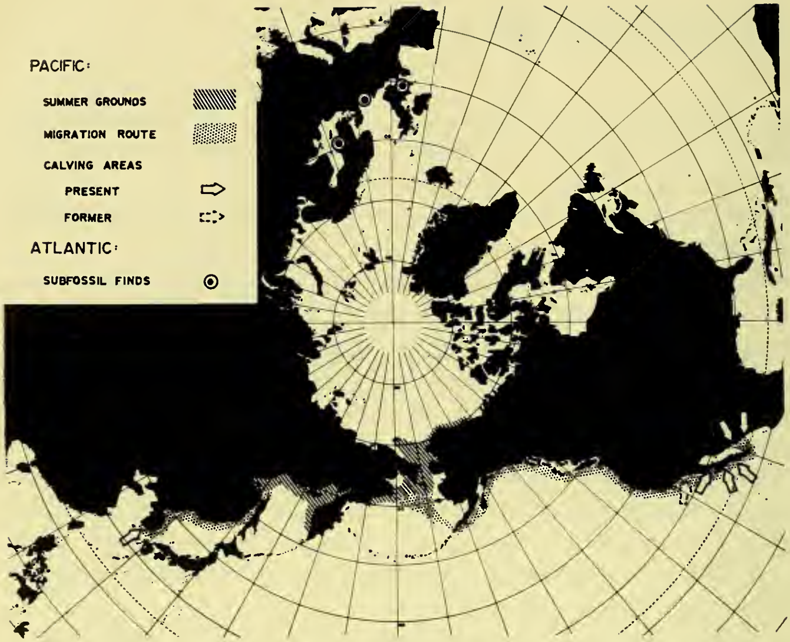

FIG. 1. Distribution of the gray whale. A few gray whales spend the summer in the migration area, especially along the coast of Washington and Oregon.

by investigators using small boats or aircraft in attempts to implant telemetering and tracking devices or drug darts may deleteriously affect reproduction (Schevill *et al.*, 1967; American Society of Mammalogists, 1967). Another threat to the survival of the gray whale is increasing industrial development and boat and ship traffic in the remaining calving lagoons (Marx, 1966). The species has long since been driven from San Diego Bay.

The gray whale is clearly an important species from the standpoint of basic scientific interest, esthetic appeal, and economic significance. If commercial exploitation is resumed it should be limited to the sustainable yield so that the scientific and esthetic values of the population may be preserved. A wise management program must be based on a sound knowledge of the biology of the species.

Beginning with Scammon's (1874) classic account, the gray whale has been the subject of many field observations (for example, Gilmore, 1960*a*, 1960*b*; Hubbs, 1959; Hubbs and Hubbs, 1967; Pike, 1962*a*). As a result, certain facets of its life history and ecology, such as distribution, migrations, and behavior, are better known than for other baleen whales.

Only five biologists have had the opportunity to examine series of gray whales. Andrews (1914) studied 23 specimens taken during southward migration and brought into the shore station at Ulsan, Korea, in January and February 1912. In his monograph he presented a historical review of earlier research on the species. Zenkovich (1934*a*, 1934*b*, 1937*a*, 1937*b*, 1937*c*) examined 104 gray whales aboard the Soviet floating factory *Aleut* during the summers of 1933 through 1936. Tomilin (1937) examined 54 specimens aboard the *Aleut* in August and September 1934. Unfortunately, neither Andrews, Zenkovich, nor Tomilin recorded reproductive information other than measurements of fetuses and condition of mammary glands. Pike (1962*a* and unpublished data) examined 10 northward migrating gray whales killed under a special scientific permit and brought into the shore station at Coal Harbour, British Columbia, during the first week of April 1953. Zimushko (1969*a*, 1969*b*) reported on 63 gray whales collected off the Chukotsky Peninsula in the summer and autumn of 1965 and 1966.

Few other original data based upon examination of dead gray whales have been published. Gilmore (1960*a*) and Eberhardt and Norris (1964) examined a number of dead calves at Laguna Ojo de Liebre, Baja California, and Maher (1960) reported on several whales killed by Eskimos at Barrow, Alaska.

Statistical data from commercial catches of gray whales in Baja California and in the Bering Sea were analyzed by Risting (1928). Unfortunately, his data are unreliable, because body lengths were estimated rather than measured (see Mackintosh and Wheeler, 1929, p. 273), and therefore the conclusions concerning fetal growth and size at sexual maturity are not valid. Mizue (1951) presented statistical data from gray whale catches in Korea.

The Bureau of Commercial Fisheries began a program of research on the species in 1952 under the leadership of Raymond M. Gilmore. During the first five years, the work consisted of field observations and censuses designed primarily to determine the extent of the calving grounds and to document fluctuations in population size (Gilmore, 1960*a*, 1960*b*).

In 1958, responsibility for whale research was transferred to the Marine Mammal Biological Laboratory in Seattle, Washington, under the direction of the senior author. Beginning in 1959, small series of gray whales have been periodically collected to obtain basic data on all aspects of the life history and ecology of the species. Particular emphasis has been given to reproduction, growth, age, and population structure. As collections and observations had to be made incidentally to studies on rorquals and sperm whales, they have been mostly confined to the periods when the gray whales were on migration along the coast of California. This report presents the results of the study from 1959 through February 1970.

NOMENCLATURE

THERE has long been a controversy over the correct scientific name of the gray whale. *Eschrichtius robustus* (Lilljeborg, 1861) is used here for the extinct Atlantic and the living Pacific populations of gray whales following Cederlund (1939). As the data and conclusions of this author have been mostly ignored by subsequent workers, none of whom has contributed new evidence to refute his conclusions, it seems desirable to briefly review the nomenclature of the gray whale.

The generic name *Eschrichtius* Gray (1864) is now used by virtually all taxonomists. There are three available species-group names (Hershkovitz, 1966) that require consideration. These are, in order of priority: (1) *Balaena gibbosa* Erxleben (1777), based on the New England "scrag whale" described by Dudley (1725); (2) *Balaenoptera robusta* Lilljeborg (1861), based on subfossil skeletal remains from Gräsö, Sweden; and (3) *Agaphelus glaucus* Cope (1868), based on gray whales from the coast of California. Two questions must be resolved: (1) which of the first two names should be used for the Atlantic population, and (2) is the Pacific population taxonomically distinct from the Atlantic population?

The applicability of Erxleben's name *gibbosa* to the gray whale depends upon the identity of Dudley's "scrag whale." Dudley's (1725) brief description reads as follows: "The Scrag Whale is near a-kin to the Fin-back, but, instead of a Fin upon his Back, the Ridge of the Afterpart of his Back is scragged with half a Dozen Knobs or Nuckles; he is nearest the right Whale in Figure and for Quantity of Oil; his Bone is white, but won't split." The lack of a dorsal fin, knobs on the back, and white baleen are diagnostic of the gray whale. It seems improbable that Dudley's description of the scrag whale is inaccurate because all other large whales described by him are readily recognizable. On the other hand, there are minor discrepancies between Dudley's description of the scrag whale and the gray whale. For one thing, the oil yield is too high; Scammon (1874) stated that right whales yielded an average of 60 barrels, but that gray whales produced only 20 with a maximum of 60 or 70. For another, the number of knobs on the back is too few; gray whales have nine to 14 knobs behind the dorsal hump, although the posterior knobs are weakly defined. These discrepancies might seem minor were it not for the fact that no other account of early whaling gives any indication of the occurrence of *Eschrichtius* in the North Atlantic (True, 1904) and the fact that the term "scrag" or "scragg" was applied to different kinds of whales, particularly small, lean, right whales (Allen, 1916; Eschricht and Reinhardt, 1866). As the identity of Dudley's scrag whale can never be unequivocally determined, we agree with Cederlund (1939) and Schevill (1952) that Lilljeborg's specific name should be used for the Atlantic gray whales.

The question of the taxonomic relationship of the Pacific and Atlantic gray whale stocks has been investigated by van Deinse and Junge (1937) and Cederlund (1939), who compared the subfossil skeletal material from the Atlantic with skeletons and published data and photographs of Pacific gray whales. These authors found no consistent differences between the Atlantic and Pacific specimens and concluded that these populations were conspecific.

FIELD AND LABORATORY PROCEDURES

Collection of Specimens

A total of 316 gray whales was examined. These were collected by the whale catcher boats of the Del Monte and the Golden Gate Fishing Companies, Richmond, California, under special scientific permits issued to the Marine Mammal Biological Laboratory. The whales were taken along the coast of central California between Half Moon Bay (37°30′ N lat.) and Point Reyes (38°00′ N lat.).

The collections were scheduled to provide representative samples for the periods of the southward (December to January) and northward (February to April) migrations. The total sample included 180 southbound migrants (85 males, 95 females) and 136 northbound migrants (81 males, 55 females). Dates of collection, numbers of specimens (in parentheses), and persons who made the examinations and measurements are as follows: 23 to 26 February 1959 (two) Rice; 27 to 30 March 1962 (four) Rice; 14 to 25 March 1964 (20) Rice; 22 to 29 March 1966 (26) Rice, Wolman, Balcomb; 14 December 1966 to 19 January 1967 (95) Rice, Wolman, Ekberg, Kasuya; 21 February to 9 March 1967 (30) Wolman, Ekberg; 14 to 25 January 1968 (35) Rice, Wolman; 26 February to 11 March 1968 (24) Wolman, Lenheim; 2 to 11 April 1968 (seven) Rice, Wolman; 20 December 1968 to 9 January 1969 (50) Rice, Lenheim; 2 to 16 March 1969 (23) Wolman, Lenheim.

Whales were delivered to the shore stations of the Del Monte and Golden Gate Fishing Companies at Point San Pablo, Richmond, California, where the following data were recorded.

Measurements and Counts.—Twenty-two standard external body measurements of the first 177 whales collected were made with a steel tape graduated in centimeters. A preliminary analysis revealed that many of these measurements were redundant, imprecise, or useless. Consequently, only nine measurements were made on the last 139 specimens. These were: total length (straight line from tip of snout to notch of flukes); head length (from tip of snout to occipital condyles); tail length (from notch of flukes to anus); maximum girth of body (determined by measuring from the mid-dorsal line to the mid-ventral line on the side of the whale that was uppermost as the animal lay on the flensing deck and multiplying by two); span of flukes; breadth of flukes (from notch to nearest point on leading edge); anterior length of flipper; posterior length of flipper; and maximum width of flipper. Sixteen skulls and one complete skeleton were collected for cranial measurements. Throat grooves, baleen plates, and knobs on the dorsal ridge of the caudal peduncle were counted on most specimens.

BODY WEIGHTS.—Weights of six whales were determined by summing the weight of the meat produced after it had been packaged in 50-pound (22.7 kilogram) bags and the weights of the blubber, viscera, and bones, which were determined by weighing each truckload of raw material on commercial truck scales. One near-term fetus was weighed in pieces.

ECTOPARASITES AND EPIZOITES.—Abundance, position, and sizes of ectoparasites and epizoites on the body surface and baleen plates were recorded, and a series of each species was collected for identification.

SCARS.—The nature and position of any scars and wounds were noted.

BLUBBER THICKNESS.—Thickness of the blubber was measured (to the nearest half centimeter) at a mid-lateral point on the body opposite the dorsal hump.

MAMMARY GLANDS.—Development of the mammary glands and presence or absence of secretory activity was noted. Maximum thickness of the glands, as determined by inspection, was measured to the nearest half centimeter. A small portion of mammary gland tissue was fixed in 10 per cent formalin or FAA (10 parts formalin, 30 parts isopropanol, 5 parts acetic acid, 55 parts water), sectioned at 10 microns, and stained with hematoxylin and eosin. The development of glandular tissue subsequently was determined by projecting a randomly selected section about one-quarter of a square centimeter onto a sheet of paper on which 100 dots were arranged in a regular 10 by 10 grid; the number of dots falling within glandular areas was used as an index of the proportion of glandular tissue.

OVARIES.—The ovaries of each female were collected and fixed in 10 per cent formalin. The preserved ovaries were weighed to the nearest hundredth of a kilogram and serially sectioned at half a centimeter on a mechanical meat slicer. Each corpus luteum and corpus albicans revealed through sectioning was measured, to the nearest millimeter, across its greatest diameter and across its maximum diameter at right angles to the greatest diameter; and the two measurements were averaged. The maximum diameter of the largest Graafian follicle also was measured to the nearest millimeter.

UTERUS.—The diameter of each uterine horn at approximately the middle was measured to the nearest half a centimeter. A sample of the uterine wall was fixed in 10 per cent formalin or FAA, sectioned at 10 microns, and stained with hematoxylin and eosin for histological study. In specimens in which a corpus luteum or recently ovulated follicle was present in either ovary, but there was no obvious indication of pregnancy, the entire uterus was removed from the carcass, each uterine horn slit open along its entire length, and the surface of the endometrium carefully searched. Embryos and small fetuses were preserved in 10 per cent formalin and their length (crown to tip of tail, with body straightened) and sex recorded. Standard body measurements were made on near-term fetuses and the sex was noted.

TESTES.—Each testis was weighed to the nearest tenth of a kilogram at the whaling station. A small sample (1 to 2 cubic centimeters) of the largest testis of each whale was taken for microscopic examination from the middle of the gonad about halfway between the surface and center and fixed in FAA, 10 per cent formalin, or Bouin's solution. Specimens were sectioned at seven microns and stained with hematoxylin and eosin. Mean diameter of the seminiferous tubules was calculated from measurements with an ocular micrometer of the greatest diameter and maximum diameter at right angles to the greatest diameter of 20 tubules cut in cross section. The presence or absence of fluid in the epididymides and deferent ducts was noted.

PENIS.—The length of the extruded penis from the base on the ventral surface to the tip and the circumference at the base were measured to the nearest centimeter. These measurements could not be made on some males, especially immature individuals, because the penis was not completely extruded.

STOMACH CONTENTS.—The quantity of any food remains in the stomach was estimated and a sample preserved for identification.

ENDOPARASITES.—The stomach, intestine, liver, kidneys, lungs, peribullary sinuses, and blubber were examined for endoparasites. The intestine was slit open at three or more randomly selected points, and in the years 1967, 1968, and 1969 the rectum also was opened for inspection. The tips of the liver lobes were examined for evidence of cirrhosis and were sliced to reveal the bile ducts. The kidneys were slit to expose the main urinary duct.

VERTEBRAL EPIPHYSES.—The degree of fusion of the epiphyses of the anterior thoracic vertebrae to their centra was determined by chopping into the ends of the vertebrae with a hatchet to a depth of several centimeters.

EAR PLUGS.—An attempt was made to collect at least one ear plug from each whale. In a few animals, however, the plug was so soft that it could not be successfully removed. Ear plugs were preserved in 10 per cent formalin. They were bisected longitudinally and gently polished on a whetstone, so that the growth layers could be counted.

BALEEN PLATES.—Several of the longest baleen plates were collected from each whale. Variations in thickness of the plates were recorded graphically by means of an apparatus similar to that used by Ruud (1940).

Field Observations

Observations on living gray whales were made from coastal lookout points, chartered whale catcher boats, and light aircraft.

Coastal Stations.—During the southward migration in 1967–68, 1968–69, and 1969–70, coastal lookout stations were established to count migrating whales. One was on Point Loma at San Diego, California (32°40′ N lat.), 130 meters above sea level (Rice, 1961) and is the site where previous counts were made (Gilmore, 1960*a*, 1960*b*; Rice, 1961). This station was manned for 52 days (27 December to 16 February) in 1967–68 and for 57 days (20 December to 14 February) in 1968–69. The second station was 2 km. S Yankee Point, Monterey Co., California (36°29′ N lat.), 23 meters above sea level and about 100 meters back from the shoreline. This was near the site where a partial count of migrating gray whales was made in 1966–67 (Adams, 1968). We manned this station for 49 days (18 December to 4 February) in 1967–68, 60 days (10 December to 7 February) in 1968–69, and 64 days (8 December to 9 February) in 1969–70.

Observations were made continuously from 0700 to 1700 hours (essentially sunrise to sunset) each day. At each station, two observers each worked a 5-hour shift; morning and afternoon shifts were alternated between the two observers. The number of whales, time of passage, estimated distance from shore, and direction of travel were recorded for each group sighted. Wind direction and force, cloud cover, precipitation, and fog were logged throughout the day.

Vessels.—Between 25 January and 9 February 1968, we ran a series of transect cruises between Point Loma and a position west of Tanner and Cortez Banks. A similar transect was run off Yankee Point on 18 January 1968. While the vessel was underway, a constant watch for gray whales and other marine mammals was maintained on the bridge. All whales sighted were approached closely enough to ensure positive identification and the number of whales in each pod, the direction of travel, and the position and time of sighting recorded.

Observations on gray whales also were made during many cruises conducted for marking rorquals (Balaenopteridae) and sperm whales (*Physeter catodon*). The area covered included the waters along the coast from Point Reyes, California (38° N lat.), south to Isla Clarion off Colima, Mexico (18° N lat.). The cruises, totaling 15 months, were made mostly between December and April from 1962 to 1969. The calving grounds in Laguna Ojo de Liebre, Laguna Guerrero Negro, Laguna San Ignacio, and Bahia Magdalena, Baja California, were briefly visited. Gray whales were sighted on 304 occasions, and a total of 1045 individuals was recorded.

Aircraft.—On 25 and 26 March 1969, an aerial survey was made in both directions along the entire coast beween San Francisco, California (38° N lat.), and Cape Flattery, Washington (48° N lat.). Two aircraft (a Cessna 177 and a Cessna 185) were used, each with two observers in addition to the pilot. The flight path was 0.3 to 2.0 kilometers offshore at an average altitude of 230 meters and air speed of 200 kilometers per hour. When pods of whales were sighted they were often circled at a lower altitude. Data were recorded on a tape recorder. Sighting conditions were optimum, with calm seas and clear skies, throughout the period of the survey.

SEASONAL MIGRATORY CYCLE

Gray whales now occur only in the North Pacific Ocean and adjacent waters of the Arctic Ocean. The species also existed in the North Atlantic until a few centuries ago. There are presently two geographically isolated stocks (Fig. 1): an eastern Pacific stock, which migrates between Baja California and the Bering and Chukchi seas, and a western Pacific stock, which migrates between South Korea and the Okhotsk Sea. These may be designated the California stock and the Korean stock, respectively, on the basis of their breeding grounds.

California Stock

Summer Grounds.—From late May through October, gray whales occupy the shallow waters of the northern and western Bering Sea, the Chukchi Sea, and the western Beaufort Sea. They are common along the Koryak coast of Siberia from Cape Navarin to Glubokoi Inlet (Berzin and Rovnin, 1966). Farther to the southwest they are rare; a few have been seen as far as Kronotskiy Bay on the Kamchatka Peninsula (Tomilin, 1957) and the Kommandorskiye Islands (Barabash-Nikiforov, 1938; Grebnitskii, 1902). In the Gulf of Anadyr, these whales are abundant along the southwest shore from Cape Navarin to Tymna Lagoon; they have not been seen in the northwestern part of the gulf from the Anadyr Estuary to Cape Kresta (Berzin and Rovnin, 1966). Gray whales are also common along the northeastern shore of the Gulf of Anadyr, from Cape Retkon to Cape Chaplino (Berzin and Rovnin, 1966), around St. Lawrence Island (Ichihara, 1958), around the shores of the Chukotskiy Peninsula as far northwest as Cape Serdtse Kamen' (Nikulin, 1946), in Kotzebue Sound (Wilke and Fiscus, 1961), and in the Chukchi Sea (north as far as 69° N lat.—Nasu, 1960). A few go westward along the coast as far as Tynkurginpil'gyn Lagoon (Berzin and Rovnin, 1966), and northwestward through the pack ice as far as Wrangel Island (Sleptsov, 1955).

Along the Arctic coast of Alaska they are found regularly from Cape Thompson (Pike, 1962*a*) east to Point Barrow, and a few have been reported by Eskimos along the shores of the Beaufort Sea as far east as Barter Island (Maher, 1960). To the southeast, there are few records of gray whales. One was found stranded at Scammon Bay, south of the Yukon Delta, in September (Fay, *in* Pike, 1962*a*). There is only one published record of gray whales from the Pribilof Islands (Gilmore, 1960*b*), but several were seen around St. George Island in the summers of 1965 and 1968 by C. H. Fiscus, A. M. Johnson, and V. B. Scheffer (personal communication). Gray whale remains have been found on St. Matthew Island (Pike, 1962*a*), and C. H. Fiscus (personal communication) saw four gray whales in Sarichef Strait between St. Matthew Island and Hall Island on 3 August 1960.

Not all gray whales migrate to the Arctic in the summer. A few remain scattered along the west coast of North America. Pike and MacAskie (1969) reported several near Langara, Queen Charlotte Islands, British Columbia, in late August and early September of 1959 and 1960, and a young male stranded near Ucluelet, Vancouver Island, on 16 August 1966. Some were seen near Lapush, Washington, in June and July 1961 by C. Munsen (personal communication) and in July 1967 by the junior author. A few were seen near Kalaloch, Washington, in July 1968, by A. M. Johnson (personal communication). Fiscus (personal communication) saw one near Cannon Beach, Oregon, in July 1969. Gilmore (1960*a*) reported that a few regularly spend the summer in the vicinity of St. George Reef and Pelican Bay in northern California and southern Oregon. Whalers working off San Francisco occasionally see gray whales during the summer. L. Newton (personal communication), captain of the catcher boat "Lynnann," saw a few near the Farallon Islands, California, throughout the summer of 1964; they remained until late September or early October. K. C. Balcomb saw a small gray whale in Bahia Magdalena, Baja California, on 11 June 1965, during one of our whale marking cruises aboard the catcher boat "Sioux City."

The northern boundary of the known summer range of the gray whale corresponds closely with the southern edge of the zone of close pack ice during the period 1 to 15 September (U. S. Navy Hydrographic Office, 1958). Close pack ice may limit their movements. Scammon (1874) and Sleptsov (1955) have reported seeing gray whales in broken pack ice. Gray whales do not arrive at Point Hope or at Barrow, Alaska, until most of the ice has gone out, long after the bowhead whales have arrived. As few observers experienced in identifying whales enter the close pack ice in ships or fly over it in the summer, the extent to which gray whales penetrate the pack ice is unknown. In the western Bering Sea, gray whales are confined to coastal waters, their seaward range being delimited by the edge of the Continental Shelf. They have never been found in the deep waters of the southwestern Bering Sea. Their feeding habits (see section on food and feeding) apparently restrict them to shallow water. Although most of the eastern Bering Sea is shallow, the scarcity of gray whales there is ✓ believed to be the result of a low biomass of benthos, 55 grams per square meter, compared with 200 to 900 grams per square meter in the northwestern region (Berzin and Rovnin, 1966; Neiman, 1963).

Migrations.—Pike (1962*a*) summarized all published information on the migration route of the California population and presented significant new data. There are few observations on southward-migrating whales in the northern part of their range. From October through January, they probably move down the eastern side of the Bering Sea, go through Unimak Pass, and then follow the coast to Baja California. A few go around Cabo San Lucas and cross to the eastern side of the Gulf of California. From late February to June, the northward migration of males and females without calves, which is much better documented, follows the reverse route.

Our observations during whale marking cruises off California and Baja California show that the majority of gray whales migrate within a few kilometers of shore when passing points, headlands, and sectors of coastline where the Continental Shelf is narrow and ✓ there are no off-lying islands. Many tend to take the most direct route, however, when crossing bights and indentations of the coastline. For example, many southbound whales, after passing Point Conception (34°27′ N lat.), head southeast through the Channel Islands, passing as much as 200 kilometers offshore from the mainland of southern California (Rice, 1965). Some gray whales make a similar offshore passage from about Punta Baja (29°57′ N lat.)

to Isla Cedros (28°22′ N lat.), Baja California, thus avoiding the long journey around the shores of Bahia Sebastian Vizcaino. Quantitative data on offshore migration are presented in the chapter on populations.

The route taken by females with calves during the spring migration is unknown. During this study, the catcher-boat crews saw only one female with a calf—near Point Reyes on 15 March 1969. From 1959 through 1967, we collected no gray whales later than 30 March, and during that time we thought females with calves moved north later in the season. Therefore, in 1968 we hunted gray whales until 25 April, 14 days after the last whale was taken, and had one boat searching exclusively for females with calves from 2 to 25 April. Each year from 1956 through 1968, the regular sperm whaling season opened on 1 April and the baleen whaling season opened on 1 May (1956–59) or 16 April (1960–68). During these years, the whalers never saw a gray whale accompanied by a calf. Shore-based whalers working from San Simeon, California, in the 1880's likewise told Townsend (1887) that they never encountered females with calves.

On whale marking cruises in 1965, 1966, 1967, and 1969, we traveled north during late February, March, and early April, by which time most females with calves had already left the calving lagoons. We put in at many points along the coast between Cabo San Lucas (23° N lat.), Baja California, and San Francisco (38° N lat.), California, but never encountered a female accompanied by a calf, although we saw many northward-migrating gray whales. During the transect cruises, we saw two females with calves on 10 February 1968 (at 32°48′ N and 118°08′ W, heading west-northwest ✓ near San Clemente Island). During the aerial surveys between San Francisco, California, and Cape Flattery, Washington, on 25 and 26 March 1969, no females with calves were identified among 816 gray whales sighted. Morejohn (1968) reported a female with a calf at Moss Landing, northeast of Monterey, California, on 2 May 1967.

Gray whales observed on migration are usually swimming steadily and continuously in a constant direction on a course ✓ parallel to the shore. They surface regularly about every 3 to 5 minutes to blow three to five times. When out of sight of land, they usually travel in a straight line. General observations indicate that the usual swimming speed is about 7 to 9 kilometers per hour (4 to 5 knots). Wyrick (1954) followed four separate gray whales migrating south past San Diego, California, for a total of more than 5 hours; their average speed was 8.5 kilometers per hour (4.6 knots). Cummings *et al.* (1968) tracked nine lone whales (some in daytime, others at night), over distances less than 1.7 kilometers and found the average speed to be 10.2 kilometers per hour (5.5 knots).

There was no consistent hourly variation in the number of gray whales migrating south past the counting stations, contrary to the opinion of Ramsey (1968). This lack of variation indicates that gray whales, on the average, maintain a constant speed throughout daylight hours.

There are few observations to show how fast gray whales travel at night. Unlike sperm whales, baleen whales are rarely, if ever, seen resting at the surface. Since they must rise to the surface regularly every few minutes to breathe, they must continue to swim at least slowly during hours of darkness. In polar regions during the summer when daylight is continuous, baleen whales appear to remain active continuously.

Cummings *et al.* (1968) used an array of hydrophones mounted on the sea bottom off San Diego to track migrating gray whales. They reported the following: "Gray whales were soniferous day and night. One hundred twenty-four signals were recorded from at least 61 whales between 1800 and 0600 h, compared with 107 signals recorded from at least 157 whales between 0600 and 1800 h. All whales seen or heard at night apparently were migrating southward, and there was no evidence of the popular notion that gray whales characteristically stopped migrating at night to rest or to sleep."

The average speed of gray whales along their entire migration route, calculated from dates of peak passage at various points along the coast, is about 185 kilometers per day, or 7.7 kilometers per hour, on the southward migration and half as fast on the northward migration (Pike, 1962*a*). If their average speed during the 10 hours of daylight is 8.5 kilometers per hour, they cover 85 kilometers; to travel the remaining 100 kilometers during the 14

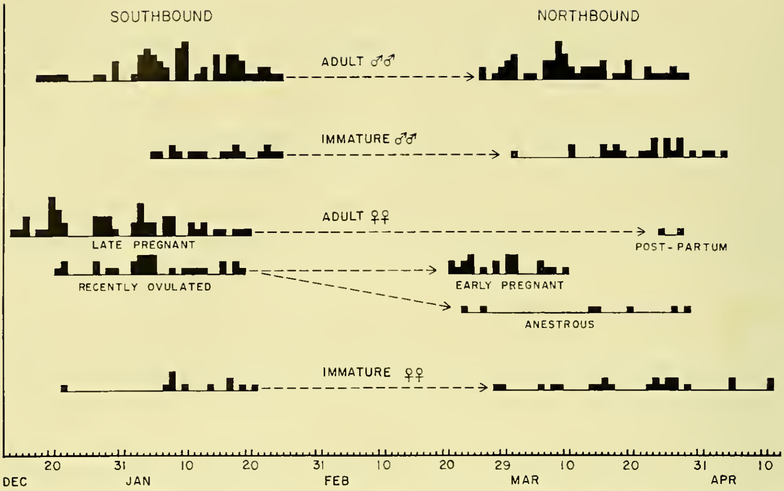

FIG. 2. Collection dates of gray whales, according to sex, age, and reproductive status. Each square represents one animal.

hours of darkness, they must average 7.1 kilometers per hour, or 92 per cent of their speed during daylight.

During migration, there is a partial temporal segregation of gray whales according to sex, age, and reproductive status. This is evident from Fig. 2 in which the collection date of each whale is plotted according to sex, maturity, and reproductive status. These data cannot be regarded as strictly representative, however, because the collecting effort was not the same throughout the season. It must be kept in mind also that the gunners doubtless tended to select the larger animals, even though we imposed no size limitations. This tends to bias the sample in favor of mature animals and females, especially those in late pregnancy. The mean and extreme dates of passage for each class (Table 1), however, should be fairly reliable.

In general, in both the southward and the northward migration, females migrate earlier than males and adults migrate earlier than sexually immature animals. The vanguard of the southward migration from mid-December to the first of January is composed predominantly of females carrying near-term fetuses. The late-pregnant females are followed by adult females that have recently

TABLE 1

MEAN PASSAGE DATES OF MIGRATING GRAY WHALES OFF CENTRAL CALIFORNIA (38° N LAT.) CLASSIFIED ACCORDING TO SEX, AGE, AND REPRODUCTIVE STATUS.

Category	Mean passage date		Days elapsed
	Southbound	Northbound	
Late pregnant (southbound); postpartum females (northbound)	31 December	26 March	85
Recently ovulated (southbound); early pregnant females (northbound)	5 January	28 February	54
Recently ovulated (southbound); metestrous and anestrous females (northbound)	5 January	14 March	68
Immature females	11 January	21 March	69
Adult males	9 January	12 March	62
Immature males	15 January	23 March	67

ovulated but have no macroscopically visible conceptus in the uterus; most of these females presumably weaned a calf a few months previously. The number of females in this class that were collected was fewer than expected. This probably resulted from gunner selection, although there also is a possibility that such females travel farther offshore. Next to pass are the immature females and, at about the same time, the adult males. Last to pass are the immature males.

During the northward migration, the first to pass are the newly pregnant females, which comprised the recently ovulated class of the preceding southward migration. Most of them pass within a limited period of about 15 days. We took them only between 21 February and 7 March in 1967, and between 26 February and 10 March in 1968. None was taken in 1969, when collecting did not commence until 2 March. The peak passage of adult males occurs more than 2 weeks later than that of the pregnant females. Adult males are followed by a few anestrous females that have failed to conceive. Immature whales of both sexes are the last to pass. Only two postpartum females were collected, both in late March. Neither was lactating; obviously their calves were stillborn or were lost shortly after birth.

Migrating gray whales travel singly or in pods of up to 16 individuals. In the course of the southward migration past Cali-

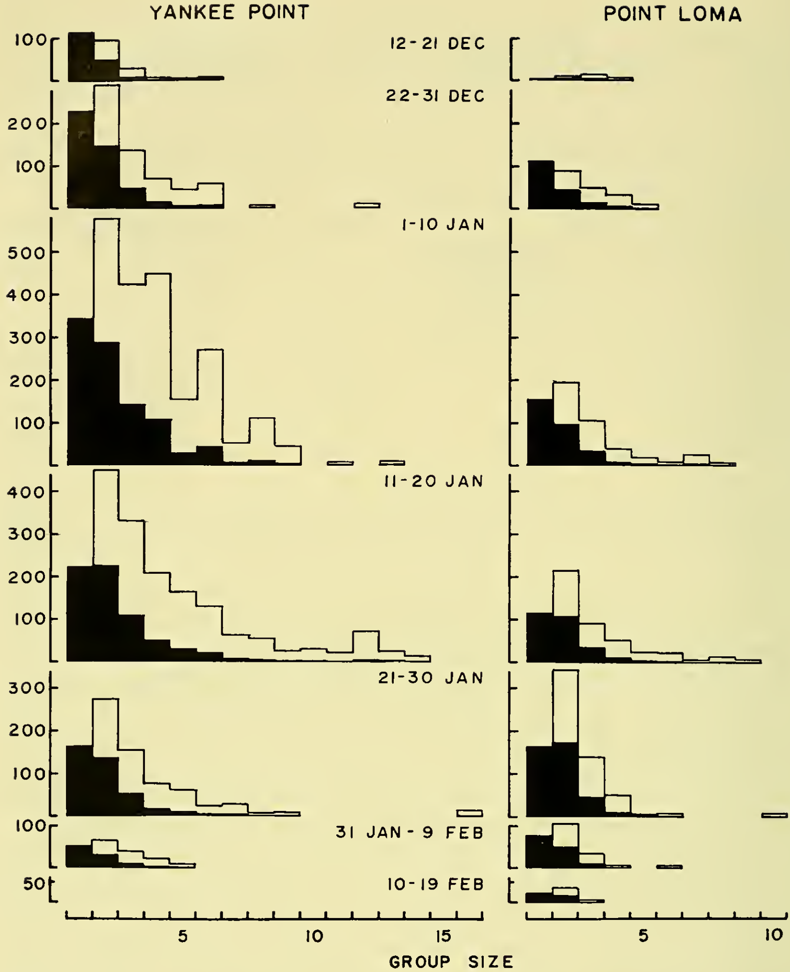

Fig. 3. Frequency distribution of group size of gray whales passing Yankee Point and Point Loma, by 10-day periods, during the southward migrations of 1967–68 and 1968–69. Solid bars indicate the number of groups, open bars the number of whales.

fornia, there are marked changes in the sizes of the groups (Fig. 3). During the early part of the migration, single whales (presumably mostly females carrying near-term fetuses) predominate, and almost no whales are in groups of more than six. During the remainder of the migration, groups of two predominate. Most of the larger groups pass in the middle of the season, and towards the end of the season no groups contain more than five whales.

Winter Grounds.—In January and February most gray whales of the eastern Pacific population are in warm temperate or tropical waters on the west coast of Baja California and the southern Gulf of California. Our southernmost sighting was at Punta Mita, Bahia de Banderas, Jalisco (20°45′ N, 105°34′ W) on 17 February 1965. Gilmore (1960*a*) reported alleged sightings of gray whales at Isla Guadalupe and at Isla Clarion; we have seen none there nor anywhere else far off the coast of Mexico.

Most calves, as far as is known, are born in certain shallow lagoons. The six known calving areas, charted in detail by Gilmore (1960*a*), are as follows: *California and west coast of Baja California*—San Diego Bay (no longer occupied), Laguna Ojo de Liebre ("Scammon's Lagoon") and the adjacent Laguna Guerrero Negro, Laguna San Ignacio, and Bahia Magdalena and adjacent waters (including Bahia Almejas, Canal San Carlos, Estero Soledad, Estero Santo Domingo, Estero Las Animas); *eastern shore of Gulf of California*—open coast south of Yavaros, Sonora (see Gilmore *et al.*, 1967), and Bahia Reforma, Sinaloa.

Korean Stock

There is little information on the distribution of the Korean stock. No gray whales have been reported in recent years in either the Okhotsk Sea or the Sea of Japan, according to (personal communications) V. A. Arseniev and M. V. Ivashin of the All-Union Research Institute for Marine Fisheries and Oceanography, Moscow; H. Omura of the Whales Research Institute, Tokyo; and M. Nishiwaki of the Ocean Research Institute, Tokyo.

Summer Grounds.—Gray whales occupy, or at least formerly occupied, the northern Okhotsk Sea. They penetrated as far north as Penzhinskaya Bay (Krasheninnikov, 1755), and ranged southward as far as Akademii and Sakhalinskiy gulfs on the west (Sleptsov, 1955), and the mouth of the Kikhchik River on the east (Ditmar, 1890).

Migrations.—The migration route of the Korean stock of gray whales lay along the mainland coast of eastern Asia from Tatarskiy Strait to South Korea. Southbound whales passed Ulsan, South Korea, from late November to late January, and northbound whales passed there from the middle of March to the middle of May (Andrews, 1914). All the whales apparently passed through Tatarskiy Strait, as none was ever seen in La Perouse Strait between northern Hokkaido and southern Sakhalin (Mizue, 1951).

Winter Grounds.—The channels, inlets, and bays along the southern coast of South Korea are believed to have been the winter calving grounds of the western Pacific gray whales. According to Andrews (1914): "In November and December, when the females are taken, almost every individual will be found to be carrying young nearly ready for birth. As these would necessarily be delivered within two or three weeks after passing Ulsan, the birth must occur in the bays among the numerous islands at the extreme southern end of the peninsula. Indeed Captain H. G. Melsom, who has hunted gray whales for 15 years along the Korea coast, has often observed them in this vicinity, but because of the abundance of other and more valuable species, they are not killed at this time by the Japanese."

Atlantic Stocks

Subfossil gray whale bones have been found at five localities along the coast of northwestern Europe: Pentuan, Cornwall, and Torquay, Devonshire, England, on the English Channel; IJmuiden and Wieringermeer Polder in the Netherlands; and on the Island of Gräsö, Sweden, in the northern Baltic (van Deinse and Junge, 1937). The most recent bones are those from IJmuiden, which date from about A.D. 500. There are no historical records of gray whales in the eastern North Atlantic. The summer grounds of the eastern Atlantic gray whales probably were in the Baltic Sea, where *Ampelisca macrocephala* (the predominant food of the California stock in the Bering Sea) is abundant (Kanneworff, 1965). Their winter grounds were perhaps along the Atlantic or Mediterranean coasts of southwestern Europe or northwestern Africa.

Discussion and Conclusions

In their annual migrations between summer feeding grounds in Arctic waters and winter breeding grounds in subtropical waters, gray whales may travel more than 18,000 kilometers each year, a distance exceeding that traveled by any other baleen whale. This extensive migration, spanning 50 degrees of latitude, exposes them to a broad range of environmental conditions. Sea surface temperatures on the summer grounds range from about 8° centigrade down to 0° or slighly less in the pack ice. On the winter grounds, temperatures range from about 18° centigrade at the latitude of Laguna Ojo de Liebre to 22° off Cabo San Lucas. In midsummer most gray whales experience more than 22 hours of light each day, and those north of the Arctic Circle experience continuous daylight for several weeks. As the whales migrate southward, they are subjected to a rapidly decreasing photoperiod, which reaches a minimum of less than 8 hours in early December. Day length increases slowly during the remainder of the southward migration and while the whales are on the winter grounds, and then increases rapidly as the animals move north in the spring. The variable photoperiods to which the species is exposed may be an important proximate factor in regulating gonadal development.

There is no evidence to suggest that gray whales slow down at night while migrating southward. The length of their migration route, and their relatively slow swimming speed, makes it necessary for them to travel almost continuously at night as well as day.

The reasons for this long migration become apparent when the food habits of the gray whale are considered. In summer, the species requires areas of shallow water with an abundant benthos. In the North Pacific, large areas with such conditions are found only in parts of the Bering Sea and adjacent waters of the Arctic Ocean, and in the northern Okhotsk Sea. For almost half the year, the ice cover on these summer grounds cuts off the whales' major food supply and forces them to migrate.

Because they cannot feed much during the winter, it is necessary that they seek warmer waters to minimize energy requirements, particularly for the newborn calves. During the winter, the eastern North Pacific from California north is cold (less than 15° centigrade) and is subject to frequent storms with northwest winds that cause heavy surf along the coast. The lagoons of Baja California are the nearest areas of warm, shallow, protected waters suitable for calving.

Females ready to bear a calf arrive on the winter grounds earlier and spend more time there than females that have recently mated. Apparently, calves must remain in warm protected waters until they have grown sufficiently to face the rigors of the long northward migration. The movements of females with calves after they leave the breeding lagoons are unknown. Unlike the other members of the population, they must travel farther offshore.

Pregnant females apparently are the first to arrive on the summer feeding grounds and spend more time there than lactating females. This is also true of fin whales, *Balaenoptera physalus* (Mackintosh, 1965), and humpback whales, *Megaptera novaeangliae* (Dawbin, 1966), and is no doubt related to the need of pregnant females to acquire more fat reserves (see discussion beyond of seasonal changes in nutritive condition).

FOOD AND FEEDING

Stomach Contents

SUMMER.—Few data are available on the stomach contents of gray whales killed on the summer grounds. Zenkovich (1934*a*, 1934*b*, 1937*c*) and Tomilin (1937) examined 104 and 54 stomachs, respectively, of whales taken in the Bering and Chukchi Seas from August to October. They did not publish quantitative data, but reported finding mostly gammaridean amphipods, of which were listed the following forms: Family Ampeliscidae—*Ampelisca macrocephala*; family Aoridae—*Lembos arcticus*; family Lysianassidae—*Anonyx nugax* and an unidentified species; family Haustoriidae—*Pontoporeia femorata*; family Eusiridae—*Eusirus* sp.; family Atylidae—*Atylus* sp.; family Gammaridae—unidentified species.

Ampelisca macrocephala predominated in the stomachs of whales killed in the Chukchi Sea and northern Bering Sea, whereas a species of Atylidae, apparently *Atylus carinatus,* predominated in those from along the coast between Natal'inskiy Bay and Cape Navarin. In addition to amphipods, several stomachs contained a few bottom-dwelling isopods, mysids (*Mysis oculata*), mollusks (*Buccinum* sp.), polychaetes (*Travisia forbesi*), and hydroids (Sertulariidae).

Pike (1962*a*) examined samples of the stomach contents of two gray whales killed by Eskimos off St. Lawrence Island in May and June. He found mostly the amphipods *Ampelisca macrocephala* and *A. eschrichti,* and a few *Anonyx nugax*; other items recorded were decapod crustaceans (including *Chionoecetes bairdi, Hyas coarcticus,* and *Liocyma fluctuosa*), cumaceans, polychaete (*Pectinaria* sp.) tubes, gastropods, and ascidians.

We examined a sample (collected by F. H. Fay) of the stomach contents of an immature female gray whale killed by Eskimos about 9 kilometers southwest of the village of Gambell, St. Lawrence Island, Alaska, in water about 30 meters deep. The sample of about 1 liter was a composite of random samples from several parts of the total contents of the stomach. More than 95 per cent of the sample consisted of gammaridean amphipods, ranging from less than 6 to more than 25 millimeters in length. A few other invertebrates were present. Following is a complete list of the species identified. Classification of amphipods at the level of family and genus follows Barnard (1969). The numbers of each species of amphipod identified are given in parentheses, but they do not necessarily represent the proportion of each species in the total sample.

- CLASS CRUSTACEA
  - Order AMPHIPODA
    - Family Lysianassidae
      - *Anonyx* sp. (16)
      - *Hippomedon ?minusculus* (1)
      - *Hippomedon* cf. *abyssi* (4)
      - *Orchomene minuta* (12)
    - Family Phoxocephalidae
      - *Paraphoxus ?milleri* (3)
    - Family Ampeliscidae
      - *Ampelisca macrocephala* (*ca.* 85)
      - *Ampelisca* sp. (fragments)
    - Family Pleustidae
      - *Pleustes* sp. (2)
    - Family Oedicerotidae
      - *Acanthostepheia malmgreni* (6)
    - Family Atylidae
      - *Atylus bruggeni* (1)
    - Family Isaeidae
      - *Protomedeia grandimana* (1)
    - Family Ischyroceridae
      - *Ischyrocerus latipes* (1)
    - Family Podoceridae
      - *Dulichia* cf. *knipowitschi* (1)
  - Order CUMACEA
    - *Diastylis bidentata*

- CLASS POLYCHAETA
  - Unidentified tube

- CLASS HOLOTHUROIDEA
  - Unidentified holothurian

- CLASS TUNICATA
  - Order ASCIDIACEA
    - ? *Phallusia* sp.
  - Order THALIACEA
    - ? Salps (attached to polychaete tube)

All of the organisms found in the stomachs of gray whales killed on the Arctic summer grounds are typically infaunal benthic species, that is, they burrow or live buried in the bottom sediments. *Ampelisca macrocephala*, the species most commonly eaten, is a large amphipod about 25 millimeters long. A study of its life history has been published by Kanneworff (1965). In the Bering and Chukchi Seas, *A. macrocephala* occurs mainly on sandy bottoms at depths of 5 to 300 meters (Gur'yanova, 1955).

Most of the amphipods in our sample were adult females, which are rarely found above the substratum during the day, although they form an appreciable part of the planktonic population at night; males alone tend to be pelagic during the day (E. L. Bousfield, personal communication).

In addition to food items, there was a considerable amount of fine gray sand or silt mixed with the stomach contents of the whale from St. Lawrence Island that we examined. Such extraneous material has also been recorded by other authors. Pike (1962*a*) found sand, silt, and bits of wood in the two samples he examined, and Zenkovich (1937*a*) found quantities of pebbles, as much as "2–3 pails," in many stomachs. Tomilin (1937) also reported finding silt, pebbles, and a large cobblestone, in addition to kelp leaves.

In northern California, Howell and Huey (1930) found a quantity of *Euphausia pacifica* in the baleen of a gray whale killed on 21 July 1926; they did not examine the stomach. This euphausiid is the chief food of rorquals in the waters off California.

The occasional infestation of gray whales with parasites that probably require fishes as intermediate hosts (see discussion of parasites in a later chapter) suggests that they sometimes eat fish.

DURING MIGRATION.—Our data confirm the reports by other authors (Andrews, 1914; Pike, 1962*a*; Scammon, 1874) that the stomachs of migrating gray whales are almost invariably empty. Stomachs of all 180 southbound migrants and those of 134 of the 136 northbound migrants examined contained no traces of food, and the intestines contained only small amounts of a thick greenish fluid, apparently bile and mucosal secretions. One of the two specimens containing food was an anestrous female taken on 20 March 1964. Its stomach contained about 20 liters of the zoea stage larvae of the littoral crab *Pachycheles rudis* (Anomura, Porcellanidae) and a few brachyuran zoeae, probably of the genus *Fabia* (Brachyura, Pinnotheridae). The other animal was an immature female taken on 11 April 1968. Its stomach contained about 50 liters of the zoea stage larvae of a pinnotherid crab, probably the same species found in the preceding specimen, and a few scattered porcellanid zoeae, which were in too poor condition to identify further.

Migrating whales sometimes have gravel and other miscellaneous items in their stomachs. We found almost a kilogram of gravel in the stomach of one southbound, recently-ovulated female; mixed with the gravel were numerous ascidian tunics, fragments of hydroid stems and polychaete worm tubes, a few gastropod opercula, one pelecypod shell, and two tiny fragments of waterlogged wood. A late pregnant female had several liters of hydroid stems and a few polychaete tubes in her stomach, but no gravel or sand. The stomachs of two immature males collected during the northward migration each contained about 10 kilograms of gravel. The stomach of an early pregnant female contained about 100 kilograms of gravel in which were a few polychaete tubes, hydroid stems, and a small bit of waterlogged wood. A northbound immature female contained about 50 kilograms of sand and silt. The stomachs of several other animals contained traces of sand and gravel. Andrews (1914) found pebbles in the stomachs of two southbound migrants taken off Korea. Gravel and sand are probably ingested accidentally while the whale is feeding.

WINTER.—Scammon (1874) appears to have been the only person to examine the stomachs of animals taken in the calving lagoons. He examined "several" and found no food—only a small quantity of vegetable matter that was no doubt accidentally ingested.

According to Matthews (1932), Norwegian whalers found gray whales feeding on the "red crab," *Pleuroncodes planipes* (Anomura, Galatheidae), at Bahia Magdalena, Baja California, in 1926. He did not indicate whether this was ascertained by actual examination of stomachs. The red crab exists in both a benthic and pelagic phase (Boyd, 1967) and at times is extremely abundant off the western coast of central and southern Baja California. We found red crabs so abundant in Bahia Magdalena on the night of 6 February 1965 that they formed a continuous, tightly packed layer on the surface, evidently attracted by the lights of our anchored vessel. On 1 March 1967, we passed through many dense shoals of these crabs, each a few meters wide and up to half a kilometer long or longer, just inside the 180-meter isobath about 45 km. SW Punta Abreojos. However, we never saw gray whales that appeared to be feeding on red crabs. *Pleuroncodes* apparently does not occur in Laguna Ojo de Liebre. According to Matthews (1932), Norwegian whalers noticed that the blubber oil obtained from "sei" whales (*Balaenoptera borealis* or *B. edeni*) on the Mexican coast was yellowish; he suggested that this was due to their feeding on *Pleuroncodes.* We have found that the blubber of gray whales is often yellow or orange during both the southward and northward migrations. A similar variation in blubber color was noted by Andrews (1914) in northbound Korean whales and by Zenkovich (1934*a*) in summer-taken specimens from the Bering Sea.

There is only one report on the stomach contents of gray whales on or near the wintering grounds in the western Pacific (Mizue, 1951). Two individuals killed in the northern waters of the Yellow Sea in May 1922 contained *Nephrops thomsoni,* a small benthic anomuran decapod similar to *Pleuroncodes.* These whales were taken unusually late in the spring and probably somewhat outside the normal range.

Seasonal Changes in Nutritive Condition

During southward migration, gray whales are fat, whereas during northward migration they are much thinner. Quantitative information on nutritive condition is provided by body weight, blubber thickness, and oil yield.

BODY WEIGHT.—We calculated and compared body weights of gray whales on southward and northward migrations, and attempted to estimate metabolic rate to determine if the difference between the two periods is sufficient to account for energy requirements in winter.

Weights and lengths of nine gray whales are given in Table 2. To calculate weights of other whales that could not be weighed, we used the formula $W = aLG^2$, where W = weight in kilograms, L = length in meters, and G = maximum girth in meters. The

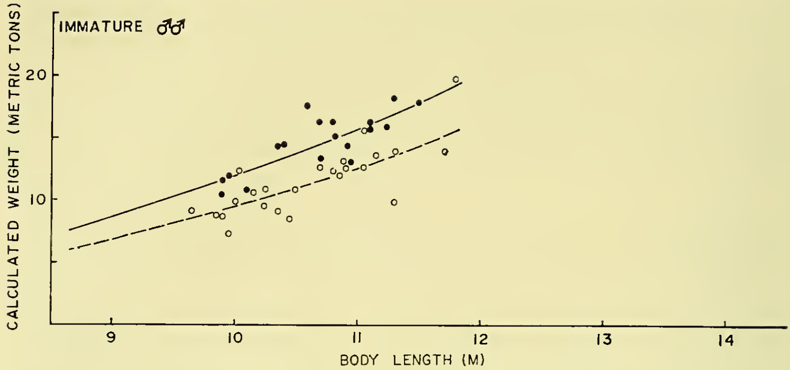

FIG. 4. Comparison of calculated weights of immature male gray whales during the southward and northward migrations. Solid circles and unbroken line indicate southbound migrants; open circles and broken line indicate northbound migrants.

value of *a* was derived from the seven gray whales of known weight, length, and girth (Table 2); this ranged from 32 to 44. The limited data suggest that *a* and body length are not correlated. This lack of correlation is not unexpected, as there is virtually no change

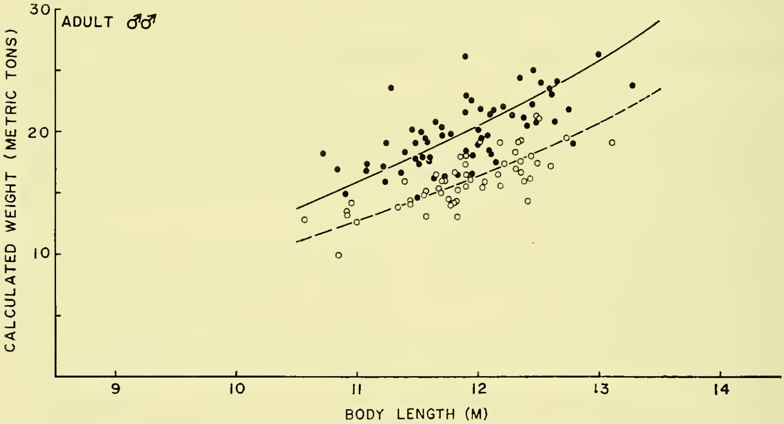

FIG. 5. Comparison of calculated weights of adult male gray whales during the southward and northward migrations. Solid circles and unbroken line represent southbound migrants; open circles and broken line represent northbound migrants.

TABLE 2

WEIGHTS AND MEASUREMENTS OF NINE GRAY WHALES. UNLESS OTHERWISE NOTED SPECIMENS WERE COLLECTED IN PRESENT STUDY.

Sex	Age	Date	Body length (meters)	Girth (meters)	Weight[1]		Value of *a*[5]
					Kilograms	Pounds	
♀	Fetus	20 January 1968	4.75	2.15	(409)	901	41
?[2]	Immature	10 January 1961	8.53	—	(6,632)	14,620	—
♂	Immature	30 March 1962	9.65	5.00	(8,808)	19,400	36
♂	Immature	28 March 1962	9.90	4.80	(8,876)	19,550	39
♂	Adult	29 March 1962	11.72	6.00	(15,686)	34,550	37
♂	Adult	27 March 1962	12.40	5.50	(16,594)	36,550	44
♀	Adult (pregnant)	23 February 1959	12.70	—	(16,360)	36,000	—
♀[3]	Adult (pregnant)	19 August 1936	13.35	8.48[4]	31,466	(69,380)	33
♀	Adult (pregnant)	14 December 1966	13.55	8.80	(33,846)	74,550	32

[1] Converted values in parentheses.
[2] Data from Gilmore (1961); originally recorded as 28 feet.
[3] Data from Zenkovich (1937*b*).
[4] Greatest height given as 270 centimeters; girth estimated as $\pi \times 2.70$ meters.
[5] See text for explanation.

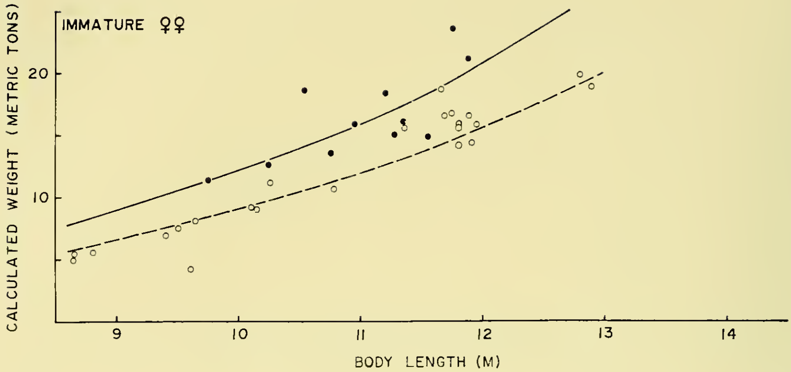

Fig. 6. Comparison of calculated weights of immature female gray whales during the southward and northward migrations. Solid circles and unbroken line indicate southbound migrants; open circles and broken line indicate northbound migrants.

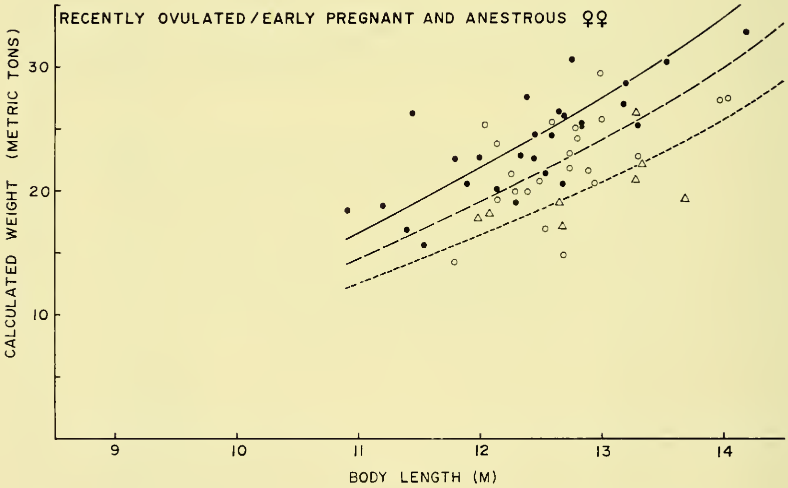

Fig. 7. Comparison of calculated weights of recently ovulated female gray whales during the southward migration and early pregnant and anestrous females during the northward migration. Symbols are as follows: solid circles and unbroken line, southbound migrants; open circles and long-dashed line, early pregnant northbound migrants; triangles and short-dashed line, anestrous northbound migrants.

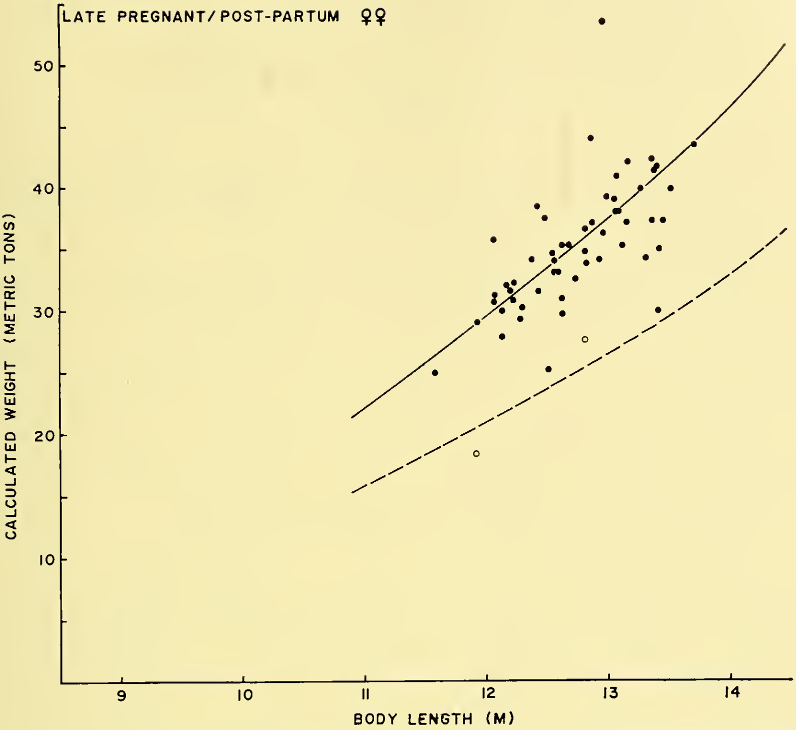

FIG. 8. Comparison of calculated weights of late pregnant female gray whales during the southward migration and postpartum females during the northward migration. Solid circles and unbroken line indicate southbound migrants; open circles and broken line indicate northbound migrants.

in body proportions with increasing length. We have used the mean value of 38. Estimates of percentage weight loss are independent of the value of *a* used.

The calculated weights of all whales (except for seven for which there were no comparable girth measurements) classified according to sex, age, and reproductive status, are plotted against body length in Figs. 4 to 8. Each class of southbound migrants is compared with the corresponding class of northbound migrants. Within each class, weight was closely correlated with length to the third power (in other words, there was no change in relative girth with increase in length), so we calculated mean weight-length curves for each class with the equation $W = bL^3$. The value of b was calculated from the formula

$$b = \frac{\Sigma (G/L)^2}{N} a.$$

The mean absolute weights of whales of any given length during their southward and northward migrations may thus be compared. Their relative weights are simply a function of G^2.

The total weight loss of gray whales between the southward and northward migrations varied from 11 to 29 per cent and was correlated with elapsed time (Table 3). Weight loss per day varied from 0.21 to 0.37 per cent. Weight lost by postpartum females is, of course, not entirely attributable to metabolism. The fetus and fetal membranes and fluids probably account for about 2000 kilograms. The nutritive condition and energy requirements of pregnant and postpartum females are discussed beyond.

To determine if the observed weight loss is sufficient to account for energy requirements during the 54 to 85 days elapsing between the southward and northward migrations past San Francisco, it was necessary to estimate the metabolic rate. For simplicity, we have estimated the metabolic rate of a near-average gray whale weighing 20 metric tons on the basis of oxygen consumption and have assumed that the number of kilocalories per day per kilogram of body weight expended is the same for all whales regardless of body length. This assumption is open to question, but more data are required before more refined estimates of metabolic rate can be made.

No data are available on the lung volume of gray whales. As the relative size and shape of the lungs are similar to those of fin whales, we have used Scholander's (1940) measurements of 800, 1500, and 2000 liters for the lung capacity of three fin whales 15.2, 20.7, and 22.0 meters long, respectively, as a basis for estimating a value for the gray whale. His estimates of the body weights of these whales were too high, so we used Ash's (1952) formula to recalculate the weights as 20, 49, and 58 metric tons, respectively. The mean lung capacity in liters is thus equal to 3.5 per cent of the body weight in kilograms. A 20-ton whale would, therefore, have a lung capacity of 20,000 by 0.035, or 700 liters. The volume

TABLE 3

Weight Loss of Gray Whales between Southward Migration (SM) and Northward Migration (NM).

Age, sex, and reproductive status	Number		Value of b[1] (mean ± SE)		Total weight loss (per cent)	Mean number of days elapsed	Mean weight loss per day (per cent)
	SM	NM	SM	NM			
Immature (males)	18	25	11.84 ± 0.26	9.47 ± 0.23	20.0	67	0.30
Adult (males)	63	54	11.83 ± 0.17	9.51 ± 0.11	19.6	62	0.32
Immature (females)	11	23	12.09 ± 0.57	9.03 ± 0.29	25.3	69	0.37
Adult (females)							
Recently ovulated (SM); early pregnant (NM)	27	22	12.43 ± 0.30	11.01 ± 0.42	11.4	54	0.21
Recently ovulated (SM); anestrous (NM)	27	8	12.43 ± 0.30	9.44 ± 0.40	24.1	68	0.35
Late pregnant (SM); postpartum (NM)	54	2	16.80 ± 0.27	11.95 ± 1.25	28.9	85	0.34

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[1] See text for explanation.

of tidal air may be estimated at 80 per cent, as Irving *et al.* (1941) found in *Tursiops truncatus,* giving an estimate of 560 liters per breath. Oxygen utilization may be estimated at 10 per cent of tidal volume, based on *Tursiops* (Irving *et al.*, 1941), giving an estimate of 56 liters of oxygen per breath. As a gray whale breathes about once a minute, it uses an estimated 80,640 liters of oxygen per day, or 0.17 cubic centimeters per gram per hour. Since 1.99 liters of oxygen are required to oxidize 1 gram of fat (Bishop, 1950), 80,640 liters is sufficient to oxidize 41 kilograms or 0.20 per cent of the animal's body weight per day.

Oxidation of 1 gram of fat produces 9.54 kilocalories (Bishop, 1950), so the whale will produce about 3.8 by 10^5 kilocalories per day or 19 kilocalories per kilogram per day. This estimate of the metabolic rate is lower, on the basis of kilocalories per kilogram of body weight, than that of smaller mammals, but lies above Benedict's (1938) "mouse-to-elephant" curve. His curve gives a value of 70 times $20{,}000^{0.75}$, or about 1.2 times 10^5 kilocalories per day for a 20-ton animal. It should be noted, however, that our estimate cannot be considered a basal rate, because it is based on the respiration rate of an actively swimming animal. In some other mammals, the energy expended over a 24-hour period ranges between 1.3 and 4.0 times the basal rate, and for animals performing a moderate amount of work the average is approximately three times the basal rate (Brody, 1945). On this basis, the metabolic rates of large whales do not appear to be far above the "mouse-to-elephant" curve (see Kanwisher and Sundnes, 1966).

Blubber Thickness.—The thickness of the blubber has long been about the only measurement that has been used as an indicator of the nutritive condition of large whales (Slijper, 1954). Blubber thickness of gray whales was not correlated with body length, so we have used absolute measurements in our analysis. All sex and age classes of gray whales showed a slight decrease in blubber thickness between the southward and northward migration (Table 4), but this decrease was not statistically significant ($P > .05$) for any class.

Blubber thickness is less sensitive than girth as an indicator of the nutritive condition of gray whales. The reduction of girth reduces body surface area, and thus tends to make the blubber

TABLE 4

Comparisons of Blubber Thickness of Gray Whales During Migration Periods.

Age, sex, and reproductive status	Number	Blubber thickness (cm)	
		Mean ± SE	Range
Immature males			
Southward	17	12.8 ± 0.3	10.5–15.0
Northward	25	12.6 ± 0.3	9.5–16.0
Adult males			
Southward	66	13.5 ± 0.2	9.5–17.5
Northward	44	12.8 ± 0.2	10.5–16.0
Immature females			
Southward	11	14.4 ± 0.4	12.5–16.5
Northward	23	12.8 ± 0.4	8.0–17.0
Adult females			
Southward (recently ovulated)	27	15.7 ± 0.4	10.5–20.0
Northward (early pregnant)	22	15.2 ± 0.4	10.0–18.5
Northward (anestrous)	8	13.3 ± 1.1	9.5–19.0
Southward (late pregnant)	53	15.7 ± 0.2	12.5–19.0
Northward (postpartum)	2	14.5	10.0–19.0

thicker. It was apparent to us while examining the viscera of southbound and northbound migrants that weight loss is due more to utilization of body fat than to utilization of blubber.

Oil Yield.—The oil yield of the carcass is probably the most reliable indicator of nutritive condition, but such data are not available for individual gray whales. The mean estimated body weight and mean yields of oil, meal, and meat from southbound whales were two and one-half to three times those of northbound animals (Table 5). The southbound sample consisted mostly of adult females carrying near-term fetuses; the northbound sample consisted mostly of males, and included many immature animals. The cubic mean length of the southbound whales was 12.62 meters, whereas that of the northbound animals was 11.23 meters. Quantities of each product were also affected by the relative amount of meat salvaged from each carcass. The remainder of each carcass was rendered for oil and meal. The difference between calculated body weight and total weight of oil, meal, and meat may be attributed to water loss during rendering of the oil and drying of the meal. Inasmuch as the samples are heterogeneous as regards

TABLE 5

MEAN WEIGHTS OF OIL, MEAL, AND MEAT PRODUCED FROM GRAY WHALES TAKEN IN SOUTHWARD AND NORTHWARD MIGRATIONS. MEAN CALCULATED BODY WEIGHT OF 26 SOUTHBOUND WHALES WAS 31,662 KILOGRAMS AND THAT OF THE 26 NORTHBOUND WHALES WAS 12,861 KILOGRAMS.

	Southward migration		Northward migration	
Products	Kilograms	Per cent	Kilograms	Per cent
Oil	7,559	39.6	2,496	38.1
Meal	6,834	35.8	2,520	38.5
Meat	4,689	24.6	1,533	23.4
Total	19,082	100.0	6,549	100.0

sex, age, and reproductive status, they are not directly comparable, but they do show the great difference in body weight between southbound and northbound migrants. The ratio of oil to meal also indicates a moderate decrease in relative oil yield between the southward and northward migrations.

Discussion and Conclusions

The predominance of gammaridean amphipods, especially *Ampelisca macrocephala,* among stomach contents indicates that gray whales, unlike other baleen whales, are primarily, if not exclusively, bottom feeders. The poor representation of polychaete worms and mollusks, which are usually dominant in the infauna, suggests that gray whales are selective feeders. Perhaps they stir up the bottom sediments with their snouts, then filter the turbid water immediately above the bottom from which the heavier mollusks have settled out. The worms presumably retreat deep into their tubes and burrows, whereas the amphipods, freely swimming, are trapped in the baleen plates. The occurrence of sand, silt, and gravel in the stomachs provides further evidence that gray whales feed on the bottom. In the Chukchi Sea, several observers (Pike, 1962*a*; Scammon, 1874; Wilke and Fiscus, 1961) have reported seeing gray whales, presumably feeding, surfacing with muddy snouts. Greater wear of the baleen on the right side suggests that gray whales swim on their right side while feeding (Kasuya and Rice, 1970). Fin whales (Gunther, 1949), Bryde's whales, *Balaenoptera edeni* (Rice, field notes), and humpback whales (Andrews, 1909) swim on their sides when feeding near the surface. Swimming on their side permits whales to turn more easily in the horizontal plane.

While migrating, gray whales apparently rarely attempt to feed, at least along the southern sector of their migration route. What little evidence is available also indicates that gray whales seldom, if ever, feed while on the winter grounds. A calculated weight loss of 0.21 to 0.37 per cent of body weight per day between the southward and northward migration past San Francisco exceeds the hypothetical value of 0.20 per cent per day based upon their estimated metabolic requirements. Thus, there is no reason to assume that gray whales must feed while on the winter grounds. This conclusion may not apply to females with calves, however, as we have no data for them.

AGE AND GROWTH

Age Determination

No gray whales of known age have been studied. Age must be deduced from indirect evidence and by analogy with other species of baleen whales. Jonsgård (1969) reviewed methods of determining the ages of cetaceans. Three criteria appeared promising for determination of age in gray whales. These are the number of growth layers in the ear plugs, corpora albicantia in the ovaries, and growth zones in the baleen plates.

Ear Plugs.—In balaenopterid whales, the number of growth layers in the ear plug is generally considered to be the most useful indicator of age (Purves, 1955; Laws and Purves, 1956). Each layer consists of one light and one dark lamina. There has been controversy, however, over the correlation between number of growth layers and absolute age. Data on ear plugs collected from fin whales marked more than 25 years previously, and several independent lines of indirect evidence, support the hypothesis that only about one growth layer is formed each year, at least in sexually mature fin whales (Ohsumi, 1964*a*). Ichihara (1966) provided evidence suggesting that in immature fin whales the rate of accumulation of ear plug laminae is irregular, varying from one to two annually, with a mean of one and one-half. Roe (1967*a*, 1967*b*), however, on the basis of histological examination of the ear plugs of fin whales collected in all months of the year, concluded that one growth layer is produced each year in both immature and adult whales of both sexes. He found that the light laminae are formed in summer and the dark laminae in winter. He also noted that the ear plugs of immature whales usually have minor laminae similar to but much thinner than the normal laminae; their significance is obscure, but he concluded that they should not be included in lamina counts for age determination.

Ear plugs of gray whales (Figs. 9–11) are soft, especially in the smaller animals, and difficult to remove without distortion or breakage. Some of the plugs have a fibrous, columnar, or amorphous

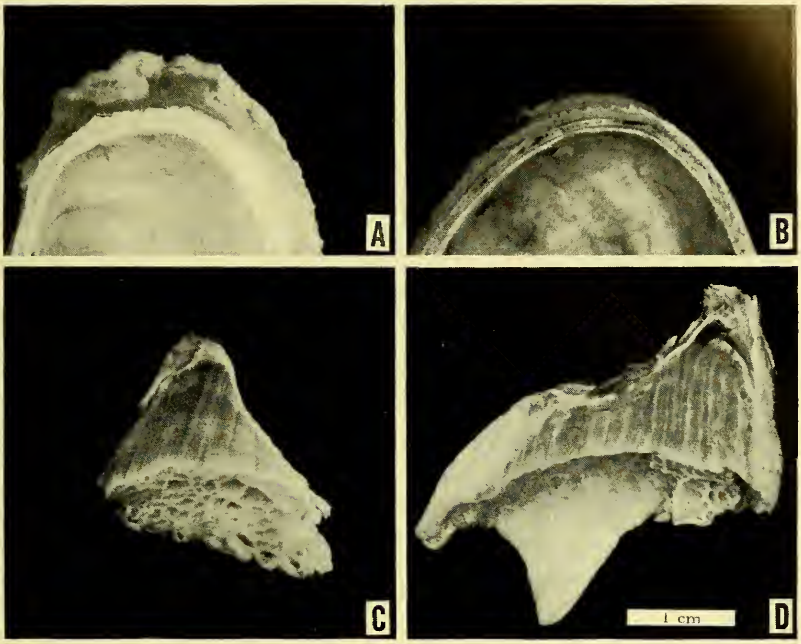

FIG. 9. Ear plugs of immature gray whales bisected longitudinally. A, 9.8-meter male, estimated age one year (attached to the "glove finger" of the tympanic membrane); B, 8.6-meter female, estimated age one year (attached to "glove finger"); C, 10.1-meter male with three growth layers; D, 11.3-meter female with six growth layers. All plugs are to same scale.

structure in which no laminae can be discerned. In the remaining plugs, laminae are vaguely to moderately well defined. Readable ear plugs were obtained from only 100 (60 per cent) of 166 males and 68 (45 per cent) of 150 females. On the better plugs, repeated counts of the laminae were consistent to within plus or minus 10 per cent of the total count. Males more often show regular laminae than do females, presumably because the annual physiological rhythm of females is modified by their longer and more irregular reproductive cycle.

The ear plug laminae are broad and poorly defined in immature whales but narrow and more sharply defined in adults. In many plugs from mature gray whales, the laminae are clear in the basal portion but indistinct or absent in the distal portion. This dif-

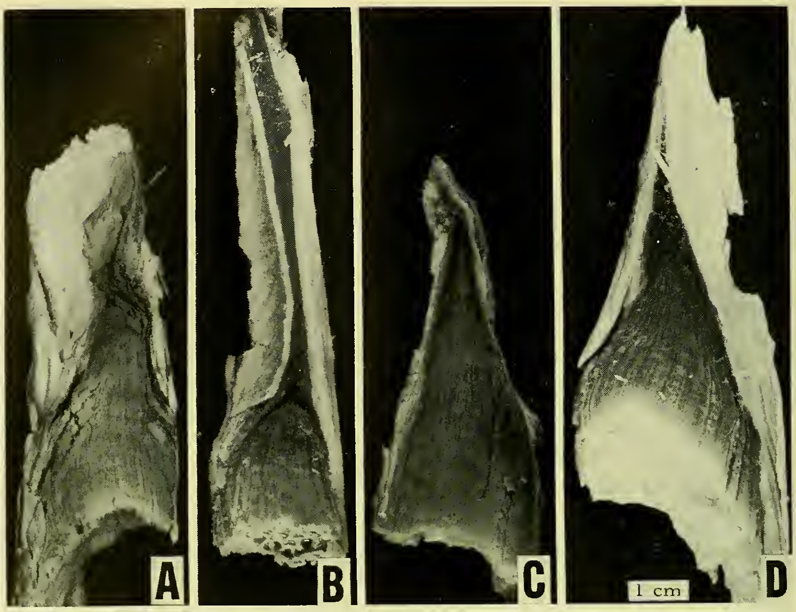

Fig. 10. Ear plugs of adult gray whales bisected longitudinally. A, 11.7-meter male with 11 growth layers; B, 11.4-meter female with 14 growth layers; C, 12.8-meter female with 18 growth layers; D, 12.3-meter male with 21 growth layers. All plugs are to same scale.

ference in the two regions suggests that the laminae laid down during immaturity may disappear as the plug grows. Another possible explanation—that some animals do not begin to produce clear laminae until they attain sexual maturity—appears unlikely, because the proportion of readable plugs was higher in immature than in mature whales (65 compared to 59 per cent in males and 56 compared to 42 per cent in females).

We found no ear plugs in several near-term fetuses that we dissected, and found no individuals with only one growth layer in the ear plugs. The smallest animals collected, 8.63 to 10.34 meters long, had two growth layers. We assumed that most of these animals were yearlings, and that the first layer forms during the nursing period and the second in late summer after weaning. As a working hypothesis, we assumed that each subsequent growth layer represented one year of growth in both immature and mature whales

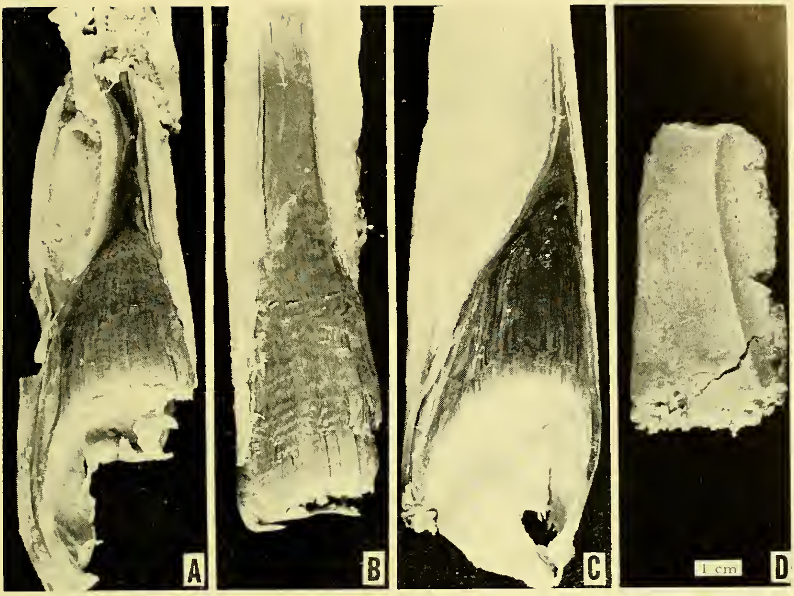

FIG. 11. Ear plugs of adult gray whales. A, 11.7-meter male with 23 growth layers; B, 12.5-meter female with 24 growth layers; C, 12.5-meter male with 40 growth layers; D, 11.7-meter male with amorphous plug showing no growth layers. All plugs are to same scale.

This interpretation is consistent with our estimate of the rate of accumulation of corpora albicantia in the ovaries (see discussion of reproductive cycle beyond). As it appears that two layers are formed the first year, the age of a whale in years should be one less than the number of growth layers in its ear plug. If, as suggested above, the earlier layers disappear in older animals, the count of growth layers provides only a minimum estimate of age.

OVARIES.—As the ovulation rate appears to be regular at about 0.50 per year, and the corpora albicantia remain permanently visible in the ovaries, the number of corpora in the ovaries provides a reliable estimate of the number of years elapsed since a female attained puberty. The mean age at puberty appears to be about 8 years (see below). Therefore, the age of a recently ovulated or early pregnant female is about twice the number of corpora (including

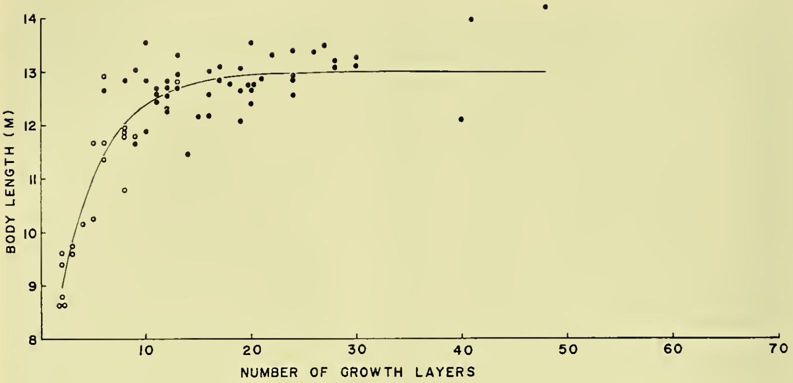

FIG. 12. Body length in relation to number of growth layers in ear plugs of female gray whales (open circles, immature females; solid circles, adult females; line, von Bertalanffy growth curve).

the corpus luteum) in her ovaries plus 6 years, and that of a late pregnant or postpartum female twice the number of corpora plus 7 years.

BALEEN PLATES.—Ruud (1940, 1945) found that the growth of baleen plates of blue (*Balaenoptera musculus*), sei (*B. borealis*), and fin whales is characterized by seasonal changes in thickness and that the pattern of variation in thickness can be used to estimate the age of the whales (see van Utrecht-Cock, 1965). Because of constant wear, there is rarely more than 5 or 6 years of growth present in a baleen plate. Thus this method is useful only for young whales.

Baleen plates of most gray whales show moderately well-defined "steps," or growth zones, each of which presumably represents one year of growth. None of the baleen plates we examined showed more than four growth zones, regardless of the age of the whale as estimated from the ear plugs. The number of growth zones in the baleen plates of most whales was less than the number of growth layers in the ear plug, and in no specimen was it greater. It thus appears that wear on the baleen plates of the gray whale is more rapid than in other baleen whales, probably because of greater abrasion resulting from bottom-feeding habits.

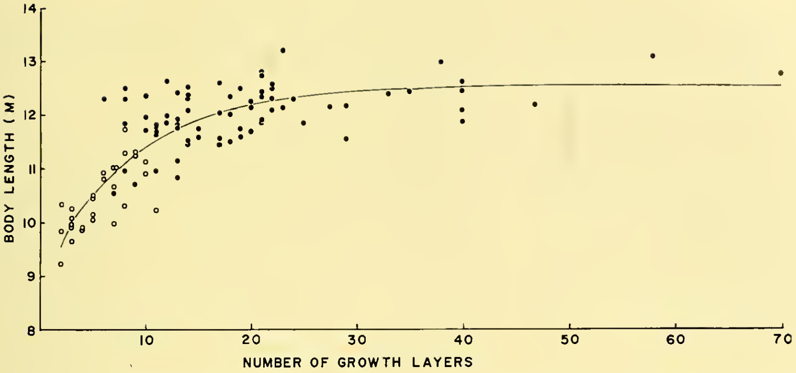

FIG. 13. Body length in relation to number of growth layers in ear plugs of male gray whales (open circles, immature males; solid circles, adult males; line, von Bertalanffy growth curve).

Growth

The external morphology and osteology of the gray whale have been described in detail by Andrews (1914), Zenkovich (1934*a*), and Tomilin (1957). Further data on growth in length, ontogenetic changes in body proportions, and sexual dimorphism were obtained in this study.

LENGTH.—Body lengths of males and females one year old and older have been plotted against the number of growth layers in the ear plugs in Figs. 12 and 13. Growth curves for each sex were calculated by using the von Bertalanffy equation (von Bertalanffy, 1938; Beverton and Holt, 1957) as follows: $l_t = L_\infty \, [1 - e^{-K(t-t_0)}]$, where l = body length in meters, L_∞ = asymptotic body length, K = rate at which length approaches the asymptote, and t = time in years. The results are given below (mean and standard deviation).

Females			Males		
L_∞	= 12.97	± 0.11	L_∞	= 12.43	± 0.12
K	= 0.246	± 0.035	K	= 0.141	± 0.021
t_0	= −2.842	± 0.772	t_0	= −8.346	± 1.721

It should be emphasized that because of the small sample sizes and the difficulty of reading ear plugs these curves are not com-

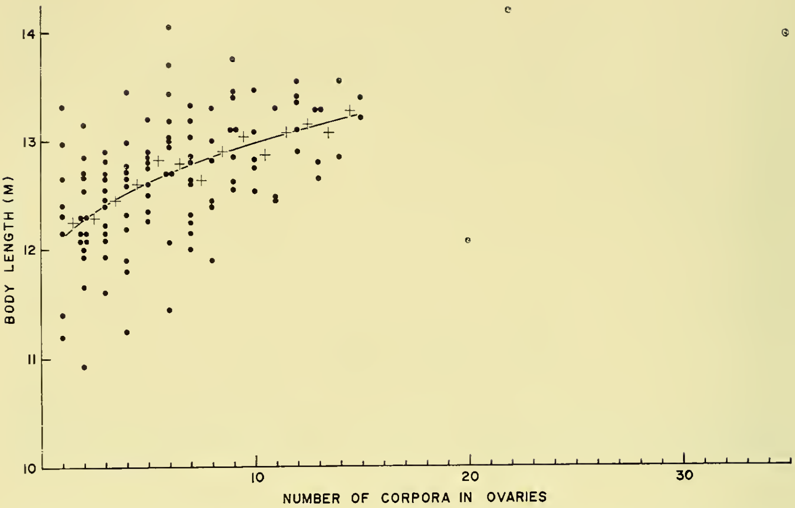

FIG. 14. Body length in relation to number of corpora albicantia and corpora lutea in ovaries of adult female gray whales. Crosses are running means of two; growth curve fitted by eye to mean values.

pletely reliable. The samples of the younger age groups are biased in favor of the larger individuals. Furthermore, possible disappearance of some ear plug laminae in older animals may have resulted in the estimated mean length at any given age being greater than the true mean.

In Fig. 14, the body length of adult females has been plotted against the number of corpora in the ovaries and a curve fitted by eye to the running means of two. This curve is probably a more accurate representation of the growth characteristics of adult females than the von Bertalanffy curve.

From a mean length at birth in January of about 4.9 meters, calves grow to a mean length of about 8.5 meters at weaning in August and to 9.3 meters by the following winter. With this first annual increment of 90 per cent of neonatal size, the females attain 66 per cent of their ultimate body length and the males 72 per cent. The growth rate drops to 7 per cent during the second year and continues to decline in subsequent years, but growth continues until at least about 30 years of age.

TABLE 6

BODY PROPORTIONS (EXPRESSED AS PERCENTAGE OF TOTAL BODY LENGTH) OF NEAR-TERM FETUSES AND POSTNATAL GRAY WHALES. SEE TEXT FOR DESCRIPTION OF MEASUREMENTS.

	Females				Males			
	Fetuses		Postnatals		Fetuses		Postnatals	
Measurement	*N*	Mean ± SD	*N*	Mean ± SD	*N*	Mean ± SD	*N*	Mean ± SD
Head length	17	22.4 ± 1.1	136	23.2 ± 1.0	25	22.5 ± 1.3	155	23.3 ± 0.9
Tail length	25	28.4 ± 2.4	147	30.3 ± 1.6	30	28.2 ± 2.6	167	29.7 ± 1.3
Fluke span	25	22.8 ± 1.8	120	24.3 ± 1.8	30	22.6 ± 1.8	138	24.9 ± 1.6
Fluke breadth	25	7.6 ± 0.6	141	7.3 ± 0.5	30	7.3 ± 0.6	152	7.3 ± 0.6
Flipper length	25	19.6 ± 1.0	147	17.3 ± 1.1	29	19.9 ± 0.8	166	17.8 ± 1.2
Flipper width	25	6.8 ± 0.5	144	6.5 ± 0.5	29	7.0 ± 0.4	166	6.7 ± 0.6

PROPORTIONS.—We have analyzed the following six body measurements to determine if body proportions change with age: (1) head length, (2) tail length, (3) span of flukes, (4) breadth of flukes, (5) length of flippers, and (6) width of flippers.

A comparison of these measurements (expressed as a percentage of body length) of near-term fetuses with those of postnatal whales (Table 6) shows that mean tail length increases from 28.2 to 29.7 per cent in males ($P < .05$) and from 28.4 to 30.3 per cent in females ($P < .001$). Relative flipper length decreases from 19.9 to 17.8 per cent ($P < .001$) in males and from 19.6 to 17.3 per cent ($P < .001$) in females. Fluke span increases from 22.6 to 24.9 per cent ($P < .005$) in males and from 22.8 to 24.3 per cent ($P < .01$) in females. Examination of near-term fetuses suggests that the apparent increase in relative fluke span does not represent differential growth, but instead is simply the result of postnatal abduction of the flukes in the horizontal plane from the adducted and folded position *in utero*. There are no significant age differences in relative head length, fluke breadth, or flipper width.

The magnitude of changes in body proportions of gray whales from one year of age to physical maturity also was examined. All postnatal animals of each sex were grouped into one-meter length classes. The mean and standard deviation of each measurement for each length class were calculated and the mean expressed as a percentage of total body length (Table 7). Only specimens for which all six measurements were available were included. For each series of measurements, we calculated the allometric equation $Y = bX^d$, where X = body length and Y = measurement being compared with X. The constant of allometry, d, does not differ significantly ($P > .05$) from unity for any of the series of measurements for either sex, indicating that body proportions change little after one year of age.

SEXUAL DIMORPHISM.—There was no significant difference between the sexes in body length of near-term fetuses. As noted above, females grow more rapidly after birth and average larger than males at any given age, as is true for all other species of baleen whales.

The data in Tables 6 and 7 reveal small but statistically significant postnatal differences between the sexes in some body proportions. Thus, males have longer flippers ($P < .01$) and shorter tails ($P < .01$) than females. There is no sexual dimorphism in number of throat grooves, baleen plates, or crenulations on the dorsal ridge of the caudal peduncle.

Puberty and Sexual Maturity

As ordinarily used by cetologists, puberty refers to the age at which gametes are first produced, and sexual maturity is the age at which the animal reaches its full reproductive power. For purposes of this study, any animal that had attained puberty is referred to as an adult.

Puberty in the female is indicated by the presence of a corpus luteum or at least one corpus albicans in the ovaries. Females are considered to be sexually mature at the onset of the first pregnancy. Evidence of sexual maturity thus is pregnancy, lactation, or the presence of mature but involuted mammary glands and a parous type uterus. In the female gray whale, attainment of puberty and sexual maturity usually coincide, but in five of 15 nulliparous and primiparous females, the presence of a corpus albicans (in one case, three corpora), in addition to a corpus luteum or recently ovulated follicle, indicated that they had attained puberty but had not conceived at least a year before their most recent estrous cycle.

Males are considered to be sexually mature when first capable of successfully impregnating females. It is impossible to make a distinction between puberty and sexual maturity in the male on

TABLE 7

Measurements (in Meters) and Relative Size (as Percentage of Body Length) of Various Body Parts of Gray Whales.

Class range of body length	N	Mean body length	Head length		Tail length		Fluke span		Fluke breadth		Flipper length		Flipper width	
			Mean ± SD	Per cent	Mean ± SD	Per cent	Mean ± SD	Per cent	Mean ± SD	Per cent	Mean ± SD	Per cent	Mean ± SD	Per cent
Females														
Near-term fetuses	17	4.69	1.05 ± 0.09	22	1.33 ± 0.14	28	1.08 ± 0.12	23	0.36 ± 0.04	7.7	0.92 ± 0.08	20	0.32 ± 0.03	6.8
8.01– 9.00	3	8.69	1.92 ± 0.03	22	2.77 ± 0.02	32	2.12 ± 0.11	24	0.65 ± 0.02	7.5	1.46 ± 0.07	17	0.54 ± 0.03	6.2
9.01–10.00	5	9.58	2.21 ± 0.13	23	3.05 ± 0.15	32	2.38 ± 0.16	25	0.70 ± 0.06	7.3	1.67 ± 0.13	17	0.63 ± 0.03	6.6
10.01–11.00	8	10.49	2.43 ± 0.19	23	3.26 ± 0.15	31	2.46 ± 0.27	23	0.76 ± 0.06	7.2	1.80 ± 0.19	17	0.68 ± 0.04	6.5
11.01–12.00	23	11.68	2.75 ± 0.10	24	3.64 ± 0.10	31	2.90 ± 0.13	25	0.88 ± 0.04	7.5	1.99 ± 0.11	17	0.76 ± 0.05	6.5
12.01–13.00	42	12.52	2.90 ± 0.10	23	3.78 ± 0.23	30	3.07 ± 0.22	25	0.91 ± 0.05	7.3	2.16 ± 0.14	17	0.81 ± 0.04	6.5
13.01–14.00	22	13.33	3.05 ± 0.11	23	3.96 ± 0.15	30	3.16 ± 0.24	24	0.93 ± 0.06	7.0	2.35 ± 0.23	18	0.87 ± 0.05	6.5
14.01–15.00	1	14.20	3.20	23	4.20	30	3.24	23	0.95	6.7	2.60	18	0.94	6.6
Males														
Near-term fetuses	24	4.56	1.02 ± 0.07	22	1.29 ± 0.13	28	1.02 ± 0.11	22	0.34 ± 0.03	7.5	0.92 ± 0.07	20	0.32 ± 0.02	7.0
9.01–10.00	9	9.81	2.26 ± 0.08	23	3.06 ± 0.12	31	2.48 ± 0.10	25	0.71 ± 0.05	7.2	1.71 ± 0.10	17	0.65 ± 0.03	6.6
10.01–11.00	27	10.62	2.51 ± 0.13	24	3.20 ± 0.19	30	2.68 ± 0.21	25	0.76 ± 0.04	7.2	1.91 ± 0.13	18	0.71 ± 0.05	6.7
11.01–12.00	56	11.62	2.73 ± 0.12	23	3.42 ± 0.15	29	2.87 ± 0.22	25	0.84 ± 0.06	7.2	2.05 ± 0.16	18	0.77 ± 0.05	6.6
12.01–13.00	33	12.36	2.23 ± 0.09	23	3.66 ± 0.14	30	3.05 ± 0.16	25	0.89 ± 0.03	7.2	2.18 ± 0.15	18	0.84 ± 0.04	6.8
13.01–14.00	3	13.21	2.90 ± 0.21	22	3.91 ± 0.07	30	3.27 ± 0.13	25	0.91 ± 0.05	6.9	2.33 ± 0.10	18	0.86 ± 0.04	6.6

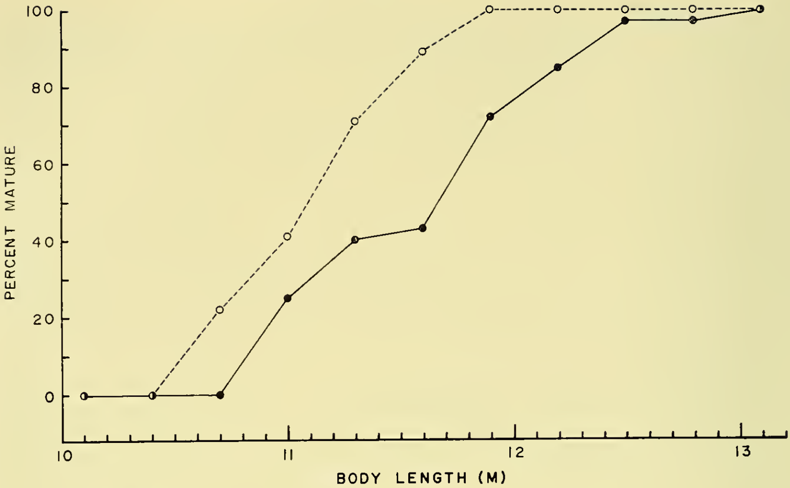

FIG. 15. Percentage of adult gray whales according to body length (grouped by 0.3-meter length classes). Open circles and broken lines represent males; solid circles and unbroken lines represent females.

the basis of our data. We determined the attainment of puberty by histological examination of the testes and regarded as adult all males whose testes showed evidence of spermatogenesis.

Fig. 15 shows that 50 per cent of the females have attained puberty by the time they reach a length of about 11.7 meters. The two smallest females that had reached puberty were 10.92 meters and 11.20 meters long; both were nulliparous and had recently ovulated for the first time. The smallest parous female was 11.24 meters long, whereas the largest immature female was 12.92 meters in length.

Fifty per cent of the males had attained puberty at a length of 11.1 meters (Fig. 15). The smallest male showing spermatogenic activity was 10.56 meters long, and the largest immature male was 11.75 meters long.

The age at puberty was estimated by plotting the percentage of animals that had attained puberty against the number of growth layers in the ear plug (Fig. 16). The mean number of growth layers at puberty was nine, giving an estimated age of 8 years. In both males and females, the fewest growth layers found in the ear plug

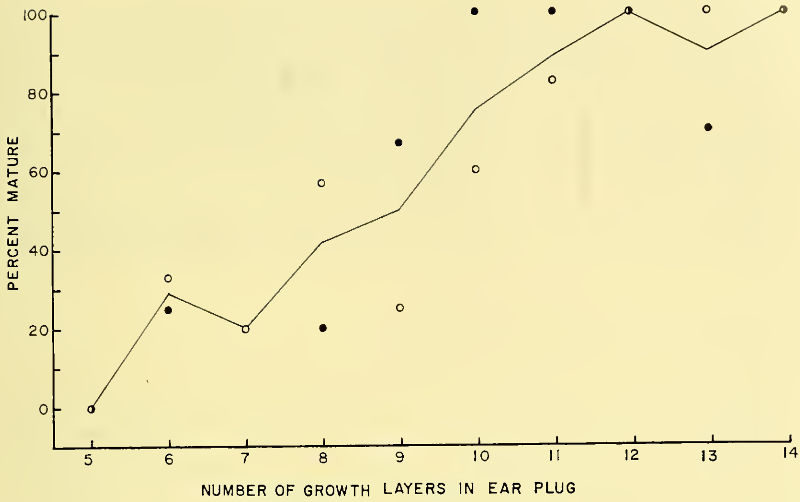

Fig. 16. Percentage of adult gray whales in relation to number of growth layers in ear plugs. Open circles represent males and solid circles represent females; line connects running means of three for both sexes combined.

of an adult animal was six, whereas the highest number in an immature animal was 11 (excepting one female with 13). On this basis, age at puberty is estimated to range from 5 to at least 11 years. Because of the difficulty of counting growth layers in ear plugs of immature animals, these figures may not be entirely reliable.

Physical Maturity

We collected few physically mature animals, as determined by the complete fusion of the vertebral epiphyses with the centra. Only two of the females examined fell in this class. They were 13.98 and 14.20 meters long. The smaller had 35 corpora in the ovaries and about 41 growth layers in the ear plugs, whereas the larger had 22 corpora and 43 laminae in the ear plugs. Physically immature females had 20 or fewer corpora and as many as 40 growth layers. Except for one individual with unreadable ear plugs that was 14.05 meters long, physically immature females were 13.75 meters or less in length.

Five males were regarded as physically mature. They ranged from 12.75 to 13.30 meters in length. The smallest had only 21 growth layers in the ear plug, whereas the others had 38 to 70 (the plugs of one were unreadable). Physically immature males did not exceed a length of 12.80 meters, except for one with 23 growth layers that was 13.23 meters long.

The largest reliably measured gray whales on record are males 14.3 meters long and a female 15.0 meters in length (Zenkovich, 1937*a*).

Discussion and Conclusions

Growth layers in the ear plugs have limited use for age determination in the gray whale because of uncertainty in counting them and because not all individuals have readable plugs. They provide a minimum estimate of age because laminae produced early in life may disappear in older whales. The number of corpora in the ovaries appears to be a more reliable method for age determination in adult females. Growth zones in the baleen plates are of little use for age determination because of the rapid wear of the plates.

Gray whales grow rapidly during their first year. Rapid initial growth is essential in large aquatic mammals that depend primarily on size for thermoregulation and protection from predators.

Between late fetal life and one year of age, relative length of the flipper decreases slightly and relative length of the tail increases slightly. There are no appreciable changes in body proportions from one year to physical maturity. The latter conclusion is contrary to the findings for blue whales and fin whales (Mackintosh and Wheeler, 1929; Ohsumi, 1960), sei whales (Matthews, 1938), humpback whales (Matthews, 1937), right whales, *Balaena glacialis* (Omura *et al.*, 1969), and bowhead whales, *Balaena mysticetus* (Eschricht and Reinhardt, 1866). In most of these species, as body length increases the head becomes relatively longer, the tail relatively shorter, and the flippers and flukes relatively shorter and narrower.

Sexual maturity is attained in both sexes at a mean age of 8 years (range, 5 to 11), at a mean length of 11.1 meters in males and 11.7 meters in females. This estimate of age at sexual maturity is in general agreement with estimates for fin whales (Nishiwaki *et al.*, 1958) and humpback whales (Chittleborough, 1959) that were based on counts of growth layers in the ear plugs. Physical maturity is attained at a mean length of about 13.0 meters in males and 14.1 meters in females, at a mean age of about 40 years. As in other baleen whales, females are larger than males. Sexual dimorphism in body proportions is slight, but males have slightly larger flippers and shorter tails than females.

FEMALE REPRODUCTIVE CYCLE

Reproduction in cetaceans has been reviewed by Harrison (1969), Rice (1967), and Slijper (1956, 1963). Our collection of 116 adult females included animals in four stages of the reproductive cycle (sample sizes in parentheses): southbound females that had recently ovulated (28); northbound females in early pregnancy (22); southbound females in late pregnancy (56, including one recently aborted individual); and northbound postpartum females (two, neither of which was lactating, apparently having lost their calves). In addition, eight northbound metestrous and anestrous females, which had failed to conceive, were included in the sample. Some anestrous females would also be expected on the southward migration, but none was collected in this study.

Where appropriate, the data on the 15 females undergoing their first reproductive cycle were analyzed separately from the data on the 101 females that had previously experienced one or more cycles. We defined a female as *nulliparous* if she has never given birth (or aborted) and was not visibly pregnant (although she may contain a macroscopically undetectable conceptus), as *primiparous* if she was in her first pregnancy or had given birth (or aborted) only once, and as *multiparous* if she had given birth (or aborted) at least twice or had given birth (or aborted) only once and was currently pregnant; *parous* refers to any female that had conceived at least once (North Pacific Fur Seal Commission, 1963). Nulliparous females and primiparous females in early pregnancy were recognized by the condition of the mammary glands and uterus as described below. Females in late pregnancy and postpartum females with a single corpus luteum and no corpora albicantia were obviously primiparous, and those with at least one corpus albicans in addition to the corpus luteum were regarded as multiparous.

Ovarian Cycle

The ovaries of the gray whale are morphologically similar to those of the fin whale (Laws, 1961; Mackintosh and Wheeler, 1929; Ommanney, 1932), and the humpback whale (Dempsey and Wislocki,

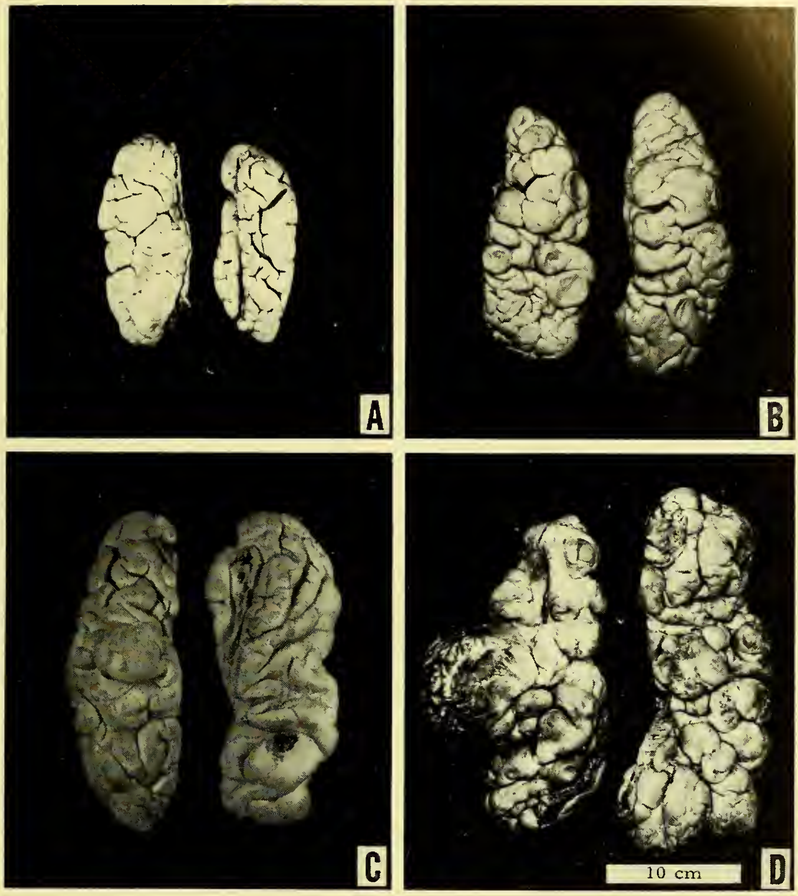

Fig. 17. Ovaries of gray whales showing various stages of ovarian cycle. A, 8.6-meter immature female with no large Graafian follicles; B, 11.2-meter immature female with enlarged Graafian follicles; C, southbound female with recently ruptured Graafian follicle in right ovary and corpus luteum of ovulation in left ovary; D, southbound, recently ovulated female with developing corpus luteum in left ovary. All ovaries are to same scale.

1941). They are elongate, flattened, and oval, with the anterior end slightly larger than the posterior end. Some are exceptionally long and narrow, being almost strap-shaped. The larger Graafian follicles and corpora albicantia protrude from the surface. Ovaries

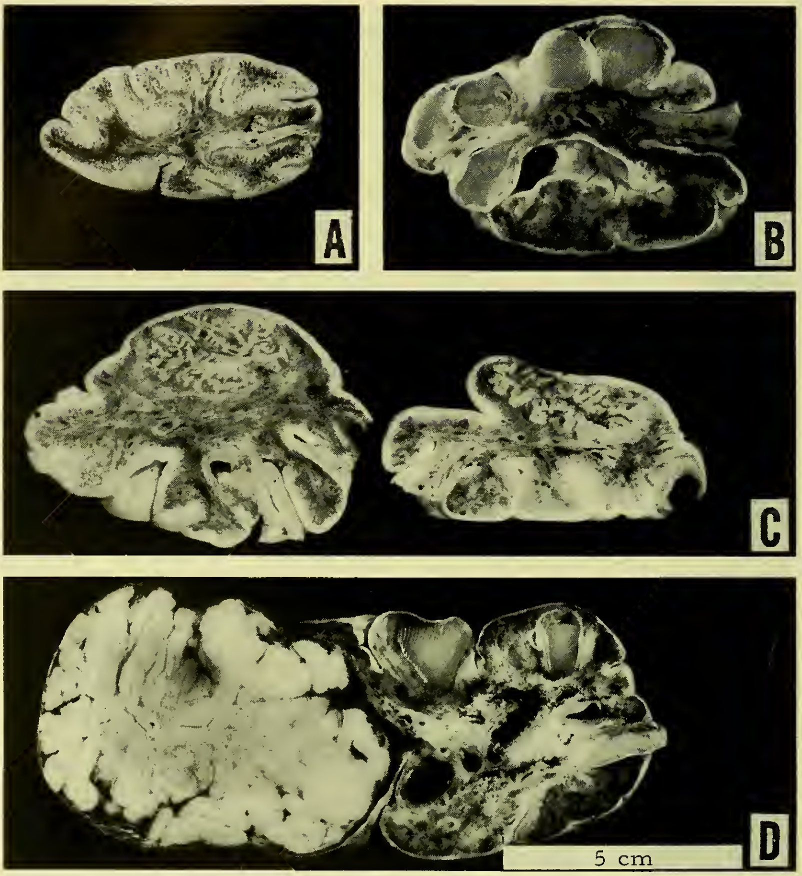

Fig. 18. Transverse sections of ovaries shown in Fig. 17. Sections shown in C and D transect the most recent corpora. All sections are to same scale.

representative of various stages of the reproductive cycle are shown in Figs. 17 to 20.

Ovary Weights.—There is no marked or consistent difference in weight between left and right ovaries. The mean weight of both ovaries of sexually immature females is plotted against body length in Fig. 21. In the smaller individuals, ovary weights range from 70 to 250 grams, with a mean of 136. At a body length of 11.2 to 11.4 meters, corresponding to an estimated age of about 5 years,

Fig. 19. Ovaries of gray whales showing various stages of the ovarian cycle. A, northbound, early pregnant female (90-millimeter fetus) with corpus luteum in left ovary; B, southbound late pregnant female (4.86-meter fetus) with corpus luteum in right ovary; C, northbound postpartum female (that had lost her calf) with regressing corpus luteum in left ovary; D, northbound anestrous female with large corpus albicans derived from the most recent corpus luteum in right ovary. All ovaries are to same scale.

ovarian weight increases abruptly to 250 to 550 grams (mean, 312), approximating that of younger sexually mature females.

The weight of the ovaries of sexually mature females is greatly increased when a corpus luteum is present. As most mature females

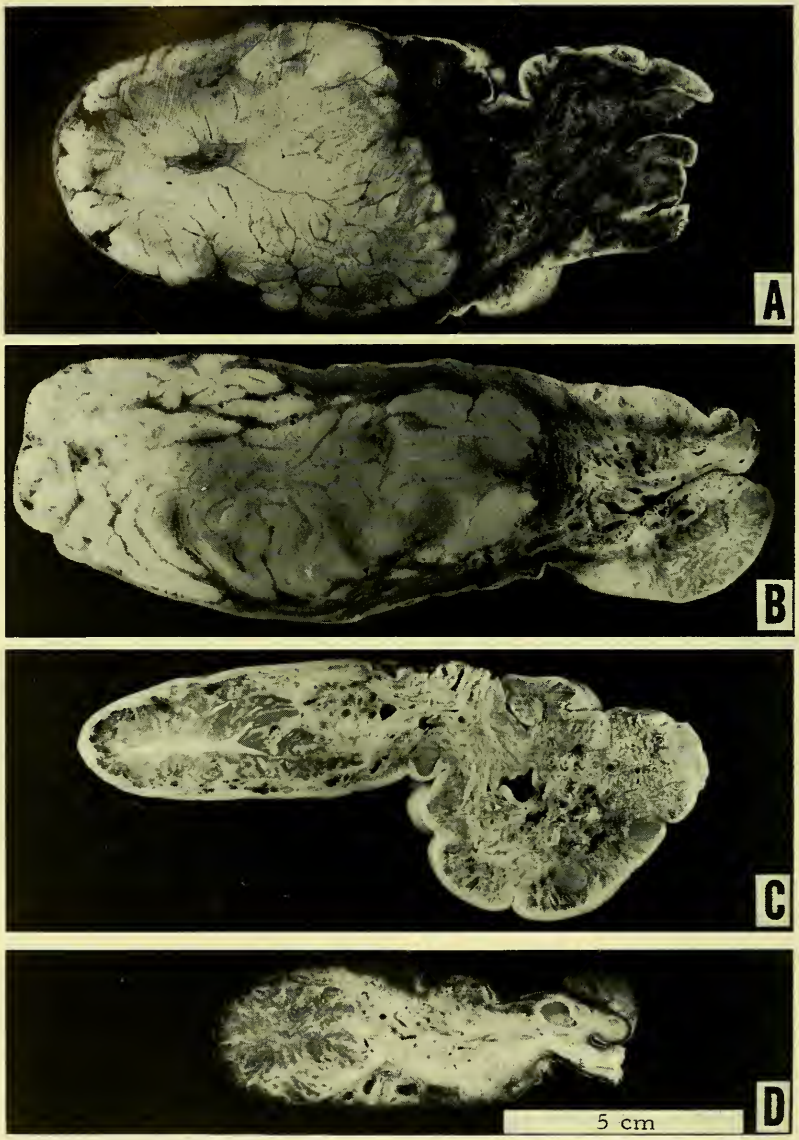

Fig. 20. Transverse sections through the most recent corpus in each pair of ovaries shown in Fig. 19. All sections are to same scale.

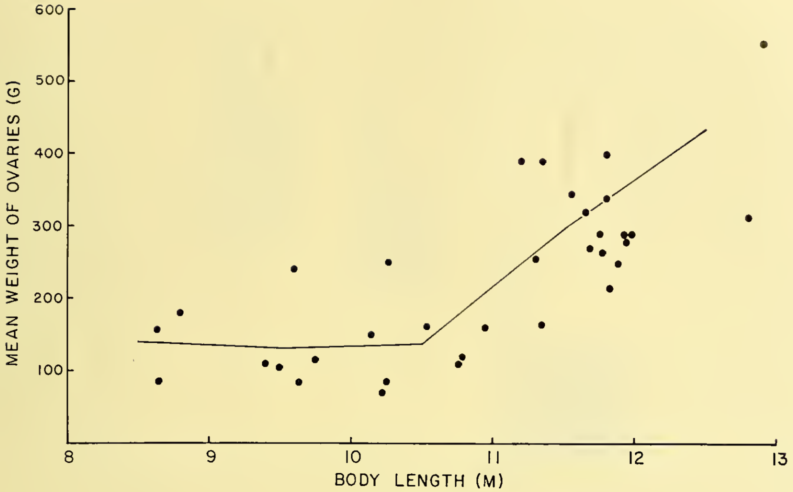

FIG. 21. Ovary weights of immature female gray whales plotted against body length. Line connects mean weights at one-meter length intervals.

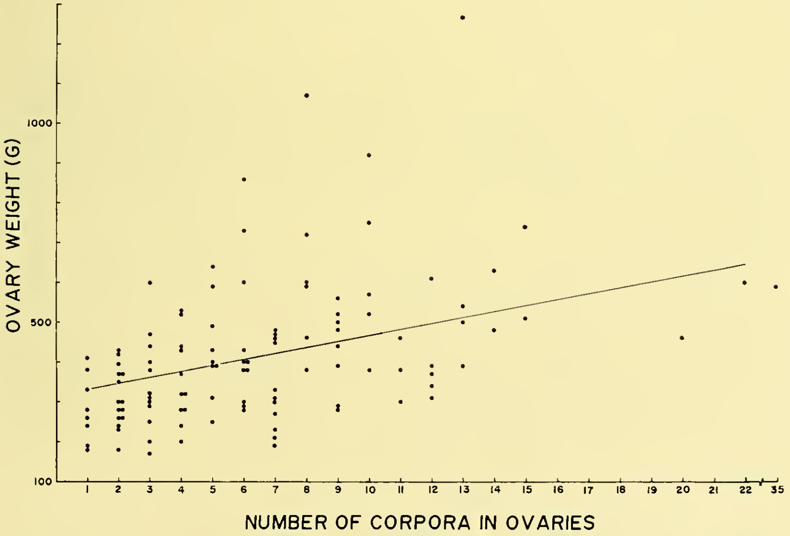

FIG. 22. Ovary weights of adult female gray whales plotted against number of corpora in ovaries.

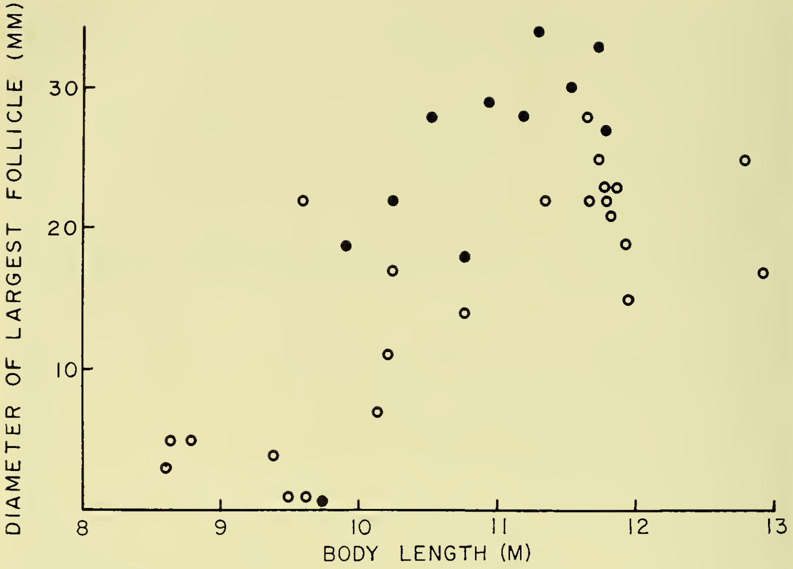

Fig. 23. Diameter of largest Graafian follicle versus body length of immature female gray whales. Solid circles indicate southbound migrants; open circles indicate northbound migrants.

had a corpus luteum in one ovary, we have used only the weight of the other ovary in making comparisons. For females without a corpus luteum, we have used the mean weight of the two ovaries. In Fig. 22, these weights are plotted against the number of corpora in both ovaries.

The weights of mature ovaries without a corpus luteum vary from 170 to 1270 grams. The regression of ovary weight on number of corpora is $Y = 316 + 15X$, where Y = ovary weight in grams and X = number of corpora. As the slope of this line differs significantly from zero ($P < .001$), ovarian weight apparently increases with age from a mean of 331 grams at puberty to 646 grams at an age of 50 years.

Follicles.—None of the follicles in the ovaries of immature females up to 9.6 meters long exceeded 7 millimeters in diameter; in all immature females longer than 10.2 meters, the largest follicle

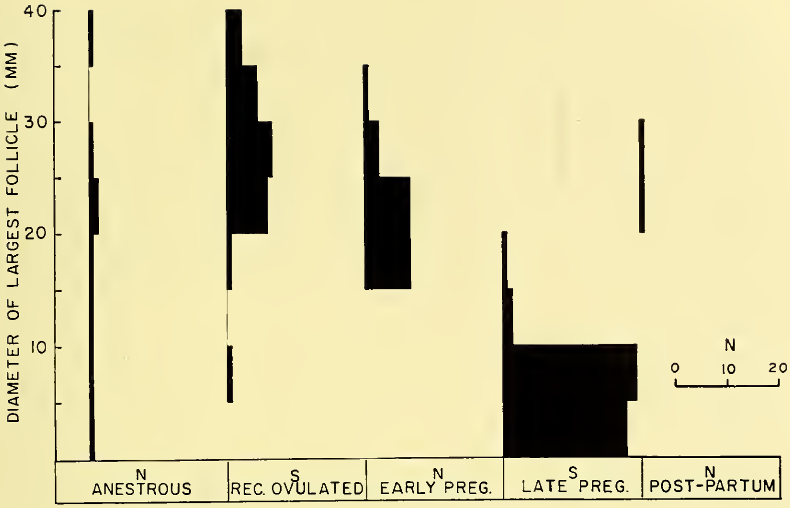

FIG. 24. Frequency distribution of diameter of largest Graafian follicle in ovaries of adult female gray whales in different phases of the reproductive cycle (N, northbound migrants; S, southbound migrants).

in either ovary exceeded 14 millimeters (Fig. 23). In the latter animals the largest follicles ranged from 18 to 34 millimeters (mean, 27) in southbound animals and from 14 to 28 millimeters (mean, 21) in northbound animals. These data suggest that females first begin to undergo a seasonal cycle of follicle-stimulating hormone secretion when they reach a length of between 9.6 and 10.2 meters at an estimated age of 2 or 3 years. Laws (1961) found a seasonal follicular cycle in immature fin whales. It should be noted that the follicles in these older immature females are significantly larger than those of late pregnant or postpartum females and slightly larger than those of northbound anestrous females. It is probable that the southbound immature females with follicles about 30 millimeters in diameter or larger (see below) are destined to ovulate for the first time later in the same season.

The size of the largest follicle in either ovary of adult females differs markedly in various phases of the reproductive cycle (Fig. 24). All southbound females not carrying near-term fetuses had recently ovulated. The largest follicle in these specimens ranged from 18 to 40 millimeters (mean, 28) in diameter (except for one nulliparous animal in which maximum follicle diameter was only 6 millimeters). Assuming that the largest follicle had ovulated, the biggest remaining follicle in these females would have been the second largest follicle just before ovulation. It thus appears that in gray whales the follicle exceeds 30 millimeters and may reach 40 before rupturing. Chittleborough (1954) found that the follicles of humpback whales exceed 30 millimeters before ovulation.

In the northbound early-pregnant females, the diameter of the largest follicles average less than two months earlier, ranging from 16 to 33 millimeters, with a mean of 22.

In strong contrast to females that had recently ovulated, southbound pregnant females carrying near-term fetuses had no greatly enlarged follicles. The largest follicle varied from 3 to 16 millimeters, with a mean of only 6. A female taken on 8 January that had apparently aborted recently likewise had no follicles larger than 6 millimeters. Such follicles are significantly smaller than those of anestrous females. The small size of follicles in late-pregnant females suggests that the progesterone secreted by the corpus luteum suppresses follicular maturation. Chittleborough (1954) found that the follicles of humpback whales in late pregnancy were smaller than those in anestrous animals. No such marked reduction has been found in blue whales and fin whales examined mostly during midpregnancy (Laws, 1961; Mackintosh and Wheeler, 1929; Nishiwaki and Oye, 1951).

In the two northbound females examined that were nonlactating and postpartum, the largest follicles were 24 and 29 millimeters in diameter. Their size suggests a resumption of follicular maturation after regression of the corpus luteum.

Northbound females that were neither pregnant nor postpartum had follicles ranging from 1 to 37 millimeters (mean, 18) in diameter. In three of these females that had recently ovulated, the largest follicles ranged from 14 to 37 millimeters, with a mean of 24. These approximate maximum follicle sizes of southbound females that had recently ovulated and were presumably pregnant. These three females probably should be regarded as being in metestrus. Five anestrous females that had not ovulated recently had follicles with maximum diameters of 1 to 25 millimeters, with a mean of 14.

This size range is probably closest to that of follicles of fully anestrous females.

Nine pairs of ovaries contained one to several thin-walled, fluid-filled cysts up to about 8 centimeters in diameter. Presumably, these are cystic follicles.

FREQUENCY OF OVULATION.—Nonpregnant adult females regularly ovulate in late November and early December (see discussion of gestation period and fetal growth beyond), while still north of central California on the southward migration. All of the adult females collected in southward migration that were not carrying near-term fetuses had recently ovulated, as revealed by the presence of recently ruptured follicles or developing copora lutea. The mean number of recent ovulations in these females was 1.14 for nulliparous animals and 1.10 for parous animals (Table 8). It is possible that some of these whales would have ovulated again later if their most recent ovulation did not result in conception.

The mean number of recent ovulations in northbound females (excluding postpartum animals) was 1.33 in the nulliparous and the primiparous pregnant females and 0.85 in the parous nonpregnant and the multiparous pregnant females. The diameter of the largest corpus albicans in the ovaries of each metestrous and anestrous female suggests, however, that some of these may have been fairly recently formed corpora whose recent origin was no longer apparent. These corpora ranged from 24 to 39 millimeters in diameter, with a mean and standard error of 32.3 ± 3.0, whereas the largest corpus albicans in each early pregnant female ranged from 18 to 42 millimeters, with a mean and standard error of 27.4 ± 1.6. The latter presumably were the corpora lutea of the previous pregnancy that had regressed after the end of lactation several months earlier.

The mean ovulation rate estimated for females during their regular biennial breeding season was 1.20 for nulliparous females, 0.96 for parous females, and 1.00 for all females (Table 8). For reasons stated above, these estimates may be slightly low.

Each of two females taken on 16 and 18 January had both recently ruptured follicles and a corpus luteum of ovulation. This observation suggests that about 40 days intervene between successive ovulations during one breeding season.

TABLE 8
Number of Recent Ovulations in Adult Female Gray Whales, Excluding Late Pregnant and Postpartum Females.

Direction of migration and reproductive status	Number of whales	Number of recent ovulations[1]				Total recent ovulations	Ovulation rate
		0	1	2	3		
Southbound							
Nulliparous	7	0	6	1	0	8	1.14
Parous	21	0	20	0	1	23	1.10
Total	28	0	26	1	1	31	1.11
Northbound							
Nulliparous or primiparous							
Nonpregnant	1	0	0	1	0	2	2.00
Pregnant	2	0	2	0	0	2	1.00
Subtotal	3	0	2	1	0	4	1.33
Parous or multiparous							
Nonpregnant	7	5	2	0	0	2	0.29
Pregnant	20	0	19	1	0	21	1.05
Subtotal	27	5	21	1	0	23	0.85
Combined northbound sample							
Nonpregnant	8	5	2	1	0	4	0.50
Pregnant	22	0	21	1	0	23	1.05
Total	30	5	23	2	0	27	0.90
All specimens							
Nulliparous or primiparous	10	0	8	2	0	12	1.20
Parous or multiparous	48	5	41	1	1	46	0.96
Grand total	58	5	49	3	1	58	1.00

[1] Figures in body of table indicate the number of whales that had the number of recent ovulations shown at the top of each column.

The only evidence for multiple (simultaneous) ovulation was one female with two recently ruptured follicles of the same size.

The nature of the estrous cycle in baleen whales has been the subject of controversy, because few specimens taken during the breeding season have been available for study, and conclusions have had to be drawn mostly from indirect evidence. Harvey (1963) reviewed the relevant literature and concluded that balaenopterid whales are monestrous. Chittleborough (1965), however, presented direct evidence that female humpback whales, although they usually conceive after ovulating only once, may undergo two or three estrous cycles if pregnancy does not intervene. Gambell's (1968) data strongly suggest a similar condition in sei whales. Potential polyestry would be of considerable selective advantage in a species that can produce no more than one offspring every 2 years, that does not form permanent pair bonds, and that may be so widely dispersed that a male might not be available when the female first comes into estrus.

As southbound female gray whales carrying near-term fetuses had no enlarged follicles, it may be concluded that there is usually no postpartum estrus in this species. However, postpartum estrus sometimes occurs in other whale species. A postpartum estrus resulting in pregnancy almost invariably occurs in the minke whale, *Balaenoptera acutorostrata* (Jonsgård, 1951; Omura and Sakiura, 1956). Postpartum estrus in a high proportion of Southern Hemisphere humpback whales also is indicated by the fact that eight (44 per cent) of 19 lactating animals examined in one study were simultaneously pregnant (Chittleborough, 1958). Likewise, 15 (12 per cent) of 129 lactating Southern Hemisphere fin whales also were pregnant (Laws, 1961). According to Gambell (1968) an estimated 11 per cent of female Southern Hemisphere sei whales experienced postpartum estrus.

The two nonlactating postpartum females examined had not recently ovulated, but the fact that they had follicles (24 and 29 millimeters) much larger than any late pregnant female and larger than the average for anestrous females indicates a resumption of follicular maturation after the corpus luteum starts to regress and progesterone secretion is reduced. It is possible that such follicles may develop sufficiently to undergo ovulation. Chittleborough (1958) has shown that humpback whales usually recommence estrous cycles immediately after stillbirth or early loss of the calf. Ovulation following stillbirth or loss of a calf would be so infrequent that it would not significantly affect the mean ovulation rate.

The possibility of postlactation ovulation, or ovulation by any nonpregnant females during the summer, remains to be considered. The southbound females that had recently ovulated, most of which presumably had ceased lactating about 5 months previously, gave no evidence of having ovulated more than once since that time.

In each, the largest corpus albicans was 22 to 38 millimeters in diameter (mean, 29); this was no doubt the regressing corpus luteum of lactation. Only data from females collected on the summer grounds can provide direct evidence on this point. There is evidence that a considerable proportion of Southern Hemisphere fin whales experience a postlactation ovulation (Laws, 1961), and about 12.5 per cent of the female Southern Hemisphere sei whales ovulate in the summer (Gambell, 1968). These summer ovulations almost never result in pregnancy. In humpback whales, which lactate for approximately 10½ months, an estrous cycle usually commences immediately following the end of lactation; this cycle corresponds with the normal winter breeding season and usually results in pregnancy (Chittleborough, 1958).

The two oldest females studied, with 19 and 34 corpora albicantia, were pregnant, so there is no indication of cessation of breeding in old females.

In summary, female gray whales normally experience one estrous cycle every 2 years, although rarely they may ovulate twice or perhaps three times during one breeding season. The mean ovulation rate for parous females is 0.96 per breeding season. A female that fails to conceive during one breeding season probably undergoes an estrous cycle again the following year. As the pregnancy rate is 0.46 (see below), the mean ovulation rate per year of parous females is 0.52 ([1.00 – 0.46] × 0.96).

CORPORA LUTEA.—Our material included three ovaries with recently ruptured Graafian follicles that provided data on early development of the corpus luteum. In one case the rupture site was still open (Figs. 17 and 18), and in the other two the rupture sites were still obvious as dark spots, although no actual openings were visible. These follicles, 24, 25, and 25 millimeters in diameter, were smaller than mature unruptured follicles. Loss of fluid presumably causes the follicle to collapse immediately after rupture. There is a marked infolding of the walls and a proliferation of luteal tissue from the membrana granulosa. The luteal tissue fills almost the entire antrum. One corpus contained a small amount of liquor folliculi in the central cavity. Subsequent development of the corpus luteum depends upon whether or not pregnancy ensues.

It is difficult to distinguish corpora lutea of ovulation from corpora lutea of pregnancy, because failure to find a visible conceptus in the uterus is not proof that an animal has not conceived. Only in the four females that had recently undergone more than one estrous cycle was it certain that corpora lutea of ovulation were present (Figs. 17 and 18). In these animals the penultimate corpora were 13, 15, 21, and 25 millimeters in diameter. Because of their small size, they did not greatly protrude from the surface of the ovaries. In cross section, the corpora were somewhat irregular or stellate in outline. The layer of luteal tissue was thin and greatly plicated, and no cavity remained. The luteal tissue was pale yellow, as in corpora lutea of pregnancy, in the larger two of the four corpora and more orange-yellow in the two smaller corpora.

Three northbound females had corpora lutea 22, 81, and 102 millimeters in diameter but showed no macroscopic evidence of pregnancy. The two larger corpora in this series were indistinguishable from corpora lutea of pregnancy.

The above data indicate that corpora lutea of ovulation do not attain a size greater than about 25 millimeters and rapidly regress if the female comes into estrus again after a brief diestrous period. The fate of the corpus luteum when the female does not become pregnant or undergo another estrous cycle requires further study.

Corpora lutea of pregnancy in the gray whale (Figs. 17 and 20) are similar to those of the fin whale (Laws, 1961) and humpback whale (Chittleborough, 1954). They protrude from the body of the ovary, from which they are separated by a constricted neck.

In most of the southbound females that had recently ovulated but were not yet visibly pregnant, the corpora lutea ranged from 37 to 87 millimeters (mean, 56; standard deviation, 16). Females with small fetuses collected two months later during northward migration had corpora lutea ranging from 61 to 100 millimeters in diameter (mean, 82; standard deviation, 11). In these animals, the size of the corpus luteum was correlated with the length of the fetus. The female carrying the smallest fetus (25 millimeters long) had a corpus luteum only 63 millimeters in diameter. In females with fetuses 120 to 140 millimeters in length (estimated age 87 to 89 days), the average diameter of the corpus luteum was 84 millimeters, which is not significantly different from that in late pregnant females.

Chittleborough (1954) has shown that it takes nearly three months for the corpus luteum of the humpback whale to reach maximum size. In southbound female gray whales with near-term fetuses, the corpora lutea varied from 61 to 115 millimeters in diameter (mean, 87; standard deviation, 12). No data were obtained on the condition of the corpora lutea in lactating females.

Twenty-one per cent of the corpora lutea of pregnancy contained central vesicles filled with liquor folliculi. Thus, in this species the presence or absence of a central vesicle is of no use in distinguishing corpora lutea of ovulation from those of pregnancy. Laws (1961) has refuted the contention of some authors (for example, Robins, 1954) that the absence of a central vesicle is diagnostic of corpora lutea of ovulation in balaenopterid whales. The largest vesicle in our animals was 54 millimeters in diameter. A few were irregularly shaped or eccentrically located. Some corpora lutea had gel-filled cavities up to 24 millimeters in diameter located around their periphery or at the base (Fig. 20). Although these structures resemble large, flattened follicles, their close association with the corpus luteum suggests that they are part of it.

Only one whale, a primiparous late pregnant female, had an accessory corpus luteum (in the opposite ovary from the primary corpus luteum). It was 14 millimeters in diameter and lacked a stigma, suggesting that it must have developed from an unruptured follicle.

Corpora Albicantia.—The corpora albicantia (Fig. 20F) of gray whales are morphologically similar to those of balaenopterid whales, and the sequence of changes during regression is essentially the same as described by Laws (1961) and van Lennep (1950) for the fin whale.

The earliest stages of regression were seen in the two postpartum females that had recently lost their calves (Figs. 19, 20). The corpora lutea in these individuals were 53 and 60 millimeters in diameter. The connective tissue septa characteristic of corpora albicantia were already obvious, and the color of the luteal tissue was more orange than is typical of the corpus luteum of pregnancy.

As the corpus albicans continues to shrink, it recedes below the surface of the ovary. The color changes to brown as collagen

TABLE 9

Diameter (mm) of Corpora Albicantia in Ovaries of Gray Whales at Different Stages of the Reproductive Cycle. See Text for Explanation of Size Class.

Size class of corpora albicantia	Recently ovulated			Early pregnant			Late pregnant			Postpartum		
	N	Mean ± SE	Range	*N*	Mean ± SE	Range	*N*	Mean ± SE	Range	*N*	Mean	Range
1	20	29.1 ± 0.9	22–38	20	27.4 ± 1.6	18–42	50	24.8 ± 0.7	17–35	2	26.5	26–27
2	18	22.0 ± 0.8	14–31	20	21.8 ± 0.7	17–30	43	20.5 ± 0.5	14–29	2	24.5	24–25
3	16	19.7 ± 0.7	14–26	16	20.4 ± 0.7	17–28	38	19.3 ± 0.6	12–29	1	23	
4	14	19.4 ± 0.7	16–26	15	18.4 ± 0.9	12–23	31	18.7 ± 0.6	10–28	1	22	
5	12	17.7 ± 0.9	12–23	11	18.0 ± 0.9	14–22	27	17.9 ± 0.5	14–24	1	20	
6	11	16.5 ± 0.8	12–21	6	17.5 ± 1.3	13–21	25	16.8 ± 0.5	12–24	1	18	
7	8	17.1 ± 0.6	15–20	3	18.0 ± 1.5	15–20	22	15.6 ± 0.6	11–23	1	16	
8	6	16.2 ± 0.5	15–18	3	17.7 ± 1.9	14–20	19	15.3 ± 0.7	10–23	1	16	
9	5	15.4 ± 0.8	13–17	33	17.0 ± 1.5	14–19	12	15.2 ± 0.6	13–20	1	15	
10	5	15.0 ± 0.9	12–17	2	17.5	16–19	9	14.9 ± 1.0	13–19			
11	4	15.0 ± 0.6	14–16	2	16.0	13–19	7	14.1 ± 1.3	8–19			
12	4	14.2 ± 0.6	13–16	2	15.5	12–19	3	16.0 ± 1.5	14–19			
13	3	13.7 ± 0.9	12–15	1	18		3	15.7 ± 1.7	14–19			
14	2	14.0	13–15	1	18		2	13.5	12–14			
15	1	15		1	18		1	13				
16	1	15		1	18		1	13				
17	1	15		1	18		1	12				
18	1	14		1	18		1	12				
19	1	14		1	18		1	10				
20	1	14		1	18							
21	1	12		1	17							
22–34				1	17–6							

replaces the luteal cells, and the proportion of connective tissue increases. Some of the smaller corpora albicantia consist almost entirely of unpigmented connective tissue.

The corpora albicantia persist throughout life in the ovaries of fin whales (Laws, 1961) and this probably applies to all large balaenopterids. This also occurs in sperm whales (Best, 1967), but not in at least some of the smaller odontocetes, such as the pilot whale, *Globicephala melaena* (Harrison, 1949; Sergeant, 1962).

The corpora persist as permanently recognizable structures in the ovaries of gray whales. The corpora albicantia of each female (excluding nulliparous and primiparous ones) were classified according to relative size in the following manner: class 1, the largest corpus in each whale; class 2, the second largest, and so on. The mean, standard error, and range for each of these classes in females in each phase of the reproductive cycle are presented in Table 9. It is apparent from the size distribution that after an initial phase of rapid regression, there is little further decrease in size of the corpora albicantia. Few were less than 12 millimeters in diameter.

In the discussion of time and frequency of ovulation, it was concluded that females usually ovulate only once every 2 years. If this is true, and the corpora albicantia persist for life, the rate of accumulation of corpora albicantia would be close to 0.5 per year. We examined two other lines of evidence bearing on this question: the size frequency distribution of the corpora albicantia and the correlation between number of corpora albicantia and number of growth layers in the ear plug.

The means, standard errors, and ranges of the diameters of the corpora lutea and two largest corpora albicantia of females in each stage of the reproductive cycle are shown in Fig. 25. We assumed that each female ovulates only once every 2 years, and adjusted the horizontal time scale accordingly. The smooth line shows the presumed rate of regression in size of the corpus albicans during the first 4 years. If the smaller corpora albicantia (Table 9) were similarly plotted, the line would gradually approach the horizontal at about 14 millimeters beyond 20 years. It is apparent from Fig. 25 that a presumed accumulation rate of one corpus albicans every 2 years is consistent with the observed size-frequency distribution of

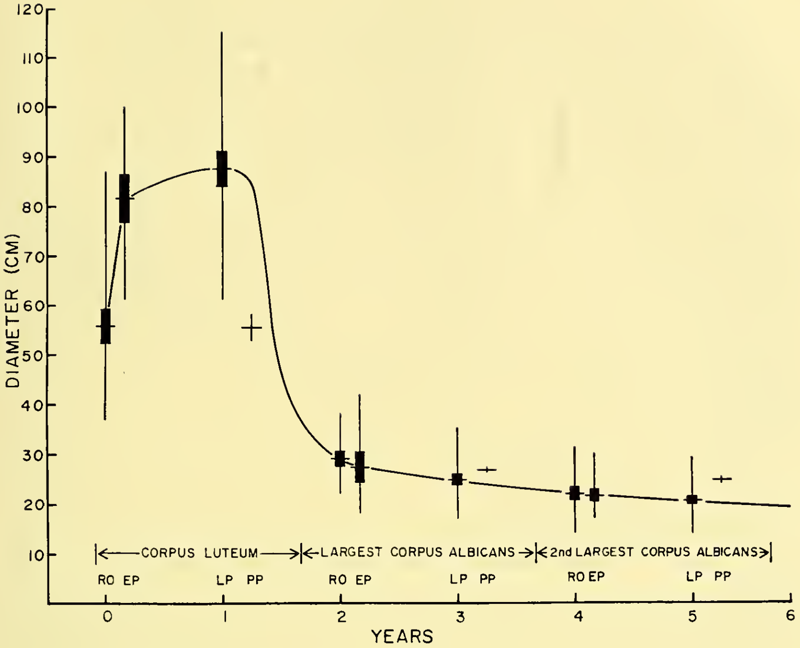

FIG. 25. Diameter of corpus luteum and two largest corpora albicantia in ovaries of gray whales in different stages of the reproductive cycle. The horizontal scale represents the age of each corpus, assuming one ovulation every two years. RO, recently ovulated females; EP, early pregnant females; LP, late pregnant females; PP, postpartum females. The two postpartum females had lost their calves, thus their corpora lutea were smaller than in lactating animals. Horizontal dashes, mean; vertical bars, two standard errors on either side of mean; vertical lines, range. Curve fitted by eye to mean diameters of corpora.

corpora. If the ovulation rate were significantly greater, the size-frequency data would not show such a regular decline. The data on ovulation further indicate that the rate cannot be less than about 0.5 per year.

The relationship between number of corpora albicantia and the number of growth layers in the ear plug is presented in Fig. 26. The solid line ($Y = 0.5X - 3.5$) represents the expected correlation between number of corpora and number of growth layers under the assumptions that two growth layers are formed the first year

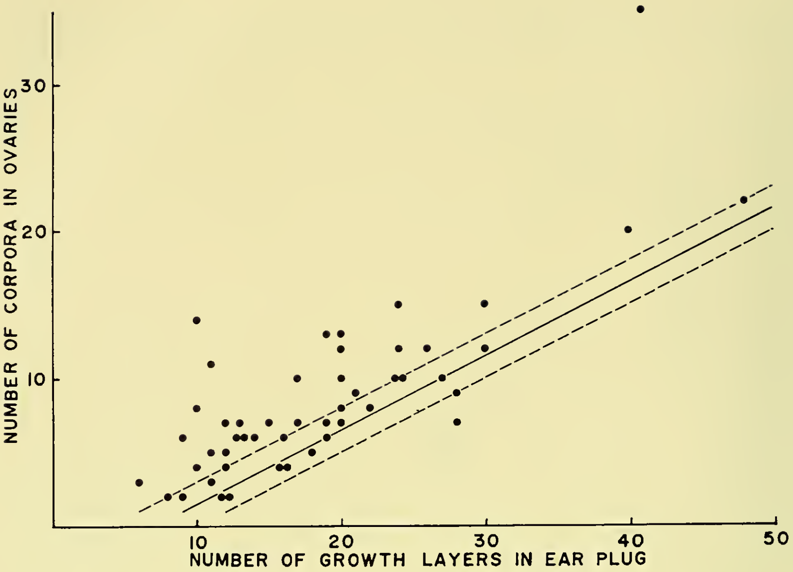

FIG. 26. Number of corpora in the ovaries versus the number of growth layers in the ear plugs of adult female gray whales. The hypothetical correlation is represented by the unbroken line (mean) and the broken lines (range).

and one each year thereafter, and that one corpus is formed every 2 years beginning at 8 years of age (mean age at sexual maturity). The two broken lines ($Y = 0.5X - 2.0$ and $Y = 0.5X - 5.0$) represent the lower and upper limits, respectively, of variation expected because of the variation in the age at sexual maturity of from 5 to 11 years. Deviations from the hypothetical mean number of growth layers are markedly skewed. The mode falls on the lower limit (–3); 41 per cent of the specimens fall within the expected limits (–3 to +3). Only one whale falls above the expected limits (+7); 57 per cent fall below the lower limit (–3 to –37), with 33 per cent falling between –3 and –7. These data are thus consistent with the conclusions that corpora accumulate at a rate of 0.5 per year and growth layers in the ear plug accumulate at a rate of one per year, although the earlier layers may not be discernible.

The only corpora albicantia that are unquestionably derived from corpora lutea of ovulation are those in nulliparous and primiparous females. These corpora do not differ in size or other respects from those representing corpora lutea of pregnancy. In three recently ovulated nulliparous females, the largest corpora albicantia were 23, 30, and 34 millimeters in diameter, and in two primiparous females in early pregnancy they were 13 and 29 millimeters in diameter. All except the smallest of these were within the size range of the largest corpora albicantia in multiparous females in corresponding phases of the reproductive cycle (Table 9).

In addition to normal corpora albicantia, the ovaries of 13 females each contained one to three small orange bodies 4 to 9 millimeters in diameter and which were either compressed and elongate, or stellate, in cross section. The total number of these structures in the 13 animals was 17, which was 2 per cent of the corpora albicantia present in all the females. They are similar to the corpora atretica described by Laws (1961) for the fin whale and presumably originate by atresia of follicles that have not ovulated. This assumption is supported by the finding of a few unruptured follicles with a partial lining of yellow-orange colored tissue. These corpora apparently do not represent ovulations and they were not included in counts of corpora albicantia.

FUNCTIONAL SYMMETRY AND POLARITY OF OVARIES.—Of the total of 756 corpora, 418 (55.3 per cent) were in the left ovary and 338 (44.7 per cent) in the right ovary. The probability of this ratio occurring in a random distribution is less than .05, suggesting that the observed dominance of the left ovary may be real. Laws (1961) found a slight but statistically insignificant dominance of the right ovary in fin and blue whales. In many odontocetes, most ovulations occur in the left ovary (Ohsumi, 1964*b*).

The position of each of 179 corpora in the anterior, second, third, or posterior quarter (measured linearly) of 52 mature ovaries was recorded. There was a significant ($P < .005$) preponderance of corpora toward the anterior pole. The numbers of corpora in each quarter, from anterior to posterior, were: 61 (34 per cent), 48 (27 per cent), 45 (25 per cent), and 25 (14 per cent). A preponderance of ovulations from the anterior pole of the ovary was also found in fin and sei whales (Laws, 1957) and in the sperm whale (Best, 1968), but not in the pilot whale (Harrison, 1949; Sergeant, 1962) or false killer whale, *Pseudorca crassidens* (Comrie and Adam, 1938).

Pregnancy

Pregnancy Rate.—The pregnancy rate is difficult to determine directly because of bias introduced into the sample by the temporal and spatial differences in migration patterns between females in different phases of the reproductive cycle and by gunner selection for the larger animals. In the series of 84 southbound migrants examined, the ratio of late pregnant females to other mature females was two to one, whereas the actual ratio in the population must be less than one to one. The sample of northbound adult females consisted of 22 early pregnant females and eight anestrous females, but only two postpartum females. As it is logical to assume that the number of postpartum females in the spring population should be nearly equal to the number of pregnant females, the sample was obviously biased.

Because the proportion of late pregnant and postpartum females in the samples was biased, these animals were excluded from calculations of the pregnancy rate and appropriate corrections made to determine the overall pregnancy rate in the adult female segment of the population.

The pregnancy rate of females that had already undergone at least one pregnancy will be considered first. During the southward migration, all females that were not carrying near-term fetuses had a developing corpus luteum. If we assume that all of them had conceived, their pregnancy rate would be 1.00. As a few may not have conceived, this figure may be a slight overestimate. During northward migration, 20 of 27 females (exclusive of postpartum females) were pregnant, giving a pregnancy rate of 0.74. Two of the females that were not visibly pregnant each had a corpus luteum that we assumed to be a corpus luteum of ovulation. Although it is possible that they had recently conceived and were carrying a conceptus too small to detect, we think this is unlikely so late in the season. Considering both the northbound and southbound migrants, 41 of the 48 were pregnant or could reasonably be assumed to have already conceived. This gives a pregnancy rate of 0.85 per breeding season.

Considering females that had not undergone a previous pregnancy, all seven taken on the southward migration had recently ovulated. Each of five animals had a single corpus luteum 19 to 62 millimeters in diameter and were assumed to have already conceived. One with a recently ruptured follicle and a corpus luteum of ovulation (25 millimeters in diameter) possibly had done so. The last had what appeared to be a corpus luteum of ovulation (27 millimeters in diameter) and Graafian follicles up to 35 millimeters in diameter, so it might have ovulated again later and then conceived. Of the three northbound animals examined, two were pregnant. The third had two fairly recent corpora lutea (22 and 13 millimeters in diameter) and was probably not pregnant. Thus, of 10 females that had not previously been pregnant, seven were pregnant, two were not pregnant but probably would have conceived later, and one probably would not have conceived that season. These data indicate a probable pregnancy rate of 0.90 per breeding season, but further data are needed to determine whether newly mature females are as fertile as older individuals.

The combined pregnancy rate for nulliparous and parous females, exclusive of late pregnant and postpartum animals, is 0.86. To determine the overall pregnancy rate for all adult females in the population, we made a correction for the biased representation of late pregnant and postpartum females in the sample. If the pregnancy rate remains constant from year to year, or if the sample was taken over a period of several years, the overall pregnancy rate may be calculated as 0.86/1.86, or 0.46 per year.

Zenkovich (1937*a*) examined a large series of gray whales taken in the Bering Sea between August and October from 1933 to 1936. Assuming that all females 12.0 meters or more in length were sexually mature, there were 57 mature females in his sample. Of these, only 16 were pregnant, giving a calculated pregnancy rate of only 0.28. G. C. Pike (unpublished data) reported that only one of three adult females he examined off British Columbia in April was pregnant.

Of the seven northbound adult females (exclusive of postpartum individuals) that were not pregnant, only three had recently ovulated, indicating that missed pregnancies may result from either failure to ovulate or failure to conceive following ovulation.

Breeding Season.—Almost all of the adult females (except those carrying near-term fetuses) taken during southward migration

TABLE 10

BODY LENGTH OF GRAY WHALE EMBRYOS AND EARLY FETUSES (CROWN-RUMP LENGTH OF EMBRYOS IN PARENTHESES).

Date of collection	Length (mm)	
	Males	Females
21 February	80	90
22 February	120	
23 February	59 (40), 85	
24 February	110	90, 110
26 February		80
28 February	85	90
1 March	75, 120	140
2 March	39 (16)	25 (10), 105
6 March		120, 120
7 March		110
8 March		135
10 March		120

probably had already conceived, although none was visibly pregnant. The mean conception date calculated from the fetal growth curve (see below) is 5 December. We calculated the duration of the breeding season by estimating the ages of the 22 embryos and early fetuses collected. The estimated ages were based on certain assumptions about early fetal growth discussed below. The calculated conception dates fall between 27 November and 13 December, except for one on 22 December and one on 5 January. The female that conceived about 22 December was multiparous and showed evidence of two recent ovulations, indicating that she had failed to conceive following her first ovulation that season. The female that conceived about 5 January was primiparous; Laws (1961) found that newly mature female fin whales conceive, on the average, later than multiparous females.

The duration of the breeding season also was estimated on the basis of length measurements for 16 fetuses collected in late summer by Zenkovich (1937*a*). The estimated conception dates of 12 (75 per cent) of these fetuses fall between 23 November and 14 December, and all fall between 13 November and 10 January. Individual variations in growth rate will give a spurious spread to the calculated range, so that the actual breeding season is doubtless even shorter than these data indicate. For the same reason, the

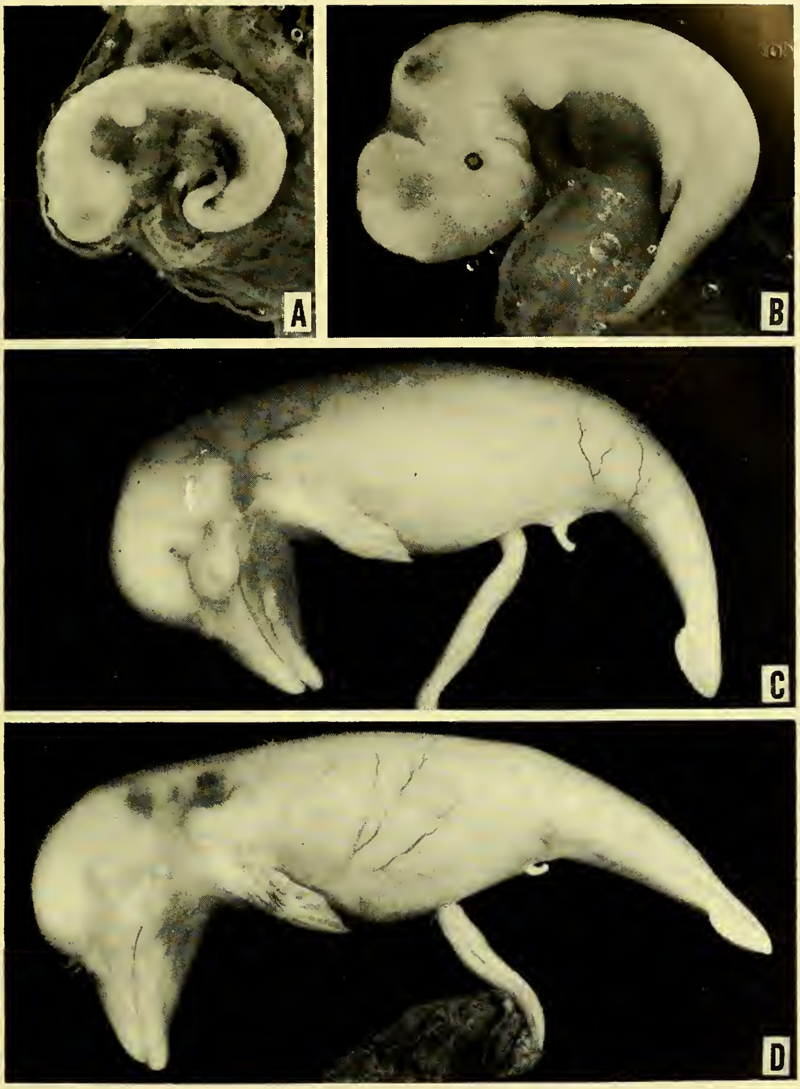

Fig. 27. Embryos and early fetuses of gray whales. A, 25-millimeter (10 millimeters crown-rump) female embryo, estimated age 55 days; B, 39-millimeter (16 millimeters crown-rump) male embryo, estimated age 70 days (note hind limb buds); C, 120-millimeter male fetus, estimated age 87 days (note size and position of penis); D, 110-millimeter female fetus, estimated age 86 days (note size and position of clitoris).

data from near-term fetuses are even less useful for calculating conception dates.

GESTATION PERIOD AND FETAL GROWTH.—Available measurements of fetuses are limited to the periods of early and late pregnancy.

A total of 22 embryos and early fetuses was collected between 21 February and 10 March (Table 10, Fig. 27). Body length, measured from the crown to the tip of the straightened tail varied between 25 and 140 millimeters (mean, 96; standard error, 6).

Additional data on fetal sizes in the gray whale are contained in a number of reports. Scammon (1874) examined five embryos taken on the California coast, but gave no measurements or dates. Andrews (1914) reported fetuses 180 and 250 millimeters long taken on 13 and 14 March 1912, on the coast of Korea. Pike (unpublished data) found a 250-millimeter fetus the first week of April from the coast of Vancouver Island, British Columbia. Zenkovich (1937*a*) published data for 16 fetuses collected in the Bering Sea between 8 August and 24 September. Their lengths ranged from 1.70 to 2.64 meters, with a mean and standard error of 2.05 ± 0.06. Townsend (1887) examined four fetuses taken in December 1885 at San Simeon, California, and stated: "Their average length was about 12 feet [3.66 meters]; the longest . . . 17 feet [5.18 meters] long." Andrews (1914) inconsistently reported one fetus taken at Ulsan, Korea, on 8 January 1912, as 4.35 and 4.76 meters long.

We measured 55 near-term fetuses (30 males, 25 females) collected during a 38-day period from 14 December to 20 January. The length varied between 3.60 and 5.31 meters, with a mean and standard error of 4.62 ± 0.05 (Table 11, Fig. 28). The average length of females (4.65 ± 0.06 meters) was slightly greater than that of males (4.60 ± 0.08), but the difference was not statistically significant ($P > .10$). If these measurements are grouped by shorter time periods, they show no change in mean length from mid-December until late January. This suggests that the timing of migration of a pregnant female depends upon how advanced her pregnancy is.

The statistics for Norwegian factory ship operations near the calving grounds on the west coast of Baja California from 1924 to 1927 (published in part by Risting, 1928) list 20 fetuses taken from 29 December to 16 February with estimated (not actually

TABLE 11

BODY LENGTH OF NEAR-TERM FETUSES OF GRAY WHALES.

Date of collection	Length (meters)	
	Males	Females
14 December	4.86	
15 December		4.58
16 December	4.53, 4.65, 4.67	
18 December		4.50
19 December	4.15	
20 December	4.07, 4.54, 4.84	4.55, 4.78, 5.12
21 December	3.85, 4.62, 4.63	5.08
22 December	4.62, 4.79	
27 December	4.22, 4.89	3.60
28 December	4.52, 4.81	4.32
29 December	4.70	5.12, 5.12
30 December		5.24
2 January	4.72	4.58
3 January	4.77, 5.31	4.42, 4.44, 4.93
4 January		4.54, 4.92
5 January	4.72	4.24
7 January	4.52, 5.24	4.43
8 January		4.11, 4.73
11 January		4.33, 5.11
12 January	4.59	
13 January	4.41, 4.48	
15 January	4.26	
16 January	4.53	
18 January		4.80
19 January	4.39	
20 January		4.75

measured) lengths ranging from 6 to 18 Norwegian feet (1.90 to 4.71 meters).

Measurements of six recently born calves found dead at Laguna Ojo de Liebre, Baja California, in late January and early February, are given by Eberhardt and Norris (1964). These ranged from 3.95 to 5.40 meters (mean, 4.68; standard error, 0.245). Gilmore (1960*a*) also listed measurements of seven recently born calves found in the same lagoon. The total lengths given for these calves (3.54 to 4.51 meters, mean, 4.05) are well below those presented by Eberhardt and Norris and even average less than our December fetuses. Therefore, we can only conclude that Gilmore made his measurements differently or that the published figures are in error.

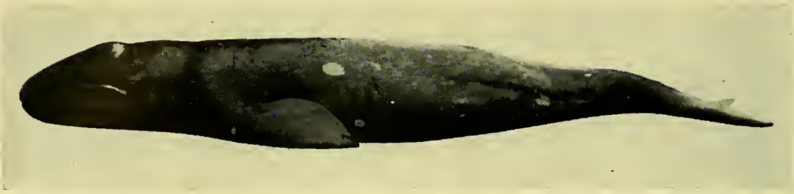

FIG. 28. Near-term gray whale fetus 4.54 meters long. Note color pattern of whitish rings and blotches (the other marks are postmortem abrasions).

Only three of the series of measurements presently available are large enough to provide statistically reliable data for use in constructing a fetal growth curve for the gray whale. These include our series of early embryos and fetuses, Zenkovich's series taken in late summer, and our series of near-term fetuses. The means for these three sets of measurements have been plotted in Fig. 29. It is apparent that the points do not fall on a straight line. Laws (1959) found that in balaenopterid whales, excepting the earliest

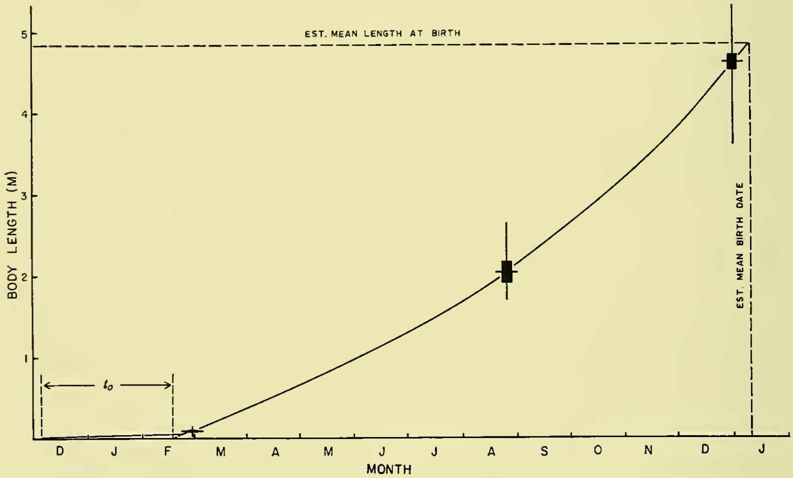

FIG. 29. Estimated prenatal growth curve based on measurements of 22 embryos and early fetuses collected in February and March, Zenkovich's (1937*a*) 16 mid-term fetuses collected in August and September, and 55 near-term fetuses collected in December and January. Horizontal dashes indicate means; vertical bars represent two standard errors on either side of mean, and vertical lines represent the range. For estimation of t_0 see text.

part of pregnancy, the length of the fetus increases linearly during the first half of pregnancy and logarithmically during the last half. A similar curve fits the present data (Fig. 29). From the slope of the lower portion of this curve, we estimated the "specific fetal growth velocity," or *a* of Huggett and Widdas (1951), as 0.95.

To determine the total gestation period, it is necessary to estimate the length of the gestation period before the beginning of the linear growth phase, termed t_0 by Huggett and Widdas (1951). J. G. Sinclair, who is studying the anatomy of two early fetuses (25 and 39 millimeters long from crown to tip of tail, and 10 and 16 millimeters in crown-rump length), has, on the basis of their stage of development, estimated their ages at about 55 and 70 days. According to Sinclair, the rapid linear growth phase starts when ossification begins, at a crown-rump length of about 35 millimeters; this is equivalent to a length of about 55 from crown to tip of tail. Judging from the estimated ages of the two early embryos, this length would be reached at an age of at least 80 days, or perhaps slightly more. An estimate of t_0 will therefore be $80 - (5.5 \times 0.95)$, or about 75 days. The growth curve, extrapolated backwards, intercepts the abscissa on 18 February (Fig. 29). Adding to this the estimate of t_0, the calculated mean conception date falls on 5 December.

If the growth curve is projected forward, it intercepts the mean length of the six newborn calves observed by Eberhardt and Norris (1964) on 2 January, only 2 days later than the mean date of passage of pregnant females past San Francisco. Considering the speed of migration, it would take the whales at least 9 to 12 days to travel from San Francisco to the major calving grounds at Laguna Ojo de Liebre, Laguna San Ignacio, and Bahia Magdalena. Therefore, the mean birth date would be about 10 January, when the projected growth curve reaches 4.90 meters. This estimate of length at birth falls within one standard error of the mean of newly born calves, so the agreement is close.

Based upon the calculated mean dates of conception and parturition, the mean length of the gestation period is estimated to be slightly more than 13 months, or about 400 days.

Applying Laws (1959) method of estimating t_0 for baleen whales to the data of this study yields values of only 31 days for t_0 and

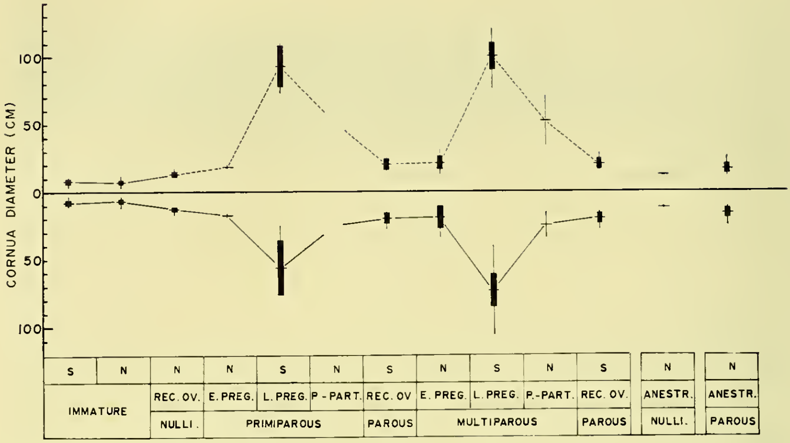

Fig. 30. Diameter of the uterine cornua of gray whales in different stages of the reproductive cycle. For pregnant and postpartum females, measurements of the horn in which implantation occurred are plotted above the base line and those for the other horn below. Symbols are as follows: horizontal dashes, mean; vertical bars, one standard deviation on either side of the mean; vertical lines, range; S, southbound migrants; N, northbound migrants.

no more than one year for total gestation period, which are not consistent with the actual data. The discrepancy results from the way in which Laws interpreted data for several species of terrestrial mammals given by Huggett and Widdas (1951) in estimating the length of t_0 for three species of odontocetes in which fetal growth is linear until the end of pregnancy. His estimates showed an *inverse* relationship between t_0 and length of gestation period (and also a). Huggett and Widdas' data show, however, that "t_0 *increases as gestation times lengthen* but forms a decreasing fraction of total gestation time" (italics added). There are no data to justify Laws' conclusions; his error appears to be the result of using imprecise, arbitrary percentage values for t_0. Laws then estimated the length of t_0 in the humpback whale as 38 days on the basis of published fetal length data and Chittleborough's (1954, 1958) data on the mating and calving seasons. Chittleborough's data suggest, however, a peak conception date in late July, not early August as stated by Laws, so Laws' estimate of t_0 is doubtless too short. Since his four estimates of t_0, for three species of odontocetes and one mysticete, showed an apparently consistent inverse relationship between t_0 and a, he extrapolated these results to other species of baleen whales. This resulted in his inexplicable and anomalous conclusion that the larger species of balaenopterid whales have shorter gestation periods than the smaller ones. Any logical extrapolation of the data presented by Huggett and Widdas would result in an estimate of at least 50 or 60 days for the duration of t_0 in larger cetaceans. In any event, it is dangerous to extrapolate from small terrestrial mammals to large cetaceans.

We suspect that when more direct evidence is available on early embryonic growth, most large mysticetes will be found to have a gestation period of about a year or somewhat longer. It is certainly approximately 13 months in the gray whale, and probably more than a year in the humpback whale. A gestation period longer than one year would not preclude an occasional pregnancy resulting from a postpartum ovulation, as has been reported in fin whales (Laws, 1961) and humpback whales (Chittleborough, 1958), but it does indicate that such pregnancies cannot occur regularly if a marked seasonality of breeding is to be maintained.

CALVING SEASON.—The mean calving date, as indicated above, is estimated to be about 10 January. The duration of the calving season should be generally similar to that of the breeding season, but slightly more prolonged because of individual variation in the length of the gestation period. As noted above, the timing of the southward migration of pregnant females depends on the stage of gestation. Because late pregnant females pass San Francisco for at least 38 days, we may assume that the calving season lasts about that many days. Therefore, we estimate that calving occupies a period of 5 or 6 weeks from late December to early February. This is corroborated by field observations of recently born calves (Eberhardt and Norris, 1964; Gilmore, 1960*a*, 1960*b*; Gilmore and Ewing, 1954; Hubbs and Hubbs, 1967).

CYCLIC CHANGES IN THE UTERUS.—Gray whales have a bipartite uterus similar to that of other baleen whales (Mackintosh and Wheeler, 1929; Matthews, 1948). The placenta is of the diffuse, nondeciduate, epitheliochorial type. Measurements of the diameter of the uterine cornua of specimens examined in this study are presented in Fig. 30. Histological characteristics of the endometrium

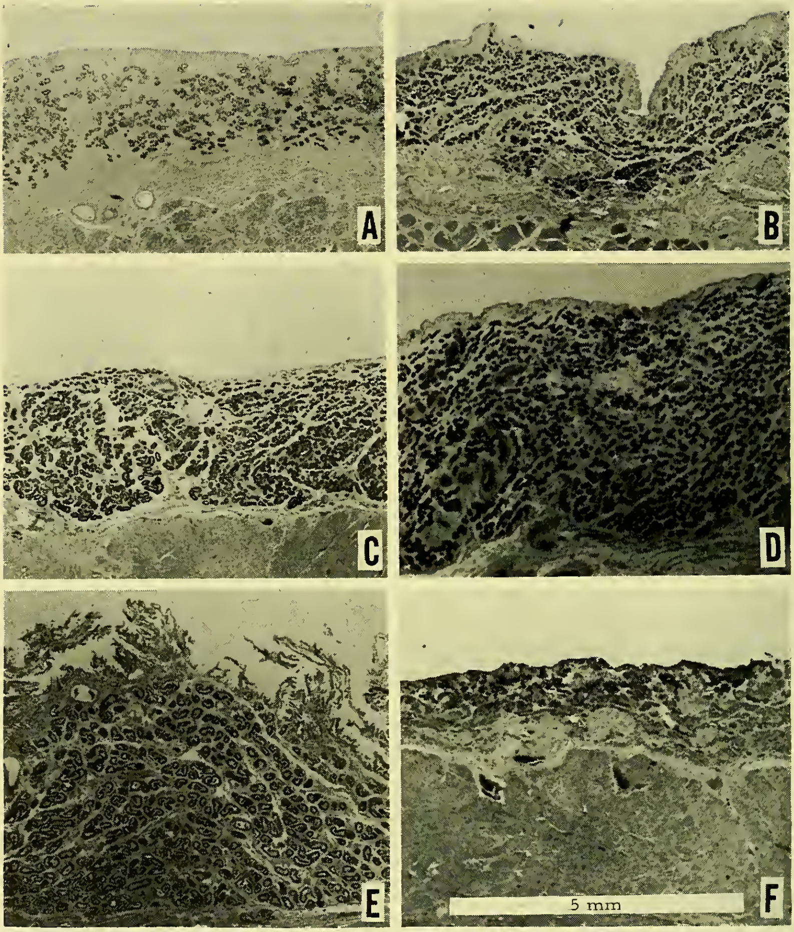

Fig. 31. Photomicrographs of sections of the endometrium of gray whales in different stages of the reproductive cycle. A, immature female; B, northbound anestrous female; C, southbound recently ovulated female; D, northbound early pregnant female (110-millimeter fetus); E, southbound late pregnant female (3.60-meter fetus); F, northbound postpartum female. All sections are to same scale.

TABLE 12

CONDITION OF THE UTERUS OF GRAY WHALES IN VARIOUS STAGES OF THE REPRODUCTIVE CYCLE.

						Endometrium thickness				Endometrial glands		
Direction of migration and reproductive status[1]	Number	Thickness of wall (mm)		Height of folds (mm)		Total (mm)		Stratum compactum (microns)		Diameter (microns)		
		Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	Spacing
Immature (S)	10	10.4 ± 3.6	4–16	8.2 ± 3.3	3–12	2.9 ± 1.5	1.1–5.4	63 ± 15.4	30–90	50 ± 12.5	30–70	Wide
Immature (N)	23	9.1 ± 3.7	4–18	10.2 ± 4.3	4–20	1.6 ± 0.8	0.9–3.8	81 ± 28.3	35–150	42 ± 8.0	35–70	Wide
Anestrous (nulliparous) (N)	1	18		11		2.5		65		50		Close
Recently ovulated (multiparous) (S)	7	16.3 ± 4.1	11–23	10.0 ± 5.0	5–20	2.9 ± 0.9	1.9–4.2	109 ± 40.3	75–175	70 ± 18.8	55–65	Close
Early pregnant (primiparous) (N)	2	17.5	17–18	9.5	9–10	4.3	2.6–5.9	165	155–175	68	60–75	Close
Late pregnant (primiparous) (S)	5	13.6 ± 4.2	7–18	3.2 ± 2.5	1–7	3.1 ± 0.4	1.2–5.1	556 ± 360.6	315–1150	102 ± 22.1	95–145	Close
Anestrous (parous) (N)	7	18.6 ± 5.8	9–26	15.1 ± 5.2	4–20	1.8 ± 1.4	0.6–4.0	96 ± 32.9	70–360	39 ± 9.9	30–60	Close
Recently ovulated (parous) (S)	21	23.0 ± 6.5	11–35	9.9 ± 7.5	0–25	3.3 ± 2.6	1.1–13.5	135 ± 54.7	75–250	61 ± 14.1	45–75	Close
Early pregnant (multiparous) (N)	17[2]	18.4 ± 5.0	8–29	9.3 ± 5.4	2–20	3.4 ± 0.9	2.4–5.3	153 ± 30.9	95–200	57 ± 10.4	45–80	Close
Late pregnant (multiparous) (S)	48[3]	24.4 ± 7.5	12–45	4.9 ± 2.7	0–21	3.9 ± 1.5	1.3–10.0	724 ± 400	190–2400	128 ± 17.9	90–170	Close
Postpartum (multiparous) (N)	2	22.5	21–24	19.5	14–25	1.6	1.0–2.1	75	70–80	40	30–50	Close

[1] (S) = southbound migrants, (N) = northbound migrants.
[2] N = 18 for wall thickness; N = 14 for stratum compactum thickness.
[3] N = 45 for stratum compactum thickness.

are illustrated in Fig. 31 and endometrial measurements are presented in Table 12. There was no endometrial epithelium in any of our specimens, probably because of postmortem changes.

In immature whales (Fig. 31A), the diameter of the uterine cornua ranges from 3.5 to 12.0 centimeters. The average thickness of the wall is 9 millimeters and the mean height of cornual folds is 10 millimeters. The average thickness of the endometrium is 2.9 millimeters in southbound animals and 1.6 in northbound animals. The surface of the endometrium is fairly smooth, with only a few small furrows, and it has few glandular ducts that have a mean diameter of 44 microns. The lumina of the glands are either small or not visible. Capillaries are scattered but fairly numerous.

At any stage of the reproductive cycle the uterine cornua of primiparous females average smaller than the cornua of females that have undergone a previous pregnancy, but they cannot be distinguished on the basis of histological criteria.

The cornua of northbound, sexually mature, anestrous females (Fig. 31B) are in the fully involuted condition. They range from 11 to 26 centimeters in diameter and 19 millimeters in thickness, and the folds are high, averaging 15 millimeters. The mean thickness of the endometrium is 1.8 millimeters, of which the stratum compactum comprises 96 microns. The area of division between the stratum compactum and the stratum spongiosum is poorly defined. The glands are small, with a mean diameter of 39 microns, and are more closely spaced than in immature females.

The cornua of southbound whales that have recently ovulated (Fig. 31C) are slightly larger than those of anestrous females. They range from 15 to 28 centimeters in diameter. Mean fold height has decreased to 10 millimeters, and the mean thickness of the endometrium and stratum compactum have increased to 3.3 millimeters and 135 microns, respectively. The inner surface of the uterus is more uneven than in immature individuals, with deeper furrows and a greater number of glandular openings. The average diameter of the glands has increased to 61 microns, and the lumina are mostly open. These data on gray whales differ from Matthew's (1948) observation (based on one specimen) that in fin whales there is a marked temporary increase in endometrial thickness and gland diameter at the time of ovulation.

In early pregnancy (Fig. 31D), the cornua range from 12 to 34 centimeters in diameter, the difference between gravid and nongravid cornua not being statistically significant. Mean fold height is 10 millimeters. The endometrium (mean, 3.4 millimeters) and the stratum compactum (mean, 153 microns) are slightly thicker than in recently ovulated animals, and there are many large vessels visible in the stratum spongiosum. The glands have a mean diameter of 57 microns, slightly less than in females that have recently ovulated. No dendritic structures are visible yet, though the surface is quite uneven and numerous crypts are visible in the stratum compactum.

Whales in advanced pregnancy (Fig. 31E) have wide cornua, ranging from 76 to 120 centimeters in diameter in the horn carrying the fetus and from 40 to 105 in the other horn. The nongravid horn contains part of the placental membranes of the fetus and is filled with fluid. The uterine wall is greatly thickened, mostly as a result of an increase in the thickness of the inner layer of circular muscles. The folds have almost disappeared, contrary to the condition reported in blue and fin whales by Slijper (1956). Their disappearance seems to be a direct result of the distension of the uterine wall, and they tend to reappear when samples of the wall contract in fixatives. The endometrium is relatively thick (mean, 3.9 millimeters) because of highly developed dendritic structures, which average 724 microns in height. One female with a length of 12.98 meters had a maximum stratum compactum thickness of 3600 microns. This is markedly thicker than that of the fin and blue whales in late pregnancy which Matthews (1948) examined, the thickest of which was 200 to 1000 microns. Vessels in the stratum spongiosum are large and many are filled with blood cells. The mean diameter of the glands has increased to 128 microns.

In the two postpartum whales examined (Fig. 31F), the cornua that had contained the fetus were 34 and 70 centimeters wide, whereas the others were 16 and 34. The uterine folds were 14 and 25 millimeters high. The thickness of the endometrium had decreased to 1.0 to 2.1 millimeters and the stratum compactum to 70 to 80 microns. Dendritic structures were absent, and blood vessels were fewer and smaller. Gland diameters also had decreased to 30 to 50 microns.

Position of the Fetus.—All near-term fetuses were positioned in the uterus with the tail towards the cervix; this would ensure caudal presentation at birth, as is usual in cetaceans (Slijper, 1956). Inasmuch as the uterine horns are curved during advanced pregnancy, the head of the fetus is actually oriented towards the tail of the mother.

There was no evidence of differential tendency for implantation to occur in the right or left uterine horns. In 76 pregnant females, the fetus was in the left cornu in 37 and in the right in 39. In three cases, the fetus was in the cornu on the side opposite the ovary containing the corpus luteum, indicating transuterine migration of the ovum.

Weight Gain During Pregnancy.—During the southward migration, females carrying near-term fetuses averaged 35 per cent heavier than those that had recently ovulated and most of which had presumably weaned a calf a few months previously (Table 3; Figs. 7–8). About 1000 to 2000 kilograms of this difference can be attributed to the fetus and fetal membranes and fluids, so that the gain in body weight attributable to fat stores is about 25 to 30 per cent. As there is no difference in blubber thickness between these two classes of females, most of the weight increase may be attributed to increased body fat stores.

Extra energy stores are necessary in late pregnant females to sustain rapid fetal growth and maintain the newborn calf, as well as provide for their own needs during the southward migration, the winter, and the northward migration. Acquisition of extra fat stores during pregnancy is characteristic of some other marine mammals that fast throughout the entire lactation period (Kenyon and Rice, 1959; Rice, 1960).

Lactation

Lactation Period.—According to Tomilin (1957), juvenile gray whales taken during August, September, and October in the Bering and Chukchi seas had already been weaned. He assumed that animals 8.5 to 9.5 meters long were calves of the year, an assumption supported by our data (see section on growth). None had milk in its stomach and even the smallest had been feeding on crustaceans, although many still accompanied their mothers (Zenkovich, 1937*a*). These Russian workers examined 57 sexually mature females (we are assuming that females 12.0 meters or more in length were sexually mature); of these, 16 were pregnant. Of the remaining 41, only three were still lactating, including one collected on 21 August and another on 1 September. The collection date for the third is not given.

Maher (1960) reported the capture of two lactating females accompanied by calves at Barrow, Alaska, on 19 July and 13 September. The calf of the specimen taken in July had an estimated length of 25 to 28 feet (7.6 to 8.5 meters) and the young of the other was also about 25 feet. On 10 August a 25-foot calf associating with an adult was killed in the same area.

Tomilin and Zenkovich estimated 6 months as the mean length of the lactation period. They believed that most calves were born in February. As the present data indicate mid-January as the peak of the calving season, 7 months seems a more reasonable estimate of the mean duration of lactation. However, more data are needed. As with other cetaceans, weaning is probably gradual and prolonged.

CYCLIC CHANGES IN THE MAMMARY GLANDS.—In gross anatomy, position, and relative size, the mammary glands of gray whales are similar to those of other baleen whales. Changes in thickness of the gland at different phases of the reproductive cycle are shown in Fig. 32. The histological specimens were not fresh enough at time of fixation to allow study of cellular details.

The mammary glands of one 11.8-meter, sexually immature female were 77 centimeters long and 17 wide. The maximum thickness of the glands of immature females was 1.0 to 6.5 centimeters. The fresh tissue of mammary glands of virgin females is pinkish in color. The glands consist mostly of stroma. The lacteal ducts are small, widely spaced, and surrounded by only a thin layer of glandular tissue.

The mammary glands of nulliparous females at puberty and females early in their first pregnancy resemble those of virgin females in their histology, but they may be slightly thicker (up to 9.0 centimeters). The mammary glands of primiparous females in late pregnancy consist of 66 to 91 per cent (mean, 81) glandular

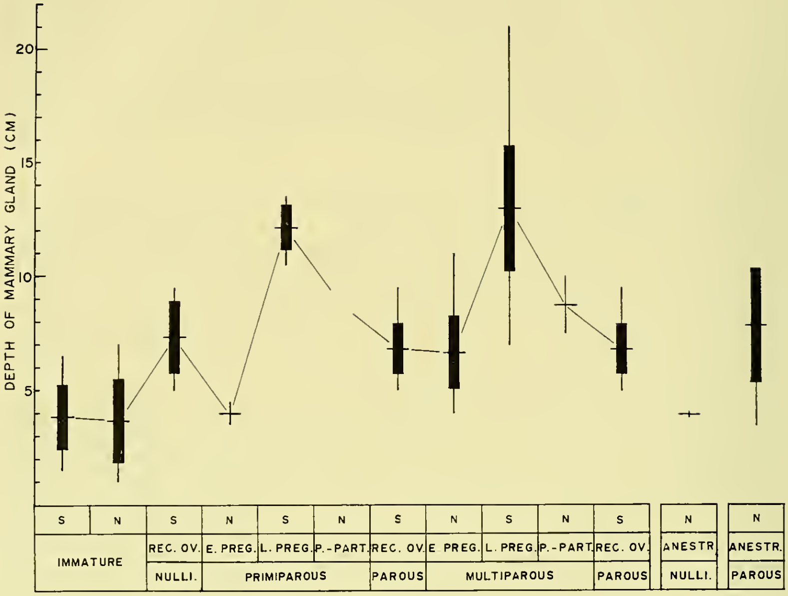

Fig. 32. Thickness of mammary glands of gray whales in different stages of the reproductive cycle. Symbols are as follows: horizontal dashes, mean; vertical bars, one standard deviation on either side of mean; vertical lines, range; S, southbound migrants; N, northbound migrants. Values plotted for post-partum females were from nonlactating individuals.

tissue and are grossly and histologically indistinguishable from those of multiparous females.

The involuted glands of parous animals in anestrus taken during the spring migration are larger than those of virgin individuals. One female 13.3-meters long had mammary glands 145 centimeters long and 32 wide. The mammary tissue varies from 3.5 to 10.0 centimeters (mean, 7.8) in thickness and is pale yellowish-brown in color. Histologically, the glands consist of 37 to 66 per cent (mean, 56) glandular tissue separated by a moderate amount of stroma. They show an extensive system of secretory lobules, which in section are somewhat polygonal and flattened. No secretory activity is apparent.

All females collected during southward migration that had recently ovulated, the majority of which had presumably ceased lactating about the previous July, had nearly or completely involuted glands 5.0 to 9.5 centimeters in thickness. They consisted of 41 to 65 per cent (mean, 53) glandular tissue, and were not distinguishable histologically from the glands of the anestrous females taken in spring. No secretory activity was noted.

The mammary glands of northbound females in early pregnancy also were grossly and histologically indistinguishable from the involuted glands of anestrous females. They consisted of 24 to 63 per cent (mean, 43) glandular tissue.

The mean depth of the lacteal tissue of females in advanced pregnancy was 13.0 centimeters. The mammary tissue is pink and softer than that of involuted glands, and histologically it shows extensive proliferation of the lobule-alveolar system. In section the lobules are large and round, comprising 67 to 91 per cent (mean, 80) of the gland, with relatively little stroma. In a few of the glands examined at this stage, no secretory activity was noticeable, but most already showed a considerable amount of secretory activity. Some had only a small amount of translucent, yellowish fluid in the ducts, others contained so much fluid (colostrum?) that it spurted from the teats when the animals were hauled onto the flensing deck. One female that apparently had recently aborted (or was immediately postpartum), killed on 8 January, had the thickest glands (21.0 centimeters) of any examined and was secreting colostrum copiously.

Unfortunately, we collected no actively lactating animals. The glands of the two nonlactating, postpartum females were grossly and histologically indistinguishable from those of females in late pregnancy. Their thickness was slightly reduced; they consisted of 56 to 72 per cent (mean, 64) glandular tissue and were secreting yellowish, translucent fluid.

Zenkovich (1938) reported that the milk of gray whales taken in August near the end of the lactation period consisted of 53.04 per cent fat, 6.38 per cent dry residue, and 40.58 per cent water. The fat content is greater than has been reported for any other species of cetacean.

Anestrus

Females are probably in anestrus for 3 to 4 months from the end of lactation about August until the onset of the next estrous period in late November or December. As noted earlier, a few females fail to come into estrus at this time and presumably would not do so again until at least a year later; they would thus undergo an anestrous period of 16 months or longer. Other females come into estrus but fail to conceive and return to the anestrous state, probably nearly a year in duration.

Discussion and Conclusions

The complete reproductive cycle of the female gray whale occupies 2 years. Females come into estrus during about a 3-week period in late November and early December. They usually conceive following their first ovulation, but if they fail to do so, they may undergo another estrous cycle about 40 days later. Pregnancy lasts for about 13 months (400 days). Parturition occurs within a period of 5 to 6 weeks from late December to early February. The calf is nursed for about 7 months. After weaning their calf about August, females are in anestrus for 3 or 4 months until November or December, when most of them go into estrus and commence a new pregnancy. A few either fail to ovulate, or ovulate but fail to conceive, and are in anestrus for another year. There is no evidence for postpartum or postlactation ovulation. Evidence for the possible occurrence of ovulation following stillbirth or early loss of the calf is suggestive but inconclusive.

The reproductive cycle of the female gray whale is basically similar to that of the larger rorquals. One important difference is that the extremely long migration route and restricted calving grounds of the gray whale impose a much stricter annual schedule. For example, the majority of gray whale calves are born during a period of 5 to 6 weeks, as contrasted with about 5 months in the rorquals.

The gray whale's ovulation rate of about 0.50 per year is less than that reported by some authors for rorquals. The ovulation rate of the fin whale was estimated as 1.40 per year by Laws (1961) and 1.25 per year by van Utrecht-Cock (1965). Laws, however, admitted that the rate may be only half his estimate. Nishiwaki *et al.* (1958) estimated the ovulation rate of southern fin whales as 0.90 per year and that of North Pacific fin whales as 0.80 per year. Chittleborough (1959) estimated the ovulation rate of humpback whales at 1.10 per year. Nishiwaki *et al.* and Chittleborough assumed that two growth layers were formed in the ear plug each year, so the true ovulation rates are probably nearer 0.40 to 0.45 per year for fin whales and 0.55 per year for humpback whales. The annual ovulation rate of Southern Hemisphere sei whales is 0.69 (Gambell, 1968). Rorquals, apparently unlike gray whales, sometimes experience postpartum and postlactation or summer ovulations.

When comparing ovulation and pregnancy rates of different species and stocks of whales, it must be borne in mind that the reproductive performances of mammals—even large, late maturing and slow breeding species—are quite labile in response to population density in relation to carrying capacity of the range. Laws (1962) and S. Ohsumi and Y. Shimadzu (personal communication) have shown a reduction in age at sexual maturity and an increase in the pregnancy rate of Southern Hemisphere fin whales in response to excessive exploitation. Among large terrestrial mammals, Buss and Smith (1966) have shown a marked decrease in pregnancy rate in a population of African elephants, *Loxodonta africana*, brought about by an increase in population density and resultant deterioration of the habitat.

Presumably population density influences reproduction through nutrition or through ethological factors. In the gray whale, nutrition could be of critical importance, because the pregnant female must accumulate enough energy stores during the summer to support herself and her fetus through a long migration, to support herself and the newborn calf for a month or more on the wintering grounds, and to sustain both herself and the rapidly growing calf during the long return migration to the summer feeding grounds. Under such conditions, selective pressure for suppression of ovulation at times when the female is not physiologically capable of carrying a new pregnancy to term might be expected. Thus it may be that in the gray whale the potentiality for a postpartum estrous cycle is being or has been genetically eliminated from the population.

MALE REPRODUCTIVE CYCLE

DATA on the reproductive biology of the male gray whale were obtained from a sample of 166 animals. Of this number, 123 had attained puberty, including 67 southbound and 56 northbound migrants.

Testes

The testes of gray whales are cylindrical, moderately elongate, and generally similar to those of rorquals.

WEIGHTS.—No significant or consistent difference in weight between left and right testes was found.

In all sexually immature males examined, both testes weighed less than 8.2 kilograms and, in all individuals except three, the combined weight of the testes was less than 5.0 kilograms (Fig. 33). With one exception, the testes of mature males weighed more than 5.7 kilograms and few had testes lighter than 17.0 kilograms. The exception was a mature northbound animal with unusually small testes that weighed only 0.8 kilogram. Following the abrupt increase in testis weight immediately after puberty, the rate of increase rapidly declines with increasing body length.

The paired testes of the southward migrating adult males taken in December and January ranged from 7.9 to 67.5 kilograms, with a mean and standard error of 38.4 ± 1.4. Mean testis weights for 10-day intervals throughout the southward migration period show no significant changes (Table 13). In northbound adults, the testes were much lighter, ranging from 5.7 to 44.8 kilograms with a mean and standard error of 22.5 ± 0.9. Mean testis weights decreased from 24.8 kilograms in late February to 18.0 kilograms by the end of March. Zimushko (1969*b*) found that the testes of 25 adults taken from July through October ranged from 14 to 27 kilograms (mean, 23).

HISTOLOGY.—Because of the rapidity of postmortem degeneration of testis tissue, detailed cytological study of our material was not possible. Representative histological sections are shown in Fig. 34.

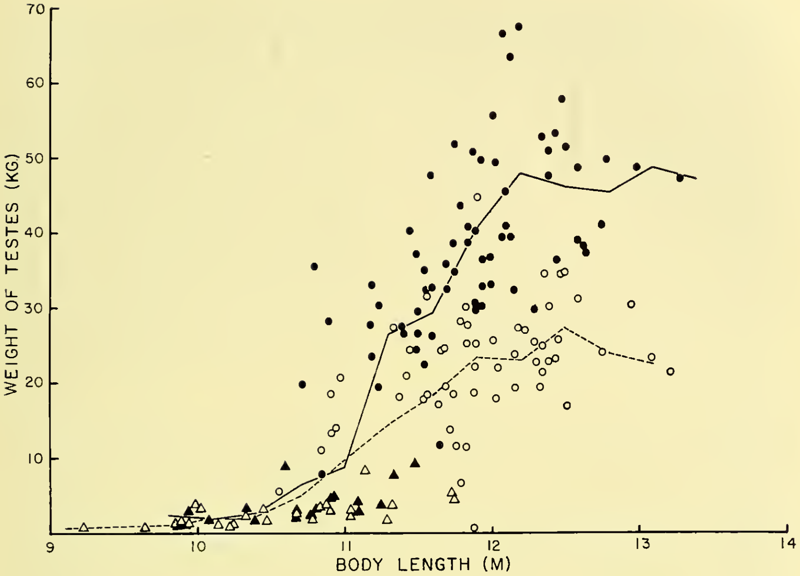

FIG. 33. Testes weights of gray whales in relation to body length. Symbols are as follows: solid triangles, southbound immature males; solid circles, southbound adult males; open triangles, northbound immature males; open circles, northbound adult males. Unbroken line connects means of 0.3-meter length groups of southbound males; broken line connects means of 0.3-meter length groups of northbound males.

In immature testes, the seminiferous tubules were closed and small, their average diameters ranging from 45 to 102 microns (mean, 75). In mature testes, the tubules had open lumina and average diameters ranging from 104 to 214 microns. In males that have reached puberty, there is a significant ($P < .001$) positive correlation between tubule diameter and testis weight (Fig. 35). This correlation is expressed by the formula $Y = 120 + 1.3X$, where Y = tubule diameter in microns and X = testis weight in kilograms.

Mean tubule diameters of the testes of southbound migrants ranged from 114 to 214 microns (mean, 177; standard error, 2). Mean tubule diameter of northbound migrants was significantly smaller, ranging from 104 to 186 microns, with a mean of 148 and a standard error of 3). Mean tubule diameters for each 10-day

TABLE 13

TESTIS WEIGHTS AND SIZE OF SEMINIFEROUS TUBULES OF ADULT MALE GRAY WHALES AT 10-DAY INTERVALS DURING MIGRATION.

	Testis weight (kg)			Tubule diameter (microns)		
Period	*N*	Mean ± SE	Range	*N*	Mean ± SE	Range
Southward migration						
12–21 December	4	41.3 ± 3.7	33.1–47.6	4	184 ± 3	177–189
22–31 December	6	36.9 ± 6.3	23.5–66.5	6	176 ± 6	154–193
1–10 January	30	36.0 ± 2.3	7.9–63.3	29	171 ± 4	114–206
11–20 January	20	40.4 ± 1.9	26.5–53.2	20	183 ± 4	153–214
21–30 January	7	43.1 ± 5.4	26.1–67.5	7	184 ± 5	161–198
Northward migration						
20 February–1 March	7[1]	24.8 ± 2.6	17.9–34.5	8	147 ± 8	111–179
2–11 March	24	24.0 ± 1.4	11.5–44.8	24	148 ± 4	104–176
12–21 March	15	21.8 ± 1.6	5.7–31.5	14	143 ± 6	107–186
22–31 March	9	18.0 ± 1.4	11.7–23.3	9	156 ± 4	142–186

[1] One male with abnormally small testes weighing 0.8 kg omitted.

interval do not reveal any significant increase or decrease within either migration period (Table 13).

The seminiferous tubules of almost all adult males appeared to be undergoing spermatogenesis, but it was difficult or impossible to ascertain the precise stages. The vasa deferentia and epididymides of all postpubertal males that were examined contained abundant fluid. Because of the long postmortem time, we did not attempt to collect vas deferens fluid for counts of sperm density.

Penis

The penis of the gray whale is an elongate, evenly tapering, conical, flesh-colored organ similar to that of the rorquals, and unlike the slender cylindrical black organ of right whales.

The length of the penis ranged from 55 to 145 centimeters in immature males and from 100 to 170 in adults. There is a significant ($P < .001$) positive correlation between penis length and body length (Fig. 36). This correlation is expressed by the formula $Y = 0.21X - 1.14$, where Y = penis length in meters and X = body length in meters. On the basis of this formula, at a body length of 11.1 meters, which is the average length at puberty, mean penis length is 1.08 meters. A penis length of 114 centimeters correctly separates 79 per cent of our specimens into immature and adult categories.

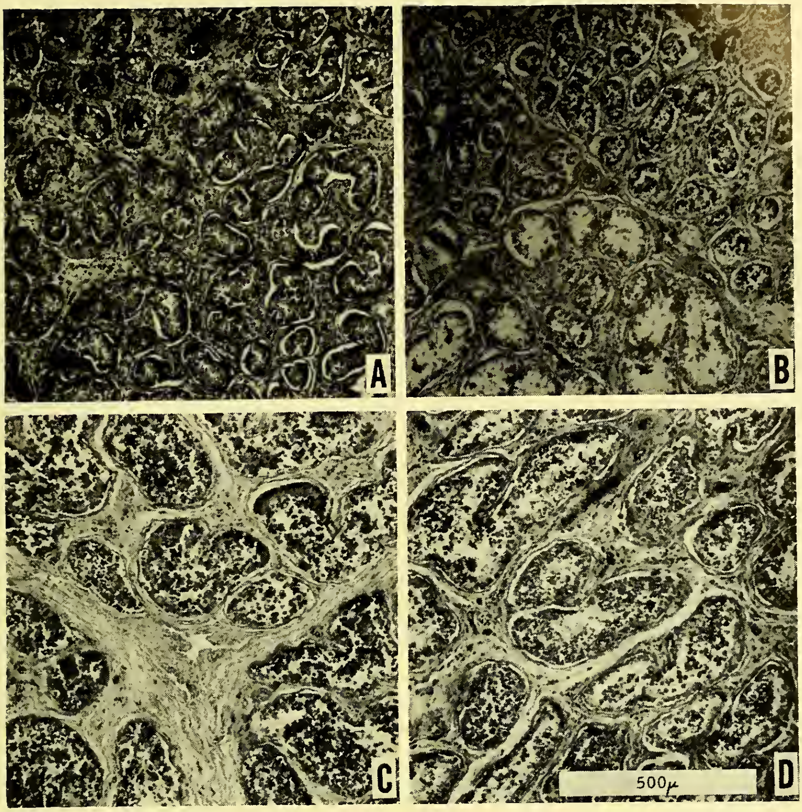

Fig. 34. Photomicrographs of sections of testes of gray whales in different stages of the reproductive cycle. A, immature male; B, pubertal male with both closed and open seminiferous tubules; C, adult southbound male; D, adult northbound male. All sections are to same scale.

Discussion and Conclusions

Testes weighing more than 5.0 kilograms are a reliable indication of maturity in male gray whales. A penis length greater than 1.1 meters also separates most mature animals from those that are sexually immature.

The much heavier testes and larger seminiferous tubules of males taken during southward migration compared with those of males collected during northward migration and on the summer grounds indicate that male gray whales have a marked seasonal sexual

Fig. 35. Relation between size of seminiferous tubules and weight of testes of gray whales. Symbols are as follows: solid triangles, southbound immature males; solid circles, southbound adult males; open triangles, northbound immature males; open circles, northbound adult males. Regression of tubule diameter on testis weight based on adult males.

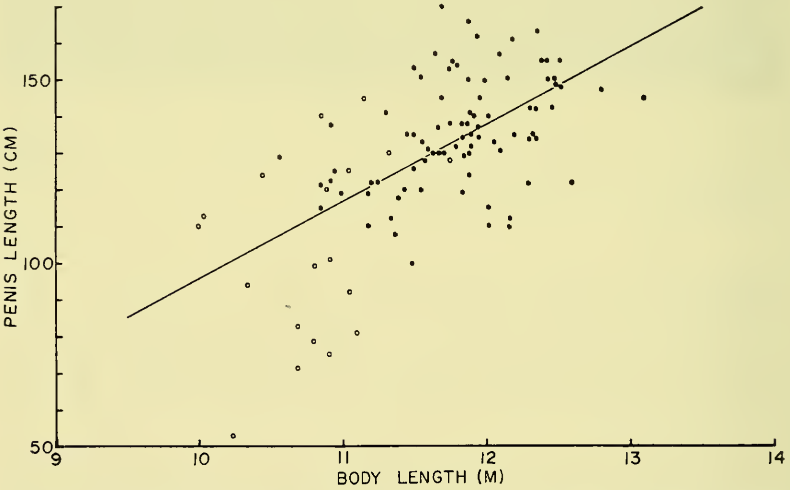

Fig. 36. Relation between penis length and body length of gray whales. Open circles represent immature males and closed circles represent adult males.

cycle, with a peak of spermatogenetic activity in late autumn or early winter. This period correlates closely with the time females come into estrus. Although there are no reported field observations of copulation at this time, biologists have not studied the behavior of gray whales in southward migration north of San Francisco. Courting and copulating gray whales often are seen on and near the calving grounds in Baja California in January (Gilmore, 1960*a*); this period coincides with the second estrous cycle of those few females that are not impregnated during their first cycle. Apparent courtship behavior, including males with an erect penis, has been observed during northward migration on the coast of California in March (Houck, 1962) and on the coast of Washington as late as April (C. E. Munsen, personal communication). Courtship behavior and apparent copulation also have been observed in the Bering Sea in June, July, August, and September (Sauer, 1963; Fay, 1963; Tomilin, 1937). Its significance at these times is unknown; certainly it never results in successful conception. In the bottlenose dolphin *(Tursiops truncatus)*, copulation behavior does not necessarily indicate sexual fertility in males, as males born in captivity may begin to copulate frequently when only a few days old (Caldwell and Caldwell, 1968).

The existence of a male reproductive cycle in other mysticetes appears to be variable. Male humpback whales show a marked seasonal variation in weight of the testes and spermatogenetic activity (Chittleborough, 1955; Nishiwaki, 1959; Omura, 1953; Symons and Weston, 1958). In blue and fin whales there is a less well-marked seasonal cycle in spermatogenetic activity, although available data do not clearly demonstrate an associated cycle in testis weight (Laws, 1961; Mackintosh and Wheeler, 1929). In sei whales there is no seasonal variation in either weight or histology of the testes (Gambell, 1968).

PREDATORS

KILLER whales, *Orcinus orca,* are the only known predators of baleen whales (Nishiwaki and Handa, 1958). Killer whales rarely have been observed attacking gray whales. However, Scammon (1874) saw three killer whales attack and kill a gray whale calf accompanied by its mother in a lagoon in Baja California. Gilmore (1961) reported an unsuccessful attack by six killer whales on two gray whales at La Jolla, California. Morejohn (1968) observed an unsuccessful attack by seven killer whales on three gray whales, including a female with a calf, at Moss Landing, California. V. B. Scheffer (personal communication) saw six killer whales unsuccessfully attack a gray whale in Monterey Bay, California, on 9 March 1952. Burrage (1964) observed avoidance behavior of a pod of six gray whales on the approach of five killer whales at La Jolla. Pike and MacAskie (1969) reported killer whales attacking a pair of gray whales off the Queen Charlotte Islands. Andrews (1914) recounted descriptions by whalers of the reaction of gray whales to the approach of killer whales in Korean waters and reported killers feeding on the carcasses of gray whales being towed by catcher boats.

We found healed parallel scars that were obviously the tooth marks of killer whales on 57 (18 per cent) of the gray whales that we examined. Other whales doubtless bore unrecognizable killer whale tooth scars. Fifty-two of the whales had scars on the flukes, and 15 animals had scars on one or both flippers. Eight other whales had scars elsewhere on the body, as follows (number of individuals in parentheses): flanks (four), caudal peduncle (one), anal region (one), dorsal hump (one), throat (one), and snout (one). The predominance of scars on the flukes and flippers suggests that killer whales usually attempt to kill gray whales by seizing their flukes and flippers so as to immobilize and drown them. The number of scarred animals indicates a fairly high frequency of unsuccessful attacks on gray whales by killer whales. The proportion of successful attacks is unknown. Like other predators such as the wolf, *Canis lupus,* killer whales probably succeed in killing only a small proportion of the large prey that they attack (Mech, 1966). Jonsgård (1968) has pointed out that there is no incontrovertible proof that killer whales are capable of killing baleen whales that are not incapacitated or otherwise at a disadvantage.

We found no gray whale remains in the stomachs of 10 killer whales taken in the eastern North Pacific, although five of the killer whales were collected at a time when gray whales were present in the vicinity (Rice, 1968).

PARASITES AND EPIZOITES

Ectoparasites and Epizoites

All gray whales examined were heavily infested with ectoparasites and epizoites, including three species of cyamids and one species of barnacle. Zenkovich (1937*a*) reported that a few gray whales, which had presumably just emerged from brackish lagoons bordering the Bering Sea, carried no cyamids and no live barnacles. He experimentally showed that brief immersion in fresh or brackish waters kills these parasites. We found small patches of an olive-colored skin film on a few whales, but were unable to find any diatoms in scrapings from such areas. Hubbs' (1959) report of kelp growing on gray whales probably was based on observation of whales that had temporarily picked up strands of kelp while swimming through kelp beds. The baleen plates of the whales examined in this study were generally clean and carried no film of microorganisms.

Barnacles.—*Cryptolepas rhachianecti* Dall, 1872 (Fig. 37), is the only barnacle found on gray whales, to which it is host-specific. This sessile species is closely related to the genus *Coronula,* which occurs regularly on humpback whales but rarely on other species. Its mode of attachment to the skin appears to be similar to that of *Coronula* (Darwin, 1854).

These barnacles were present on every whale examined, which has been the experience of other workers who have studied gray whales. They may occur in small clusters almost anywhere on the trunk or on the surfaces of the flukes and flippers, but are most abundant on areas that are exposed to the air when the whale surfaces. They often form a continuous mass on the dorsal aspect of the rostrum and the most anterior part of the back. These areas also are those most directly exposed to food-carrying water currents as the whale stirs up the bottom sediments. The barnacles are oriented with their cirri generally directed towards the anterior end of the whale (Kasuya and Rice, 1970).

Virtually all barnacles on whales taken during the southbound migration are large (20 to 40 millimeters in diameter). Only one

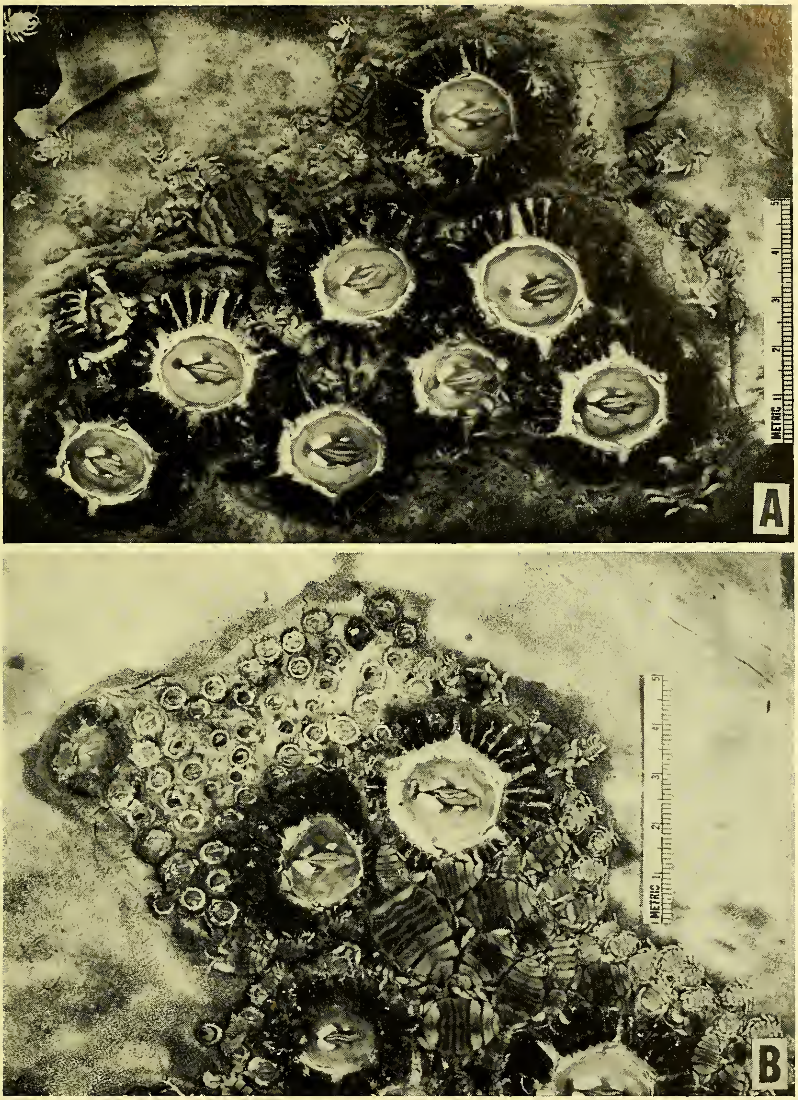

FIG. 37. Barnacles *Cryptolepas rhachianecti* on skin of gray whales. A, southbound whale with large barnacles only; B, northbound whale with many small as well as large barnacles. The anterior end of each whale is to the left. Note the many *Cyamus scammoni* on the barnacle clusters and a few *C. ceti* mostly around the periphery of the clusters.

southbound whale, a pregnant female taken on 27 December 1968, bore small barnacles (3 to 5 millimeters in diameter). Northbound whales carry two discrete size groups of barnacles. Besides the large individuals that are 20 to 40 millimeters in diameter, there are usually large numbers of small individuals that range from 2 to 5 millimeters in diameter. Thus it is apparent that barnacles spawn while the whales are concentrated on their winter grounds and when the cypris larvae of the barnacles have the greatest opportunity for finding a new host. The small barnacles often are located close together, so there must be much mortality due to crowding as they grow.

Cyamids.—Gray whales are host to three species of cyamids (Fig. 37). Most previous workers have reported only one species, the unique and easily recognized *Cyamus scammoni,* but they doubtless overlooked the other species. Hurley and Mohr (1957) were the first to report the other two, *Cyamus ceti* and *C. kessleri.* Few cetaceans are host to more than one species of cyamid. The only other cetaceans on which three species have been found are the right whale and the sperm whale (Leung, 1967), but it is not known how frequently three species of cyamids may occur on a single individual of these host species. All except one of our gray whales were lightly to heavily infested with cyamids, and the three species occurred together on 310 (98.1 per cent) of the 316 examined. However, they tended to segregate on different parts of the body as described below.

Cyamus scammoni Dall, 1872, is invariably the most abundant cyamid on the gray whale and is restricted to this host. We found it on 315 (99.7 per cent) of the 316 whales examined. It is found mostly around clusters of barnacles. A few individuals may be scattered elsewhere on the body, most often in the fold at the axilla of the flippers, in the notch of the flukes, in the umbilicus, and sometimes in the genital groove. We found no trace of the cornified area on the dorsal surface of the rostrum reported by Andrews (1914) and supposed by him to be produced by the action of cyamids. On several whales, we found large numbers of *C. scammoni* in fairly fresh wounds. The two most notable cases were a large adult male taken on 25 March 1964 with a deep wound 1.40 meters long and 0.35 of a meter wide in the blubber of the back slightly to the right of the middorsal line opposite the flipper; and a female taken on 20 December 1968 with a wound 0.85 by 0.85 meters and 14 centimeters deep on the back about 2 meters anterior to the dorsal hump. In both specimens, the wounds were completely filled with tightly packed masses of cyamids, mostly, if not entirely, *C. scammoni.* More than 100,000 were collected from the male (Leung, 1965). Many of the individuals were exceptionally large.

Cyamus ceti Linnaeus, 1758, was originally described from the bowhead whale from the Atlantic sector of the Arctic Ocean. Hurley and Mohr (1957) first found it on the gray whale at Barrow, Alaska. They reported that their specimens agreed closely with descriptions of this species and with specimens taken from bowhead whales captured at Barrow. L. Margolis (letter, July 1959), however, is somewhat doubtful about the identification of specimens from gray whales as *C. ceti,* because he has found minor differences between specimens from gray whales and those from Atlantic-Arctic bowheads. As most cyamids are host-specific, it would be most unusual for one species to infest hosts belonging to different families. This specificity is, no doubt, primarily a result of cyamids spending their entire life upon the host, so that transference can rarely occur except between members of a pair during copulation or between mother and calf during birth or suckling. This species is much less numerous than *C. scammoni,* but usually more frequent than *C. kessleri.* We recorded it on 314 (99.4 per cent) of 316 whales. It most commonly lives in grooves and skin folds on the body as follows: around the blowholes; in the angle of the gape; in the throat grooves; around the eyes; at the bases of the flippers; on the umbilicus; in the mammary slits; and, rarely, in the genital and anal grooves. Small patches of them are sometimes found elsewhere on bare skin. A few may be found adjacent to *C. scammoni* around the edges of clusters of barnacles, but competition with the larger species appears largely to exclude *C. ceti* from barnacle clusters.

Cyamus kessleri Brandt, 1872, was first described from an unidentified species of whale from the Bering Sea. Hurley and Mohr (1957) rediscovered it on a gray whale killed at Barrow, Alaska. It has subsequently been found only on gray whales. This is usually the least abundant species of cyamid on the gray whale. We found it on 310 (98.1 per cent) of 316 whales. It occurred almost exclusively around the anus and in the genital grooves. A few were occasionally located in the mammary slits and elsewhere on the body.

Endoparasites

Before these studies, no endoparasites had been identified from the gray whale, although an unidentified cestode was reported by Tomilin (1937) from individuals of this species in the Chukchi Sea. We found eight species of endoparasites in the digestive system, including three trematodes, two cestodes, one nematode, and two acanthocephalans. Some of these seem to represent undescribed species. The taxonomy of the cestodes is being studied by R. Rausch and that of the acanthocephalans by K. Neiland. We found no parasites in the kidneys, lungs, peribullary air sinuses, or blubber. Treshchev *et al.* (1969) have published an abstract of recent studies on the helminthofauna of gray whales in the Bering and Chukchi seas.

TREMATODES.—*Lecithodesmus goliath* van Beneden, 1959, was found in only two gray whales. These large flukes live in the bile ducts of the liver. Specimens from gray whales range from 35 to 54 millimeters (mean, 45) in length and 10 to 14 millimeters (mean, 12) in width. This species differs from *L. spinosus* Margolis, 1955, in its incompletely spined cuticle. *L. goliath* has been reported from many species of baleen whales (Delyamure, 1955). Two flukes were found in an immature female whale taken on 16 March 1969; no pathological conditions were grossly visible in the liver. Forty-seven flukes were recovered from a mature male whale taken on 13 March 1969, and many others were doubtless present. The bile ducts of this whale had distorted, inflamed biliary epithelium and were rimmed with thick walls of dense scar tissue. We have never observed such marked pathogenic effects associated with heavy infestations of *Lecithodesmus* in sei whales, which suggests that the gray whale is not a normal host for these flukes.

Orthosplanchnus pygmaeus was described by Yurakhno (1967) from the intestine of a gray whale taken off the Chukotskiy Peninsula. Other members of this genus infest the bile ducts and gall bladder of Arctic pinnipeds.

Ogmogaster pentalineatus Rausch and Fay, 1966, was described as a new species on the basis of our specimens and the type series collected by Fay from a gray whale at St. Lawrence Island, Alaska. The name *Ogmogaster delamurei* Treshchev (1966*a*), based upon specimens found in gray whales taken in the Chukchi Sea near Enurmino on the Chukotskiy Peninsula, is a junior synonym of *O. pentalineatus* (Skriabin, 1969). *O. pentalineatus* has been found only in gray whales. Entire specimens are easily recognized by the smoothly rounded or weakly undulate edge of the body and by the five ridges on the ventral surface. The species usually does not attain a length greater than about 3.5 millimeters, although one specimen measured 5.6 millimeters.

Field inspection of the surface of the mucosa of the small intestine at several randomly selected points revealed *O. pentalineatus* in only eight (2.5 per cent) whales. A more careful search of a section of the small intestine in a tray of water sometimes showed these flukes to be present in whales in which our spot-check had revealed none. The type series of more than 200 individuals was found in the small intestine (Rausch and Fay, 1966). In 1967, large numbers of this species were discovered in the rectum of one whale, so in 1968 and 1969 that portion of the rectum exposed on the inner side of the blubber after the blubber had been flensed from the whale was routinely examined. *O. pentalineatus* was recorded from 31 (22 per cent) of 139 whales examined in this manner. In all except seven cases, this species was living alongside *O. antarcticus*, although usually in lesser numbers. Of 1280 *Ogmogaster* collected from the rectum of 53 whales, only 227 (18 per cent) were *O. pentalineatus*. Usually fewer than 20 individuals of the latter species were present, but one whale contained well over 100.

Ogmogaster antarcticus Johnston, 1931, occurred in 46 (33 per cent) of 139 whales examined in 1968 and 1969. This species is distinguished from *O. pentalineatus* by the greater number of ridges (12 to 15) on the ventral surface, the 15 to 20 conspicuous marginal crenulations on each side of the body, and the four or five lateral loops in each intestinal caecum. It also typically attains larger size, reaching 6.0 millimeters in length. In rorquals (*Balaenoptera* species), this species has a maximum length of 10 millimeters (Rausch and Fay, 1966). Our specimens agree well with the descriptions of *O. antarcticus* as diagnosed by Delyamure (1955) and Rausch and Fay (1966). *O. antarcticus* has been reported previously from the intestines of Antarctic seals (tribe Lobodontini) and from the intestines of rorquals in the North Pacific and North Atlantic as well as the Southern Hemisphere. In this study *O. antarcticus* was found only in the rectum. The maximum number recovered from one whale was 199. In 24 of the 139 whales examined it was associated with lesser numbers of *O. pentalineatus.* Treshchev *et al.* (1969), strangely enough, did not find this species in gray whales collected on the summer grounds.

Ogmogaster plicatus Creplin, 1829, was reported in a gray whale obtained off the Chukotskiy Peninsula (Treshchev *et al.*, 1969). Otherwise the species has been found only in the intestines of rorquals in the North Pacific and North Atlantic; we have found it in fin whales collected off San Francisco. This species differs from *O. antarcticus* in having more ventral ridges (19 to 28), more than 20 marginal crenulations on each side of the body, and larger size (maximum length 14 millimeters).

The life histories of the species of *Ogmogaster* are unknown. The food habits of their definitive hosts suggest that their second intermediate hosts are crustaceans.

CESTODES.—The genus *Priapocephalus* includes cestodes characterized by a bulbous scolex that lacks suckers and has a basal collar. *P. eschrichtii* recently has been described by Murav'eva and Treshchev (1970) from gray whales in the Chukchi Sea. The other two described species are *P. grandis* Nybelin, 1922, from rorquals (*Balaenoptera* species) and right whales in the Southern Hemisphere, and *P. minor* Nybelin, 1928, from rorquals in the North Atlantic and North Pacific (Baer, 1954; Delyamure, 1955; Markowski, 1955). The larval host of *Priapocephalus* is unknown. We collected two kinds, apparently different species, from the gray whale.

The commonest species has a narrow (less than 1 millimeter wide) strobila that is of uniform width throughout. It is difficult to collect complete strobilae, but they attain a length of at least 25 centimeters. The proglottids are about 0.3 to 0.4 of a millimeter long, and the scolex is about 3 millimeters in diameter. This species was found in the small intestine of 94 (30 per cent) of the 316 whales. Usually infestations were light and rather local, although a few whales were heavily infested.

The second species differs from the previous species in that its strobila is much wider—2 to 4 millimeters. Although the proglottids adjacent to the scolex are as narrow as those of the previous species, they rapidly become wider distally. The proglottids are about 0.5 to 0.8 of a millimeter long. The scolex is similar to that of the previous species. This cestode was found in the large intestine of an immature female whale taken on 11 April 1968. The whale was heavily infested with this parasite, and no other species of cestode was present.

Tomilin (1937) reported an unidentified cestode from the gray whale. He stated (translation): "In 1934, internal parasites (tapeworms) Cestoda Ord. Pseudophaliidae [sic] (species not determined) 40 meters in length (deposited in parasitological laboratory of the Institute of Zoology, MGU) were found in the intestines of two gray whales. Their segments attained a width of 2 centimeters. The worms equaled about 48 liters in volume, in each animal." From their size, we would guess that these must be *Diplogonoporus balaenopterae* Lönnberg, 1891, a species frequently found in rorquals (*Balaenoptera* and *Megaptera*). The life cycle of *Diplogonoporus* is unknown, but the plerocercoids can be expected to occur in fishes (Rausch, 1964).

Nematodes.—*Anisakis simplex* Rudolphi, 1809, was found in only one gray whale. There were many immature individuals, 20 to 35 millimeters long, of this species in the first and second chambers of the stomach of an immature male killed on 3 April 1968. They were not attached to the mucosa. In a recent revision of this genus, J. T. Davey (personal communication) recognized only three species. Our specimens differ from *A. physeteris* Baylis, 1923, in the possession of a sigmoid esophagus. Only mature males of *A. simplex* can be distinguished from *A. typica* Diesing, 1860. *A. simplex* occurs in all species of balaenopterid whales as well as many other species of marine mammals from all over the world, especially from colder seas, whereas *A. typica* is known only from delphinids from warmer seas. Therefore Davey (personal communication) had little hesitation in assigning our specimens to *A. simplex*. The life cycle of *Anisakis* is unknown, but it is probable that two intermediate hosts are needed (Berland, 1961). Fishes are the usual source of infestations in marine mammals (van Thiel, 1966), in which these worms reach maturity.

ACANTHOCEPHALANS.—*Corynosoma* sp. was found in 18 (5.7 per cent) of the 316 gray whales studied. They were rather loosely attached to the mucosa of the small intestine. Most infestations were light, the heaviest being a whale that had 60 individuals within a 0.3-meter section of intestine. Specimens from gray whales are 4 to 5 millimeters long; the anterior half of the trunk is bulbous, the posterior half elongate and tapering. Treshchev (1966*b*) described a new species, *C. septentrionalis,* and reported (Treshchev *et al.*, 1969) *C. semerme* Forssell, 1904, *C. strumosum* Rudolphi, 1802, and *C. validum* Van Cleave, 1953, from gray whales collected off the Chukotskiy Peninsula. The life cycles of a few species of *Corynosoma* are known. All these involve crustaceans as first intermediate hosts, and fishes as second intermediate hosts (Golvan, 1959). Seals and aquatic birds are the definitive hosts of most species of this genus; a few species parasitize toothed whales (Delyamure, 1955; Golvan, 1959). The discovery of species of this genus in gray whales is the first known occurrence in a baleen whale, although we recently have found *Corynosoma* in fin whales.

Bolbosoma sp. was present in the small intestine of an immature male whale captured on 3 April 1968. The two specimens found were white and about 30 millimeters long. The trunk (when turgid after being placed in fresh water) was slightly more than a millimeter in diameter. One was loosely attached to the mucosa; the head of the other was imbedded in a small, thick-walled, pus-filled cyst in the mucosa. The life cycles of species of *Bolbosoma* are unknown.

Discussion and Conclusions

The gray whale is more heavily infested with a greater variety of ectoparasites and epizoites than any other species of cetacean. This may be at least partly due to the fact that they swim slowly and live throughout the year in shallow coastal waters rich in nutrients. In contrast, they are infrequently infested with endoparasites. Their long period of fasting each year may inhibit the survival of parasites in the digestive tract. Except for liver flukes, none of the ectoparasites or endoparasites appears to have any significant pathogenic effects.

POPULATION

Although a reasonably complete understanding of the population dynamics of the California stock of gray whales will require further investigation, data obtained in the present study provide a basis for some tentative conclusions.

Present Numbers

Because gray whales migrate close to the coast, a large proportion of the population may be counted from vantage points on shore, providing an index of population size. Between the migration seasons of 1952–53 and 1960–61, four essentially full-time counts were made at the Point Loma coastal station (Gilmore, 1960*a*, 1960*b*; Rice, 1961). In the course of offshore cruises for marking whales of other species, beginning in 1964, we found unexpectedly large numbers of southbound gray whales passing the coast of southern California far offshore (Rice, 1965; unpublished data). However, in the area of the counting station south of Yankee Point, observations during whale marking cruises indicated that few gray whales pass so far offshore that they cannot be seen from land.

Daily counts of southbound whales migrating past these two points are shown in Fig. 38. In 1967–68, 3120 whales were counted at Yankee Point and 1324 at Point Loma. In 1968–69, 3280 were counted at Yankee Point and 1154 at Point Loma. Thus, of the number of whales that passed Yankee Point only 35 to 42 per cent were seen passing Point Loma. In 1969–70, 3345 were counted at Yankee Point, and no count was made at Point Loma.

To calculate total population size from these counts, we must estimate the number of whales that were missed because of poor visibility, the whales that passed too far offshore to be seen, and the whales that passed at night. We estimated the number of whales missed because of poor visibility by considering only the counts made during days when visibility was good. As visibility is limited most by fog, drizzle, or rain, and by winds strong enough to create whitecaps, we considered only the days when there was no precipitation or fog and winds were below 19 kilometers per

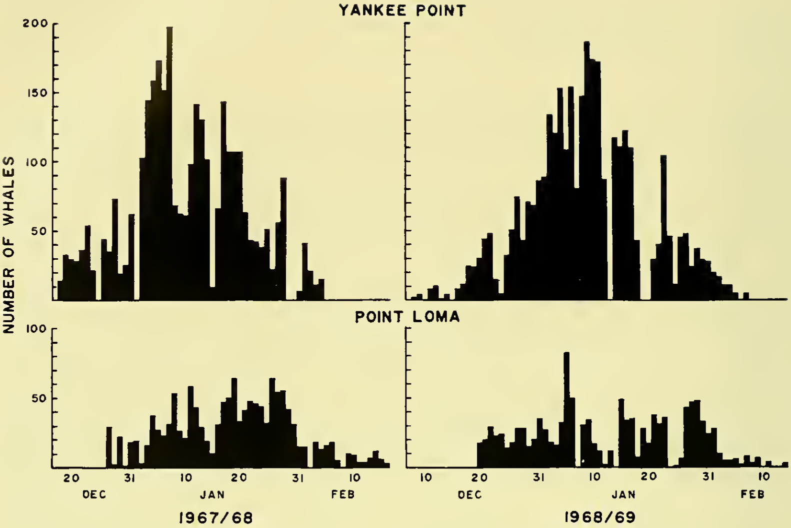

FIG. 38. Daily counts of gray whales passing Yankee Point and Point Loma, California, during the southward migrations of 1967–68 and 1968–69.

hour (10 knots). Days with good visibility and days with poor visibility were interspersed at random throughout each census period, so we extrapolated the counts made during the days with good visibility to include the entire period of each census. Some whales were doubtless missed even during days with good visibility, and, of course, a few passed early in the season before the counts began and late in the season after the counts ended.

To determine the number of whales passing too far offshore to be seen, we ran transect cruises from Yankee Point and Point Loma across the migration path of the whales. In a transect from Yankee Point on 18 January 1968, extending 37 kilometers offshore, no gray whales were seen farther from shore than 6 kilometers, and only nine of the 33 whales sighted were beyond 4.5 kilometers from shore. The remaining 24 were within 1.5 kilometers of land. Under conditions of good visibility, observers on shore could detect whales at an estimated distance of 7.4 kilometers, but 95 per cent of the whales were estimated to be within 1.9 kilometers of shore. Therefore, we conclude that the number of whales passing too far offshore from Yankee Point to be seen by the observers during periods of good visibility was insignificant.

Between 25 January and 9 February 1968, we ran seven transects totaling 1572 kilometers between Point Loma and longitude 119°20′ W, just beyond Tanner and Cortez Banks. During 100 kilometers of cruising within 9.3 kilometers of shore, 37 gray whales were seen, an average of 0.37 per kilometer cruised. During 1472 kilometers of cruising beyond 9.3 kilometers from shore, 40 gray whales were sighted, an average of 0.027 per kilometer. The width of the migration path at this latitude is at least 194.5 kilometers, of which 9.3 kilometers is within sight from Point Loma. The ratio of whales passing offshore to those passing within sight of land is thus (185.2 × 0.027) : (9.30 × 0.37) = 5.00 : 3.44. This ratio indicates that only 41 per cent of the whales migrating south past southern California passed within sight of Point Loma. This agrees with our estimates of 35 to 42 per cent based upon a comparison of the Point Loma and Yankee Point counts. Therefore, we have multiplied the Point Loma counts by 2.44 (100/41), to estimate the total number of whales moving past the latitude of Point Loma during daylight hours.

Because there is no evidence that migrating gray whales slow down at night, we have multiplied the estimated number of whales passing during the 10 hours of daylight during which counts were made by 2.4 to estimate the total number of whales passing each counting station during each of the two seasons.

Estimates of total population size, based on the foregoing corrections, are shown in Table 14. The Yankee Point estimates are probably more accurate than the Point Loma estimates, because of the greater possibility of error in adjusting for offshore migration at Point Loma. The 1968–69 and 1969–70 estimates are probably more accurate than those for 1967–68 because the counts started earlier in the season. The best estimate of the present population size of the California gray whale stock is approximately 11,000.

The reliability of this estimate is difficult to assess. A probable lower limit may be estimated by multiplying the actual counts at Yankee Point by 2.4 to allow for the whales passing at night, which gives figures of about 7500 for all three seasons. An upper

TABLE 14

COUNTS OF SOUTHWARD MIGRATING GRAY WHALES AND ADJUSTED ESTIMATES OF TOTAL GRAY WHALE POPULATION SIZE, 1967–68 TO 1969–70.

		Entire period		Days with good visibility					
Season	Locality	No. of days	No. of whales	No. of days	No. of whales	Whales per day	Estimate of whales passing during daylight	Adjusted for offshore migration	Adjusted for night migration
1967–68	Yankee Point	49[1]	3,120	32	2,430	76	3,724		8,938
	Point Loma	52	1,324	29	879	30	1,560	3,806	9,134
1968–69	Yankee Point	60	3,280	29	2,174	75	4,500		10,800
	Point Loma	57	1,154	26	758	29	1,653	4,033	9,679
1969–70	Yankee Point	64	3,345	32	2,257	71	4,544		10,906

[1] No count made on two of these days.

limit was estimated by drawing a line connecting the highest daily counts at Yankee Point and measuring the area under the line to estimate the number of whales passing during daylight. The total was then calculated by multiplying this value by 2.4 to compensate for night migration. The resulting estimates of the upper limit were about 13,000 in 1967–68, and 12,000 in 1968–69 and 1969–70.

Population Trends

In the decades prior to 1947, before legal protection was afforded by the International Convention for the Regulation of Whaling, the gray whale population is believed to have been considerably lower than it is now, but there are no quantitative data available upon which to base an estimate of its size during this period.

The estimated population size based upon four complete counts made at Point Loma from 1952–53 to 1959–60 (Gilmore, 1960*a*; Rice, 1961) showed a rather consistent increase of about 11 per cent per year. A regression analysis of the logarithms of these counts gives an estimate of the rate of population change as +12.2 per cent per year, with a 95 per cent confidence interval of –4.0 to +31.2 per cent. This study, however, has thrown doubt on the reliability of estimates of absolute population size based upon these counts.

The most questionable factor is the estimate of the extent of offshore movement, which Gilmore arbitrarily estimated at 5 per cent of the inshore movement. In contrast, present evidence indicates that offshore movement is about 144 per cent of the inshore movement along this stretch of coast.

The 1967–68 and 1968–69 counts at Point Loma were 44 and 51 per cent, respectively, below the 1959–60 count of 2344. Either some factor such as increase in small boat traffic has caused a larger proportion of the population to pass farther offshore at Point Loma, or the population in 1959–60 actually was much higher than estimated and has since decreased.

Hubbs and Hubbs (1967) made aerial surveys of the gray whale wintering grounds in Baja California between late January and early March in most years from 1952 to 1964. They suggested that the population increased from 1952 to 1954 and thereafter remained constant at about 3000. A regression analysis of the logarithms of their five complete counts from 1954 to 1964 gives an estimated rate of population change of +0.8 per cent per year, with a 95 per cent confidence interval of –4.5 to +6.4 per cent. Their estimate of absolute population size was based on an "admittedly rather intuitive estimate that about half of the population was observed on the flights." Between soundings, gray whales are at the surface or sufficiently near it to be visible for only about 1 out of every 5 minutes. Therefore, applying this correction to the data of Hubbs and Hubbs would give an estimate of about 7500 animals. Gilmore (1960*a*), who participated in some of these aerial counts, came to a similar conclusion.

In 1966–67, Adams (1968) made a partial count during the southward migration at Yankee Point. His counts were conducted only during periods of optimum visibility and included only 9.16 per cent of the daylight hours during the migration period. The number of whales actually counted was 1084. This count was adjusted to cover all daylight hours, increased by 5 per cent to account for offshore migration and 70 per cent for night migration, to yield a total estimate of 18,300. This estimate is probably too high because the counts were made only during limited periods when the most whales could be seen. Adams reported an average of up to 55 whales passing per hour, which extrapolates to a rate of 550 per 10-hour day; we never counted more than 46 whales in one hour nor more than 197 per day during our full-time counts from 1967–68 to 1969–70.

Our counts at Yankee Point suggest that the population remained essentially stable from 1967–68 to the 1969–70 season.

Density and Biomass

Population density is ecologically most significant in relation to the feeding grounds. The summer range of the gray whale in the Bering and Chukchi seas occupies about 1,000,000 square kilometers. With a population of about 10,000, the average density is approximately one whale per 100 square kilometers. Density, of course, may vary markedly between different portions of the summer grounds (Berzin and Rovnin, 1966).

The total biomass of the gray whale population based on estimated numbers, sex and age structure, and mean body weights of each sex, age, and reproductive category is estimated at approximately 1.4×10^5 metric tons. The weight of an average gray whale is thus about 14 metric tons. The mean biomass on the summer grounds would thus be about 14 metric tons per 100 square kilometers, or 140 kilograms per square kilometer.

As a gray whale requires an estimated 19 kilocalories per kilogram per day, a 14-ton individual will require about 2.7×10^5 kilocalories per day, or 9.7×10^7 kilocalories per year. Inasmuch as gray whales must consume enough food during about half the year to sustain them the entire year, their daily energy requirements on the summer grounds would be about 5.3×10^5 kilocalories. Thus, if one kilogram of amphipods supplies 500 kilocalories, a gray whale weighing 14 tons must consume about a ton, or approximately 7 per cent of its weight, of amphipods per day.

The gray whale population consumes about 10 kilograms of food per day, or nearly 2 tons a year, per square kilometer. This quantity represents about 0.2 to 1.0 per cent of the standing crop of benthos (Neiman, 1963). Energy exchange amounts to 5.3×10^3 kilocalories per day. Although these figures are rough approximations, they provide some indication of the magnitude of the ecological role of the gray whale in the shallow waters of the Bering and Chukchi seas.

TABLE 15

SEX RATIOS OF GRAY WHALE AGE GROUPS.

Age group	No. males	No. females	Per cent males
Early fetuses	9	13	41
Near-term fetuses	30	25	55
Immatures	43	34	56
Adults	123	116	51
Combined total	205	188	52

Population Structure

SEX RATIO.—The combined sex ratio of fetal, immature, and adult gray whales was 52 per cent males to 48 per cent females (Table 15). In none of the age classes does the ratio differ significantly from one to one. The observed slight preponderance of males is probably not real, especially in view of the fact that lactating females were not represented in the sample.

TABLE 16

AGE COMPOSITION OF ADULT FEMALE COMPONENT OF SAMPLE BASED ON COUNTS OF CORPORA IN OVARIES.

Number of corpora	Estimated age (years)	Number of individuals
1	8–9	8
2	10–11	15
3	12–13	12
4	14–15	11
5	16–17	9
6	18–19	11
7	20–21	11
8	22–23	6
9	24–25	8
10	26–27	5
11	28–29	3
12	30–31	5
13	32–33	4
14	34–35	2
15	36–37	2
20	46–47	1
22	50–51	1
35	76–77	1

TABLE 17
AGE COMPOSITION OF GRAY WHALE SAMPLE BASED ON COUNTS OF GROWTH LAYERS IN EAR PLUGS.

No. of growth layers	Estimated age (years)	Number of individuals		
		Males	Females	Total
2	1	3	5	8
3	2	5	2	7
4	3	2	1	3
5	4	4	2	6
6	5	3	4	7
7	6	5		5
8	7	7	5	12
9	8	3	3	6
10	9	5	3	8
11	10	6	3	9
12	11	3	5	8
13	12	6	4	10
14	13	6	1	7
15	14	2	1	3
16	15		3	3
17	16	4	2	6
18	17	3	1	4
19	18	3	3	6
20	19	3	5	8
21	20	6	1	7
22	21	4	1	5
23	22	2		2
24	23	1	4	5
25	24	1		1
26	25		1	1
27	26		1	1
28	27	1	2	3
29	28	2		2
30	29		2	2
33	32	1		1
35	34	1		1
38	37	1		1
40	39	4	1	5
41	40		1	1
47	46	1		1
48	47		1	1
58	57	1		1
70	69	1		1

AGE COMPOSITION.—Age composition of our sample, based on counts of corpora in the ovaries of adult females and counts of growth layers in the ear plugs of both sexes, is given in Tables 16 and 17. Although corpora counts are believed to be more reliable than the data from ear plugs, the latter are useful because they are the only known means of determining the ages of males and of immature whales, and they permit a comparison between the sexes.

Immature whales comprised 24 per cent of the sample (26 per cent males, 23 per cent females). The data for this age class are biased because gunners select against smaller animals and because a larger proportion of immature whales have "readable" ear plugs. The proportion of immature whales in the population is certainly higher than indicated by our sample. If the apparent annual survival rate (S) of immature whales were the same as that of adults (0.92—see below) and sexual maturity were attained at 8 years of age, the proportion of immature whales 1 to 7 years old in the population would equal $1-S^7$, or 44 per cent. This is probably an underestimate, as the mortality of immatures is more likely to be greater than that of adults.

Another method of estimating the proportion of immature whales in the population based on the birth rate is applicable only if the population is stable. The birth rate is about 0.23 of the adult stock (see below). Since births must balance deaths in a stable population, the birth rate would be $(1-S)/S$, or 0.09 of the total stock alive at the beginning of the calving season. With a birth rate of 0.23 of the adult stock, the proportion of immature whales in the population would be $(0.23 - 0.09)/0.23$, or 61 per cent.

Population Dynamics

NATALITY.—On the basis of our estimate of a pregnancy rate in adult females of 0.46 per year and an assumption of an equal sex ratio, the birth rate in the California gray whale population is about 0.23 of the adult stock. As the present data indicate that adults constitute no more than 56 per cent of the population, the overall birth rate would not exceed 0.13. The approximate potential maximum rate of increase would approach this value.

MORTALITY.—The mean annual mortality rate of the adult female component of the sample, based on ages estimated from corpora counts, was calculated using Chapman and Robson's (1960) formula $M = 1 - (T/[N + T - 1])$, where M = annual mortality rate and T = Σ(age–8) (frequency). The resulting estimate of the mortality rate is 0.082.

The mortality rate for each sex was also calculated from the ear-plug data. As the proportion of immature whales in the sample is apparently biased, only whales of estimated ages of 8 years or older were used in the analysis, thus making the estimates directly comparable with those based on ovarian data. The resultant mortality values are 0.081 for males and 0.095 for females, which agree well with the estimates based on ovary analysis. They also indicate that there is probably little sex difference in mortality rate, a conclusion further supported by the essentially equal sex ratio at all ages.

Discussion and Conclusions

The California gray whale population was probably at least 8000 but less than 13,000 during the southward migration in 1969–70, with 11,000 being the most reasonable estimate.

Estimates of population size in earlier years based on shore counts at Point Loma (Gilmore, 1960*a*, 1960*b*; Rice, 1961) and aerial censuses in Baja California (Hubbs and Hubbs, 1967) are probably too low. However, they suggest that the population increased moderately from the early 1950's to 1960. The evidence for population trends from 1960 to 1967 is equivocal. The counts at Yankee Point suggest that the population has remained essentially stable from 1967–68 to 1969–70.

The sex ratio is about one to one at all ages. Probably at least 44 per cent of the population is sexually immature. The birth rate is 0.13 or slightly less. The age structure of the population suggests that the mortality rate has been 0.08. The size of any age class at a given time depends on its initial size and on its mortality rate. Therefore, the mortality rate calculated from the age composition represents the true mortality rate only if the initial size of each age class was the same, a situation likely to exist only in a stable population with a constant birth rate. In an increasing population with a constant birth rate, the initial size of each succeeding age class is greater. If the gray whale population was increasing at a rate of about 0.12 per year between 1952–53 and 1959–60, as the counts from Point Loma suggest, mortality would have to have been almost zero to produce the observed age structure. A low mortality rate would be expected in an initially small, rapidly increasing population comprised predominantly of younger animals. Inasmuch as the population has been stable since 1967, the mortality rate must have increased to equal the birth rate, but this change would have been too recent to have had a noticeable effect on the age structure of the population. However, additional data are needed, particularly on the actual age structure of the immature segment of the population and on population trends, before recruitment and mortality can be more accurately estimated.

EXPLOITATION

Aboriginal Whaling

The Nootka, Makah, Quillayute, and Quinault indians, the renowned aboriginal whalers living on the west coast of Vancouver Island and the State of Washington, regularly hunted gray whales since prehistoric times. Gray whale bones have been found in ancient middens near Lapush, Washington (Reagan, 1917). Indians chased whales in dugout canoes and struck them with harpoons attached to a line and float (Swan, 1870; Swanson, 1956; Waterman, 1920). Aboriginal whaling survived until 1928 on the coast of Washington (Anonymous, 1949).

Indians of the Kodiak Island and eastern Aleutian area killed whales with aconite-poisoned lances, a method also used by the Kamchadal in Kamchatka (Heizer, 1943). It is not known to what extent these people captured gray whales; their usual quarry was probably the right whale or the humpback whale.

The Koryaks who lived on the shores of Olyutorskiy Gulf north of the Kamchatka Peninsula in the 18th century regularly caught gray whales in large nets made of strips of walrus skin, which they set at the mouths of inlets (Krasheninnikov, 1755; Steller, 1774). Gray whales still are occasionally caught in this manner (Tomilin, 1957).

The Eskimos of Arctic Alaska and the Chukchi of eastern Siberia have for thousands of years hunted the bowhead whale and the gray whale from skin-covered "umiaks." In aboriginal times they used hand harpoons. After contact with American whalers in the late 19th century, they adopted the darting-gun and bomb-lance (Rainey, 1947). Whaling is still regularly practiced by the Eskimos of the villages of Barrow, Wainwright, and Point Hope on the Arctic coast of Alaska. In this area the catch is mostly bowhead whales. From 1954 through 1959, only nine gray whales were killed at Barrow and one at Wainwright (Maher, 1960). The natives of the village of Gambell on St. Lawrence Island (Francis H. Fay, personal communication) and the villages of Sireniki, Imtuk, Chaplino, Naukan, Uelen, and Enurmino on the Chukotskiy Peninsula

(Tomilin, 1957; Treshchev, 1966*a*) also still hunt whales. The catch in these areas is almost entirely gray whales. One hundred fourteen were killed in 1965 and 53 in 1966 off the Chukotskiy Peninsula (Zimushko, 1969*a*).

Commercial Whaling

Whaling in Japan dates back more than a thousand years, but it was not until about 1606 that commercial whaling was established. From the town of Taiji, the industry spread rapidly throughout the islands. At first, hand harpoons were used, but in 1674 the use of nets was introduced and widely adopted. Early 19th century Japanese illustrations show that gray whales were hunted in addition to the commonly taken right and humpback whales (Fraser, 1937; Japanese Fisheries Agency, 1954; Omura *et al.*, 1953).

The possibility that gray whales survived in the North Atlantic until the early 18th century and were pursued by New England whalers is suggested by Dudley's (1725) account of the enigmatic "scrag whale" mentioned earlier.

During the late 18th and 19th centuries the American high-seas, open-boat whale fishery developed and gradually spread to all oceans. In 1846, the whalers discovered the winter grounds of the Pacific gray whale along the west coast of Baja California. Scammon (1874) estimated the gray whale population as "probably not over 30,000" between 1853 and 1856. The annual congregations of gray whales in the lagoons attracted the American whalers, and by the winter of 1860–61 about 60 whaling vessels were engaged in lagoon whaling in Baja California (Starks, 1922). The first shore whaling station was established in 1854 (Starks, 1922), and by 1874, 11 shore stations were operating along the coast of California and Baja California (Scammon, 1874; Jordan, *in* Clark, 1887). Scammon estimated that about 10,800 gray whales were killed there between 1846 and 1874. Others were killed in the Bering Sea and Arctic Ocean. Scammon estimated the population of gray whales as 8000 to 10,000 in 1874. By 1886 only five shore whaling stations remained; they took 58 gray whales in 1883–84, 68 in 1884–85, and 41 in 1885–86 (Townsend, 1887). During the latter season, Townsend estimated that only 160 southbound gray whales passed

San Simeon, California, in December and January. Regular shore whaling ceased about 1900 (Starks, 1922).

During the early 20th century there was little exploitation of gray whales, although American whaling ships doubtless took a few; 31 were taken in waters off Mexico and California, and one off Alaska, by the whaling schooner "Carolyn Frances" as late as 1921 (Starks, 1922; Bower, 1923). During this period the stock probably increased.

The perfection of the modern harpoon gun in 1864 by the Norwegian whaler Svend Foyn ushered in the era of modern whaling. Captain H. G. Melsom of the Toyo Hogei Kabushiki Kaisha [Oriental Whaling Co., Ltd.] of Osaka, Japan, inaugurated a winter fishery for the gray whale at a shore station at Ulsan on the east coast of Korea, about 1899 (Andrews, 1914). A total of 1474 gray whales was killed off Korea from 1910 to 1933. Catches were declining by the 1920's, and whaling ceased after 1933, when only two gray whales were taken. This rapid decline suggests that the Korean stock numbered only some 1000 to 1500 whales in 1910, and was virtually extinct by 1933.

Exploitation of the California stock of gray whales by modern methods began with the establishment of several shore whaling stations along the west coast of North America, the first in 1905. Few gray whales were killed, however, because they were rare and could be taken only during the winter and early spring when the weather was bad. The few taken were brought into the stations at Port Hobron on Sitkalidak Island and Port Armstrong on Baranof Island, Alaska, Bay City, Washington, and Trinidad and Moss Landing, California.

The introduction of floating factory ships gave modern whalers a mobility that greatly increased their efficiency. Because whales were flensed while floating alongside the ship, these early floating factories could operate only in sheltered anchorages. A Norwegian factory ship, "Capella I," took 19 gray whales off Baja California in the spring of 1914. From 1924–25 until 1928–29, Norwegian whaling interests operated factory ships each winter and spring at Bahia Magdalena and other points along the coast of Baja California. Catches of gray whales steadily declined from 100 in 1924–25 to two in 1928–29 as the whalers turned their attention

TABLE 18

Recorded Catch of Gray Whales by Modern Style Whaling from 1910 to 1946. See text for Sources of Data.

	California stock														Korean[1] stock
	Baja California				California			Washington	Alaska		Bering and Chukchi seas			Total	
Year	Fl. F. *Capella I*	Fl. F. *Kommandören I*	Fl. F. *Mexico*	Fl. F. *Esperanza*	Sh. St. Moss Landing	Sh. St. Trinidad	Fl. F. *Lansing*	Sh. St. Bay City	Sh. St. Port Armstrong	Sh. St. Port Hobron	Fl. F. *Kommandören I*	Fl. F. *Aleut*	Fl. F. *Tonan Maru*		
1910															6
1911															121
1912															193
1913									1					1	131
1914	19													19	155
1915															139
1916															178
1917															69
1918															104
1919															46
1920					2									2	68
1921					1									1	78
1922					5									5	40
1923															27
1924								1						1	17
1925		82	18								33			133	10
1926		36	5			1								42	11
1927		16		13			3							32	10
1928				9			1			2				12	9
1929				2										2	12
1930															30
1931															11
1932															7
1933										2		2		4	2
1934												54		54	
1935												34		34	
1936												102		102	
1937												14		14	
1938												54		54	
1939												29		29	
1940												47	58	105	
1941												57		57	
1942												101		101	1
1943												77		77	
1944															
1945												30		30	
1946												22		22	

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[1] Catch by shore stations, almost all in Korea; for particulars see Mizue (1951). The whale taken in 1942 was killed in the Kuril Islands.

to the abundant and more profitable blue and humpback whales. A total of 181 gray whales was killed during these five seasons. One of these Norwegian factory ships, the "Kommandören I," took 33 gray whales in Natal'inskiy Bay, northeastern Kamchatka, in the summer of 1925. An American floating factory, the "Lansing," began operating in California in 1927. In 1932 she was replaced by the "California," which operated until 1937.

The invention of the stern slipway in 1925 made it possible to haul whales aboard the factory ship, thus permitting whalers to operate on the high seas and freeing them from regulation by national governments. The Soviet floating factory "Aleut" began operating in the western Bering Sea in 1933. Gray whales were an important part of her catch. The Japanese floating factory "Tonan Maru" took 58 gray whales in the Chukchi Sea in 1940, and the "Aleut" continued to take gray whales until 1946. From 1933 to 1946, a total of 681 gray whales was killed in the Bering and Chukchi seas. Annual catches provide no clear evidence of any changes in population size during this period.

The 1937 International Agreement for the Regulation of Whaling, which forbade the killing of gray whales, was adhered to by the governments of many whaling nations, including the United States, Canada, and Mexico, but not Japan or the Soviet Union. The 1946 International Convention for the Regulation of Whaling was ratified by the Governments of 17 nations, including Canada, Japan, Mexico, the Soviet Union, and the United States. This convention forbids the killing of gray whales, except by aborigines or a contracting government on behalf of aborigines and only when the meat and products are to be used exclusively for local consumption by the aborigines. Contracting governments may also grant special permits authorizing the collecting of gray whales for scientific research.

Statistics on catches of gray whales by modern style whaling as published in the International Whaling Statistics (IWS) are incomplete and in some instances erroneous; many data from prior to 1937 are combined under the category "North Pacific." We have attempted to compile a complete record of all gray whales killed from 1910 to 1946 (Table 18). No data are available on Korean catches before 1910. Although modern style whaling began on the west coast of North America in 1905, no gray whales were killed until 1913. No gray whales have been taken commercially since the International Convention for the Regulation of Whaling went into effect in 1947, except for one taken in error by the shore station at Coal Harbour, British Columbia, in 1951. In 1953, 10 specimens were taken under a special scientific permit at Coal Harbour. As far as we can ascertain, these statistics are complete except for possible catches off California during the years 1930 and 1932–36, as noted below, and for any that might be included under a few unspecified whales taken in California, British Columbia, and Alaska. The sources of our data for each area in which modern whaling has been conducted are given below.

Baja California.—Data on the 1914 catch of the floating factory "Capella I" are from Tønnessen (1967). Catch figures for 1924–25 through 1929 and for 1935 are from original daily catch records submitted by whaling companies to the Bureau of International Whaling Statistics and kindly made available by Einar Vangstein.

California.—Data from 1918 through 1929 are from Starks (1922), Radcliffe (1933), and Kellogg (1931). Catch statistics by species are not available for the floating factory "Lansing" in 1930 or the floating factory "California" from 1932 through 1936 (total catches for all species are listed in the annual statistical issues of "Pacific Fisherman"). No whaling was conducted in 1931. Catch statistics subsequent to 1936 are from files of the U. S. Bureau of Commercial Fisheries.

Washington.—Catch statistics of the shore station at Bay City, Washington, from 1911 to 1925, as compiled by Scheffer and Slipp (1948).

British Columbia.—Catch statistics for 1905 through 1946, compiled by Gordon Pike (1962*b*) from Annual Reports of the Canadian Department of Fisheries, list no gray whales.

Alaska.—Catch statistics are on file with the U. S. Bureau of Commercial Fisheries.

Bering and Chukchi seas.—Catch statistics for the Norwegian floating factory "Kommandören I" are from IWS, those for the Soviet floating factory "Aleut" are from Sleptsov (1955), and those for the Japanese floating factory "Tonan Maru" are from Sakiura *et al.* (1953).

Korea.—Catches by Korean shore stations are from Mizue (1951) and IWS. Their figures for the period 1920 to 1930 are erroneous; correct figures were published by Tønnessen (1967) and in Norsk Hvalfangst-Tidende, 16:13 (1927), 19:161 (1930), and 20:142 (1931).

Kuril Islands.—Mizue (1951) recorded one gray whale taken by a shore station at Otomae (on Shiashkotan Island), in the northern Kuril Islands, in 1942; this locality is outside the normal range of the species.

SUMMARY

1. This study is based on data obtained from 316 gray whales collected off the coast of central California between 1959 and 1969 and on field observations. The latter included counts of southward migrating whales from shore stations during the winters of 1967–68 to 1969–70, observations made during cruises off California and Mexico from 1962 to 1969, and aerial observations along the coast of Washington, Oregon, and California in 1969. In addition, the stomach contents of a gray whale killed by Eskimos at St. Lawrence Island, Alaska, were analyzed.

2. Gray whales usually travel within a few kilometers of shore while migrating from their summer grounds in the Bering and Chukchi seas to their winter grounds along the coast of Baja California, but off southern California the majority take a more direct offshore route from Point Conception to northern Baja California. The northward migration follows the same route, except that females with calves apparently travel offshore. Migrating gray whales swim at about 8.5 kilometers per hour; on the southward migration they travel about 185 kilometers per day. There is no evidence that the whales travel slower at night than during daylight. Migrating gray whales are temporally segregated according to sex, age, and reproductive status. During southward migration, the sequence of passage is as follows: females in late pregnancy, females that have recently ovulated, adult males, immature females, and immature males. During northward migration, the sequence is as follows: newly pregnant females, anestrous females, adult males, immature females, immature males, and postpartum females. The earliest southbound migrants (mostly late pregnant females) usually travel singly, whereas later migrants usually are in pods of two or more.

3. Food of gray whales on their summer grounds in the northern Bering and Chukchi seas includes at least 17 species of benthic gammaridean amphipods, among which *Ampelisca macrocephala* predominates. The nature of the food indicates that gray whales are bottom feeders. Virtually no food is consumed during migration,

although rarely small quantities of decapod nauplii (*Pachycheles rudis* and ?*Fabia* sp.) are eaten. There is little evidence that gray whales feed on their winter grounds off Baja California. In the interval between their southward and northward migration past San Francisco, the whales lose from 0.21 to 0.37 per cent of their body weight per day. This weight reduction is sufficient to account for the estimated energy expenditure during the winter. Blubber thickness and oil yield also decrease during winter.

4. Age may be estimated from the number of growth layers in the ear plug, indirect evidence suggesting that two layers are formed the first year and one each year thereafter. However, the value of ear plugs for age determination is limited because many plugs do not have clear laminations, and earlier laminations may disappear in older animals. The number of corpora albicantia in the ovaries provides a more reliable estimate of the age of adult females. Growth zones in the baleen plates are of little use for age determination because of rapid wear.

5. Mean body length at birth is about 4.9 meters. Mean length at weaning at an age of 7 months is about 8.5 meters. Puberty is attained at an estimated mean age of 8 years (range, 5 to 11 years) and a mean body length of about 11.1 meters in males and 11.7 meters in females. Physical maturity is attained at about 40 years at a mean body length of about 13.0 meters in males and 14.1 meters in females.

6. Ontogenetic changes in body proportions are slight. From late fetal life to a year of age, relative length of the flippers decreases and relative length of the tail increases. There are no significant changes in body proportions between the end of the first year and physical maturity. Females have slightly shorter flippers and longer tails than do males.

7. In immature females, seasonal enlargement of the follicles begins at a body length of about 9.9 meters and an age of 2 or 3 years. Mean weight of individual ovaries increases rapidly from about 140 to 300 grams when body length reaches about 11.3 meters at about 5 years of age. The ovaries weigh about 340 grams at sexual maturity and continue to increase slowly throughout life,

reaching about 646 grams at 50 years of age. The uterine cornua are 3.5 to 12.0 centimeters in diameter in immature females and more than 11.0 centimeters in adult females. The mammary glands do not develop until the female is well into her first pregnancy.

8. Female gray whales normally come into estrus biennially in late November and early December. Most individuals ovulate only once each season, although whales failing to conceive after their first ovulation may experience a second estrous cycle the same season. Multiple ovulations are extremely rare. Mean ovulation rates are 1.20 per breeding season for nulliparous females and 0.96 per breeding season (0.52 per year) for parous females. There is no evidence for postpartum ovulation or for ovulation at any other time of year. However, increase in follicle size following stillbirth or early loss of the calf suggests that females might ovulate following such an event. Females continue to breed at an advanced age. Corpora lutea of pregnancy average 8.7 centimeters in diameter, whereas corpora lutea of ovulation do not exceed 2.5 centimeters (at least if another estrous cycle soon follows). Corpora albicantia derived from corpora lutea of ovulation are indistinguishable from those derived from corpora lutea of pregnancy. Corpora albicantia persist in the ovaries throughout life. About 55 per cent of ovulations occur in the left ovary and 61 per cent occur in the anterior half of the ovaries.

9. Most conceptions occur within a 3-week period during southward migration, with a peak about 5 December. The pregnancy rate is 0.86 per breeding season (0.46 per year). The gestation period is about 13 months, and fetal growth is accelerated during the last half of pregnancy. During southward migration, late pregnant females (exclusive of their conceptus) average 25 to 30 per cent heavier than the other adult females. Births occur within a period of 5 to 6 weeks, with a peak occurring about 10 January. Caudal presentation at birth is normal.

10. Lactation lasts an average of about 7 months, ending in August.

11. Females are usually in anestrus from August to November or December. However, females that fail to ovulate or conceive

during the winter are probably in anestrus for the following 12 months.

12. In immature males, the weight of both testes is usually less than 5 kilograms, and the seminiferous tubules average 45 to 102 microns in diameter. Testis weight of sexually mature males is more than 5 kilograms, and the average diameter of the seminiferous tubules exceeds 104 microns. Penis length is correlated with body length and is usually less than 1.1 meters in immature males.

13. The average weight of the testes of adult males during southward migration in December and January is 38 kilograms, and the mean diameter of the seminiferous tubules is 177 microns. During northward migration in February and March, mean testes weight and tubule diameter are 22 kilograms and 148 microns, respectively. From July through October, the testes average 23 kilograms. These differences suggest a marked seasonal sexual cycle in the male, with a peak of spermatogenetic activity in autumn or early winter.

14. The killer whale, *Orcinus orca,* appears to be the only predator on gray whales. The mortality rate from killer whale attacks is unknown. However, frequency of tooth scars indicate that killer whale attacks on gray whales are often unsuccessful.

15. Epizoites of gray whales include the following (percentage of occurrence in parentheses): the barnacle *Cryptolepas rhachianecti* (100) and the cyamids *Cyamus scammoni* (99.7), *C. ceti* (99.4), and *C. kessleri* (98.1). Endoparasites collected include the trematodes *Lecithodesmus goliath* (0.6), *Ogmogaster pentalineatus* (more than 22), and *O. antarcticus* (33); two apparently undescribed species of the cestode *Priapocephalus,* one in the small intestine (30) and the other in the large intestine (0.3); the nematode *Anisakis simplex* (0.3); and two acanthocephalans, *Corynosoma* sp. (5.7) and *Bolbosoma* sp. (0.3). Obvious pathogenic effects were noted only for the liver fluke, *Lecithodesmus goliath.*

16. Population size of the California stock during the southward migration of 1969–70 was estimated to be about 11,000. Although previously published estimates of numbers of the California stock are questionable, the population appears to have increased from

1947 to 1960. Trends from 1960 to 1967 are uncertain. Since 1967, population size has remained essentially stable.

17. The sex ratio is essentially equal in all age groups. The birth rate does not exceed 0.13. The calculated annual death rate of adults is 0.08. This is probably an overestimate, although, if the population is now stable, the death rate must have recently increased to near the birth rate.

18. The California gray whale stock was severely overexploited between 1846 and 1900. During the present century this population has been only lightly exploited. Factory ships took an average of 36 gray whales per year in Mexico from 1924–25 to 1928–29 and an average of 48 per year in the Bering Sea from 1933 to 1946. Since then the species has been protected from commercial whaling by the International Convention for the Regulation of Whaling. The Korean stock was virtually exterminated between 1899 and 1933.

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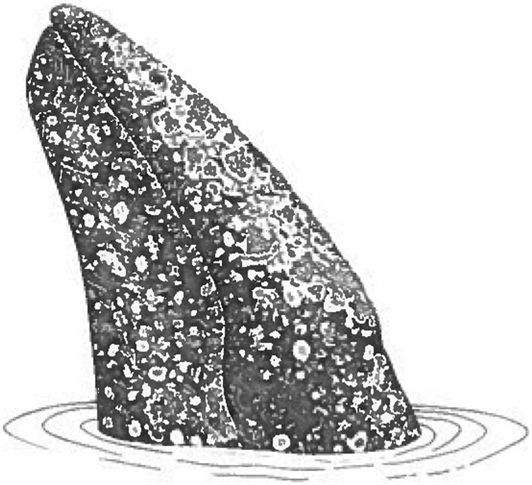

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Demography and Phenology of Gray Whales and Evaluation of Whale-Watching Activities in Laguna San Ignacio, Baja California Sur, Mexico

Mary Lou Jones and Steven L. Swartz

Introduction

As whale-watching tourism, local fishing, and industrial activities increased throughout the southern range of the gray whale in the 1970s, the government of Mexico expressed a desire for detailed information on gray whales in their winter range with which to formulate management policy. The U.S. government raised the concern that

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visits to the gray whale breeding lagoons by U.S.-based excursion companies may create environmental disturbance detrimental to the whales and thus constitute "harassment" and a violation of the U.S. Marine Mammal Protection Act[1] and the Endangered Species Act (Reeves, 1977; Bean, 1980; U.S. Marine Mammal Commission, Washington, D.C., personal communication. Literature on gray whale breeding biology and on the possible effects of whale-watching activity (or human activities) on gray whales was extremely limited, mostly anecdotal, and not quantified. One line of reasoning suggested that whale-watching activities or the mere presence of humans within the breeding lagoons would displace the whales and cause them to seek alternate, perhaps suboptimal, areas in which to mate and calve (Rice and Wolman, 1971; Reeves, 1977). Gard (1974) stated that the gray whales may abandon important habitats and shift their distribution from lagoon to lagoon in response to human activities, but the results of his surveys were not sufficiently conclusive to demonstrate any shift. During the 1960s, gray whales apparently abandoned the small lagoon of Guerrero Negro while it was used as a port for salt barges, and then reoccupied the lagoon following the departure of the salt company and its associated vessel traffic (Reeves, 1977; Chapter 15, this volume). Several investigators suggested "that disturbance from whale-watching may draw needed energy from the finely tuned energy budget of these animals" (Kaza, 1980); however, there were no data to substantiate this point. Still others proposed that if whale-watching operations (and other human activities) resulted in general disturbance that interrupted mating behavior frequently enough to lower reproductive success and increase calf mortality and was not benign over the long term, a decrease in the whale population and its productivity would be expected (Swartz and Cummings, 1978). None of the proposed consequences of disturbance due to whale watching within the lagoons could be evaluated as there was a scarcity of information available on the sensitivity of the whales to human activites.

In full recognition of the paramount importance of the breeding lagoons to the reproductive success and continued recovery of gray whales and of the economic, educational, and aesthetic value of controlled visitation to wildlife areas, the government of Mexico enacted as protective measures a series of legal and administrative provisions that established Laguna Ojo de Liebre (Scammon's Lagoon) and Laguna Guerrero Negro (Black Warrior Lagoon) as national refuges for gray whales, the first of their kind for any cetacean (Vargas, 1981). Beginning in 1972, all commercial vessels, domestic and foreign, were required to obtain permits before entering Laguna Ojo de Liebre, and in 1974 they were restricted to one lower channel near the lagoon inlet (Kaza, 1981).[2] With the restrictions on entry to Laguna Ojo de Liebre, the focus of whale-watching tourism shifted to the largely undisturbed Laguna San Ignacio approximately 150 km further south.

Lagura San Ignacio, the third largest breeding area of gray whales, is the least developed of all the major lagoons. Local Mexican fishing from outboard-powered, 5- or

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[1] United States Marine Mammal Protection Act 1972, 16 U.S.C. 1361 et seq. and the Endangered Species Act 1973, 16 U.S.C. 1531 et seq.

[2] Diario Oficial de la Federation de los Estados Unidos Mexicanos, 14 January 1972.

6-m "pongas" was the only commercial activity prior to 1975, when large-vessel traffic associated with whale-watching tourism began to visit the lagoon. Nearly 100% of the visitors to Laguna San Ignacio utilized vessels to enter the lagoon or to explore the interior, after arriving by aircraft or overland. Considering the dearth of information on gray whale abundance and distribution in this lagoon and because of the recent influx of tourism, we conducted a reconnaissance study in 1977 to assess the need for and feasibility of an intensive long-term research program in Laguna San Ignacio (U.S. Marine Mammal Commission Contract No. MM7AC008). This initial investigation indicated that the majority of females and their calves occupied the middle and upper lagoon "nursery" areas early in the winter when the calves were young. These areas were separated from the lower lagoon and inlet area by a constriction of the main entry channel at Punta Piedra. The width of this constriction (1.5 km) relative to the middle and upper lagoon suggested that human activities there, if adverse, could impede the movement of pregnant near-term females and females with newborn calves into and out of the nursery areas. Also, disturbance in the lower lagoon could disrupt courtship and mating activity of whales without calves and possibly reduce reproductive success. It was clear that knowledge of "normal" gray whale abundance, distribution, and behavior was a prerequisite for understanding the biological significance of responses to any human disturbance (Swartz and Cummings, 1978).

In 1978 we initiated the first long-term systematic study of gray whales in Laguna San Ignacio with the two-fold aim of providing baseline information on the demography and phenology of breeding gray whales and evaluating the impact of whale-watching activities within the lagoon on the whales. It was hoped that the information generated by this research, in conjunction with on-going monitoring programs, would be used to detect and evaluate changes in the wintertime abundance, distribution, and movements of gray whales that may be correlated with future human development.

Following the second year of this study, Mexico declared Laguna San Ignacio a refuge for gray whales and enacted regulations to control the number of whale-watching vessels that visited the lagoon and restrict their activities to specific areas within it. The intent of this action was to protect areas essential to the females and their calves (nursery areas), while at the same time permitting controlled commercial activity in the lower lagoon nearest the sea.

The Laguna San Ignacio research program continued for five consecutive winters, beginning in 1978 and concluding in 1982. We felt that 5 years was the minimum period required to develop a meaningful data base on gray whale trends and to determine whether frequent or continuous vessel disturbance caused changes in gray whale utilization of the lagoon.

The specific objectives of the Laguna San Ignacio research program were to

1. Document the seasonal timetable of lagoon occupation by whales
2. Determine the number and distribution of gray whales inhabiting the lagoon interior and inlet
3. Estimate the proportion of females with calves to whales without calves that utilize the lagoon throughout the season

4. Identify specific nursery areas and the abundance of calves in these areas
5. Ascertain the seasonal mortality of calves, immatures, and adult whales
6. Monitor the level of whale-watching tourism and other human activities and evaluate its impact on the abundance and distribution of whales wintering in the lagoon.

In this chapter we report new findings on gray whale demography and phenology in Laguna San Ignacio; we provide detailed data on patterns of movement into and out of the lagoon, compare changes in the timing of the whales' occupation of the lagoon among all years, evaluate trends in relative abundance across the 5-year study, and present information on the impact of whale-watching activity on the whales. These findings are also compared with studies of gray whales in other breeding lagoons within their winter assembly area. This research establishes a data base on which to evaluate changes in abundance and habitat utilization of gray whales wintering in Laguna San Ignacio which may occur as a result of increasing vessel traffic, industrial development, and petroleum and natural gas production throughout virtually the entire range of this cetacean.

This research was conducted under Permit No. 163 issued by the U.S. Department of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service. Permission to conduct scientific research in Mexico was authorized under permits No. 14203 (1977), No. 12-459-498 (1978), No. 920 (1979), No. 10919 (1980), No. 10455 (1981), and No. 4048 (1982) issued by the Secretaria de Pesca, Direccion General De Regulacion Pesquera de Mexico.

Methods

STUDY SITE

Description

Laguna San Ignacio is located on the Pacific coast of Baja California adjacent to Bahia Ballenas, approximately 680 km south of the International Border between 26°42′ and 27°00′N and 113°7′ and 113°18′W (Fig. 1). The lagoon is part of the Vizcaino Desert and borders a gently sloping, dry, coastal flood plain the sediments of which are presumed to be Cretaceous and Tertiary, capped by Pleistocene alluvium (Mina, 1957; Phelger and Ewing, 1962). The climate is arid with an annual average rainfall of 56 mm (2 in.) which falls mainly during winter months; there is no runoff and no freshwater streams or rivers flow into the lagoon (Bostic, 1975).

Prior to our study, the most recent hydrographic chart dated from 1896 (U.S. Hydrographic Chart No. 1494) and did not accurately represent the lagoon in its present state. Therefore, it was necessary for us to conduct a habitat study to establish the physical characteristics of the lagoon and to construct an accurate chart. The present-day shoreline, the location of major shoals, and an accurate estimate of the total lagoon acreage were determined from satellite imagery (LANSAT). Lagoon bathymetry was

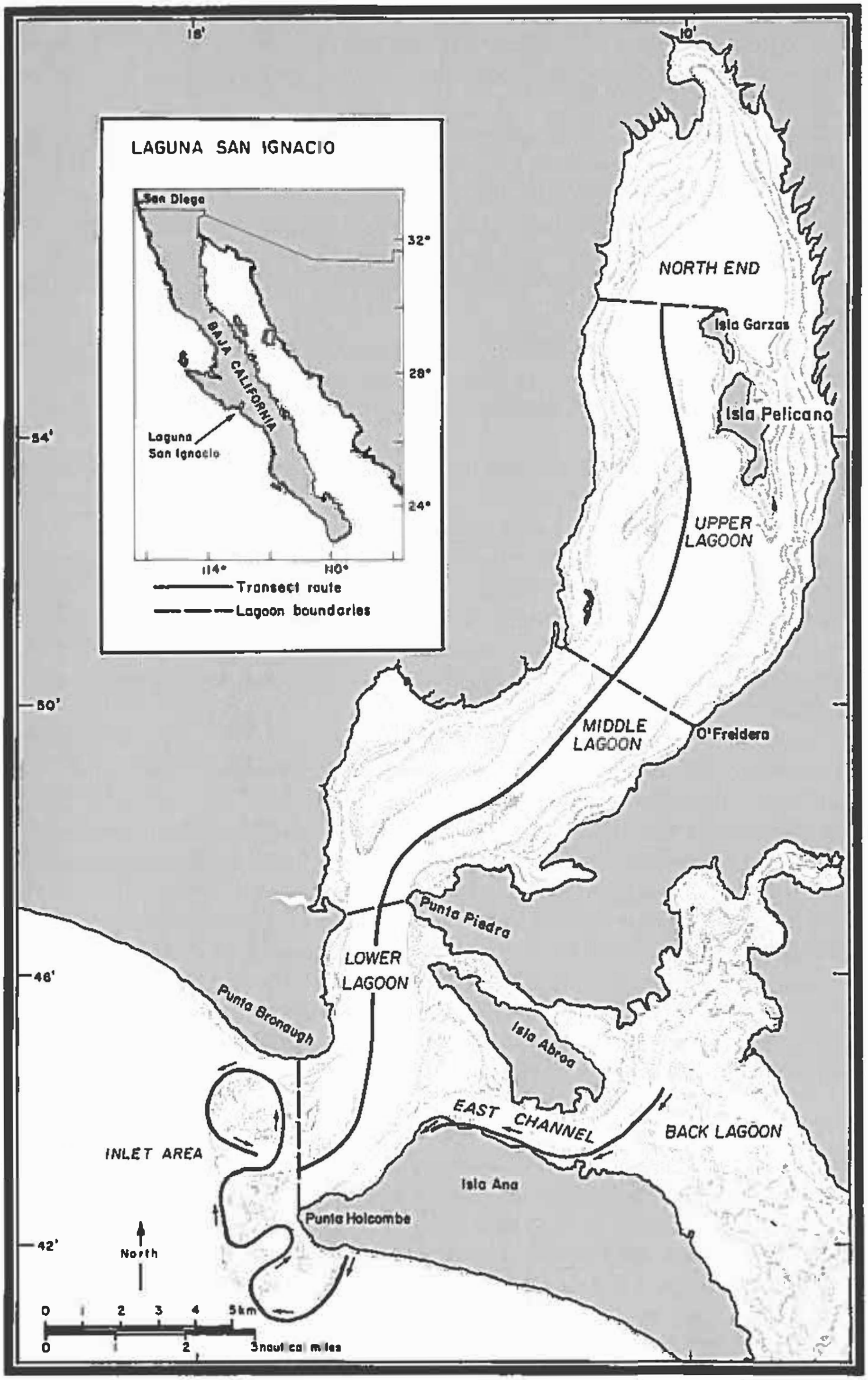

Fig. 1. *Laguna San Ignacio showing the boat transect trackline in the lower, middle, and upper lagoon areas and the aerial transect trackline in the east channel and inlet area. Arrows indicate the direction of flight of the aircraft.*

discerned from "echograms" made by a continuous-recording fathometer. Scuba divers made visual observations of the lagoon floor and sampled bottom sediments (Swartz and Jones, 1981).

The lagoon is a system of narrow, relatively deep channels surrounded by large intertidal flats. It lies on a north-to-south axis, extends inland approximately 32 km, ranges from 1.8 to 6.5 km wide, and has an area of 152 km^2, of which only approximately 57% or 87 km^2 is of sufficient depth (>2 m) to be navigable by whales. The area of the inlet is approximately 20.5 km^2, and the east channel adds approximately 3.6 km^2. The semidiurnal tide ranges from 0.9 to 2.4 m, and the tidal currents in the inlet and channels are very turbulent.

Laguna San Ignacio has a distinctive topography characteristic of lagoons with an appreciable tidal range. The bathymetry and sedimentology may be divided into five areas: the inlet, east channel, and the lower, middle, and upper lagoons (Swartz and Jones, 1981).

The 3.8-km-wide inlet is defined by a breaker line and includes a 1-km-wide entry channel with a maximum depth of 16.8 m, bordered by the inner inlet delta that averages 3.6 m in depth (Fig. 2, Profile 1). This steep-walled channel runs northward and parallels the west shore of the large barrier island, Isla Ana. The delta ends 1.5 km inside the inlet and the channel becomes deep over its entire width (Fig. 2, Profile 2). Sediments range from well-sorted, hard-packed, medium-grained sand with large shell fragments on the inner delta to irregular rock rubble covering the floor of the inlet channel. The delta is devoid of macroscophic plants, but the channel supports sparse algal vegetation in the rocky areas.

The lower lagoon consists of a steep-walled channel with a maximum depth of 25.9 m. It narrows from 3-km wide near the inlet to a constriction 1.8-km wide at Punta Piedra, where it terminates as the lagoon trends northeast. This segment is the widest relatively deep channel in the lagoon (Fig. 2, Profiles 3 and 4). West of Isla Ana, the 0.5-km-wide and 9.1-m-deep east channel tributary leaves the main lagoon, turns southeast behind Isla Ana, and runs 5.1 km to a shallow lagoon 1.5- to 2.4-m deep (Fig. 2, Profiles 13–15). Here the bottom is composed of poorly sorted coarse- and medium-grained sand with crushed shells. Extending north from Isla Ana, the main channel floor varies from a series of irregular sand ridges perpendicular to the lagoon axis to rocky areas (*coquina*) overlain with sand. The deepest regions of the channel are covered with poorly sorted, hard-packed, fine- to coarse-grained sand. West of Punta Piedra, medium-grained sand ridges are interspersed with occasional rock outcroppings 4- to 6-m tall.

The middle lagoon is characterized by a system of three channels ranging from 7.6 to 21.3 m deep, which become shallower and irregular in profile west of O'Freidera (Fig. 2, Profiles 5 and 6). Sediments are poorly sorted, fine- to coarse-grained sand with crushed shell, and some rocky areas. Extensive sand bars support stands of eelgrass (*Zostera marina*), but the channels contain little plant life.

The upper lagoon is a gently sloping basin with an average depth of 4.6 m. Two islands, Isla Garzas and Isla Pelicano, are separated by a shallow isthmus and located approximately mid-lagoon (Fig. 2, Profiles 8–12). The areas at the head of the lagoon

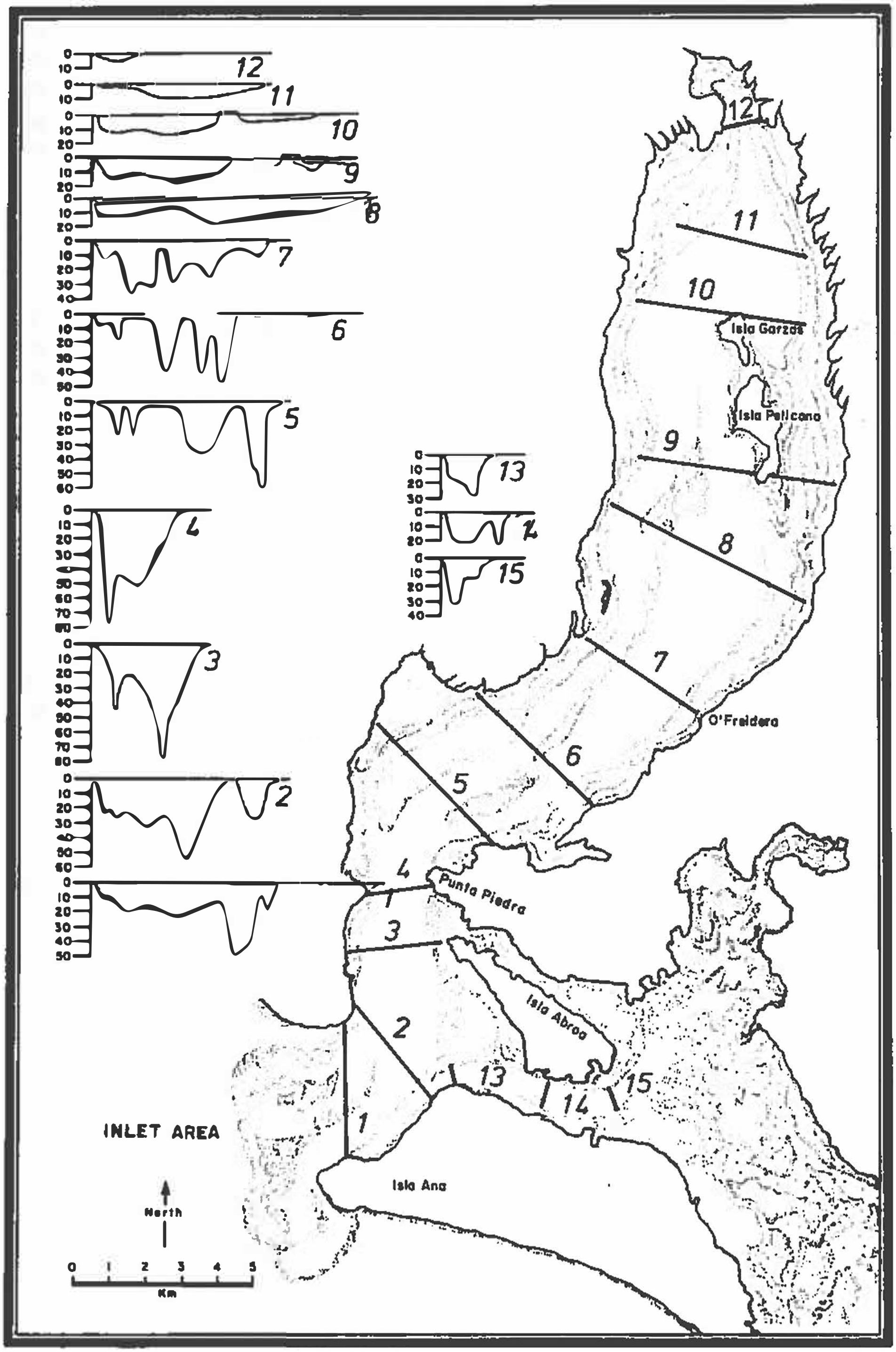

Fig. 2. *Depth profiles of Laguna San Ignacio based on echograms. Horizontal scale approximate. Soundings are in feet, and vertical exaggeration is 100×.*

north and east of the islands contain fine sand, silt, and clay. The bottom in the north is dominated by dense stands of eelgrass containing a variety of crustaceans, gastropods, pelecypods, encrusting hydroids, sponges, and tunicates. Red and brown algal epiphytes and encrusting invertebrates are attached to rocks, shells, and eelgrass blades.

Refuge Regulations

By 1975 almost all whale-watching tourism had switched from Laguna Ojo de Liebre to Laguna San Ignacio, and the need for regulation of commercial activities in this lagoon became apparent (Reeves, 1977). Our first two winters of research, 1977 and 1978, indicated the majority of females and their calves utilized the middle and upper lagoon areas early in the winter when the calves were young. In 1979 Mexico declared Laguna San Ignacio as a gray whale refuge, and our initial findings were used to designate the boundaries of the "closed" nursery area (middle and upper lagoon areas) and the "open area" in the lower lagoon where controlled tourism and fishing were permitted and to formulate regulations for the kinds of activities that would be permitted within the lagoon.[3] The regulations specify that between December 15 and March 15 each year all vessel traffic is restricted to the lower lagoon south of Punta Piedra, thus providing the upper two-thirds of the lagoon as a sanctuary free of human activities. In addition, no more than two commercial vessels are allowed within the lagoon at any one time. Individual permits issued to each vessel specify the number of days a vessel may remain within the lagoon, the number of passengers it may carry, the number of skiffs it may launch, and the kinds of activities permitted, such as whale watching, shore explorations, etc.

BOAT SURVEYS

Each of the field seasons was timed to coincide with the period during which most of the gray whales that utilized the lagoon could be observed. We began the first field season (1977–1978) on December 23, 1977, in an attempt to document the arrival of the earliest whales to the lagoon. In subsequent winters (1979–1982), field work began the second week in January, and in all years it continued until mid-April.

Each week, line transects (Eberhardt, 1978) of the entire lagoon interior were conducted to estimate whale abundance, to elucidate whale distribution and movement, and to document the seasonal timetable of lagoon occupation. Transects were executed in a 4.7-m inflatable boat powered by a 20-hp outboard engine and traveling at approximately 11 km/hr. Each transect required approximately 7 hr to complete. The crew included a left and a right observer and a vessel operator. Transects were run along an imaginary line drawn midlagoon from Punta Piedra south to the breaker line near the lagoon inlet, north to Isla Garzas at the northern end of the lagoon, and then south again to the starting point at Punta Piedra. In this way, the entire transect line was traversed twice. The maximum distance from the boat to the 2-m depth contour along shore was 2.6 km and the minimum 0.8 km; thus, whale-inhabitable water and both

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[3] Diario Oficial de la Federation de los Estados Unidos Mexicanos, 16 July 1979.

shorelines were clearly visible at all times within the lagoon. Whales in the "North End" of the upper lagoon north of the transect termination were observed through binoculars from a 5-m-high bluff on the northern tip of Isla Garza (Fig. 1).

All whales sighted from the boat were counted when they were approximately abeam of the boat, and all observations were recorded on a cassette tape recorder. The higher number of whales counted from the two replicate transects was used as a minimum abundance count, an index of the whale population for that week. Because only two replicates could be obtained per census day, we did not estimate errors for these abundance counts. Whale distribution was determined by recording transect starting time, time each whale or group of whales was encountered, passage of landmarks, progression of tidal stages, and time of completion. To prevent observer anticipation of whales previously counted, observers viewed a different side of a transect leg on each replicate. Transects were discontinued when wind and wave conditions exceeded Beaufort Sea State No. 3 (winds 12–18 km/hr), which obscured whale blows, diminished the sightability of inconspicuous behaviors, and lowered the overall probability of sighting whales (particularly calves). Corrections for whales missed are discussed in the results.

Unless otherwise noted, "female–calf pairs" were considered a single unit, and counts of these pairs are equivalent to calf counts; "single whales" refer to nonparturient females, adult males, and immatures. Single whales often occurred in pairs or groups.

AERIAL SURVEYS

Aerial surveys augmented the boat surveys in 1980, allowing simultaneous estimation of whale abundance and distribution in areas not accessible by boat, namely the east channel, inlet, and nearshore waters adjacent to the lagoon. These surveys were flown in a Piper Super Cub (a two-passenger, single-engined, high-wing aircraft) at an altitude of 330 m and an average ground speed of 123 km/hr. Total coverage (100%) was attempted (Eberhardt, 1978) by flying a serpentine course over the inlet with observers making counts from each side of the aircraft. The east channel was surveyed by flying along its southeastern shore (Fig. 1). As with boat surveys, all observations were recorded on a cassette tape recorder. For larger whale groups, the aircraft diverted from course and circled until the observer's count stabilized, then returned immediately to the original course. Practice flights were flown to familiarize the pilot and observers with the transect route and survey procedure. Surveys were conducted during Beaufort Sea State No. 3 conditions or better, and surveys were flown between 0900 and 1500 hr to reduce the effects of surface glare on the water. Sighting cues indicating the presence of whales, such as bubble bursts, mud upwellings, or a series of whale "foot-prints," were counted as single animals.

MORTALITY

Beaches were searched by boat or aircraft for stranded dead whales at least twice per week, and additional information was requested of local fishermen who participated by reporting sightings of whale carcasses. The sex of dead whales was determined, and standard measurements were recorded. Length was measured as the distance from the tip of the snout (rostrum) to the notch of the flukes. Whale carcasses were marked and photographed, and their locations were recorded to prevent duplicate sightings of individuals in the event that the tide and winds moved bloated carcasses from their original site of discovery. The calf mortality rate for Laguna San Ignacio was calculated from the number of dead calves discovered and the estimated total calf production. Finally, we researched the records on natural mortality in other breeding areas for comparison with the Laguna San Ignacio data.

WHALE-WATCHING ACTIVITIES

When we began the gray whale study in Laguna San Ignacio in 1977, there was little information available from which to judge the possible reactions of the whales to the growing tourist industry within the lagoon. Gray whales seemed particularly vulnerable to human activities within the confinement of the lagoons because they cannot readily flee from an adverse disturbance as they can in the open ocean. Also, given that the lagoon is a critical habitat necessary for successful reproduction, exclusion from one or more lagoon areas could cause overcrowding in remaining areas or force whales to seek alternate and perhaps suboptimal areas in which to breed that may not provide the protective features offered by the lagoons.

To document the relative amount of disturbance introduced into the lagoon each winter by human activities, our first step was to qualitatively and quantitatively characterize human disturbance. A log was kept of the number, location, and hours of activity of all vessels entering or transiting through the lower lagoon, the area designated for commercial activities. For the whale-watching excursions, we determined the number of hours that vessels were present in the lagoon, the number of hours they were underway and at anchor, and the number of hours whale-watching skiffs were in operation. The sum of the hours of each disturbance category was then expressed as a percentage of each entire season, and these percentages were compared among years. It was, however, beyond the scope of the program to identify the specific attributes of vessels that might cause significant changes in the utilization of the lagoon by gray whales.

In our study, we employed natural experimental and observational approaches to evaluate the demographic reactions of gray whales to potential sources of disturbance from whale-watching activities over the 5 years. To determine whether whales showed a response to human disturbance in the lagoon among years, seasonal trends in whale abundance and distribution were statistically compared among years as levels of tourism increased and decreased. Specifically, we sought to identify the following possible responses to disturbance:

1. A decrease in seasonal abundance of gray whales utilizing the entire lagoon
2. A decrease in the number of females and calves utilizing the nursery area
3. A decrease in the seasonal abundance of gray whales in the lower lagoon, the area utilized by tour vessels, and
4. An increase in the seasonal mortality of whales, especially calves.

Although interactions between whales and people have a variety of forms, in designing our study we believed that the consequences of changes in these parameters would be immediately "meaningful" from a management point of view. Findings on gray whale behavioral reactions to vessel disturbance such as changes in the relative frequency, duration, and context of social behavior, aerial behavior, sexual behavior, swimming direction, and breathing rates are reported elsewhere (Swartz and Jones, 1978, 1981; Jones and Swartz, 1984).

In addition to the analysis of seasonal demographic trends among years, we compared gray whale abundance and distribution within years during "control" periods without human activity and "experimental" periods with human activity (specifically tourism) in the lagoon. Here, the potential adverse effects of whale-watching tested for were responses 1, 2, and 3 mentioned earlier.

To evaluate these potential effects, boat transect counts from consecutive pairs of days were compared; these pairs included a day preceding and a day following the arrival of a vessel, two days with vessel activity, and a day before and a day following a vessel departure. We tested the null hypothesis that whale-watching activities did *not* cause significant changes in gray whale abundance, density, and distribution in the lagoon as a whole, in the nursery area, and in areas where whale and human activities occurred simultaneously.

The proposed consequences of exposure to human disturbance (i.e., whale-watching activities) constituted our operational definition of "harassment" or disturbance to whales.

Results

ABUNDANCE, DISTRIBUTION, AND OCCUPATION TIMETABLE

Correction for Unseen Whales

Raw boat transect counts may be biased toward underestimating the actual number of whales in an area for two primary reasons, (1) some whales that are present but are below the water's surface while the transect vessel passes through the survey area are not detected, and (2) some whales that are at the surface may be missed by the observer (Caughley, 1977; Eberhardt, 1978; Eberhardt *et al.*, 1979; Davis *et al.*, 1982). The first source of bias is a function of the length of time the observer has to view the survey area and the whale's surface interval and duration of dives. A correction factor to determine the probability that a whale will surface while the observer is viewing the survey area is given by Eberhardt (1978) as

$$P = \frac{s}{s+u} + \frac{t}{s+u} = \frac{s+t}{s+u} \qquad (1)$$

where s is the mean duration of surfacings (i.e., the mean surface interval), u is the mean duration of dives, and t is the length of time a point along the transect line is visible to the observer. To allow for submerged animals, raw whale counts should be divided by P. Two of the assumptions of this formula are that t is less than or equal to u and that s and u are constant; however, because our gray whale values for u were very much less than t and because the duration of surface intervals and dive durations varied with the behavior of the whales in Laguna San Ignacio, these assumptions were not valid for our boat surveys. Under these conditions, Eberhardt (1978), and Eberhardt *et al.* (1979) suggest that $P = (s + t)/(s + u)$ is inappropriate to compute the probability that a whale will be detected, but, to our knowledge, no alternate method has been published.

We employed a different approach to determine whether to adjust our raw whale counts for whales missed while they were below the surface. First, to calculate t, the duration of potential detectability during our boat survey, we divided the observer's field of view by the boat survey speed. We estimated that the length of the observer's field of view was 1.5 km, beginning approximately 1.0 km ahead of the boat and ending 0.5 km behind. The survey speed of 11 km per hour was selected for three reasons: (1) it was faster than the observed range of normal gray whale swimming speeds of up to 6 km per hour (Gilmore, 1960; Pike, 1962; Sumich, 1983) and thereby reduced the possibility of counting the same whale twice; (2) it allowed adequate time to view most whales more than once (see below); and (3) it allowed us to complete two transect replicates per census. Thus, our value of t was

$$t = \frac{1.5\ \text{km}}{11\ \text{km/hr}} = 8.18\ \text{min}, \tag{2}$$

the period during which a point along the transect line was within the observer's view.

Our next step was to determine how many times a whale was likely to surface within the period of potential detectability. To do this we used the mean surfacing rate and mean surfacing interval calculated by Mate and Harvey (1981) and Harvey and Mate (Chapter 24, this volume) for 10 radio-tagged gray whales in Laguna San Ignacio. Because their radio tag only transmitted signals when the antenna broke the surface, Harvey and Mate obtained the most precise estimates available for these parameters during 307 hr of monitoring.[4] Their mean surfacing rate for adult whales was 35.6 ± SE 0.8 surfacings/hr ($n = 202$), or 0.59 surfacings/min. In addition to the data for radio-tagged whales, from their shore observations they reported a rate of surfacing for gray whale calves of 100.2 surfacings/hr, or 1.67 surfacings/min (sample size not reported). Adult whales, then, would be expected to surface once every 1.69 min (1 min and 41 sec) and calves once every 0.59 min (35 sec). From these surfacing rates, the mean number of times an adult whale would be expected to surface within the observer's duration of detectability was calculated as 8.18 min × 0.59 surfacings/min = 4.8 surfacings. Simi-

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[4] Surface intervals may have been slightly longer than those reported by Mate and Harvey because their radio tags were placed behind the whale's blowholes; thus, as the animals arched and rolled while beginning a dive the antenna would submerge a moment before the entire animal.

larly, the mean number of surfacings expected for a calf would be 8.18 min × 1.67 surfacings/min = 13.7 surfacings.

To determine how many seconds a whale would be visible during the period of potential detectability, we used Harvey and Mate's mean surface interval for adult whales of 0.07 ± SE 0.01 min ($n = 11{,}229$ surfacings) or 4.2 sec. They did not report a mean surface interval for calves. The mean proportion of the duration of potential detectability that an adult whale would be visible was calculated as the number of surfacings multiplied by the surface interval, divided by the duration of potential detectability or

$$\frac{4.8 \text{ surfacings} \times 0.07 \text{ min}}{8.18 \text{ min}} = 0.041 \qquad (3)$$

or approximately 20 sec during every 8.18 min.

Our estimate of a mean of 4.8 surfacings and a mean total surface duration of 20 sec during the period of potential detectability suggests that we had an opportunity to see most if not all whales (including calves) one or more times during a transect. For this reason, we did not adjust our raw whale counts for whales missed because they were below the surface.

The second source of bias, whales at the surface but missed by the observer, is a function of environmental conditions affecting visibility during the survey and the observer's sighting ability and experience (Leatherwood *et al.*, 1978; Davis *et al.*, 1982). Again, we did not correct for this bias, but, to minimize this source of error, transects were conducted only during ideal conditions, Beaufort Sea State No. 3 or less, and excellent through-air visibility (no rain, mist, or fog). In addition, all observers were experienced at surveying gray whales in Laguna San Ignacio; new observers participated in training transects and accompanied experienced observers on actual transects before they conducted counts on their own. Despite these precautions, some whales were undoubtedly missed. For this reason, we chose the highest count from the two transect replicates as the minimum whale abundance estimate for that day.

Inlet and Lagoon Interior

Counts of gray whales in the inlet and the east channel of the lagoon (Fig. 1) were obtained from 16 systematic aerial surveys conducted between January 16 and March 28, 1980. Seasonal counts of single whales and female–calf pairs in the inlet are shown in Fig. 3. An overview of the total seasonal whale abundance for the entire Laguna San Ignacio system was obtained for 1980 by combining aerial counts with corresponding boat counts of the lagoon interior (Fig. 4A).

The maximum combined count (single whales + female–calf pairs) for the entire system occurred on February 16 and was 458 whales (333 single whales and 125 female–calf pairs). These whales were distributed as follows: 27% (119 single whales and 5 female–calf pairs) were in the inlet, 72% (214 single whales and 118 female–calf pairs) were in the lagoon interior, and 1% (2 female–calf pairs) was in the east channel (Fig. 4A).

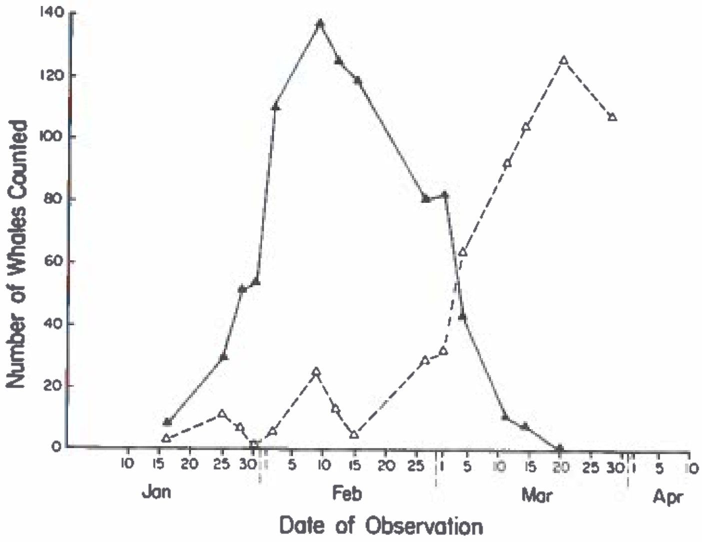

Fig. 3. *The number of single whales (solid triangles) and female-calf pairs (open triangles) counted in 16 aerial transects of the inlet of Laguna San Ignacio during the 1980 winter.*

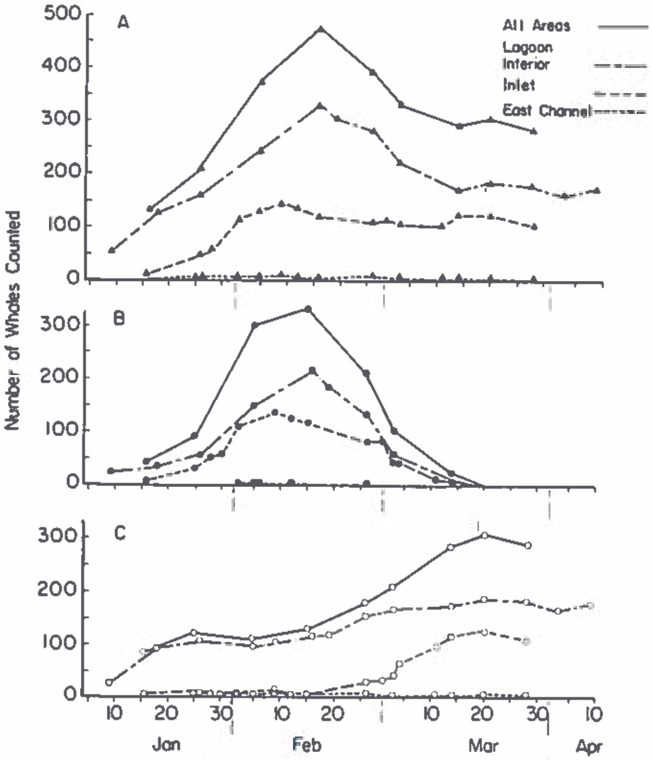

Fig. 4. *Total number of whales counted in the entire Laguna San Ignacio system in 1980. (A) Triangles are total adult whales. (B) Closed circles are single whales. (C) Open circles are female–calf pairs.*

The maximum single whale count of 351 animals also occurred on February 16, 1980. Thirty-nine percent of these animals were in the inlet, and 61% were in the lagoon interior. No single whales were in the east channel (Fig. 4B). By March 3, single whales in the inlet had declined to 26% of their maximum count for the entire lagoon system, and by March 14, only 3% remained.

In contrast to the single whales, at the maximum combined count only 8% of the 125 female–calf pairs counted were in the inlet, while 90% were in the lagoon interior, concentrated in the upper lagoon nursery area (Fig. 4C). The east channel, the smallest inner-lagoon area, never contained more than 2% of the lagoon whale population.

Following the departure of single whales from the lagoon, counts of female–calf pairs continued to increase and reached a maximum of 315 pairs on March 19. At this time, 40% were in the inlet, 59% were in the lagoon interior, and 1% was in the east channel. During the final aerial survey on March 28, 108 female–calf pairs were counted in the inlet. Local fishermen informed us that some females and their calves may be

Table 1
Abundance of Gray Whales in the Inlet and Interior of Laguna San Ignacio at Two Key Time Periods in 1980

	Lagoon area					
	Inlet[a]	Lower[b]	Middle[c]	Upper[d]	East channel[e]	Total
Maximum combined counts (February 16)						
Total whales						
Number	124	153	69	110	2	458
Density[f]	7.75	9.28	3.40	4.50	1.11	—
Percentage of total	27	33	15	24	1	100
Single whales						
Number	137	144	60	10	0	351
Density	6.68	8.25	2.62	0.21	0	—
Percentage of total	39	41	17	3	0	100
Female–calf pairs						
Number	11	9	9	100	2	131
Density	1.07	1.03	0.79	4.29	1.11	—
Percentage of total	8	7	7	76	2	100
Maximum female–calf counts[g] (March 20)						
Number	126	163	23	0	2	314
Density	12.29	18.68	2.01	0	1.11	—
Percentage of total	40	52	7	0	1	100

[a] Inlet area = 20.50 km².
[b] Lower lagoon area = 17.45 km².
[c] Middle lagoon area = 22.91 km².
[d] Upper lagoon area = 46.62 km².
[e] East channel area = 3.60 km².
[f] Whales/km². Female–calf pairs were considered as two animals in density calculations.
[g] No single whales present.

seen in the surf areas of the inlet through April and May of some years, but they are rarely seen in June.

To illustrate the utilization of the inlet relative to the lagoon interior at the maximum combined count and at the maximum female–calf pair count, a more detailed breakdown of the number of whales utilizing the complete lagoon system is presented in Table I. The inlet was utilized extensively throughout the season and was clearly a major area. On the date of the maximum combined count, 39% of the single whales occupied the inlet at a density of 6.68 whales/km^2, while only 8% of the female–calf pairs were present in this area. Coinciding with the departure of single whales, however, the number of female–calf pairs gradually increased in the inlet and at their maximum count, the inlet contained 40% of these animals at a density of 12.29 whales/km^2, or double the density of single whales (female–calf pairs were counted as two animals for densities).

Lagoon Interior

To identify trends in gray whale abundance, distribution, and duration of season, the counts of whales were analyzed at two key time periods. The first period was the annual date of maximum combined counts, which coincided with the period of single whale maximum counts. For this time category, an overview of the total whale abundance and distribution in the lagoon is presented first. Then, the total whale population is subdivided into single whales and female–calf pairs and these two components are analyzed as separate but interacting groups. The second time period was the date of maximum female–calf pair counts which occurred after the departure of single whales from the lagoon each year. To determine whether whale abundance at the two time periods changed significantly among years, a least squares exponential regression line was fitted to the yearly maximum counts for each whale category (i.e., total whales, single whales, and female–calf pairs); the regression (significance of trend) and significance of slope (significance of increase or decrease) were evaluated with analysis of variance (ANOVA) (Sokal and Rohlf, 1981).

During the 1977 reconnaissance study, we learned that gray whales were distributed differentially within the lagoon. Whales occupied some areas throughout the season, while other areas were occupied only part of the winter. Therefore, to more precisely elucidate whale distribution, the lagoon interior was divided into three sections, the lower, middle and upper lagoon, based on our preliminary observations of whale distribution, and on the bathymetric features of the lagoon. The seasonal distribution of whales within each section was determined by subdividing the weekly censuses of the entire lagoon into the number of whales counted per area.

The dynamics of gray whale distribution in the lagoon interior was assessed by investigating three parameters: abundance, density, and the percentage of the total lagoon population that was within each area. We first tested for differences among lagoon areas, and then tested for changes within each area during the 5 years. A Kruskal–Wallis nonparametric test was used to evaluate differences in the three variables among the lower, middle, and upper lagoon areas. In the situation where the null hypothesis of the Kruskal–Wallis was rejected, nonparametric multiple comparisons

(Zar, 1974) were done to determine between which of the locations significant differences occurred.

Differences in the abundance of whales within each lagoon area over the 5 years were evaluated by using G-tests to compare each yearly count to the mean count for all years. Trends in abundance within each area were evaluated by fitting least squares, exponential regression lines to the counts for all years, and the significance of regression was evaluated with ANOVA.

To examine whether whale density (whales/km^2) varied significantly within each of the three areas, counts were analyzed with three separate Kolmogorov–Smirnov tests, where the expected frequency was the mean density in each location for the 5 years. In addition, least squares regression lines were fitted to the densities for each year and the significance of each regression was evaluated with ANOVA.

To determine whether there was a pattern to the whale distribution in the lagoon over the 5 years, the number of whales within each of the three areas was expressed as a percentage of the total number of whales in the lagoon, and changes in the proportion of the whales in each area were evaluated by calculating G-statistics for the log-likelihood ratios of observed percentages versus the mean percentage for each area.

Maximum Combined Counts. Gray whale counts from 60 boat transects, 10–14 each winter between 1978 and 1982, were used as an index of the weekly whale abundance within the lagoon interior. In all years, whales were present in low numbers when field work began. During the 1977–1978 season when transects were begun in December, the first count (5 single whales and 1 female–calf pair) on December 26, was only 2% of the eventual maximum count, and the second count (29 single whales and 2 female–calf pairs) on January 4, was 9% of the eventual maximum count for that year. In subsequent years, the first transects were conducted during the second week in January, and these counts averaged 20% (mean = 67 whales) of the annual maximum count.

The seasonal distribution of the overall whale population in the lagoon was bimodal: the major mode represented the maximum combined counts for each year and was composed primarily of single whales and some female–calf pairs (Fig. 5). Maximum combined counts occurred as early as February 2 in 1978 and as late as March 1 in 1979 with a mean day for the five winters of February 15 ± SE 3.9 days, and a 95% confidence interval of 21 days from February 5 to February 26. In 1978 and 1979, the dates of maximum combined counts were the most widely separated (27 days) and were significantly different from the mean day; the dates of maximum combined counts for the 1980 to 1982 seasons, however, were clustered about the mean day; these dates were February 16 in 1980, February 12 in 1981, and February 14 in 1982

Maximum combined counts increased significantly, 7.3% per year, from 300 adult whales in 1978 to 407 whales in 1982 [$F_{(1,3)} = 32.88$, $p < .025$, $r^2 = 0.916$] (Fig. 6). This increase was primarily attributable to greater counts of female–calf pairs each year. Counts of these whales increased significantly, 18.3% per year [$F_{(1,3)} = 16.13$, $p < .05$, $r^2 = 0.843$], from 65 pairs in 1978 to 137 pairs in 1982. In contrast, the 2.7% per year increase in the single whale counts was not significant [$F_{(1,3)} = 0.52$, $p > .50$, $r^2 = 0.147$].

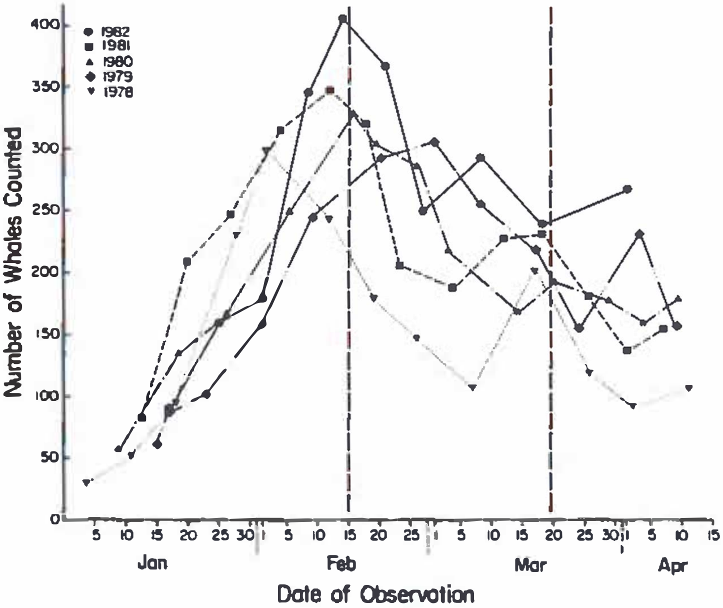

Fig. 5. *The number of whales (except calves) counted in 60 vessel transects of Laguna San Ignacio between 1978 and 1982. Broken vertical lines represent the mean date of combined maximum counts (February 15) and the mean date of maximum female–calf pair counts (March 19).*

The seasonal abundance and distribution of gray whales in the lower, middle, and upper lagoon areas between 1978 and 1982 are shown in Table II and in Figs. 7–9. A Kruskal–Wallis test of equality among lagoon areas revealed that whale abundance was not the same in all three areas [$X^2_{(2)} = 12.02$, $p < .01$]. The nonparametric multiple comparison test disclosed that abundance was significantly different in each lagoon area.

Whale abundance was greatest in the lower lagoon during all years. A G-test

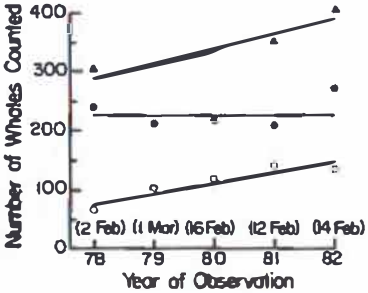

Fig. 6. *Maximum combined counts of gray whales (triangles) in Laguna San Ignacio between 1978 and 1982. Closed circles are the single whale component and open circles are the female–calf pair component of the maximum combined count. Dates of maximum counts are in parentheses. Black lines are least squares regression lines.*

Table II
Abundance of Gray Whales in the Three Lagoon Interior Areas and Inlet Between 1978 and 1982

Lagoon area	Year	Maximum combined counts			Maximum[a] female–calf pair counts
		Total adults	Single whales	Female–calf pairs	
Inlet	1980	124	119	5	126
Lower lagoon	1978	137	129	8	179
	1979	168	144	24	198
	1980	153	144	9	163
	1981	158	134	24	190
	1982	202	187	15	200
	G	13.97**[b]	13.61**	15.54**	5.11
	$P_{(G)}$	<.01	<.01	<.005	>.10
	F	4.97	3.43	1.57	0.38
	$P_{(F)}$	>.10	>.10	>.10	>.50
	r^2	.62	.53	.34	.11
Middle lagoon	1978	73	69	4	16
	1979	50	33	17	29
	1980	69	60	9	23
	1981	72	56	16	32
	1982	67	52	15	49
	G	5.63	14.11**	11.76*	19.90***
	$P_{(G)}$	>.25	<.01	<.025	<.001
	F	0.03	3.90	2.43	11.80*
	$P_{(F)}$	>.90	>.10	>.05	<.05
	r^2	.01	.57	.45	.80
Upper lagoon	1978	92	37	55	7
	1979	90	31	59	0
	1980	110	10	100	0
	1981	118	17	101	7
	1982	138	31	107	33
	G	14.15**	22.24***	31.61***	74.59***
	$P_{(G)}$	<.01	<.001	<.001	<.001
	F	42.45**	0.25	14.96*	1.44
	$P_{(F)}$	<.01	>.50	<.05	>.50
	r^2	.90	.08	.85	.32

[a] No single whales present.

[b] * = significant at $\alpha \leq .05$, ** = significant at $\alpha \leq .01$, and *** = significant at $\alpha \leq .001$.

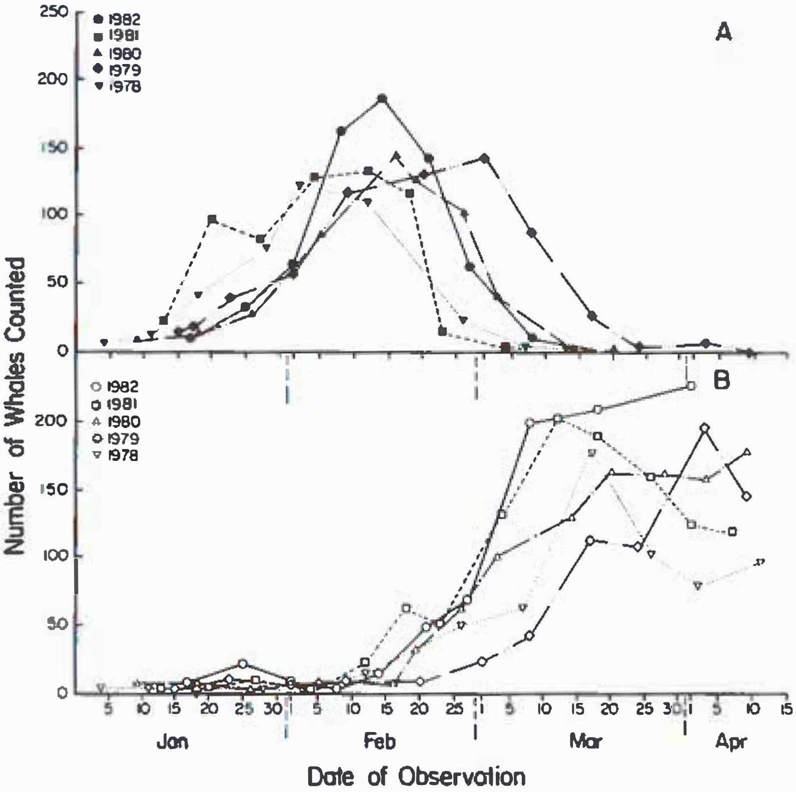

Fig. 7. *The number of single whales (A) and female–calf pairs (B) counted in 60 vessel transects of the lower lagoon between 1978 and 1982.*

indicated that the number of whales in this area at the date of maximum combined counts was significantly different each year [$G = 13.97 > X^2_{.05(4)} = 9.49$, $p < .01$] (Table II). The slope of the least squares, exponential regression line fitted to these counts indicated that the population in the lower lagoon increased 7.1% per year from 137 whales in 1978 to 202 in 1982, but, this increase was not statistically significant [$F_{(1,3)} = 4.97$, $p > .10$, $r^2 = 0.624$] (Fig. 10A, top). Thus, the heterogeneity in the counts among years was not explained by the regression.

The number of whales in the middle lagoon did not change significantly among years [$G = 5.63 < X^2_{.05(4)} = 9.49$, $p > .10$], and the 3.8% per year decrease in these counts from 73 in 1978 to 67 in 1982 was also not significant [$F_{(1,3)} = 0.03$, $p > .90$, $r^2 = 0.010$].

Finally, whale counts in the upper lagoon nursery did change significantly [$G = 14.15 > X^2_{.05(4)} = 9.47$, $p < .01$] showing a significant 8.9% per year increase from 92 in 1978 to 138 whales in 1982 [$F_{(1,3)} = 42.45$, $p < .01$, $r^2 = 0.934$]. Notably, the 7.3% per year overall increase in the whale population in the lagoon between 1978 and 1982 was

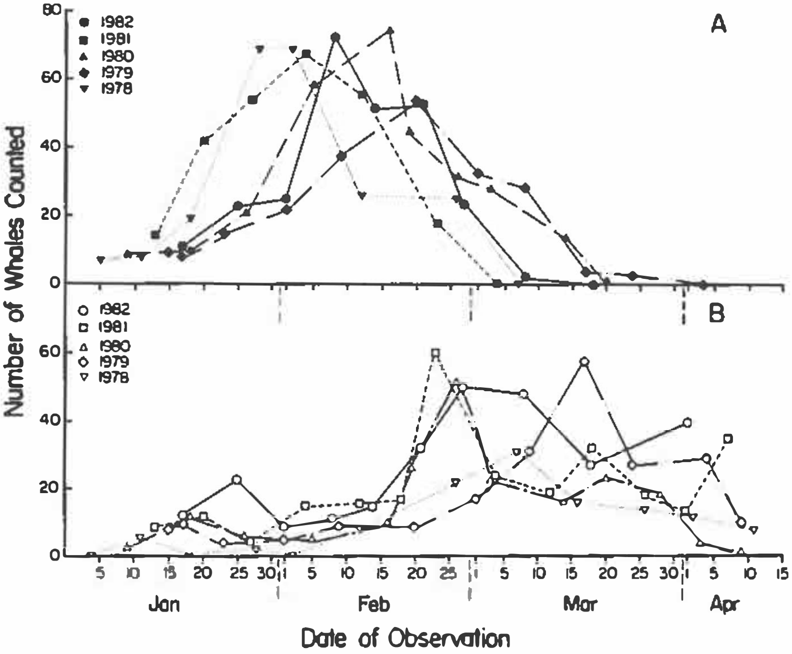

Fig. 8. *The number of single whales (A) and female–calf pairs (B) counted in 60 vessel transects of the middle lagoon between 1978 and 1982.*

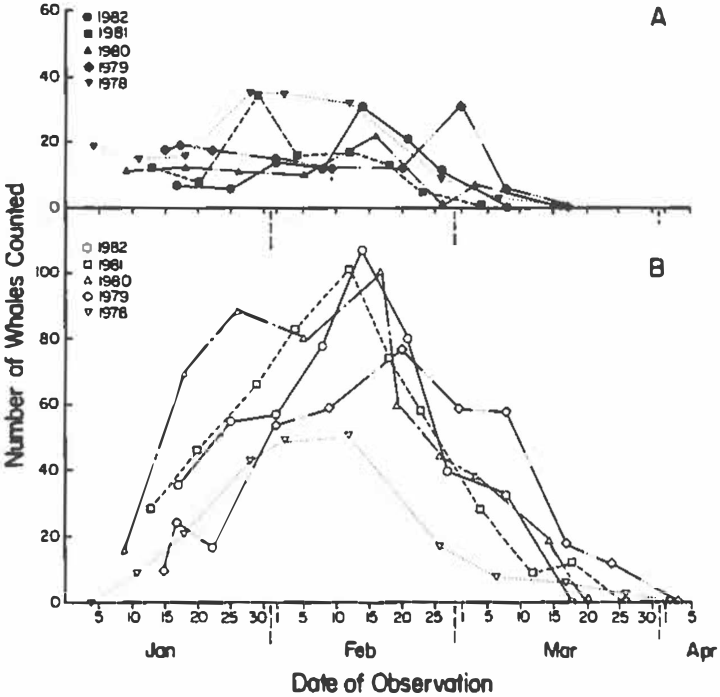

Fig. 9. *The number of single whales (A) and female–calf pairs (B) counted in 60 vessel transects of the upper lagoon between 1978 and 1982.*

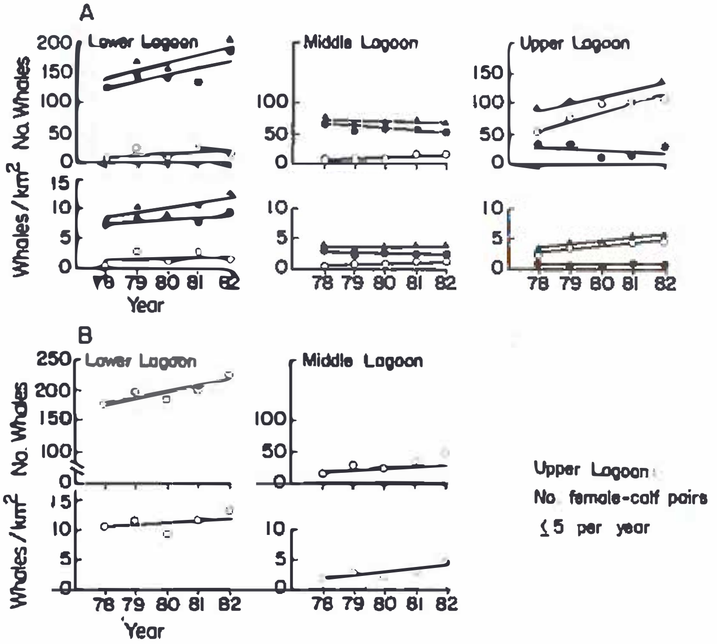

Fig. 10. *The abundance and density of whales in the lower, middle, and upper areas of Laguna San Ignacio between 1978 and 1982. Section A represents whale counts (top) and densities (bottom) on the date of the maximum combined count each year. Section B represents the female–calf count (top) and density (bottom) on the date of their maximum count each year. Triangles are combined counts (single whales + female–calf pairs), solid circles are single whales, and open circles are female–calf pairs. Black lines are least squares regression lines. Female–calf pairs were counted as two animals in density calculations.*

seen primarily as an increase in the use of the upper lagoon area, while whale abundance in the lower and middle areas remained relatively unchanged.

As with whale abundance, densities of whales in the lower and middle lagoon areas did not change significantly between 1978 and 1982, and averaged 10.29 and 3.42 whales/km² respectively. The density of whales in the upper lagoon, however, did increase significantly from 3.16 whales/km² in 1978 to 5.25 whales/km² in 1982 [$F_{(1,3)} = 27.14$, $p < .02$, $r^2 = 0.900$].

The densities of whales within each area by year and the results of the Kolmogorov–Smirnov comparisons and ANOVAs for significance of regression are presented in Table III. The abundance and densities of whales per lagoon area and the least squares regression lines are shown in Figure 10A.

At the maximum combined count, the percentage of the total whale population in the lagoon that was present in each area did not change significantly between 1978 and 1982. These percentages and the results of the G-tests for significant differences within each area among years are summarized in Table IV. The lower lagoon contained an average of 48.3 ± SE 5% of the population, the middle lagoon contained an average of 20 ± SE 3.7%, and the upper lagoon contained an average of 32 ± SE 2.5% of the

Table III
Densities of Gray Whales in the Three Lagoon Interior Areas and Inlet, 1978–1982

Lagoon area	Year	Maximum combined counts			Maximum[b] female–calf pair counts
		Total whales	Single whales	Female–calf[a] pairs	
Inlet (20.5 km²)	1980	7.75	6.68	1.07	12.29
Lower lagoon (17.5 km²)	1978	8.31	7.39	0.92	20.52
	1979	11.00	8.25	2.75	22.69
	1980	9.28	8.25	1.03	18.68
	1981	10.43	7.68	2.75	21.78
	1982	12.44	10.72	1.72	22.92
	$D_{(n)}$	0.044	0.053	0.099	0.019
	$p_{(D)}$	>.50	>.50	>.50	>.50
	F	4.28	3.43	0.51	0.39
	$p_{(F)}$	>.10	>.10	>.50	>.10
	r^2	.59	.53	.14	.11
Middle lagoon (22.9 km²)	1978	3.36	3.01	0.35	1.40
	1979	2.92	1.44	1.48	2.53
	1980	3.40	2.62	0.79	2.01
	1981	3.84	2.44	1.40	2.79
	1982	3.58	2.27	1.31	4.28
	$D_{(n)}$	0.033	0.055	0.134	0.143
	$p_{(D)}$	>.50	>.50	>.50	>.50
	F	1.95	0.00	2.44	11.88*
	$p_{(F)}$	>.25	>.99	>.25	<.05
	r^2	.39	.00	.45	.80
Upper lagoon (46.6 km²)	1978	3.15	0.79	2.36	0.30
	1979	3.20	0.66	2.53	0.00
	1980	4.50	0.21	4.29	0.00
	1981	4.70	0.36	4.33	0.30
	1982	5.25	0.66	4.59	1.42
	$D_{(n)}$	0.095	0.141	0.130	0.501
	$p_{(D)}$	>.50	>.50	>.50	>.50
	F	27.14*	0.25	14.59*	0.58
	$p_{(F)}$	<.02	>.50	<.05	>.50
	r^2	.90	.08	.83	.16

[a] Female–calf pairs were counted as two whales in densities.
[b] No single whales present.
[c] * = significant at $\alpha \leq 0.05$.

Table IV
Percentages of the Total Gray Whales in the Lagoon Areas Between 1978 and 1982

Lagoon area	Year	Maximum combined counts			Maximum female–calf pair counts
		Total adults	Single whales	Female–calf pairs	
Lower lagoon	1978	46	55	10	89
	1979	54	69	10	87
	1980	46	67	8	88
	1981	46	65	17	88
	1982	50	69	11	85
	$\bar{X} \pm$ SE	48 ± 5	65 ± 2	11 ± 1	87 ± 6
	G	1.04	2.17	3.87	0.10
	$P_{(G)}$	>.50	>.50	>.10	>.95
Middle lagoon	1978	24	29	6	9
	1979	16	16	9	13
	1980	21	28	7	12
	1981	21	27	11	9
	1982	17	20	11	15
	$\bar{X} \pm$ SE	20 ± 4	24 ± 2	9 ± 1	12 ± 1
	G	2.17	5.70	2.42	2.35
	$P_{(G)}$	>.50	>.10	>.50	>.50
Upper lagoon	1978	30	16	84	2
	1979	29	15	81	0
	1980	33	5	85	0
	1981	34	8	72	3
	1982	34	11	78	0
	$\bar{X} \pm$ SE	32 ± 2	11 ± 2	80 ± 2	1 ± 0.6
	G	.69	8.31	1.39	9.32
	$P_{(G)}$	>.90	>.05	>.50	>.05

population. Thus, despite the significant annual increase in the abundance of whales in the upper lagoon, the proportion of the total yearly population that utilized each section of the lagoon remained nearly constant.

Following the maximum combined count each year, single whale abundance declined in all areas (see Single Whales), while female–calf pair abundance continued to increase, resulting in a second smaller peak in abundance around March 19, the minor mode of the population curves. At this time, the lagoon was occupied entirely by female–calf pairs (see Female and Calf Pairs).

Single Whales. Each year single whale counts increased rapidly during the 6-week period approximately from the last week in December through the second week in

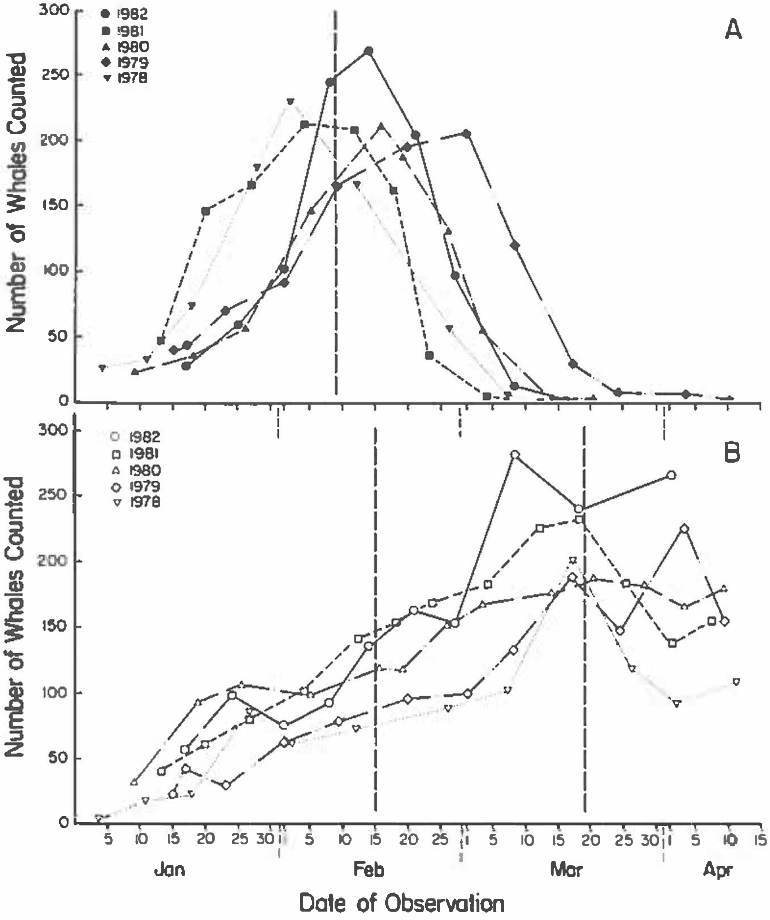

Fig. 11. *The number of single whales (A) and female–calf pairs (B) counted in 60 vessel transects of Laguna San Ignacio between 1978 and 1982. Broken vertical lines indicate the mean date of the maximum single whale counts on February 9 (A), the female–calf counts at the end of the birth period on February 15, and the mean date of maximum female–calf pair counts on March 19 (B).*

February (Fig. 11A). During our earliest census on December 26, 1977, five single whales or 2% of the eventual maximum single whale count for that year were already present. Single whale counts reached 50% of their eventual maximums as early as January 17 in 1981 and as late as February 2 in 1979 and 1982, with a mean date of January 27 ± SE 3 days.

The maximum single whale counts each year occurred on the same day as the combined maximum count; the average date of maximum single whale counts for all years was February 15 ± SE 3.9 days, with a range from February 2 in 1978 to March 1 in 1979 (Fig. 4). Both of these dates fell outside the 21-day 95% confidence interval for the mean date. Maximum single whale counts ranged from a low of 207 animals on February 12, 1981 to a high of 270 whales on February 14, 1982, with a mean maximum count of 227 whales. The slope of the exponential regression line fitted to these counts for all years indicated a 2.7% per year increase in single whale maximum counts, but this slope was not significantly different from 0, indicating there was no significant change in the abundance of single whales over the 5 years [$F_{(1,3)} = 0.516$, $p > .50$, $r^2 = .147$] (Fig. 6). Following peak abundance, single whale counts rapidly declined to 50% of their maximum counts on dates which ranged from February 19 in 1978 to March 11 in 1979, with a mean date of February 27 ± SE 3 days. Single whale counts had dropped further to 2–4% of their maximums as early as March 4 in 1981 and as late as March 24 in 1979, with a mean date of March 11 ± SE 3 days.

The duration of the single whale season was defined as the time elapsed between the first and last sighting of a single whale during the boat transects each year. We assumed that the single whale season began on December 26 each year (see p. 325). The weekly counts were scaled so that December 26 was equal to day one each year, rather than the calendar date.

Single whale seasons ranged from 76 days in 1981 to 104 days in 1979 with a mean duration of season of 84 days, and a 95% confidence interval of 72 to 97 days (Table V). Only the 1979 season of 104 days was significantly different from the mean length of season. That year, approximately seven whales, 3% of the maximum single whale count, remained in the lagoon 20 days longer than the overall mean season length. The mean length of the season for the four similar years was 79 ± SE 2.9 days, with a range of 6 days among years. The last day that single whales were counted in the boat transects ranged from March 12 in 1981 to April 9 in 1979 (Fig. 11). In summary, the length of the single whale season in Laguna San Ignacio averaged 11 weeks for the four similar years, but was 14.8 weeks in 1979.

To evaluate shifts in the timing of the single whale seasons, we calculated the mean day and its accompanying variance for each year and compared these among years (Reilly, 1981) (Table V). The mean day $\bar{j}$ is expressed as

$$\mu = \bar{j} = \frac{\Sigma j f_j}{n} \tag{4}$$

Table V
Summary of the Single Whale Seasonal Occupation of Laguna San Ignacio Between 1978 and 1982

Year	Number of transects	Maximum count day[a]	Duration of season	Mean day[a]	Variance of mean
1978	8	Feb 2	81	Feb 1	154.01
1979	9	Mar 1	104	Feb 16	292.74
1980	9	Feb 16	78	Feb 13	155.42
1981	12	Feb 12	76	Feb 4	130.68
1982	8	Feb 14	82	Feb 12	101.02
Average		Feb 15	84	Feb 9	

[a] Maximum count and mean days are scaled so that December 26 = day 1.

where $\bar{j}$ = the day of the season expressed with December 26 = day 1, f_j = the single whale count (as a proportion of the total count for the year), and n = the total number of days. The variance, (σ^2), is

$$\sigma^2 = \frac{\Sigma j f_j^2 - \dfrac{(\Sigma j f_j)^2}{n}}{n - 1} \qquad (5)$$

The mean days ranged from February 1 in 1978 to February 16 in 1979. A Bartlett's test indicated that the variances for each year were homoscedastic [$B_c = 2.71$, $p = .61$], and the ANOVA indicated the means were not significantly different [$F_{(4,39)} = 2.07$, $p < .05$], permitting the calculation of a pooled mean for all years of February 9. The 95% confidence interval for this pooled mean was 14 days, from February 2 to 16. The February 1, 1978 mean day was the only date to fall outside this confidence interval. The greatest shift in timing of the single whale season was 15 days between February 1, 1978 and February 16, 1979.

The seasonal distribution of single whales in the lower, middle, and upper lagoon areas between 1978 and 1982 are shown in Figs. 7A, 8A, and 9A. At their maximum counts, single whale abundance was not the same in the three lagoon locations [Kruskal–Wallis test: $X^2_{(4)} = 12.00$, $p < .01$]. Multiple comparison tests at $\alpha = .05$ confirmed that the abundance was unique in each area; moreover, counts of single whales were heterogeneous within each area over the 5 years, but did not show a significant increase or decrease. The G-tests of equality of abundance and ANOVAs for significance of regression in each area among years are summarized in Table II.

Single whales were most abundant in the lower lagoon, where their counts were different each year [$G = 13.61 > X^2_{.05(4)} = 9.49$, $p < .01$]. Maximum counts in the lower lagoon increased 6.7% per year from 129 in 1978 to 187 in 1982 (Fig. 7A); however, this increase was not statistically significant [$F_{(1,3)} = 3.43$, $p > .10$, $r^2 = .533$] (Fig. 10A, top).

Maximum counts of single whales in the middle lagoon were also significantly different each year [$G = 14.11 > X^2_{.05(4)} = 9.49$, $p < .01$] (Fig. 8A). The slope of the regression line fitted to these counts indicated a nonsignificant 5.3% per year decrease [$F_{(1,3)} = 3.90$, $p > .10$, $r^2 = .565$] (Fig. 10A, top).

Finally, single whales were least abundant in the upper lagoon nursery area where their counts were significantly different each year [$G = 22.24 > X^2_{.05(4)} = 9.49$, $p < .05$] (Fig. 9A).

In general, single whale maximum counts were heterogeneous in all areas in all years, and their slight increase in the lower lagoon and decrease in the middle and upper lagoon areas were not significant.

The density of single whales was homogeneous within each section of the lagoon; thus, the five yearly densities were pooled and a mean density calculated for each area (Table III). In the lower lagoon, single whale density averaged 8.46 ± SE 0.53 whales/km^2, in the middle lagoon it averaged 2.36 ± SE 0.23 whales/km^2, and in the upper lagoon single whales were least dense averaging 0.54 ± SE 0.09 whales/km^2 (Fig. 10A, bottom).

The Kruskal–Wallis test revealed that the proportion of single whales among areas was significantly different [$X^2_{(2)} = 12.29$, $p < .01$]. Single whales were distributed in a gradient each year being most abundant in the lower lagoon nearest the inlet and becoming less abundant toward the upper lagoon. As would be expected, since there were no significant changes in single whale abundance or density within each area during the 5 years, a G-test of the proportions of the total single whales that were within each area did not indicate any significant changes. An average of 65 ± SE 2% of the single whale population was in the lower lagoon, 24 ± SE 2% was in the middle lagoon, and 11 ± SE 2% was in the upper lagoon (Table IV).

In summary, the distribution of single whales at their maximum counts analyzed as abundance, density, and proportion of whales in each area did not change significantly between 1978 and 1982.

Female and Calf Pairs. The pattern of abundance and distribution of female–calf pairs in Laguna San Ignacio was more complex than that of single whales. Counts of female–calf pairs increased continuously between early January and late March or early April in all years (Fig. 11B). However, following approximately mid-February, the increase was not caused by continued births; rather, late season calves were judged by their size, color, and degree of barnacle infestation to be at least 1.5 to 3.0 months old. For this reason, the analysis of female–calf pairs was conducted in two stages.

The first stage was the time during which most births occurred and females with newborn calves occupied the lagoon. It is believed that most gray whale births occur during a period of at least 66 days from December 26 to March 1 (Swartz and Jones, 1983) with a mean birth date of about January 27, and that the majority of births have taken place by February 15 (Rice *et al.*, 1981). During 6 years we observed only two newborn calves after February 15; therefore, we assumed that late births were relatively rare events and that February 15 was best representative of the date by which a high percentage of the births had taken place. Counts of female–calf pairs on February 15 were used to estimate the number of females using Laguna San Ignacio as a nursery for newborn calves.

The second part of the analysis was the time of maximum female–calf pair counts. The increase in the number of female–calf pairs that utilized the lagoon after the birth period was representative of the number of whales that used the lagoon as a staging area (see below).

The Birth Period. The seasonal distributions of females with calves from January 4 to February 15 between 1978 and 1982 are shown in Fig. 11B. The number of female–calf pairs that occupied Laguna San Ignacio on February 15, the end of the birth period, increased significantly each winter. Female and calf counts rose from 81 pairs in 1978 to 137 pairs in 1982, a significant increase of 14.3% per year [$F_{(1,3)} = 33.56$, $p < .025$, $r^2 = .914$] (Fig. 12).

The significant increase in the number of female–calf pairs was accompanied by a significant increase in their abundance in one of the three lagoon areas. The seasonal distribution of females and calves in the lower, middle, and upper lagoon are shown in

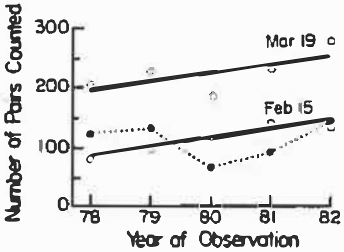

Fig. 12. *A comparison of the maximum female–calf pair counts (average date of March 19) and February 15 female–calf pair counts between 1978 and 1982 (open circles). Closed circles are the differences between these counts and represent minimum estimates of whales utilizing the lagoon as a staging area. Fitted lines are least square regression lines.*

Figures 7B, 8B, and 9B. A Kruskal–Wallis test revealed that the female–calf pair abundance was not the same in all three areas $[X^2_{(2)} = 9.555, p < .01]$; abundance in the upper and lower, and upper and middle lagoon areas was significantly different, but in the lower and middle lagoon it was not significantly different.

In all years, females with newborn calves were least numerous in the lower lagoon nearest the inlet. Counts were generally low, ranging from 8 pairs in 1978 to 24 pairs in 1979 and 1981, and were significantly different $[G = 15.54 > X^2_{.05(4)} = 9.49, p < .001]$ (Table II). The slope of the least squares regression line fitted to these counts indicated that female–calf pairs increased 32.2% per year, but this trend was not statistically significant $[F_{(1,3)} = 1.57, p > .10, r^2 = 0.345]$ (Fig. 10A, top).

Counts of female–calf pairs in the middle lagoon were also significantly different among years $[G = 11.76 > X^2_{.05(4)} = 9.49, p < .025]$ (Table II), but their 25.8% per year increase was not significant $[F_{(1,3)} = 2.43, p > .05, r^2 = .448]$ (Fig. 10A, top).

The increase in the annual female–calf pair counts was seen primarily as a significant positive rate of increase in their numbers in the upper lagoon nursery (Table II). Counts in this area were different each year $[G = 31.61 > X^2_{.05(4)} = 9.49, p < .001]$ increasing significantly 16.2% per year from 55 pairs in 1978 to 107 pairs in 1982 $[F_{(1,3)} = 14.96, p < .05, r^2 = .833]$ (Fig. 10A, top).

The densities of female and calf pairs within each area and the values for the Kolmogorov–Smirnov tests and ANOVAs are presented in Table II. Densities of female–calf pairs in the lower and middle lagoon did not change significantly among years and averaged 9.83 ± SE 0.72 and 1.06 ± SE 0.17 whales/km^2 respectively (Fig. 10A, bottom). For the upper lagoon, the Kolmogorov–Smirnov test suggested that the differences in whale densities among years were nonsignificant; nevertheless, the ANOVA for the least squares regression analysis of density showed that the steady increase in density from 2.36 whales/km^2 in 1978 to 4.59 whales/km^2 in 1982 was statistically significant $[F_{(1,3)} = 14.59, p < .05, r^2 = .829]$ (Fig. 10A, bottom). The conflicting results of the Kolmogrov–Smirnov test and the ANOVA can best be explained by the fact that the regression analysis is sensitive to the small but steady increase in density from year to year.

On February 15 each year, female–calf pairs were concentrated in the upper lagoon nursery area and became less abundant toward the inlet. In addition, the percentage of the total female–calf pairs in the lagoon that occupied each area remained essentially the same each year (Table IV). The percentage of female–calf pairs was smallest in the lower lagoon where they averaged 11 ± SE 2% of the total, the middle lagoon contained an average of 9 ± SE 9%, and the upper lagoon had the highest percentage of female–calf pairs, averaging 80 ± SE 2%. Although the number of female–calf pairs utilizing the upper lagoon increased significantly, the proportion of the population utilizing this area remained the same each year.

Maximum Female–Calf Pair Counts. The maximum count of female–calf pairs occurred late each season following the departure of single whales from the lagoon. After February 15, females and calves continued to increase steadily to their maximum counts that occurred as early as March 2 in 1982 and as late as April 3 in 1979, with a mean date of March 19 (Fig. 11B). The maximum counts increased approximately 6.9% per year from 202 pairs in 1978 to 281 pairs in 1982; however, this increase was not statistically significant [$F_{(1,3)} = 2.69$, $p > .25$, $r^2 = .473$] (Fig. 12).

To determine the degree to which Laguna San Ignacio was utilized as a staging area, we fitted a least squares regression line to the annual February 15 counts and the annual maximum female–calf counts and compared their slopes and elevations. There was no significant difference between the slopes of the lines [$t_{(6)} = 0.058$, $p > .80$], but the elevations were significantly different [$t_{(6)} = 13.17$, $p << .001$]. The difference between the elevations of the lines averaged 110 ± SE 0.7 female–calf pairs and represented a minimum estimate of the number of female–calf pairs that were gathering at Laguna San Ignacio late in the season and using it as a staging area. The maximum counts, the February 15 counts, and the difference between them are plotted in Fig. 12. The average difference was 111 ± SE 12 female–calf pairs and ranged from 67 in 1980 to 144 female–calf pairs in 1982. As mentioned previously, this late season increase included older calves and not newborn animals.

Following the combined maximum counts, single whales began to decrease and averaged only 3% of their maximum count by March 14. As the single whales departed, the female–calf pairs continued to increase and gradually shifted their distribution to the lower and middle lagoon (Figs. 7B and 8B); they were seen only rarely in the upper lagoon nursery after the third week in March (Fig. 9B). At their maximum counts, the abundance of females and calves was not the same in all three areas [Kruskal–Wallis test: $X^2_{(2)} = 10.86$, $p < .005$]. The multiple comparison tests of equality of abundance among years indicated that the lower and upper, and lower and middle lagoon areas were significantly different from each other, while the middle and upper areas were not significantly different.

In all years, females and calves were most abundant in the lower lagoon where their counts averaged 186 ± SE 6 pairs and did not change significantly (Table II; Fig. 10B, top).

In the middle lagoon, the number of female–calf pairs was significantly different each year [$G = 19.90 > X^2_{.05(4)} = 9.49$, $p < .001$], and their counts increased significantly 22.9% per year from 16 pairs in 1978 to 49 pairs in 1982 [$F_{(1,3)} = 11.80$, $p < .05$, $r^2 = .797$] (Table II; Fig. 10B, top).

Female–calf pairs were least abundant in the upper lagoon nursery area in late March each year (Fig. 9B). Here, counts ranged from no whales in 2 years to 33 pairs in 1982, and were significantly different each year [$G = 74.59 > X^2_{.05(4)} = 9.49$, $p < .001$] (Table II; Fig. 10B, top). The slope of the regression line fitted to the upper lagoon counts was not significantly different from zero [$F_{(1,3)} = 1.44$, $p > .50$, $r^2 = .324$].

Densities of female–calf pairs in the lower and upper lagoon areas did not change significantly between 1978 and 1982, averaging 21.3 ± SE 0.7 whales/km^2 and 0.4 ± SE 0.2 whales/km^2 respectively (Table II; Fig. 10B, bottom). As would be expected from the significant increase in abundance of female–calf pairs in the middle lagoon, the density of these whales also increased significantly in this area from 1.4 whales/km^2 in 1978 to 4.28 whales/km^2 in 1982 [$F_{(1,3)} = 11.88$, $p < .05$, $r^2 = .80$].

The percentage of the female and calf population in the lagoon that was in each area remained essentially the same (Table IV). The lower lagoon averaged 87.4 ± SE 6.0%, the middle lagoon contained 11.6 ± SE 1%, and the upper lagoon averaged 1.0 ± SE 0.6% of the population each year.

To summarize, at their maximum counts, female calf pairs were distributed in a gradient being most dense in the lower lagoon near the inlet and becoming less dense with increasing distance from the inlet. This gradient was consistent each year, as the abundance of female–calf pairs in each area and the percentage of the lagoon female–calf pair population that utilized each area remained the same.

Female and calf counts generally declined after mid-March, although a substantial number of female–calf pairs remained in the lagoon at the termination of our field work each April. The percentage of the maximum female–calf pair count remaining in the lagoon at the last transect each winter was 53% in 1978, 68% in 1979, 96% in 1980, 66% in 1981, and 96% in 1982.

Time limitations of field studies prevented us from documenting the entire female–calf pair occupation of the lagoon. Therefore, to estimate their minimum abundance and duration of season, we utilized late April and early May sightings of whales reported by other observers. J. Harvey and B. R. Mate (personal communication) reported that 25–35 female–calf pairs remained in Laguna San Ignacio and that an unknown number were outside the lagoon inlet in the breakers on April 26, 1980. In addition, Storro-Patterson (1982) reported that a few (no number specified) females and calves remained in the inlet in early May; and Mexican fishermen (Abreojos Fishing Cooperative, personal communication) indicated that gray whales could be found outside the lagoon in the inlet as late as early June of some years. The earliest arrival of female–calf pairs in Laguna San Ignacio during our study was December 26. The combination of our early season observations with these late season sightings yielded an estimate of a 4- to 4.5-month (16- to 18-week) duration of season for female–calf pairs in Laguna San Ignacio. This was 1–1.5 months longer than single whales that arrived at approximately the same time, but departed from the lagoon by mid-March.

Table VI

Summary of Length Measurements and Sex Composition of Dead Gray Whale Calves in Four Breeding Areas, 1954–1983

		Number of calves		Body length (m)		Sex			
Location	Year	Total	Number measured	$\bar{X}$ ± SE	Range	M	F	?	Reference
Laguna San Ignacio	1977	4	4	4.56 ± 0.13	4.40–5.00	—	—	4	Swartz and Cummings (1978)
	1978	5	4	4.45 ± 0.12	4.10–4.80	1	3	1	Swartz and Jones (1979)
	1979	4	3	4.63 ± 0.14	4.42–4.98	2	1	1	Swartz and Jones (1980)
	1980	4	4	4.87 ± 0.14	4.40–5.10	4	0	0	This chapter
	1981	4	4	4.43 ± 0.22	4.04–5.16	3	1	0	Swartz and Jones (1981)
	1982	4	4	4.20 ± 0.22	3.84–4.95	2	2	0	This chapter
	1983	9	6	4.42 ± 0.29	3.76–5.94	5	2	2	Dahlheim (1983)
	Total	34	29	$\bar{X}_p$ = 4.47 ± 0.09					
Laguna Ojo de Liebre	1954–57	12	7	4.05 ± 0.14	3.54–4.51	2	—	10	Gilmore (1960)
	1962	6	6	4.68 ± 0.19	3.95–5.40	4	2	0	Eberhardt and Norris (1964)
	1975	20	13	4.54 ± 0.10[a]	3.96–5.05	5	8	7	White and Griese (1978)
	1979	4	4	4.47 ± 0.16	4.00–4.88	1	2	1	D. W. Rice (personal communication)
	1980	12	8	4.30 ± 0.09	3.84–4.60	3	3	2	Rice *et al.* (1981)
	1982	10	10	4.31 ± 0.15	3.45–4.94	4	3	3	Fleischer *et al.* (1983)
	1983	12	7	4.48 ± 0.18	4.00–5.47	7	3	2	Fleischer *et al.* (1983)
	Total	76	55	$\bar{X}_p$ = 4.40 ± 0.05					
Isla Arena[b]	1980	20	0	— —	—	—	—	20	Chapter 15, this volume
	1981	10	10	4.46 ± 0.13	3.76–5.05	5	1	4	Bryant *et al.* (1981), Chapter 15, this volume
	1982	20	18	4.42 ± 0.15	3.5–6.4	3	1	16	Bryant and Lafferty (1982), Chapter 15, this volume
	1983	2	1	4.37 —	—	[illegible]	2	0	Fleischer *et al.* (1983)
	Total	52	29	$\bar{X}_p$ = 4.43 ± 0.10					
Laguna Guerrero Negro	1980	7	2	3.77 ± 0.23	—	—	2	5	Bryant (1980), Chapter 15, this volume
	1981	4	4	4.49 ± 0.13	4.27–4.95	2	2	0	Bryant *et al.* (1981), Chapter 15, this volume
	1982	2	2	3.85 ± 0.11	3.7–4.0	1	—	1	Fleischer *et al.* (1983)
	1983	1	1	3.90 —	—	0	1	0	Fleischer *et al.* (1983)
	Total	14	9	$\bar{X}_p$ = 4.13 ± 0.13					
Boca de Soledad	1982	6	4	4.50 ± 0.16	4.13–4.92	1	3	2	Lawson (1983)
				Grand $\bar{X}$ = 4.43 ± 0.06	Σ =	55	42	81	

[a] Individual lengths were not reported; mean length was used in the calculation of the pooled mean.

[b] Isla Arena separates the inlets of Guerrero Negro and Ojo de Liebre lagoons.

MORTALITY

The basic unit of the mortality section is the Laguna San Ignacio data from 1977 to 1982. In brief, we give a general account of mortality and then examine four aspects of mortality, (1) the number of dead whales, (2) whale lengths, (3) age class composition, and (4) the calf mortality rate. In addition, data on natural mortality from 1954 to 1983 which were available for Laguna Guerrero Negro, Laguna Ojo de Liebre, and the Boca de Soledad area of the Bahia Magdalena complex are compared and integrated with the Laguna San Ignacio information to determine (1) the age class composition of dead whales, (2) the proportion of carcasses in each age class among years, (3) the mean length of dead calves for comparison with the length of near-term fetuses, and (4) the sex ratio of calves and all whales combined. A summary of calf mortality is presented in Table VI, and immature and adult mortality is shown in Table VII.

Age frequencies were determined by grouping the carcasses into three broadly defined categories—calves, immatures, and adults. Animals between 3 and 8.99 m were considered to be calves of the year, those measuring 9–10.99 m were regarded as immatures, and whales 11 m and larger were classified as adults (based on Rice and Wolman, 1971; Zimushko and Ivashin, 1980; and Chapter 21, this volume).

Table VII
Summary of Length Measurements and Sex Composition of Dead Immature and Adult Gray Whales in Three Breeding Areas[a]

Location	Dates of observations	Dates of sighting	Age[b] class	Length (m)	Sex[c]	Source
Laguna San Ignacio	1977–1983	1978	I	8.41	M	Swartz and Jones (1979)
		1978	A	13.80	U	Swartz and Jones (1979)
		1979	I	10.40	U	Swartz and Jones (1980)
		1980	I	8.00	U	This chapter
		1980	I	7.40	U	This chapter
		1981	I	7.51	U	Swartz and Jones (1981)
		1981	I	7.50	U	Swartz and Jones (1981)
		1983	I	10.41	F	Dahlheim (1983)
Laguna Ojo de Liebre	1980, 1982, 1983	1980	A	—	U	Bryant (1980)
		1982	I	7.82	U	Fleischer *et al.* (1983)
		1982	A	11.00	U	Fleischer *et al.* (1983)
		1983	I	—	U	Fleischer *et al.* (1983)
Isla Arena[d]	1980–1983	1980	A	—	U	Bryant (1980)
		1982	A	—	U	Bryant and Lafferty (1982)
		1983	A	11.00	F	Fleischer *et al.* (1983)
Laguna Guerrero Negro	1980–1983	1980	I	8.4	M	Bryant (1980)

[a] No dead immature or adult gray whales were sighted in Boca de Soledad in 1982.
[b] A = adult, I = immature.
[c] M = male, F = female, and U = sex unknown.
[d] Isla Arena separates the inlets of Guerrero Negro and Laguna Ojo de Liebre lagoons.

Thirty-two recently dead gray whales including 25 calves, 6 immatures, and 1 adult were examined in Laguna San Ignacio. The cause of death was not determined for any of these whales; however, it appeared that one immature died as the result of a killer whale (*Orcinus orca*) attack and that many calves were stillborn or had died shortly after birth as evidenced by intact umbilical cords or bleeding umbilical wounds that had not healed prior to death. In addition, the 23 calves that were discovered in January and February lacked epizoic barnacles compared to 2 stranded calves discovered in March which possessed these parasites.

The minimum calf mortality rate for each 97-day season in Laguna San Ignacio from 1978 to 1982 was estimated by dividing the number of dead calves discovered per season by the estimated gross calf production per season (i.e., the number of living calves at the maximum combined count + the number of dead calves per season) (Caughley, 1966, 1977). The calf mortality rate was 5.81% in 1978, 4.00% in 1979, 3.25% in 1980, 2.78% in 1981, and 2.84% in 1982.

The average, minimum, calf mortality rate for the 5-year period was calculated as the sum of the dead calves discovered in all years divided by the sum of the estimated gross production for all 5 years, or

$$\frac{21}{573 + 21} \approx 0.0354 \tag{6}$$

A G-test indicated that the seasonal calf mortality rates were not significantly different from the mean rate for all five seasons [$G_{(4)} = 3.67 < X^2_{.05(4)} = 9.49$, $p > .25$].

To determine whether the number of dead calves, immatures, and adults discovered per year in Laguna San Ignacio was the same over the 5 years, each age category was tested for heterogeneity by computing a G-statistic of the difference between the observed mortality per year and the mean number of carcasses per class. All categories were homogenous among years; the number of dead calves ranged from 4 to 5 per year and averaged 4.17 whales per year [$G = 0.15 < X^2_{.05(4)} = 9.49$, $p > .99$] (Table VI). The number of immatures ranged from 0 to 2 per year with a mean of 0.67 whales per year [$G = 1.64 < X^2_{.05} = 9.49$, $p > .75$]. And finally, the number of dead adults ranged from 0 to 1 with a mean of 0.17 whales per year [$G = 3.49 < X^2_{.05(4)} = 9.49$, $p > .10$] (Table VII). Because the frequency of carcasses within each category was not significantly different during the 5 years, we pooled the frequencies per class, and calculated the percentage of the total sample that was in each age class. Seventy-eight percent were calves, 19.5% were immatures, and 2.5% were adults.

In order to compare age class frequencies of dead whales from different breeding areas in which there was unequal search effort within years, we converted the total number of whales in each category to a percent of the total number of whales counted in each area. For each age class, we pooled the percentages from all areas, including Laguna San Ignacio, and calculated a mean percentage. These means were used as the expected frequencies in three separate G-tests of the null hypothesis of equality between the mean proportion and the observed proportion per class for each area. The percentages of calves among areas were homogeneous, ranging from 78 to 100% with a mean of 91.4% [$G = 3.13 < X^2_{.05(4)} = 9.49$, $p > .50$]. The percentages of immatures, however, were significantly different in each area, and ranged from 0 to 19.5% [$G = 42.07 > X^2_{.05(4)} = 9.49$, $p < .001$]. The percentages of dead adults were also significantly different in each area, ranging from 0 to 5% [$G = 12.73 > X^2_{.05(4)} = 9.49$, $p < .025$]. Due to the small sample sizes for dead immatures and adults, these estimates may not be representative.

Sex was determined for 101 of the 194 dead gray whales reported from all the lagoons. These included 57 males and 44 females (Tables VI and VII). The sex ratio of calves, immatures, and adult whales combined was 56.4% males to 43.6% females. A G-test with a William's correction (Sokal and Rohlf, 1981) indicated that the observed ratio of dead male to female whales was not significantly different from 1:1. Here, the expected sex ratio was 1:1, as reported by Rice and Wolman (1971, p. 118).

To determine whether male and female calves died in equal numbers, we tested for a difference in the sex ratio of these animals. Of the 125 calves from all areas combined, sex was determined for 97. The ratio of 55 males (56.7%) to 42 females (43.3%) was not significantly different from unity [$G_{adj}(1) = 1.747 < X^2_{.05(1)} = 3.841$, $.10 < p < .20$]. This suggests that the slight preponderance of male calves was not indicative of differential mortality between the sexes.

Sample sizes of the immature and adult age classes were too small to evaluate the significance of their observed sex ratios.

A Bartlett's test for homoscedasticity of calf carcass lengths for samples among years from Laguna San Ignacio between 1977 and 1983 indicated that the variances were not significantly different [$B_c = 6.99 < X^2_{.05(6)} = 12.59$, $p = .32$]. The ANOVA disclosed that the mean lengths for each year were also not significantly different [$F_{(6,22)} = 0.866 < F_{.05(6,22)} = 2.55$, $p = .53$]. This permitted the calculation of a pooled mean for calf carcass lengths in Laguna San Ignacio which was 4.47 ± SE 0.086 m. The mean calf lengths per year are shown in Table VI.

The lengths of dead whales in different breeding areas were tested for significant differences. A Bartlett's test revealed that the samples from each breeding area were highly heteroscedastic [$B_{(c)} = 200 >> X^2_{.05(4)} = 12.59$, $p < .001$]; but, the Kruskal–Wallis test of the null hypothesis that the "location" of the sample populations were the same was not rejected. Therefore, we concluded that the lengths of the dead calves from each area were not significantly different [$H_c = 4.79 < X^2_{.05(4)} = 9.49$, $p > .25$]. The grand mean of the lengths of dead calves for all areas was 4.43 ± SE 0.06 m.

The lengths of dead calves have been used as indicators of gray whale calf length at birth (Rice and Wolman, 1971; Rice *et al.*, 1981; Rice, 1983). To determine the validity of extrapolating the mean length of calves at birth from dead calf data, we compared the lengths of dead calves reported from the lagoons to lengths of near-term fetuses.

The series of length measurements for near-term fetuses reported by Rice and Wolman (1971) was the only sample presently available that was large enough to provide statistically reliable data for comparison with the sample of length measurements of recently born, dead calves from the breeding lagoons. Other data on lengths of near-term fetuses taken from females in the Korean or California populations were reported by Scammon (1874), Townsend (1887), Andrews (1914), Risting (1928) and Mizue (1951). These accounts, however, were of limited use because many of the calf lengths were estimated and not actually measured, ranges of lengths were often given rather than individual lengths, and the collection dates of individual whales were frequently not reported.

Rice and Wolman (1971) measured 55 near-term fetuses taken from female gray whales collected off San Francisco during a 38-day period from December 15 to January 20 from 1959 to 1969. These ranged in length from 3.60 to 5.31 m with a mean of 4.62 ± SE 0.007 m. To ascertain whether the "location" of the calf lengths from the lagoons was significantly different from the length of near-term fetuses, we tested the null hypothesis that the lengths of dead gray whale calves in the southern range were greater than or equal to the length of near-term fetuses collected during migration. A one-tailed Mann–Whitney U-test failed to accept the null hypothesis $[Z = 3.819 > t_{.05(1),\infty} = 1.96, p < .005]$. Therefore, we concluded that the mean length of 4.43 m for dead neonates from the southern range in January and February was highly significantly smaller than the mean length of 4.62 m for near-term fetuses collected during migration.

Seven (78%) of the nine immature whales measured in three breeding areas fell into the yearling (8.2 to 9.6 m) age category, suggesting that next to calves, yearlings had the second highest mortality rate. The lengths of immatures ranged from 7.4 to 10.41 m with a mean length of 8.20 ± SE 0.43 m (Table VII).

The analysis of the lengths of some immatures was problematic. According to Rice and Wolman (1971), Zimushko and Ivashin (1980), and Blokhin (Chapter 21, this volume), the length of a gray whale at 1 year of age should range from 8.2 to 9.6 m; but, four of the seven dead immatures in Laguna San Ignacio were too small to be classified as yearlings and two were too large to be classified as calves of the year (>7.3m). All of these carcasses were infested with adult barnacles, further suggesting they were yearlings, as newborn calves do not develop adult parasites while in the breeding lagoons.

Only one dead adult whale was discovered in the lagoon. In addition to the whale mortality in Laguna San Ignacio, five adult and three immature carcasses were reported from other lagoon areas, and all are summarized in Table VII. Sample sizes of these whales were too small for statistical comparisons.

WHALE-WATCHING ACTIVITIES

Nature of Human Activities

Human activities within Laguna San Ignacio during the winter included local fishing, U.S. based overland and seagoing commercial whale-watching excursions, and visitation in private yachts.

Local Mexican fishermen operated 4- to 6-m fiberglass and wood pongas powered by 40- to 65-hp outboard engines throughout each winter, but their numbers and working days fluctuated with the condition of the fisheries and the weather. During the winters of 1978 and 1979, six to eight pongas operated approximately 5 days each week in the lower lagoon. Following the designation of the lagoon as a refuge in 1979, only three pongas operated in the lower lagoon between 1980 and 1981. In 1982, again only three pongas regularly operated in the lower lagoon; however, between 15 and 18 pongas with hooka-assisted divers operated in the middle and upper lagoon areas in response to an emergent bay-scallop (*Pectin* sp.) fishery in the shallow eelgrass beds north of Punta Piedra.

Individuals aboard private yachts continued to visit the lagoon following its designation as a refuge, averaging six visits each winter lasting from 1 to 10 days each.

Between 1977 and 1979, three or four land-based whale-watching excursions visited Laguna San Ignacio, but these companies ceased operation when the refuge was established in 1979 because the regulations prevented their access to the lower lagoon whale-watching area which can only be reached by boat.

Seagoing whale-watching excursions based in San Diego, California accounted for 90% or more of the human activities within the lagoon each winter. These excursions were conducted aboard 100-ton vessels that carried an average of 25 passengers each and typically spent 2½ days (3 days and 2 nights) or approximately 60 hr in the lagoon each visit. These vessels are powered by two or three diesel engines (V-12 to V-16, 550 to 965 hp range) with two 60- to 100-kW diesel generators (Fig. 13). During a typical visit to the lagoon, these vessels were underway with their main engines running approximately 1.5 hr (2% of 60 hr) and moved around the lagoon at speeds between 5 and 8

Fig. 13. *Typical whale-watching excursion vessel in Laguna San Ignacio. Note gray whale spyhopping in foreground.*

knots; total running time within the lagoon included entry (30 min), at least one change of anchorage (30 min), and their departure (30 min). The remainder of the time (97.5% of 60 hr) these vessels were at anchor with only their power generators operating. While underway they produced broadband waterborne noise ranging from 125 Hz to 20 kHz at source levels ranging from 124 to 170 dB *re.* μPa at 1 m depending upon hull construction and engine type (Dahlheim, 1984; Chapter 22, this volume).

Each excursion vessel launched three or four inflatable, wooden, or aluminum 4- to 5-m skiffs powered by 20-hp outboard engines to take their passengers whale watching and to visit various places of interest within the lagoon. These skiffs normally operated 8 hr per day between 07:00 and 16:00 hr for approximately 24 running hr per visit (40% of 60 hr); during the remaining 36 hr the skiffs were not in operation. Besides the presence of vessels at anchor (generators on), whales did not have to contend with skiff activity at night. Therefore, whales were followed less than 50% of the day. While whale watching at idle speeds, skiff waterborne noise source levels ranged from 75 to 120 dB *re.* μPa at 1 m, and while motoring at half throttle, source levels ranged from 105 to 120 dB *re.* μPa at 1 m (Dahlheim, 1984; Chapter 22, this volume).

Whale-Watching Excursion Visitation

The number of whale-watching excursions that called at Laguna San Ignacio during the 97-day period from January 5 to April 15 between 1978 and 1982 is summarized in Fig. 14.

In 1978, 28 commercial whale-watching excursions visited Laguna San Ignacio during 50 days (51%) of the 97-day winter season. The number of these excursions increased 28% in 1979 to 36 excursions visiting during 56 days (58%) of the winter, and in 1980 they increased another 5.5% to 38 excursions during 72 days (73%) of the winter.

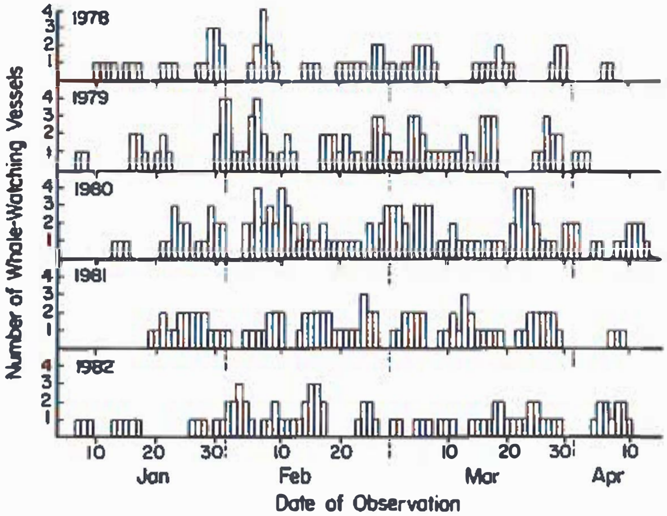

Fig. 14. *The number of whale-watching excursion vessels that visited Laguna San Ignacio from January 5 to April 12 between 1978 and 1982.*

Table VIII
Whale-Watching Excursion Vessel Visitations to Laguna San Ignacio during each 97-day[a] Winter Season between January 5 and April 12 for the Years 1978 to 1982

		Vessel days		Number of vessels per vessel day				Vessels with engines engaged[b]		Vessels at anchor[c]		Skiffs operating[d]	
Year	Number of trips/passengers	Number	% season	1	2	3	4	hr/season	% season	hr/season	% season	hr/season	% season
1978	28/700	50	51	36	11	2	1	42	1.8	800	34	400	17
1979	36/900	56	58	29	15	9	3	54	2.3	896	38	448	19
1980	38/950	72	73	34	23	10	5	57	2.4	1152	49	576	25
1981	28/700	60	62	31	27	2	0	42	1.8	960	41	480	21
1982	30/750	63	65	46	14	3	0	45	1.9	1008	43	664	29
Average	32/800	60	62	35	18	5	2	45	2.0	963	41	514	22

[a] Ninety-seven days = 2328 hr.
[b] Engines engaged based on 1.5 hr per trip.
[c] At anchor with generators running based on 16 hr per vessel day.
[d] Skiffs in operation based on 8 hr per vessel day.

In 1981, the number of whale-watching excursions declined by 28% (primarily in response to a 125% fare increase from 1978) to 28 excursions visiting during 60 days (62%) of the winter and then increased slightly in 1982 to 30 excursions visiting during 63 days (65%). The number of days without vessel activity within the lagoon declined from 49% in 1978 to 27% in 1980 and increased to 35% in 1982. Between 1978 and 1982, the number of excursion vessels within the lagoon at any one time averaged one vessel during 35 days (40%), two vessels during 18 days (20%), three vessels during 5 days (5%), four vessels during 2 days (2%), and no vessels in the lagoon the remaining 33% of the time (Table VIII).

Although the Mexican refuge regulations and commercial vessel permits allow only two commercial vessels in the lagoon at any time, three to four vessels occupied the lagoon together on 32 days over the 5 years. Because of the extensive shoals and strong currents at the lagoon inlet, multiple entries and exits occurred when one vessel followed another into or out of the lagoon, particularly if one operator was more familiar with the inlet channels. At these times excursion trips overlapped and when a third or fourth vessel arrived on the day that another vessel was scheduled to depart. This overlap resulted in three to four vessels occupying the lagoon simultaneously for approximately ½ day. On other occasions more than two vessels occupied the lagoon for one to three days. In both situations, there was a concomitant cumulative increase in the noise disturbance.

Ambient noise in the lagoon comes from both biological and nonbiological sources. Dahlheim *et al.* (Chapter 22, this volume) reported that levels of biological noise were lowest below 2 kHz, increased to high levels between 2 and 5 kHz, and declined gradually through 20 kHz. The average ambient noise levels attributable to biological sources (excluding cetaceans) ranged from 94 to 110 dB *re* μPa. The amount of nonbiological waterborne noise of human origin introduced into the lagoon habitat each season was dependent upon the number of hours that vessels were in the lagoon, the class of the vessel, and the amount of time each vessel or skiff was engaged in various activities.

One-hundred-ton class excursion vessels while underway produced the greatest levels of noise; however, on the average, these vessels ran their main engines only 48 hr of each 2328 hr- (97-day) season or approximately 2.0% of the winter. While at anchor, with only their power generators running, excursion vessels produced noise levels of 70 to 110 dB re. μPa at 1 m (Chapter 22, this volume) for approximately 963 hr or 41% of each winter. Outboard-powered skiffs were active an average of 514 hr or 22% of each winter season (Table VIII) and produced noise levels between 75 and 120 dB re. μPa at 1 m (Chapter 22, this volume).

In 1978, excursion vessels introduced noise distrubance during 51.5% (50 days) of the 97-day winter season. By 1980 these trips were introducing noise during 73% (72 days) of the winter, but the noise disturbance declined to 65% (63 days) by 1982. The 22.5% increase in the amount of time vessel noise was present in the lagoon between 1978 and 1980 represented a substantial change in the acoustical environment of the lagoon, particularly in the low-frequency range characteristically used by gray whales to communicate (Dahlheim, 1984). The 1980 winter saw the greatest amount of visitation and the greatest amount of nonbiological noise introduced into the lagoon.

Vessel Versus Nonvessel Day Comparison

Our goal of comparing gray whale abundance and distribution during control and experimental conditions was not fully realized. Almost continuous vessel visitation in some years combined with unstable winter weather severely hindered the opportunity to obtain data for pairwise comparisons between consecutive days with and without whale-watching activity. Only seven pairs of days were satisfactory for analysis.

To evaluate the short-term impact of whale-watching disturbance on gray whale demography in Laguna San Ignacio, we tested the hypotheses that gray whale abundance and distribution on days with and without tour vessel activity remained the same in the lagoon as a whole, in the lower lagoon where whales and human activities occurred simultaneously, and in the upper lagoon nursery area.

There was no evidence that gray whales moved out of the lagoon on days during the presence of whale-watching activities. In our three samples of paired-days prior to and following the arrival of a vessel, lagoon whale abundance increased in two instances and declined in one. In four samples of paired-days prior to and following the departure of a vessel, whale abundance decreased three times and increased only once. A Wilcoxon's paired-sample test (Sokal and Rohlf, 1981) of the nonvessel control days

Table IX
Comparison of Whale Abundance on Paired Days with and without Vessel Activity in Laguna San Ignacio, 1978–1982

Test comparison days	Date	Number of vessels	Number of whales		
			Entire lagoon	Lower lagoon	Upper lagoon
Preceeding vessel arrival versus vessel present	Jan 15	0	64	18	28
	Jan 16	2	86	24	43
	Mar 24	0	155	113	15
	Mar 25	1	139	92	15
	Apr 1	0	219	174	—
	Apr 2	2	234	205	—
Vessel present versus following vessel departure	Feb 1	2	129	64	45
	Feb 2	0	138	54	41
	Feb 9	1	245	126	61
	Feb 10	0	235	92	53
	Feb 26	2	137	74	23
	Feb 27	0	108	50	19
	Mar 7	1	107	66	10
	Mar 8	0	82	56	11
Wilcoxon's paired-sample test			$T_s = 5$ $p > .20$ $n = 7$	$T_s = 4$ $.10 < p < .20$ $n = 7$	$T_s = 1$ $.05 < p < .10$ $n = 6$

versus the vessel disturbance, experimental days revealed that the observed differences were not statistically significant [$T_s = 5 > t_{.05(2)7} = 2$, $.10 < p < .20$] (Table IX).

We suspected that any change in gray whale abundance in the area designated for vessel activity might be local, possibly masked, and not detected when the overall lagoon abundance was used as an estimator. We therefore repeated the above analysis using whale abundance data for only the lower lagoon. Whales were slightly more abundant in the lower lagoon while vessels were present. With the arrival of a vessel in the lower lagoon, whale abundance increased twice and decreased once. Following the departure of a vessel from the lower lagoon, whale abundance decreased in four instances; however, these differences in abundance were not significant [$T_s = 4 > t_{.05(2)7} = 2$, $.10 < p < .20$].

Finally, there was no conclusive evidence of an alteration in abundance or distribution of whales in the nursery area relative to the presence or absence of vessel activity in the lower lagoon. In two samples of paired days prior to and following the arrival of a vessel, whale abundance increased once and was unchanged once. In four samples of days prior to and following the departure of a vessel, female-calf pair abundance decreased in three instances and increased only once. The Wilcoxon's test revealed these changes were not significant [$T_s = 1 > t_{.05(2)7} = 0$, $.05 < p < .10$].

Friendly Whales

One of the unexpected effects of commercial whale watching in Laguna San Ignacio was the appearance of curious or "friendly whales." Friendly whales, as nicknamed by Gilmore, were first described for Laguna San Ignacio in 1975–1976 by Gilmore (1976), Wolfson (1976), and B. Cauble (personal communication), who reported that a few gray whales were soliciting human attention by deliberately approaching tour boats and whale-watching skiffs and allowing the passengers to pet them (Fig. 15).

During the course of this study, the friendly whale phenomenon rapidly expanded. In 1977–1978 friendly or curious whale behavior was a rare event involving a small number of individual whales (Swartz and Cummings, 1978; Larsen, 1978). But, by 1982 the incidence of this behavior had increased dramatically such that we personally had encounters with at least 200 friendly whales during 70 days of our 97-day field season. Moreover, virtually all whale-watching excursions that visited the lagoon between 1980 and 1982 have had encounters with friendly whales. For instance, in 1981, 26 of the 28 excursion vessels had contacts with curious whales, and nearly all 700 passengers were able to "pet a whale." Similarly, in 1982, each of the 30 excursions had repeated encounters with friendly whales (Swartz and Jones, 1981; Jones and Swartz, 1984).

Reports by investigators working in other areas indicate that friendly whale behavior has spread and is no longer unique to Laguna San Ignacio. At La Entrada (Bahia Magdalena) in 1979, Norris *et al.* (1983) reported two instances of friendly whale behavior when whales approached their research vessel, the *Regina Maris*, while she lay at anchor. In 1982, a chronic friendly whale that had been photographed for four consecutive winters in Laguna San Ignacio was encountered by researchers working in Laguna Guerrero Negro (Chapter 15, this volume). During the same year in Laguna Ojo

Fig. 15. *Friendly gray whale calf allowing whale watchers to pet it on the head. Note the tip of the mother whale's rostrum below and between calf and skiff.*

de Liebre, a team of Mexican scientists reported an encounter with a "curious" whale (Anonymous, 1983[5]). Similarly, in 1983, Lawson (1983) encountered a friendly whale in the Boca de Soledad area of Bahia Magdalena that nudged and rubbed against the skiffs tied astern a large excursion vessel. Most recently, a gray whale that was feeding along the west coast of Vancouver Island, British Columbia approached a skiff and exhibited friendly behavior (Hudnall, 1983). This whale remained in the area for a week or more where it was "friendly" to numerous vessels (J. D. Darling personal communication). Lastly, while recording gray whale vocalizations on the Bering Sea feeding grounds in July of 1982, M. Dahlheim (personal communication), who has experienced friendly whales in Laguna San Ignacio (Chapter 21, this volume), encountered a friendly whale that followed her boat for approximately 20 min.

Salient features of friendly whale behavior in Laguna San Ignacio have included: (1) participation by whales of all sex–age classes, (i.e., females and calves, males, females, groups of adults and immatures, and single individuals, (2) a seeming attraction toward a skiff with its engine idling in neutral gear, (3) frequent approaches to skiffs from astern, as though curious about the source of the engine sound, (4) frequent departures when the engines were shut off, (5) blowing large bubble bursts under and around the skiffs,

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[5] Cetacean workshop discussion, VIII Reunion Internacional Sobre Mamiferos Marinos de Baja California, La Paz, Baja California Sur, Mexico.

(6) producing airborne "Bronx cheer" sounds from slightly pursed blowholes, (7) allowing physical contact (patting, rubbing, stroking, etc.) by passengers, (8) probing and frequently lifting the skiff, (9) occasionally jostling skiffs hard enough to knock a passenger overboard, (10) approaching and remaining near or directly alongside excursion vessels at anchor, (11) an accumulative effect where the presence of a single curious whale or female–calf pair appeared to attract additional passing whales creating groups of friendly whales of up to 20 individuals, (12) whales leaving the company of others to follow a skiff, (13) chronic curious behavior from some individual whales which continued throughout an entire day, and from week to week, month to month, and year to year for up to 6 years, (14) following slow moving whale-watching skiffs for up to 5 km and resuming friendly behavior when the skiffs stopped, (15) following skiffs attempting to leave an area, even at speeds in excess of 11 km/hr (6 knots).

The large majority of curious whale encounters have occurred without incident. Most friendly whales were cautious to the point of being timid. Whales when first making contact, generally probed the skiffs with the tip of their rostrum. We discovered that the whales were very sensitive to the slightest touch and often flinched if touched unexpectedly before they made the initial contact with the boat. On occasion, however, energetic "friendlies" have prodded skiffs with sufficient force to cause concern for the safety of the passengers. During six encounters, whales bumped whale-watching skiffs hard enough to knock six people overboard and cause slight damage to one of the skiffs and outboard engines. Skiff operators reported that the initial behavior of these whales toward the boats was gentle, but over time became increasingly rambunctious. In no instance, however, did this behavior appear as either aggressive or defensive behavior as described by Scammon (1874), Norris and Gentry (1974), or Norris *et al.*, (1977). On subsequent encounters with the same whales, the more forceful behavior was pronounced throughout and the whales did not revert to the formerly gentle contact. In addition, twice during curious encounters adult whales were observed breaching and lob-tailing within a distance of less than one body length from the skiffs, sending a cascade of water over the occupants. Furthermore, instances of near collisions with whales surfacing directly in the path of skiffs underway were observed.

Discussion

ABUNDANCE, DISTRIBUTION, AND OCCUPATION TIMETABLE

The demographic study of gray whales in Laguna San Ignacio provides a detailed picture of whale abundance and use of this breeding area between 1978 and 1982. An important finding is that the Laguna San Ignacio whale population at maximum combined counts has increased moderately at a statistically significant rate of 7.3% per year over the 5 years. This increase was chiefly due to significantly greater numbers of females and calves that primarily occupied the upper lagoon nursery during the birth period. The 18.3% per year increase in their counts indicated that greater numbers of females were either utilizing Laguna San Ignacio for parturition or were entering the lagoon with newborn calves. This increase, however, was not accompanied by a change in the timetable of female–calf pair occupation or their duration of stay, which remained the same each year. In contrast to the female–calf pairs, our results provide good evidence that the demography and phenology of the single whale population has remained essentially stable since 1978. There were no significant changes in the maximum abundance, distribution, or density of single whales, and, with the exception of one season, their timetable of occupation remained the same.

Prior to our research, mid-February aerial surveys of gray whale abundance in Laguna San Ignacio were conducted between 1947 and 1965 by Hubbs and Hubbs (1967) and later by Gilmore (1960). A second series of aerial counts was conducted by Gard (1978) between 1974 and 1976. Although all of these investigators attempted 100% coverage, each utilized unstandardized procedures and transect track lines; consequently, their results preclude quantitative comparisons. These early surveys are valuable, however, because they provide an index of gray whale abundance in Laguna San Ignacio over the past 35 years. An exponential curve fit to the counts since 1947 along with our boat counts between 1978 and 1982 suggests that the number of gray whales utilizing the lagoon has increased at least 7.9% per year [$F_{(1,18)} = 97.01$, $p < < .001$, $r^2 = .851$] (Fig. 16). This rate of increase agrees closely with the 7.3% per year rate of increase of our maximum combined counts between 1978 and 1982; however, it also suggests an annual rate of increase for the lagoon in excess of the population growth. The best estimate for the annual rate of increase of the California–Chukotka gray whale population is 2.5% per year, based on Reilly's (1981) analysis of 13 years of shore censuses of the fall migration past Monterey, California between 1968 and 1980; this was concurrent with an annual exploitation of 1.2% per year, yielding a 3.7% per year net realized rate of increase. During our 5-year study, then, gray whale counts in the lagoon increased approximately 4.8% per year above the growth rate of the population itself. At the beginning of our study in 1977–1978, the size of the gray whale herd was estimated to be 14,811 ± SD 2,272 whales and would have increased to approximately 16,000 by 1982 (Reilly *et al*., 1983).

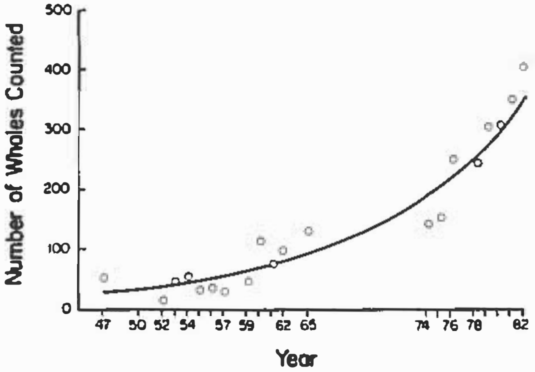

Fig. 16. *Gray whale abundance counts in Laguna San Ignacio from surveys conducted between 1947 and 1982. Aerial surveys were flown between 1947 and 1976 by Gilmore (1960), Hubbs and Hubbs (1967), and Gard (1978). Boat counts between 1978 and 1982 were conducted by the authors. Black line is a least squares exponential regression line fitted to the counts.*

There are at least two possible explanations for the overall increase in whale abundance in Laguna San Ignacio between 1978 and 1982. The first is that the gray whale herd is continuing to grow following its recovery from exploitation, and, therefore, counts in the lagoons continue to increase. An alternate explanation is that the higher overall whale counts could be due to a larger fraction of the total herd utilizing this lagoon. With the exception of Laguna Guerrero Negro, where whale counts did not increase significantly between 1980 and 1982 (Chapter 15, this volume), we do not know if increases in abundance occurred in other breeding areas, or whether Laguna San Ignacio is unique in attracting larger numbers of whales per year.

Notably, Laguna San Ignacio supports the second largest number of whales of all the major winter breeding areas. This is demonstrated by the results of boat surveys of gray whales (not including calves) reported from other breeding areas during the same time period (Fig. 17). Total adult whales in Laguna Ojo de Liebre reached a maximum of 829 animals on February 1, 1980 (Rice *et al.*, 1981); in Laguna San Ignacio the maximum count was 407 whales on February 14, 1982; in Boca de Soledad the maximum count was 225 adults on February 8, 1982 (Lawson, 1983); and maximum counts ranged from 120 to 207 whales between 1980 and 1982 in Laguna Guerrero Negro (Chapter 15, this volume). In addition, Rice *et al.* (1981), who conducted extensive aerial surveys of the west coast of Baja California, showed that two other areas were utilized by substantial numbers of adult grays; their unadjusted counts revealed that 170 whales were in San Juanico Bight on February 4, 1980, and 139 whales were in Bahia Almejas on February 5, 1980.

A main difference in the composition of the whale population in Laguna San Ignacio compared with other lagoons is that Laguna San Ignacio, at the time of maximum combined counts, is a single-whale-dominated system, whereas female–calf pairs predominate in the other lagoons during the same time period. For example, single whales averaged 70% of the population in Laguna San Ignacio at maximum combined counts, compared to 44% in Laguna Ojo de Liebre, 32% in Boca de Soledad, and an average of 19% in Laguna Guerrero Negro. Thus, Laguna San Ignacio supports a relatively small proportion of female–calf pairs while these animals outnumber single whales in the other areas at maximum combined counts.

To evaluate the relative importance of Laguna San Ignacio as a calving area for females and as a breeding area for single whales, we compared maximum counts of both groups in Laguna San Ignacio with maximum counts of these whales in other breeding areas. In terms of overall female–calf pair usage, Laguna San Ignacio appears to host the second highest number of females and calves with a maximum of 281 counted on March 8, 1982 (Fig. 17). The area with the greatest abundance of female–calf pairs was clearly Laguna Ojo de Liebre with 571 pairs counted there on February 4, 1980 (Rice *et al.*, 1981). One hundred and fifty-four mothers and calves were counted in Boca de Soledad on February 4, 1982, making it the third largest female–calf area (Lawson, 1983). Finally, Laguna Guerrero Negro contained the least number of these whales, averaging 127 pairs between 1980 and 1982 (Chapter 15, this volume). Laguna San Ignacio also appears to host the second greatest number of single whales, with an average maximum count of 227 (Fig. 17). Again, this is second only to Laguna Ojo de

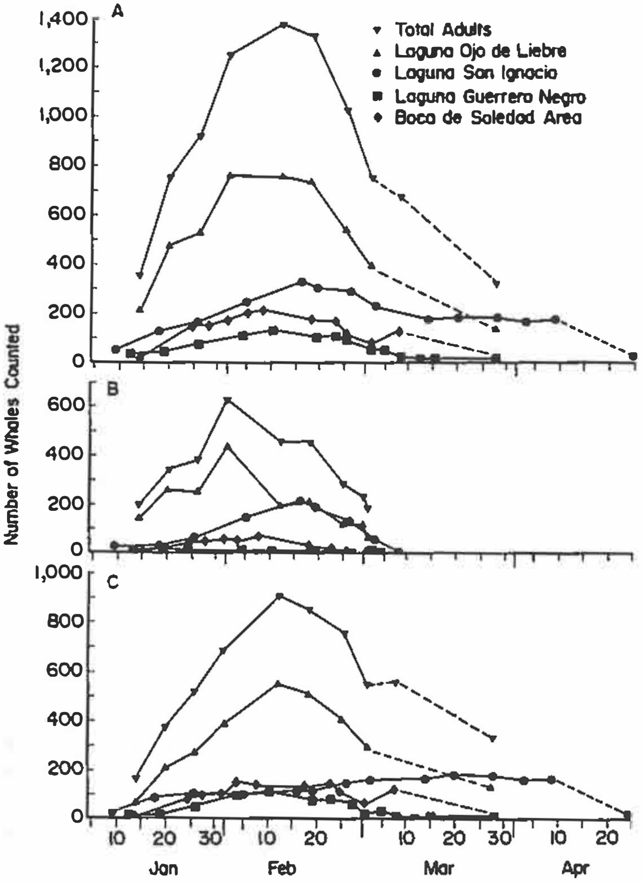

Fig. 17. *The number of gray whales (excluding calves) counted in four major breeding areas:* ▼, *total adults;* ▲, *Laguna Ojo de Liebre (Rice* et al., *1981);* ●, *Laguna San Ignacio (Swartz and Jones, 1981);* ■, *Laguna Guerrero Negro (Chapter 15, this volume);* ◆, *Boca de Soledad area (Lawson, 1983). All counts are for the 1980 winter except the data for Boca de Soledad which are from the 1983 season. (A) Total whales for all areas, (B) single whales, (C) female–calf pairs. Counts connected by solid lines are from boat surveys; those connected by broken lines are from 100% aerial surveys (see text for explanation).*

Liebre which contained 438 single whales at their maximum count on February 1, 1980 (Rice *et al.*, 1981). Boca de Soledad contained the third largest number of single whales, with 75 on February 8, 1982 (Lawson, 1983), and Laguna Guerrero Negro supported the smallest number of single whales of all these areas; single whale counts in this lagoon ranged from 19 to 43 in mid-February between 1980 and 1982 (Chapter 15, this volume).

We cannot explain why the single whale maximum abundance remained the same each year rather than increasing significantly; however, we believe that the total number of single whales using Laguna San Ignacio during a winter season is far greater than the number counted in the lagoon at maximum combined counts. The boat surveys provide an index of the minimum number of whales in the lagoon at specific points in time throughout a season; but, we do not mean to imply that the population is a static group or that the same individuals are being counted repeatedly each week as the number of whales builds to its maximum each year. In other words, we suspect that single whales have a high turnover rate in the lagoon. Evidence supporting the notion of a relatively continuous exchange of whales through the lagoon during each season comes from our photographic identification study between 1977 and 1982, and our shore-based observations of the main entry channel of the lagoon inlet in 1982. Photographic identification results revealed that 81% of the single whales photographed in Laguna San Ignacio had a duration of stay of 1 week or less. In addition, the fact that two single whales photographed by D. Withrow (personal communication) in Laguna Oje de Liebre were resighted approximately 1 week later in Laguna San Ignacio during the same season suggests the possibility of a relatively rapid circulation of whales between breeding areas as well (Jones, 1984). Finally, our census of whale movement through the inlet demonstrated that substantial numbers of single whales enter and exit the lagoon every day. For example, at the time of the maximum combined count in 1982, when 270 whales were counted within the lagoon, a minimum of 341 others entered and 185 exited the lagoon during a 7-hr. period. Because the majority of the singles present in the inlet throughout the season were actively transiting and their movement was independent of the tide, counts of these whales through the inlet were indicative of a real exchange of animals rather than being repeat counts of the same individuals passively moving into and out of the lagoon with the tide (Jones and Swartz, 1984).

The duration of the single whale season in Laguna San Ignacio was statistically consistent during 4 of the 5 years when it averaged 79 days (11 weeks). In 1979, however, the season was significantly longer, as seven whales (3% of the maximum count) remained in the lagoon approximately 2 weeks longer that usual. Since the number of whales present during the tail end of the deviant year was small, we think that the 4 year average is the best estimate for the single whale duration of stay in Laguna San Ignacio between 1978 and 1982. Nevertheless, there are two obvious reasons why this estimate may be somewhat biased toward overestimating the actual length of the single whale season. First, late-pregnant females are believed to be the first animals to arrive at the lagoons (Rice and Wolman, 1971), and because these females are indistinguishable from single whales until they give birth to their calves, census counts early in the winter probably extend the length of the single whale season beyond its actual length. Similarly, whale counts late in the season may include some females that lost their calves and would be counted as single whales.

The durations of stay of single whales were nearly the same in Laguna San Ignacio, Laguna Ojo de Liebre, and Boca de Soledad, and each of these areas hosted single whales longer than Laguna Guerrero Negro. In Laguna Ojo de Liebre, the minimum length of the single whale season in 1980 was 75 days (10.7 weeks). This period is based on an estimated beginning date for the season of December 20 which Rice *et al.* (1981) extrapolated from the timing of the southbound migration past Point Loma, California, and from the date of their last lagoon boat census on March 3. Because their final count included 67 single whales, and our March 28 aerial survey of the same area revealed no single whales, we suspect that the season probably extended to at least March 10, 1980 and, therefore, was at least 80 days (11.4 weeks) in duration. Single whales were present in Boca de Soledad for a minimum of 78 days (11.1 weeks) from January 9 to March 28, 1982 (Lawson, 1983). Lawson stated that approximately 15 whales were already present at the beginning of her study, thus, the duration of the season was probably a few days longer. Lastly, Bryant *et al.* (Chapter 15, this volume) reported that the single whale season in Laguna Guerrero Negro began on approximately January 3 and usually ended by March 10 for the 3 years from 1980 to 1982. This yields a 66-day (9.4-week) duration of single whale season, which is approximately 2 weeks shorter than that reported for any of the other breeding areas. This shorter single whale season may be related to Bryant *et al.*'s (Chapter 15, this volume) finding that Laguna Guerrero Negro consistently hosted only a small number of single whales that averaged 16.2% of the total adult whales. In summary, the period of lagoon occupation for single whales in these areas ranged from 9.4 to 11.4 weeks, beginning in late December or early January and ending by approximately mid-March. Their departure from these lagoons occurred approximately 1 month before the departure of female–calf pairs.

Knowledge of the duration of a behavior contributes to the understanding of an animal's time budget. In the case of the gray whale, the duration of stay in the lagoons has important implications in terms of the whales' energy requirements. Because single whales leave the breeding areas approximately 1 month earlier than many of the female–calf pairs, they presumably arrive on the summer feeding grounds earlier and spend more time there than females that give birth to calves during the same year (Rice and Wolman, 1971). Given that females normally reproduce biennially, this suggests that adult females would alternate between a longer period on the summer range when newly pregnant and a shorter period on the summer range when lactating. Males, however, would be able to spend the same amount of time feeding on the summer range each year. For newly pregnant females, this extra summer feeding time is of obvious energetic significance related to their need to acquire more fat reserves for the gestation of a calf and a 7-month lactation period.

The variation in the timing of the single whale seasonal occupation of Laguna San Ignacio is best expressed as differences between the mean day per season, rather than as changes in the dates of the maximum counts. The timing of maximum counts may be more a function of the weekly sampling schedule than of actual variations in the timing of single whale abundance. For example, the dates of single whale maximum counts in Laguna San Ignacio differed as much as 27 days between winters and were significantly different, whereas the mean days differed by 15 days and were not significantly different from one another or the pooled mean day. For predictive purposes, the pooled mean day of February 9 is the best estimate of the midpoint of the single whale season between 1978 and 1982. The variation in the seasonal timing, expressed as differences between mean days, may occur as a result of environmental factors such as changes in the timing of the advance of the Arctic ice sheet (Chapter 10, this volume) or extremely favorable or unfavorable weather in the summer range and along the migratory route.

Estimates of the mean day of the single whale season are not available for other breeding areas. At present, the timing of peak abundance of single whales among breeding areas can only be evaluated by comparing the dates of maximum counts. A comparison of the 5-year average day of maximum counts in Laguna San Ignacio with the date of maximum counts in other areas indicated that the timing of single whale maximum counts is variable among breeding areas. Peak counts coincided in the northernmost lagoon of Guerrero Negro and the southernmost lagoon of Bahia Magdalena, but occurred a few days earlier than in Laguna San Ignacio; for example, in Laguna Guerrero Negro maximum counts were obtained between February 8 and 10 during the period 1980 to 1982 (Chapter 15, this volume), and in Boca de Soledad they occurred on February 8, 1982 (Lawson, 1983). In Laguna Ojo de Liebre maximum counts were obtained on February 1, 1980 (Rice *et al.*, 1981), 2 weeks earlier than in Laguna San Ignacio. The variation among the different areas may be the result of real changes in the single whale season or of the survey schedules employed in the various breeding areas. Clearly though, the timing of single whale counts from these lagoons is not suggestive of a sequential occupation of areas from north to south (Norris *et al.*, 1983); rather, the timing of the occupation appears to be independent of geographical location.

The pattern of temporal distribution of female–calf pairs in Laguna San Ignacio was virtually the same each year, but was strikingly different from that in other lagoons. In Laguna San Ignacio, the number of females with calves increased steadily throughout the birth period from late December through mid-February, and reached peak numbers in late March or early April. At maximum counts, abundance was nearly double that in mid-February and averaged 226 pairs compared to 116 pairs. In Laguna Guerrero Negro, Laguna Ojo de Liebre, and Boca de Soledad, however, maximum counts of females and calves occurred much earlier. In these areas, counts increased in early January to maximums in mid-February and then decreased. For instance, maximum counts of female–calf pairs were obtained between February 8 and 10 between 1980 and 1982 in Laguna Guerrero Negro (Chapter 15, this volume), on February 12, 1980 in Laguna Ojo de Liebre (Rice *et al.*, 1981), and on February 4, 1982 in Boca de Soledad (Lawson, 1983).

One explanation for the difference in timing of female and calf peak counts between Laguna San Ignacio and the other areas is that this lagoon serves as a staging area for female–calf pairs prior to their departure from the southern range. There are two sources of evidence supporting this idea. First is the observation that the late season influx is not due to continued births; rather, these late season females have calves that are approximately 2 to 3 months old (Swartz and Jones, 1981). Second, the results of our 6-year photographic identification study, in combination with a 3-year program in Laguna Guerrero Negro by Bryant and co-workers and a 1-year project in Boca de Soledad by Lawson, revealed that some females with older calves were immigrating to Laguna San Ignacio after leaving these breeding areas. Prior to the extension of photographic identification studies to other breeding areas, we and other investigators had speculated that the late season influx of whales consisted of females with calves that were moving northward from Bahia Magdalena (Swartz and Jones, 1978; Rice *et al.*, 1981). But this is only partly true. In addition to northbound immigrants, some females with calves photographed early in the season in more northerly lagoons, vacated these areas and moved south to Laguna San Ignacio late in the season (Jones, 1984).

Recently, a late season influx of female–calf pairs was reported for Boca de

Soledad; however, this influx occurred on March 8 and was preceded by a decrease in abundance from their maximum count on February 4, rather than showing the continual increase seen in Laguna San Ignacio (Lawson, 1983). Lawson speculates that this late season influx in Boca de Soledad consists of whales moving north from the main bay of Bahia Magdalena or from the Gulf of California. Additional observations will be required to determine if this influx is an annual event in Boca de Soledad.

The reason why females and their calves are attracted to Laguna San Ignacio late in the season is unknown, but may be related to a combination of factors. For example, females may utilize potential food resources in Laguna San Ignacio, as there is a growing body of direct and indirect evidence indicating that a subgroup of gray whales, particularly females with calves, may opportunistically consume appreciable amounts of prey within the lagoon and its nearshore waters (Swartz and Jones, 1981; Jones and Swartz, 1984). Another possibility is that this aggregation of whales is related to the social structure of the herd or to the "socialization" of older calves. Gray whales have been characterized as being unsocial animals, partly because of the solitary nature of mothers and calves during the early part of the winter (Gilmore, 1960). However, the contention that these gatherings may have a social function is supported by the observation that in the latter part of the season in Laguna San Ignacio when calves are older, mothers and young frequently join to form large groups characterized by intense physical contact (Swartz and Jones, 1981). Group members cavort, rolling and rubbing against each other, wheeling and diving at the surface and below. Multiple bubble bursts frequently mark their location while submerged. The size and duration of these groups vary, but can involve up to 20 mother–calf pairs at a time, and can last from a few minutes to over 3 hours. The groups are fluid, with pairs coalescing and exchanging continually (Jones and Swartz, 1984). Another hypothesis is related to the physical development of the calves; that is, Laguna San Ignacio may serve as a resting area where females stop over to rest and nurse their growing young after periods of oceanic swimming. Additional study will be required to evaluate the validity of these tentative hypotheses.

A major objective of the study was to learn how gray whales use Laguna San Ignacio. This lagoon is an important calving and breeding area for single whales and female–calf pairs, and during our study, the whales exhibited a regular distribution that did not vary significantly over the 5 years. During the period from late December to late February, when single whales and females with calves occupied the lagoon jointly, 50% of the total whale population was distributed in the lower lagoon, 20% in the middle, and 30% in the upper lagoon. However, there was a consistent separation between the calving and breeding portions of the lagoon population. Females with calves and single whales utilized the lagoon quite differently. As whales entered the lagoon, the population became segregated spatially and temporally such that the distribution, gross movement, and timetable of occupation differed for each group. Single whales were dispersed in a gradient being most dense near the inlet and becoming less dense with increasing distance from the inlet, while most female–calf pairs were concentrated in the upper lagoon nursery farthest from the inlet. To illustrate, at the date of combined maximum counts each year, the average distribution of single whales was 65% in the lower lagoon, 24% in the middle, and 11% in the upper lagoon. In contrast, the average female–calf pair distribution at the same time was 11% in the lower lagoon, 9% in the middle, and 80% in the upper lagoon nursery.

The single whales' definite preference for the lower lagoon may be related to access to the relatively deep and wide channel, which is unrestricted even at low tide, or to close proximity to the inlet and open ocean areas, or both. While in this area, single whales are predominantly engaged in social activities associated with courtship and mating. The lower lagoon is 2–4 times deeper than the middle and upper lagoon respectively, and may be more conducive to sexual behavior by allowing the whales greater mobility.

The localization of single whales in the inlet and lower lagoon region of Laguna San Ignacio is a feature of lagoon use by single whales that also occurs in other breeding areas. Gilmore (1960) reported that lone adults, courting adults, and immatures also predominate at the entrances to Laguna Ojo de Liebre and Bahia Magdalena, and suggested that courting and mating are the primary activities of the whales in these areas. In addition, Samaras (1974) stated that adult male and female grays use the inlet of Laguna Ojo de Liebre as a staging area for precopulatory behavior, while pregnant females occupy the inner lagoon calving area. Norris *et al.* (1983), who studied lagoon entrance aggregations of gray whales at La Entrada, the main entrance to Bahia Magdalena, and Canal Rehusa, the entrance of the southernmost calving lagoons at Bahias Almejas and Santa Maria, reported that the entrance aggregations were composed entirely of males, nonparturient females, and juveniles whose primary behaviors appeared to be courtship, mating, and possibly feeding. On the other hand, Bryant *et al.* (Chapter 15, this volume) described Laguna Guerrero Negro as hosting very few single whales and they did not appear to aggregate in the area nearest the inlet. They also noted, however, that this lagoon does not have any deep-water areas comparable to those in the larger breeding lagoons, but further remarked that a large number of singles have been observed in the deep-water area just offshore. This finding, then, is reminiscent of the pattern of single whale distribution in other breeding areas.

The predominance of female–calf pairs in the upper lagoon nursery area of Laguna San Ignacio is undoubtedly related to a number of features that are conducive to the rearing of very young calves. First, the upper lagoon area is relatively shallow and least affected by tidal currents, but the area available to the whales is greatly reduced at low tide. Evidently, these inner lagoon features are attractive to females with newborn calves since they consistently utilize the innermost areas when single whales are present in the lagoon. Mothers and calves in the upper lagoon are primarily engaged in the more tranquil activities of resting, nursing, and moving about with the changing tides. Moreover, it is generally accepted that the nursery area furthest from the inlet provides an area of relative solitude for the females following parturition and during early calf development. In addition, we feel that harassment by courting whales is probably a major factor in the segregation of females and calves away from single whales inhabiting the outer lagoon areas. Females with calves avoid courting groups; despite their avoidance of single whales, they are occasionally pursued by groups of single whales that appear to harass and attempt to mate with these females (Swartz and Jones, 1981; Jones and Swartz, 1984). Mating bouts appear to be very disruptive events and may involve as many as 15 individual whales thrashing at the surface and throwing their flukes and flippers about as they jocky for mating position. It is certainly reasonable to think that a calf might be separated from its mother or could sustain injuries or even be killed in these circumstances. We agree with Norris *et al.* (1977) that "courting–mating aggregations are almost certainly disruptive places for mother–calf pairs."

The pattern of female–calf pair distribution in Laguna San Ignacio during the first half of each winter is consistent with the findings of investigators working in other lagoons who report that the uppermost lagoon areas farthest from the open sea are utilized extensively by female gray whales with newborn calves (Scammon, 1874; Gilmore, 1960; Rice and Wolman, 1971; Samaras, 1974; Gard, 1974; White, 1975; Norris *et al.*, 1977). The dynamics of female–calf pair distribution in Laguna Guerrero Negro appears to correspond to that observed in the upper portions of the larger breeding areas of Laguna Ojo de Liebre, Laguna San Ignacio, and Bahia Magdalena; that is, the duration of female–calf pair occupation in Laguna Guerrero Negro and in the upper regions of these areas begins and ends at approximately the same time, their periods of peak abundance coincide, and very few single whales are found in these areas.

The middle lagoon consistently hosted the lowest density of whales early in the season. One explanation for the decrease in single whales in the middle lagoon and nursery is that the significantly larger numbers of female–calf pairs using these areas, in effect, may have displaced single whales. In addition, this region may serve as a "buffer" between courting single whales and females with their newborn calves. Norris *et al.* (1983) commented that an almost whale-free "buffer-zone" existed at Bahia Magdalena between single whales in the area nearest the inlet and the female–calf pairs deepest within the lagoon interior.

Following the period of combined maximum counts, and with the gradual departure of single whales from Laguna San Ignacio, female–calf counts continued to increase to their maximum counts and these whales gradually shifted their distribution to the lower lagoon and inlet, essentially abandoning the upper lagoon nursery. Thus, throughout each season, gray whales are most numerous in the lower lagoon and inlet. The average distribution of female–calf pairs at this time is: 87% in the lower lagoon, 12% in the middle lagoon, and 1% in the upper lagoon.

The trend for female–calf pairs to occupy the area nearest the sea following the end of the birth period and the departure of single whales from the lagoon was prevalent during all winters in Laguna San Ignacio, and suggests that females prefer the inlet and lower lagoon over other areas when their calves are 2–3 months old. We conducted aerial surveys (100% counts) of Lagunas Guerrero Negro and Ojo de Liebre on March 28, 1980 and found that female–calf pairs had abandoned the innermost regions of these lagoons as well and were concentrated in the lower lagoon and inlet areas; in Laguna Guerrero Negro, we counted 17 mother–calf pairs in the lower lagoon entry channel and 73 pairs in the inlet, and in Laguna Ojo de Liebre we counted 22 pairs in the upper portion of the lagoon, 83 pairs in the lower portion, and 121 pairs in the inlet, indicating that a late-season shift in the distribution of female–calf pairs toward the inlet also occurs in these lagoons. The tendency for whales to shift their distribution from the inner regions of the breeding areas to the lower and inlet areas is also seen in Boca de

Soledad (Lawson, 1983) and Bahia Magdalena (Norris *et al.*, 1983). Scammon (1874) and Norris *et al.* (1977) interpreted this shift as being the first stage of the migration preparatory to leaving the lagoons.

MORTALITY

Age-specific mortality is a vital parameter in any demographic study. The pattern of gray whale mortality in the winter range that emerged from the evaluation of mortality data in Laguna San Ignacio, Laguna Guerrero Negro, Laguna Ojo de Liebre, and Boca de Soledad between 1954 and 1983 can be characterized by three age-class components: (1) a very high proportion of calves, consistent in all areas, that averaged 91.4% of the total dead whales, (2) a relatively high, but unstable proportion of immatures that ranged from 0–19.5% among areas, and (3) a consistently low, but unstable proportion of adults ranging from 0 to 5% between areas.

This mortality pattern supports both the contention that calves are more susceptible than adults to fatal strandings in the lagoons and the idea that calf and yearling mortality is higher than that of adults (Eberhardt and Norris, 1964; Gard and Gard, 1972; Gard, 1976) and further implies that gray whale age specific mortality is typically mammalian. That is, in most mammal species, young and immatures have higher mortality rates in relationship to older individuals, whose mortality rates remain relatively constant following maturity (Allen, 1981). Caughley (1977) states that mammal mortality rates typically follow a U-shaped trend with age, where prepubertal mortality varies greatly compared to adult mortality rates which remain less variable with age. Gray whale mortality appears to fit such a trend, with calf and immature mortality rates significantly greater than that of adults. Since the gray whale population is changing demographically as it continues to grow, records of strandings, particularly calf mortality, are valuable for monitoring changes in age-specific mortality and will provide a more accurate profile of the population age structure.

The preponderance of dead gray whale calves discovered in the breeding areas in all years suggests that the period including birth and the time immediately following birth within and near the breeding lagoons is critical for the survival of the young. Calf carcasses were commonly discovered in the lagoons throughout the birth period from January 5 to February 15, but were infrequently encountered in March and April, suggesting that the probability of dying is greatest for a calf just after birth and decreases with time.

The mean calf mortality rate of 3.54% calculated for whales in Laguna San Ignacio (1978–1982) is comparable to the 2.5% mean rate for calves in Laguna Guerrero Negro (1980–1982) and the 2.9% rate in Laguna Ojo de Liebre in 1980 (Swartz and Jones, 1983). Unfortunately, data on calf mortality prior to the exploitation and subsequent depletion of gray whales are nonexistent, making it impossible to determine whether the mortality rates for Laguna San Ignacio and the other areas are high, low, or typical for the species. Counts of dead calves undoubtedly underestimate actual calf mortality because not all carcasses are discovered: some dead whales are washed out to sea with the tides, some are consumed by scavengers, others strand on beaches not visited by investigators, and still others are missed by researchers altogether. Nonetheless, mortality rates based on dead whales are useful as minimum estimates.

From our analysis of the body size of dead calves stranded in Boca de Soledad, and Guerrero Negro, Ojo de Liebre, and San Ignacio lagoons, we concluded that the mean lengths of the calves in all these areas were consistent and together averaged 4.43 m. It has been generally assumed that the lengths of dead calves in the lagoons are representative of the lengths of gray whales at birth (Rice and Wolman, 1971; Rice *et al.*, 1971; Rice, 1983). However, our comparison of the lengths of dead calves from the breeding areas with the lengths of near-term gray whale fetuses collected by Rice and Wolman (1971) clearly indicated that the dead neonates were significantly shorter than the fetuses (4.43 to 4.62 m respectively) and suggests that the typical length at birth of most viable gray whale calves would be longer than the lengths of the dead lagoon calves. Presumably, had the fetuses developed to full term, only a small percentage of them, equal to the calf mortality rate in the lagoons, would be expected to die, and we would expect the lengths of *these* calves to be similar to the lengths of dead neonates from the lagoons.

Rice *et al.* (1981) also noted the smaller size of dead neonates in the breeding lagoons compared to near-term fetuses, and proposed that ". . . the body length shrinks after birth, possibly due to compression of the intervertebral disks." An alternate explanation for the dead neonates being shorter is that they might be premature, and as premature animals their lengths would not be representative of full term neonates. The fact that they are dead, also suggests that these whales are abnormal and not representative of normally developed young. Another possibility is that neonatal mortality is higher for smaller calves. It is generally known that among mammal species, the bigger the offspring, the better are its chances of survival (Ralls, 1976), and that for humans and some species of nonhuman primates and some ungulates, small offspring have higher mortality than larger individuals. Although we have no hard evidence to support any of these ideas for gray whale neonate mortality, we feel that the deaths of these smaller whales are probably related in some way to reduced fitness at birth.

Theoretically, gray whale yearlings should attain a length of about 8.2–9.6 m by the time they make their first return trip to the southern range. The dead immatures from Laguna San Ignacio that were either too small to be yearlings or too large to be calves of the year, perhaps, were animals that became ill before or following separation from their mothers, or failed to learn how to forage for themselves, or did not spend their first summer in a suitable feeding area with the result that their growth was stunted. These "runt" animals could then have followed the fall migration of the population to the southern range where they died as undersized yearlings.

Most population biologists agree that accurate aging of animals is important because knowledge of the dynamics of a population depends heavily on the ability to age individuals (Caughley, 1977). Many also agree that errors are inevitable especially when the criterion of age is a morphological feature, like body size, that changes continuously with age. In the case of gray whales where body length is used to age individuals, the problem of correctly categorizing small gray whales as yearlings rather than calves points out an obvious bias with this or any fixed length–age interval classification scheme. Alternative methods of aging small whales are limited primarily because small whale carcasses decompose rapidly (Eberhardt and Norris, 1964), and short-term clues as to their age, such as the presence of adult barnacles, are lost relatively soon after death. Thus, small yearlings could be misidentified by age as calves of the year. One important effect of this error is that calf mortality rates might be biased upward. In this instance, it would be important to know what proportion of dead calves is actually undersized yearlings. A second effect is that yearling lengths misclassified with calf lengths would contribute error when these data are used to assess calf growth rates (i.e., it would bias calf growth rates upward). In the future, it will be valuable to know how often the gray whale age classification index leads to error, so that researchers can reduce bias in their results and better evaluate the significance of age-specific mortality in this species.

Sex Ratio

The 1:1 sex ratio of dead gray whale calves, immatures, and adults combined reported from the four breeding lagoons is in agreement with the findings of Rice and Wolman (1971), who report that gray whales have an equal sex ratio at all age classes. Based on the sex ratio of gray whales collected during migration, Rice and Wolman (1971) state that ". . . there is probably little sex difference in mortality rate, a conclusion further supported by the essentially equal sex ratio at all ages." While this may be true for gray whale calves, the sample of dead immatures and adult whales from the lagoon was too small to permit the evaluation of differential mortality between males and females of these age classes. If gray whale mortality is typically mammalian, we would expect proportionately greater male mortality in older age classes (Caughley, 1966; Ralls *et al*., 1980). However, additional data are needed to clarify this issue.

WHALE-WATCHING ACTIVITIES

Concern about the potential detrimental consequences of the intrusion of human activities into the breeding lagoons of the gray whale has been widespread since whale-watching excursions began to visit these areas in the early 1970s. Gard (1974) and Villa-Ramirez (1975) maintained that the presence of people seeking to view the whales close-up displaces gray whales from their preferred breeding areas, but they provided no conclusive evidence. Rice (1975) stated that "considerable harassment is caused by commercial cruise boats which take people into the calving lagoons to see the whales." Additional speculation came from Gilmore (1978) who wrote that the "entry of man with his industrial or recreational activities into the calving and courting lagoons . . . , could only have an adverse effect on the reproduction and survival of the newborn [whales]."

In seeking a biological basis for the argument that whale-watching excursion vessels pose a significant threat to breeding gray whales in Laguna San Ignacio, we attempted to assess the long and short-term demographic effects on gray whales including changes in abundance, distribution, and mortality that may occur as the result of repeated encounters with excursion vessels and their related activities. To our surprise, none of the adverse consequences that we proposed might result from exposure to human activities were substantiated. Rather, our findings to date suggest that the gray whales possess sufficient resiliency to tolerate the physical presence and activities of whale-watching vessels and skiffs and the noise produced by this level of activity without major disruption.

Gray whales did not shift their distribution from Laguna San Ignacio in response to human activities. They continued to return to the lagoon, and there was no decrease in whale abundance concurrent with the growth of the thriving whale-watching industry within the lagoon. In fact, the whale population in Laguna San Ignacio has steadily increased since whale-watching activities began in 1974, as demonstrated by the comparison of previous aerial surveys over the past 35 years with our 5 years of abundance counts. Moreover, the increase in gray whale abundance in the lagoon each year exceeded the estimated rate of growth of the population, suggesting that gray whales were preferentially utilizing this lagoon even with the presence of whale-watching activity. Further evidence of the grays' apparent tolerance of whale-watching disturbance, which is of major importance to their reproductive success, is the fact that the number of female–calf pairs inhabiting the lagoon during the birth period also increased significantly at a rate approximately 10% per year above the population growth between 1978 and 1982. We feel that a key factor responsible for maintaining the stability of the whale population in Laguna San Ignacio was the establishment of the gray whale refuge in the lagoon, which serves to regulate the number of vessels operating in the lagoon and provide an area free of all vessel activity as a sanctuary for the use of the whales (particularly females with calves) (Vargas, 1981).

Our index of whale abundance in all regions of the lagoon throughout the season revealed that patterns of use of the three lagoon interior areas have been essentially the same in all years despite increased levels of tourism. The upper lagoon and the lower lagoon merit special consideration. For instance, the number of females and calves that utilized the upper lagoon nursery area showed a significant increase, indicating that human activities in the constriction of the main entry channel at Punta Piedra did not impede their access to and from the upper area or prevent them from entering the lagoon. If tranquility within the lagoon is important to females with calves, then perhaps containment of whale-watching activities in the lower lagoon has had a beneficial influence on the whales in that the closed middle and upper lagoon nursery areas provide a refuge where females with calves remain relatively undisturbed.

In the lower lagoon, gray whales have continued to co-exist next to whale-watching activities. The whale population has made no detectable shift away from the lower lagoon toward areas of less human contact. Although the lower lagoon is the smallest of the three lagoon sections, it was the region most heavily utilized by the whales. This area consistently contained 65% of the single whales during the first half of each winter, and later was occupied by 87% of the female–calf pairs. In fact, each year, whale density was greatest in this area when female–calf pairs occupied it exclusively during the last half of each season. Thus, it is reasonable to conclude that the single whales and female–calf pairs have not been displaced from their preferred habitat as a result of whale-watching activities in the lower lagoon from 1978 to 1982.

The whales' continued utilization of the lower lagoon during the presence of whale-watching activities may be related to the fact that whale-watching skiffs were operated only during 8 daylight hours, or approximately 33% of each day that they were present in the lagoon, while the remaining 66% of the day, the whales were free to move about the lower lagoon unencumbered by interruptions caused by whale-watching skiff activity. On a seasonal basis, in fact, skiffs were only in use during approximately 22% of the time. Similarly, excursion vessels were underway only during daylight hours, and operated their main engines (which produced the greatest amount of waterborne noise) for only 2% of each season. If night movement is an important element in the gray whale's winter life cycle, then the lessened vessel traffic during this time is likely to contribute to their apparent ability to tolerate vessel activity within the lagoon. Indeed, there is some evidence from behavioral observations in Laguna San Ignacio which demonstrates that the whales are active at night. For instance, from nighttime observations with a starlight scope, Swartz and Jones (1981) determined that there were no outstanding differences in the types of behaviors exhibited by females and calves, lone single whales, and groups of single whales during the night and the day in Laguna San Ignacio. At night, whales jumped out of the water (breached), held their heads above the surface (spy-hopped), moved around the lagoon as singles or in groups, rolled at the surface, or remained motionless, drifting with the current (Swartz and Cummings, 1978). Furthermore, Mate and Harvey (1981) and Harvey and Mate (Chapter 24, this volume) reported that "radio-tagged whales generally left the lagoon during the night and returned in the morning hours."

Another factor that may contribute to the continued use of the lower lagoon by gray whales is the method of whale-watching employed by the skiff operators. The primary objective of the whale-watching excursions is to provide an opportunity for the passengers to view free-ranging gray whales in their natural habitat. Paying passengers and crew generally show a genuine respect for the whales and a desire to minimize their disturbance (Gilmore, 1976). Most skiff operators have had years of experience at operating skiffs around whales and have learned that gray whales are not seen by forceful pursuit (Storro-Patterson, 1981). Thus, practices that overtly disrupt whale behavior or cause the whales to flee from whale-watching skiffs are not generally employed. On the contrary, when following whales, skiff operators typically move at slow speeds, usually following a whale for only a short distance or remaining stationary with the engine running in neutral waiting for whales to pass by. It is to their advantage not to "run" a female with a newborn calf or to "spook" the whales and cause them to leave the whale-watching area. Additionally, because gray whales are so numerous in Laguna San Ignacio, if one individual shows avoidance behavior, many other whales are available for skiff operators to follow instead.

It is also possible that because of their continued exposure to boat noise and whale watching at the controlled level observed during our study, gray whales may have, to some degree, become habituated to the vessel activity in the lower lagoon. In other words, gray whales may be growing accustomed to the presence of tourist vessels in this lagoon. A finding that lends support to this idea is the widespread increase in the incidence of friendly whales in this lagoon. Previously, Gilmore (1976) remarked that friendly whale behavior "suggests that sport-fishing [i.e., whale-watching] boats and their skiffs have not been harassing the whales, disturbing their calving, nursing, and courting, as have been contended." Likewise, Reeves (1977, p. 20) quotes Hubbs (in litt.) as stating that the San Ignacio whales "have shown very definite indications of becoming accustomed to the party boats [i.e., whale-watching vessels] and the small craft, and have actually, in some instances, given every indication of inviting attention and even physical, friendly contact." At the time these encounters were first reported, one could argue that the friendly whale phenomenon was aberrant behavior by a few animals. During our project, however, we witnessed the incidence of friendly whale behavior grow from a few isolated encounters each season to a commonplace event that involved numerous whales and was experienced by nearly every whale watcher aboard the whale-watching excursions to the lagoon.

Finally, we obtained no conclusive evidence that whales move out of the general area of whale-watching activities during or on the day following human disturbance, which further suggests that whale-watching did not significantly disturb gray whales in the lagoon. Support for this comes from the pairwise comparison of the whale abundance on days with and without the presence of excursion vessels. These activities did not seem to alter the overall distribution of whales in the lagoon or change the distribution of whales in the area of chronic disturbance. Gray whale demography in the upper and lower lagoon, and in the lagoon as a whole did not change significantly with the arrival or departure of excursion vessels in the lower lagoon. Unfortunately our sample size of paired days with and without disturbance was relatively small and, therefore, may not be sufficiently representative to allow the formulation of a conclusion regarding the short-term cause–effect relationship between the whales and whale-watching activities. Given the small sample size, caution should be used when interpreting these results as additional data will be required to fully evaluate the short-term significance of vessel disturbance on whales in the lagoon.

A very important consequence of the disruption of gray whales by whale-watching activities in the lagoon as a whole would be the potential for increased mortality of calves, either as the direct result of collisions with vessels or separation from their mothers, or as the indirect result of severe vessel-induced stress. Reeves (1977) speculated that whale-watching activity may cause calves to be separated from their mothers and possibly abandoned, which would result in the death of the abandoned calf. From our findings in Laguna San Ignacio, it does not appear that whale-watching activity has caused an increase in calf mortality. Calf mortality was highly consistent at four dead calves per year during five winters and five calves in one winter between 1977 and 1982. There was no indication that vessel activity contributed to any of these deaths. Additional evidence indicating that the effects of whale watching on calf mortality in Laguna San Ignacio must not be too severe is the finding that calf mortality in this lagoon was proportionately the same as calf mortality in three breeding areas not visited by significant numbers of whale-watching excursions.

There have been several studies in recent years which suggest that grays and other species of whales are able to accommodate to various kinds of human disturbance. Reeves (1977), who investigated the problem of whale harrassment at the breeding lagoons, stated that the continued high level use of Laguna Ojo de Liebre by gray whales following relocation of commercial salt shipping operations from Laguna Guerrero Negro to Laguna Ojo de Liebre after 1967, suggests that the movement of salt barges "may not be such a nuisance to them." Laguna Ojo de Liebre is, by far, the largest and perhaps the most important single breeding area of the gray whale, and Reeves contends that because it is a large area, "the whales there simply may have been able to 'move-over' and co-exist next to the barges." Based on his aerial surveys of this lagoon in the 1970s, Storro-Patterson (1981) agrees that the whale distribution in Laguna Ojo de Liebre seems to be only minimally effected by salt barge traffic. A similar apparent accomodation to vessel disturbance was reported by Fraker *et al.* (1982) who concluded that bowhead whales (*Balaena mysticetus*) did not permanently vacate areas where they had been exposed to short-term noise from seismic surveys, dredges, and vessel disturbance and that "flight" response seemed brief in duration and was usually followed by a return to normal activities. Watkins and Schevill (1979) reported that feeding humpback whales (*Megaptera novaeangliae*) were not disrupted by the passage of an oil tanker to within 800 m of the animals. Humpback whales wintering off Maui, Hawaii also appear to habituate to routine vessel traffic activity associated with the harbor (Darling, 1983).

On the other hand, although the current levels of whale-watching activity in Laguna San Ignacio do not appear to be having a detrimental effect on the demography of gray whales in this lagoon, there is some evidence from other geographical areas that gray whales and other mysticetes are sensitive to and may be displaced by human disturbance under different circumstances. For example, during the gray whales' recent recovery from depletion, their utilization of Laguna Guerrero Negro has varied widely (Storro-Patterson, 1981). By 1967, the evaporative salt works located in the town of Guerrero Negro was shipping approximately 3 million tons of salt per year out of the lagoon. Prior to the growth of the salt industry, Gard (1974) stated that the number of gray whales using Laguna Guerrero Negro had increased steadily during the 1950s. As salt-barge traffic and dredging activities increased with the growth of the salt industry, Gard's aerial counts of gray whales decreased to zero by 1964. Following the relocation of the salt works to Laguna Ojo de Liebre in 1967, salt shipping ceased in Laguna Guerrero Negro and counts of whales increased to 104 animals by 1973. Gard speculates that the "shipping of salt from this lagoon between 1957 and 1967 apparently drove out the whales, but they reinvaded the lagoon in substantial numbers after shipping was eliminated." In assessing the effects of human activities on the whales, however, it has been very difficult to determine whether salt shipping was entirely responsible for the whales abandonment of the lagoon. Concurrent dredging operations to maintain the channel of the lagoon, natural variations in water temperature or chemistry in the habitat, or biological changes within the population itself may have also contributed to the changes in lagoon use (Storro-Patterson, 1981). In the case of humpback whales, it has been proposed that the apparent sudden abandonment of Glacier Bay, Alaska, by humpback whales in 1978 may be due to a dramatic increase in whale watching and other fishing and recreational vessel traffic within the confines of the bay, suggesting that the whales' tolerance for vessel activity had been exceeded (U.S. Marine Mammal Commission, 1980; Baker *et al.*, 1982).

During the course of this study from 1978 to 1982 we have accrued no statistically significant evidence to substantiate the contention that whale watching has had a detrimental effect on the demography of gray whales in Laguna San Ignacio. However, it may well be that human activities in the lagoon, if they negatively impact the whales, do so in an indirect manner. For instance, the cumulative effects of continual exposure to increased water-borne noise, visual stimuli, restriction of space available to whales, or stress associated with vessels being in and passing through whale areas could have serious biological implications if, for example, gray whale reproductive fitness is reduced over the long term (U.S. Marine Mammal Commission, 1980). Studies of other species of large mammals suggest that stress may have distinct physiological and population effects (Geraci and St. Aubin, 1980; Eisenberg, 1981), and that significantly loud noise could mask important environmental noise and/or interfere with communication between whales (Davis *et al.*, 1983). Clearly, the degree to which the gray whale is affected over the long term by habitual exposure to human activities will require continuous evaluation of their abundance, distribution, and productivity. The breeding lagoons provide an excellent opportunity to continue to obtain this information.

In conclusion, to date, whale-watching activity in Laguna San Ignacio does not seem to pose a serious threat to the gray whales, but its potential for becoming one should be acknowledged so that future developments can be monitored carefully for the benefit of whales and for humans.

Friendly Whales

The apparent interest in human activities exhibited by friendly whales in Laguna San Ignacio confounds the argument that whale-watching activity harasses gray whales. The friendly whale phenomenon has also given rise to many important questions. For instance, if whale-watching activity is not benign and seriously disturbs gray whales, why has curious behavior developed? Why has this behavior persisted year after year? And, are recent reports of friendly whale behavior outside Laguna San Ignacio indicative of the spread of this behavior throughout the gray whale's range? The interaction involving calves is perhaps the single most astounding case, as calf participation contradicts most previous beliefs about maternal protection. Friendly mother gray whales seemingly do not perceive the interaction between the boats and their calves as a threatening situation.

Speculation as to why whales appear to demonstrate curiosity is widespread among the scientific and lay communities alike. In a letter to the editor of *Science Magazine*, Wolfson (1976) suggested that the present gray whale population, recovering from near depletion, and composed of primarily young animals, has never been severely harassed by the whaling industry, and therefore has never become conditioned to avoid boats.

Gilmore (1976) proposed that the whales are curious about the small boats that hover over them in the lagoons. He felt that continued exposure to boat noise has probably conditioned most gray whales to tolerate the vessels and has encouraged some whales to approach and even explore whale-watching skiffs.

Storro-Patterson (1981) commented that this behavior may be the result of the method of whale-watching employed by the skiff operators in the lagoon. In his opinion, the skiff operators do not forcefully pursue the whales, but instead "almost seem to 'tease' the whales by refusing to follow them for more than 20–50 yards. They move at very slow speeds or stay in one place waiting, but always with the motor running, often in neutral."

Finally, it is widely accepted that the acoustical sense of cetaceans is their most important sensory process, and we believe that gray whales are initially attracted to some sounds of the outboard engines. They appear to show an interest in the submerged portion of the outboard engine running in neutral, such as the nonrevolving propeller and exhaust ports from which sound emanates. Some whales repeatedly bumped the still propeller of the engine with their rostrum and even took it into their open mouth. The whales avoided Mexican fishing boats with 40-hp engines running at high speed. However, they approached and even followed 20-hp engines running at moderate or low speed. Curious whales usually left the vicinity of idling outboard engines when they were shut down, and they also avoided nonmotorized vessels including kayaks, canoes, and small sail boats. Many of the sounds from gray whales fall within the frequency range of slow-running (or idling) outboard engines (Swartz and Cummings, 1978; Chapter 22, this volume). We agree with Dahlheim *et al.* (Chapter 22, this volume) that in addition to engine sounds, other factors may be involved in maintaining the friendly behavior once the whales physically contact the boat. We suspect that tactile stimulation from rubbing against the boat and from the "strokes" of the passengers act in concert with engine sounds and other stimuli to reinforce curious behavior over the long term.

To determine whether gray whales had displayed this behavior before the 1975–1976 reports from Laguna San Ignacio, we and our assistant Mike Bursk searched the literature and spoke to individuals that had worked in the breeding lagoons prior to 1975. There were no reports of friendly whale behavior in the literature prior to 1975, and investigators that had studied gray whales in the lagoons had not experienced these animals (R. M. Gilmore, C. L. Hubbs, K. S. Norris, T. J. Walker, and others, personal communications). At the San Diego Natural History Museum, we found a chart of Laguna Ojo de Liebre made by Jim Mills, a Santa Barbara Pharmacist. The chart, dated in the early 1960s, noted "curious and friendly whales" in the lagoon. Captain Bill Lang, an excursion vessel operator, spoke of a few experiences with curious gray whales while running whale-watching trips to Laguna Ojo de Liebre in the late 1960s. Captain Lang recalled that small whales lingered behind the excursion vessel, apparently inspecting the empty skiffs tied astern. And, occasionally whales approached the skiffs filled with whale watchers, as they cruised about in the lagoon (Swartz and Bursk, 1979). But, at this time, gray whales were not to be trusted. From the days of commercial whaling, the whales, particularly females with calves, held a notorious reputation for inflicting violent attacks on pursuers. The name "devilfish" was well earned; and, consequently, close contact with whales was avoided. Perhaps the forerunners of friendly whales were in

Laguna Ojo de Liebre, but cautious skiff operators were hesitant to let any whale get too close to his skiff full of passengers.

With the closing of Laguna Ojo de Liebre, attention focused on Laguna San Ignacio as the prime whale-watching location. Because Laguna Ojo de Liebre was closer and easily accessible for U.S.-based excursions operators, Laguna San Ignacio had received few visitors; thus, we found no records of past expeditions. We spoke to the residents of La Laguna, a San Ignacio fishing village, and none were familiar with friendly whales. However, for these people any whale encounter was unlikely because the local fishermen avoid all contact with them. When traveling across the lagoon, the fishermen usually motor their pongas over sand bars to minimize the risk of colliding with a whale. While crossing deep channels, they pound on the hulls of their boats and sing loudly as if to alert the whales (Swartz and Bursk, 1979). The first bonafide reports of friendly whales in Laguna San Ignacio, then, were the encounters during the 1975–1976 winter.

In summary, the phenomenon of friendly gray whales in Laguna San Ignacio between 1975 and 1982 suggests that not all interactions with boats are necessarily disturbing to the whales. The bottom line that virtually all whale watchers have agreeded upon is that whether or not a whale exhibits curious behavior is entirely up to the animal; in other words, friendly whales find you, you don't find them. The educational, recreational, and economic importance of carefully controlled whale-watching activities is evident; however, the observation that grays occasionally jostle boats or appear to act rambunctiously (Swartz and Jones, 1981) signifies that there can be some degree of potential threat to humans as well as harassment of whales. As noted by Baker *et al.* (1982), the increased incidence of "jostling" of boats by gray whales "may indicate aggressive behavior or may only reflect the actions of the laws of probability: that accidental contact is increasingly more likely with increased human use of the whale habitat." In any event, it is imperative that the whale-watching community be reminded that gray whales are wild and immensely powerful animals and need to be treated with great caution.

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SC/34/PS4

Gray Whale (*Eschrichtius robustus*) Calf Production and Mortality in the Winter Range

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ABSTRACT

Annual gray whale (*Eschrichtius robustus*) calf production and mortality were empirically estimated from data collected in Laguna Guerrero Negro, Laguna Ojo de Liebre, and Laguna San Ignacio, Baja California Sur, Mexico between 1980 and 1982. A gross annual production of 1,185 calves with a 5.4% mortality based on lagoon strandings yielded a net production of 1,121 calves. This represents a 7.0% annual rate of production based on the best estimate of the current population size of 15,942 gray whales. By comparison, the proportion of calves passing Pt. Piedras Blancas, California in 1980 and 1981 was 4.3% (679) and 4.8% (769) respectively, suggesting a 31% calf decrease may occur between the lagoons and central California. Two periods critical to calf survival are postulated; the first period immediately follows birth, and the second corresponds to the calves departure from the lagoons and the beginning of the northward migration.

INTRODUCTION

Empirical data on calf production and mortality are not available for most cetacean species. Recent studies within the breeding and calving lagoons, and along the migratory route of the gray whale (*Eschrichtius robustus*) provide an opportunity to examine newborn calf gross production, mortality, and net calf production during the winter breeding season. This information is useful for analyzing gray whale population growth and recovery from depletion, and it may be useful in understanding other depleted cetacean populations. This paper will:

1. Estimate maximum theoretical calf production based on current gray whale population estimates, proportion of breeding females in the population, and pregnancy rates.
2. Examine empirical data on gray whale calf production and calf mortality in breeding lagoons.
3. Compare observed net calf production within lagoons with calf population estimates from shore counts of the northward spring migration.

ESTIMATED MAXIMUM ANNUAL GRAY WHALE CALF PRODUCTION

Population estimates for gray whales based on shore censuses of the fall migration at Monterey, California between 1968 and 1981 indicated an annual 2.25% rate of increase (Reilly *et al.*, 1980a). The 'best estimate' from a regression of thirteen annual counts was 15,587 for 1980 (Reilly *et al.*, 1980b), and at the above rate of increase would be 15,942 in 1981 and 16,304 in 1982. Additional studies supporting population estimates of this size include an age structured simulation of gray whale population history using Monterey data which yielded a 1980 population of 15,400 (Reilly, 1981), and two years of shore censuses of the northward migration from Pt. Piedras Blancas, California resulting in population estimates of 15,725 for 1980 and 16,140 in 1981 (Poole, 1981). These population size estimates are further supported by earlier independent estimates of 14,400 for 1976 (Hall, 1977), and 15,099 for 1977 (Rugh and Braham, 1979) from fall counts of southward migrating gray whales passing through Unimak Pass, Alaska.

Rice and Wolman (1971) proposed that the maximum theoretical rate of gray whale calf production was 12.8% based on an equal sex ratio (50:50), an adult breeding proportion of 56%, and an annual female pregnancy rate of 46%. Based on the current population estimates given above (Reilly *et al.*, 1980b), the maximum expected number of calves produced assuming a 12.8% rate of increase would be 2,072 for 1981, and 2,119 for 1982.

CALF COUNTS IN THE BREEDING LAGOONS

Gray whales give birth during a 66 day period approximately from 26 December to 1 March (Jones and Swartz, 1983) with a mean birth date of 27 January (Rice *et al.*, 1982). Evidence supporting this proposed calving period comes from studies of the passage of southbound late-pregnant females past San Francisco, California in December and January (Rice and Wolman, 1971), the peak counts of cow/calf pairs in Laguna Ojo de Liebre (Rice *et al.*, 1982) and Laguna Guerrero Negro (Bryant and Lafferty, 1983), and the range of birth dates observed in Laguna San Ignacio (Jones and Swartz, 1983). In Laguna San Ignacio the number of cow/calf pairs counted continued to increase after mid-February. This increase did not include newborn calves; rather, these calves were judged by their size, coloration, and extent of barnacle encrustation to be 1–2 months old and presumably emigrated from areas outside Laguna San Ignacio (Swartz and Jones, 1980; 1981; Jones and Swartz, 1983). Annual calving, then, appears to be near completion by mid-February, and calf counts made during this period would best represent gross calf production in each respective lagoon or coastal area.

Aerial surveys in the breeding lagoons and along the near-shore waters of Baja California, Mexico tend to underestimate abundance of gray whale calves when compared to simultaneous vessel surveys (Fleischer, 1980; Bryant and Lafferty, 1980; Rice *et al.*, 1982; Swartz and Jones, 1981; Storro-Patterson, 1982). Results of aerial surveys by various researchers, although available, are difficult to compare because of differences in survey dates, aircraft census techniques, and environmental sea state. Vessel surveys utilizing the same techniques were conducted in mid-February for three seasons in Laguna Guerrero Negro (Bryant and Lafferty, 1980, 1983), one season in Laguna Ojo de Liebre (Rice *et al.*, 1982), and for three seasons Laguna San Ignacio (Swartz and Jones, 1980; 1981; Jones and Swartz, 1983); therefore, we have elected to use only the results of vessel surveys in the following analysis. These surveys were limited to lagoon interiors because high surf conditions preclude vessel surveys of lagoon inlets and adjacent near-shore waters even though these areas are utilized by a significant proportion of whales throughout the winter (Swartz and Jones, 1980; Storro-Patterson, 1982; and Norris *et al.*, 1983).

The number of calves counted during vessel surveys, and the number of dead calves discovered in the three breeding lagoons of Laguna Guerrero Negro, Laguna Ojo de Liebre, and Laguna San Ignacio between 1980 and 1982 are summarized in Table 1. The average mid-February calf count in Laguna Guerrero Negro was 129.7. This number of calves, combined with the average of 3.3 dead calves/year, suggests an average annual gross calf production of 133 individuals. Similarly, for Laguna San Ignacio, an average count of 132 calves/year plus four dead calves/year yields an annual gross calf production of 136 animals. Data are available for only one season in Laguna Ojo de Liebre: in 1980 557 calves were counted in mid-February, 12–16 dead calves counted within the lagoon and 23 stranded on the ocean side of the barrier island. This makes an annual gross production at Laguna Ojo de Liebre of 573 if 16 dead calves are added to the 557 living calves counted.

There was no significant difference in the yearly stranded calf and calf counts for Laguna Guerrero Negro, Laguna Ojo de Liebre, and Laguna San Ignacio (chi-square = 0.148, p = 0.9287); thus, these data from within the lagoons were combined to yield a grand average mid-February calf count of 818.7, an average stranded calf count of 23.3, which give a combined gross calf production of 842 calves. Because bloated calf carcasses are known to move about and even out of lagoon interiors with the winds and tides (Swartz and Jones, 1978; Rice *et al.*, 1982), we strongly suspect that 23 calves found stranded on the beach between Laguna Guerrero Negro and Laguna Ojo de Liebre belonged to this lagoon system. If these 23 calves are not included, calf mortality and gross production would be underestimated. Adding these calves to the combined totals the gross calf production becomes 842 + 23 = 865 calves for all three lagoons.

LAGOON CALF MORTALITY RATE

Minimum calf mortality may be estimated from the number of dead calves discovered divided by the estimated gross annual calf production. The combined annual mortality for all three lagoons (Laguna Guerrero Negro, Laguna Ojo de Liebre, and Laguna San Ignacio) of 23.3 calves divided by the total estimated gross production of 842 gives an annual lagoon calf mortality rate of 2.8% (Table 1). If the 23 calves found stranded outside of Laguna Guerrero Negro and Laguna Ojo de Liebre are included, the mortality rate becomes 46.3/865 = 5.4%.

ESTIMATED TOTAL ANNUAL CALF PRODUCTION

Aerial surveys by Rice *et al.* (1982) examined major gray whale calving areas and ranked them by the proportion of the total calves counted within each area. These surveys were conducted in mid-February using the same observers and were flown during sea states of Beaufort No. 3 or less, at a constant altitude and air speed. We assume that the bias toward underestimation of calf abundance (as discussed earlier) was uniform during all surveys and the proportions of calves counted in each area are good estimates of actual distributions. The results of these surveys suggest that Laguna Guerrero Negro contained 9%, Laguna Ojo de Liebre 53%, and Laguna San Ignacio 11% of all the calves born that year, or 73% of all the calves produced in a given year. The remaining 27% of the calves were in the Bahia Magdalena lagoon complex and along the Pacific coast of the Baja Peninsula.

If the rates of production and mortality are

Table 1

Gray whale mortality and production in three breeding/calving lagoons between 1980 and 1982.

Lagoon	Year	Stranded calves	Mid-Feb. calf counts	Gross calf production	Mortality rate
Guerrero Negro	1980	4	115	119	0.034
	1981	4	161	165	0.024
	1982	2	113	115	0.017
Average		3.3	129.7	133	0.025
Ojo de Liebre	1980	16	557	573	0.029
Outer Beach LGN & LOL	1980	23	—	—	—
San Ignacio	1980	4	119	123	0.033
	1981	4	140	144	0.028
	1982	4	137	141	0.028
Average		4	132	136	0.029
Grand average (all 3 lagoons)		23.3	818.7	842	0.028
Grand average (including outer beach count)		46.3	818.7	865	0.054

equivalent for all the breeding/calving areas, including Bahia Magdalena and the coastline between lagoons, then the total expected gray whale gross calf production extrapolated from the above proportions would be 865/0.73 = 1,185 calves. The expected total annual calf mortality would be 5.4% of the total gross production, or approximately 64 calves. Thus, the net annual production would be 818.7/0.73 = 1,121 calves.

CALF ABUNDANCE ESTIMATES FROM MIGRATION COUNTS

The 1981 population estimate of 15,942 gray whales (Reilly *et al.*, 1980b) and the estimated net lagoon production of 1,121 calves generated above combine to suggest a 7% annual rate of production, compared with the theoretical maximum rate of 12.8% calculated by Rice and Wolman (1971) (Table 2).

Proportions of calves to adults observed during two short censuses of the spring northward migration are available for comparison with the estimated net annual lagoon production. Poole (1981) utilized Reilly's (1981) model to estimate that 15,725 gray whales passed Pt. Piedras Blancas, California in 1980, and 16,140 passed in 1981; of these 679 (4.3%) in 1980, and 769 (4.8%) in 1981 were calves. The difference between Poole's 1981 calf abundance estimate and the estimated annual net calf production (1,121 − 769 = 352) suggests a calf attrition or loss of up to 31% between the lagoons and central California.

A calf loss of 31% may be the result of an underestimate of northward migrating whales; however, Poole's gray whale population estimates of 15,725 for 1980 and 16,140 for 1981 agree with other independent estimates (Hall, 1977; Rugh and Braham, 1979; Reilly, 1981), and the increase between both years of 415 whales (2.6%) is consistent with the 2.25% annual rate of increase established for gray whales (Reilly *et al.*, 1980a). Unfortunately, estimates of the variance of these calf estimates are not available. Poole states that during the period corresponding to the northward spring migration of cow/calf pairs (from mid-April to the end of May), of 1,790 whales passing Piedras Blancas 264 (15%) were not cow/calf pairs, but may have been postpartum females that had lost their calves. These whales were almost always observed travelling in the presence of a cow/calf pair rather than alone.

If we add 264 to Poole's 1981 estimate of 769 calves to compensate for females that presumably lost their calves, we can account for 1,033 calves which is within 88 calves (8%) of our estimated net annual lagoon production of 1,121. This corroborates our estimated 31% loss rate of calves. If the missing calves do not die but disperse below central California, we would expect approximately 352 gray whales per year to be detected somewhere in the southern range. Except for two verified sightings of gray whale calves unattended by adults off Isla Guadalupe, Baja California, Mexico in April of 1973 and June of 1974 (Leatherwood, pers. comm.), a 13 meter long gray whale in Bahia de San Quintin, Baja California Norte in July 1977 (Aguayo, 1980), and a handful of unsubstantiated reports over the past 15 years, there is no evidence that gray whales in the numbers calculated above remain in the southern range.

DISCUSSION

The best available data suggest approximately 5.4% of the gray whale calves produced annually die within the breeding/calving lagoon areas and that an additional 31% decrease (presumed mortality) of the net lagoon production occurs during the first leg of their northward migration before reaching central California.

The strength of this analysis lies in the accuracy of data from the lagoons and the abundance estimates extrapolated from shore-based migration counts. Estimates of lagoon calf production and mortality are minimum estimates based on counts of cow/calf pairs and of dead calves found within the lagoons during the same time periods. Estimates of calves migrating past central California and estimates of gray whale population size are extrapolated from daytime shore-based counts corrected for whales missed due to poor visibility, whales missed before the first and following the last day of the census, whales that passed during the night time, and whales not sighted as a function of their distance from shore (Reilly *et al.*, 1980b). Although the majority of cow/calf pair sightings are well inshore, we cannot discount the possibility that a few pairs may migrate offshore beyond the sight of coastal census stations. Between 1969 and 1972 Leatherwood (1974) reports five cow/calf pairs migrated northward offshore through the Southern California bight. Similarly, in his 1982 aerial survey off central California, Poole (In Press) observed one cow/calf pair (4%, n = 24) 10.4 km offshore, while all other pairs sighted were within 1.2 km of the beach.

Evidence exists that the tail-end of the cow/calf northward migration may not have passed central California when Poole ceased his observations at the end of May. J. Harvey and B. R. Mate (pers. comm.)[1] reported 25 to 35 cow/calf pairs remained in Laguna San Ignacio and an unknown number were outside the lagoon inlet in the breakers on 26 April 1980. Throughout April and May sportfishing vessel operators sailing between San Diego and Baja California Sur report sightings of gray whale females with their calves moving northerly along kelpbeds and up to a few kilometers offshore (pers. comms)[2]. Storro-Patterson (1982) reports a few females and their calves remain at the lagoon inlets into May, and local

Table 2

Summary of gray whale calf production estimates based on the 1981 population estimate of 15,942 whales (Reilly, 1980b).

		No. calves	Source
Maximum theoretical rate of production	0.128	2,072	Rice & Wolman, 1971
Observed net production in lagoons	0.07	1,121	This paper
Pt. Piedras Blancas estimate	0.043 (1980)	679	Poole, 1982
	0.048 (1981)	769	

Mexican fishermen (pers. comms)[3] indicate gray whales may be found outside the lagoons as late as early June of some years. These observations imply that an unknown number of cow/calf pairs were not included in the central California abundance estimate, and if included they would reduce the disparity between estimated lagoon calf production and estimated calf abundance during the migration.

The frequency of dead gray whale calves found in the lagoons and the apparent loss of calves between the lagoons and central California suggest that two periods critical to the survival of calves occur during the first few months of a gray whale's life. The first period includes birth and the time immediately following birth. The physical appearance and condition of stranded gray whale calves examined in the lagoons indicate some are under-sized and may have been stillborn, while others drowned during birth or died within a few days after birth (Rice and Wolman, 1971; Rice *et al.*, 1981; Jones and Swartz, 1983). Because the gray whale population is recovering from very low levels, we would expect it to include a higher proportion of young females (perhaps first time mothers) than when the population reaches a stable age distribution, and that these females may not be as successful at reproducing as older females that have bred previously. Dead newborn calves are discovered throughout the birthing period (26 December to 1 March), but they are found only infrequently later in the season, suggesting that the probability of dying is greatest just after birth and decreases with time.

The second critical period of calf mortality would correspond to the cow/calf pairs' departure from the lagoon areas and their northward migration. It is reasonable to think some calves are unable to withstand the rigors of coastal migration, fall prey to sharks and killer whales (*Orcinus orca*), or become lost, disoriented, and ultimately separated from their mothers prior to weaning. Killer whale harassment of gray whales is well documented (Rice and Wolman, 1971; Baldridge, 1972; Poole, 1982; Norris, pers. comm.) and probably contributes significantly to the deaths of very young gray whales. Calves of the year comprised 43% of 97 gray whale strandings reported along their migratory route between 1950 and 1981, suggesting that calves die in significantly higher proportion to other gray whale age classes (Jones and Swartz, 1983).

In the present context, caution must be used in drawing strong conclusions about gray whale calf mortality and production in the breeding/calving lagoons because the data are incomplete as follows:

1. Estimates of the variance of the calf estimates from shore censuses, the variance of the population rate of increase, and the variance for the estimated lagoon calf production are not available and are necessary to assess the significance of these numbers.
2. Not all dead whales are discovered; some carcasses strand on beaches not visited by investigators, are lost at sea, or are consumed by scavengers. These data tend to underestimate mortality.
3. Not all calves born each year are detected; census counts represent minimum estimates of annual gross calf production. These data tend to underestimate calf production.
4. Census counts from different sites made at different times and seasons cannot be assumed to be independent; there may be mixing of gray whales (and calves) between lagoons, particularly just prior to northward migration. Census data should be collected simultaneously from all areas to be compared.
5. Lagoon censuses do not include the near-shore waters adjacent to lagoon inlets. These areas are utilized extensively by significant numbers of whales throughout the breeding season (Swartz and Jones, 1980; Norris *et al.*, 1983). Additional cow/calf pairs counted outside the lagoons would decrease the mortality rate but consequently increase the discrepancy between observed net calf production within lagoon areas and calf population estimates from shore counts of the northward migration.
6. Data are not available for all birthing areas; however, we must assume the rate of production and mortality observed in the three lagoons studied is representative of all areas. Additional data from these and other areas is needed.

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GRAY WHALE MORTALITY AT OJO DE LIEBRE AND GUERRERO NEGRO LAGOONS, BAJA CALIFORNIA SUR, MEXICO: 1984–1995

Gray whales migrate annually from their northern feeding grounds in the Bering and Chukchi Seas to their winter breeding and calving grounds along the coast of Baja California, Mexico. Swartz and Jones (1983) estimated that 5.4% of gray whale calves of the year die near or in the lagoons, and an additional 31% of calf mortality occurs by the time they reach central California in the first part of their northward migration. This increase in calf mortality outside the lagoons emphasizes the apparent advantage of the coastal lagoon habitats to reproductive success of this species. Calf survival may be enhanced by the combination of factors found in the breeding and calving lagoons (Rice and Wolman 1971, Jones and Swartz 1984, Sanchez 1991).

The objectives of this study were to (1) identify stranding locations within and adjacent to the lagoons, (2) determine periods of peak mortality during the winter reproductive season, (3) determine the sex ratio of stranded whales, (4) determine the age and sex class of stranded whales, and (5) identify and describe key factors that may influence the mortality of gray whales in and adjacent to the lagoons.

The outer coasts from the southern end of the entrance to Ojo de Liebre Lagoon north along Arena Island to the northernmost portion of Manuela Lagoon were surveyed each winter from 1984 to 1995 except for 1986 and 1994. We photographed, measured, sexed and noted the location of each dead whale encountered. In addition, we estimated date of death from the state of the decomposing carcass, location on the shore, and time elapsed since our previous search. Any unique markings or scars were noted. Each carcass was marked with a line tied around a flipper to prevent double counting.

A total of 191 whales were found. Length was determined for 176 whales, sex was determined for 146, and time of death was estimated for 117.

The southwest coast of Arena Island had the highest incidence (34%) of stranded dead whales (Fig. 1). Interactions among ocean currents, prevailing northwest winds, and tidal flow into and out of the lagoon are likely responsible for depositing floating carcasses in the area. Similar abundance of stranded whales at this same location was noted by Rice *et al.* (1981). These authors

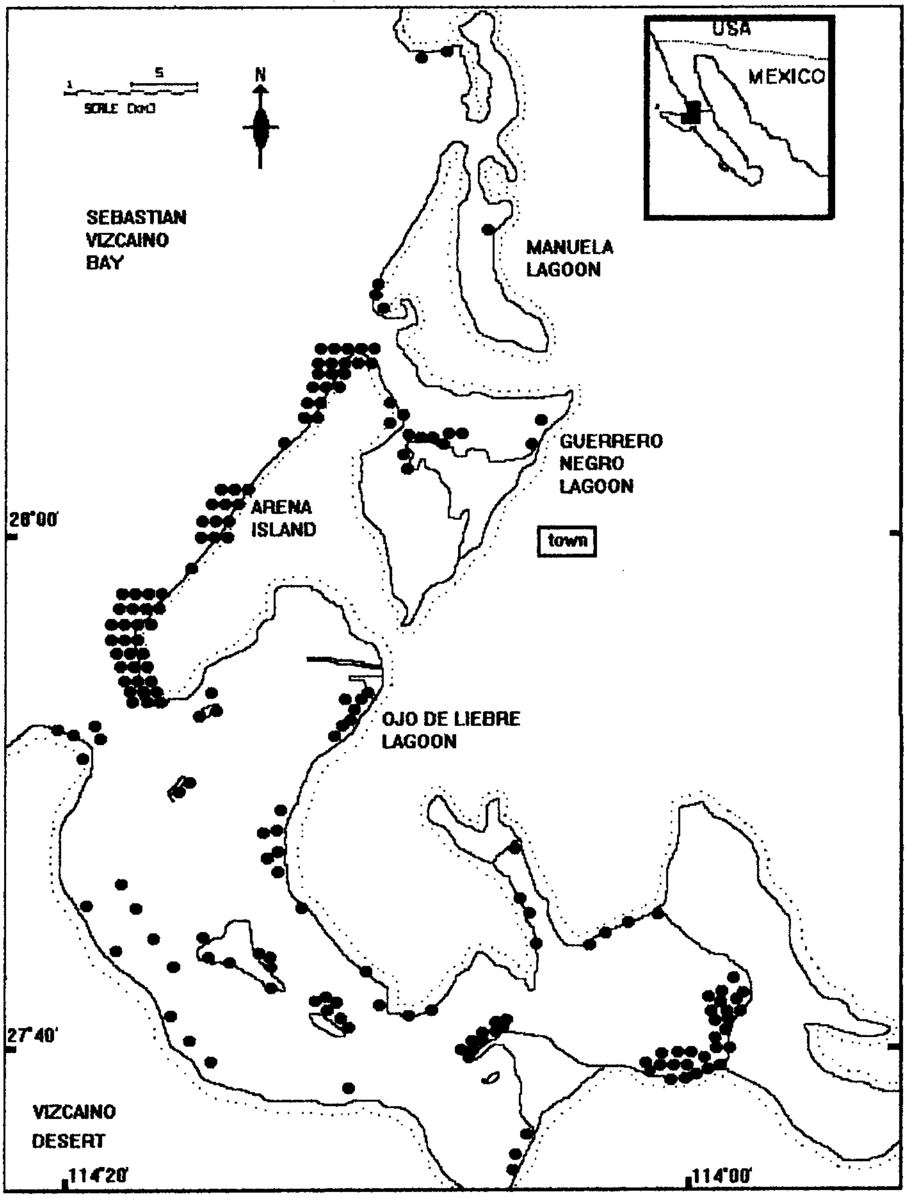

Figure 1. Stranding locations of gray whales (1984–1995).

stated that it could not be determined if calves found on this outer beach died inside or outside the lagoon. As they suggest, if the latter were true, it would support the contention that the lagoon interior offers conditions that contribute to increased survival of neonates.

The earliest calves of the season were observed in Ojo de Liebre and Guerrero Negro Lagoons on 27 December. The earliest that dead newborn calves

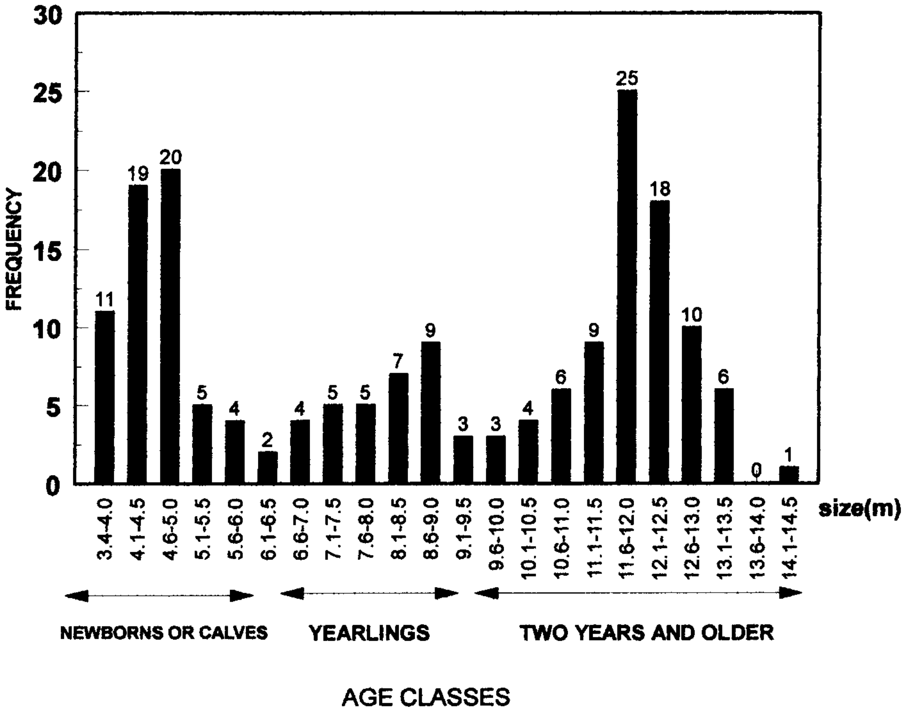

Figure 2. Size frequency of dead gray whales at Ojo de Liebre and Guerrero Negro Lagoons (1984–1995).

were found was 4 January and the latest was 9 March. This range of dates suggests a calving season of 73 d. Mean mortality date for calves was estimated at 2 February ($n = 39$, SD = 14.9), which is approximately one week later than the mean birth date of 26 January described by Rice (1983).

Fifty percent of the calves found were estimated to have died between 24 January and 10 February, and 77% between 15 January and 15 February. After the first half of February, the number of dead calves discovered declined, which suggests a higher survival rate for calves older than two weeks and/or a decline in the number of births during this period.

Only six calves between 5.6 and 6.2 m long were found. Sumich (1986) predicted a mean length of 5.69 m (range 5.35–6.03 m) at three months. This could mean that at this size/age range, calves leave the area or that survival chances are better so that fewer, more mature calves are found dead.

We found that 44.8% of whales larger than 6.0 m died between 1 and 28 February. The average mortality date for these whales was estimated at 15 February ($n = 78$, SD = 22.0), which is close to the peak of whale abundance in Ojo de Liebre Lagoon of 12 February reported by Rice *et al.* (1981) and Sanchez (1991).

The stranded whales can be divided into three size/age classes based on the frequency distribution of their lengths (Fig. 2). As Sumich (1986) proposed, the first class can be delimited by the low frequency of stranded whales measuring 6.1–6.5 m, which appears to separate the calf and yearling age classes. The average size of newborn calves was 4.63 m (n = 61, SD = 0.62, range 3.4–6.2 m). Our results are similar to the average calf length reported by Jones and Swartz (1984) (4.47 m), Rice (1983) (4.57 m), and Sumich (1986) (4.58 m). Whales measuring 3.4–6.5 m accounted for 34.6% of all the stranded whales measured. This supports the findings of Swartz and Jones (1983) and Sumich and Harvey (1986) that the most critical survival period with the highest calf mortality rate occurs during the first few weeks following birth.

Determining the limits for whales in the second size/age class was more difficult. Jones and Swartz (1984) observed, based on the growth rate of symbiotic barnacles in the breeding lagoons, that gray whale calves do not display adult barnacles during the season in which they are born, and it is only after at least one year that adult barnacles are observed on whales. The smallest stranded whale observed in this study with barnacles was 7.3 m long. We used this individual to set the lower size limit for this age class. The upper size limit for this class was set at 9.5 based on the low frequency of individuals between 9.1 and 10.0 m (Fig. 2). Whales measuring 6.6–9.5 m were considered yearlings. This age class had a mean length of 8.13 m (n = 33, SD = 0.82) which corresponds to other published ranges for yearlings by Jones and Swartz (1984) (9.0–10.0 m), Rice *et al.* (1981) (8.2–9.6 m) and Sumich (1986) (8.0 m). Whales in this size class accounted for 18.7% of all stranded whales measured.

The third size class includes whales larger than 9.6 m, which were all estimated to be two years and older. Mean length for whales in this class was 11.94 m (n = 82, SD = 0.86). Whales of this size class represented 46.5% of all stranded whales measured, compared to only 2.5% reported for San Ignacio Lagoon between 1977 and 1982 (Jones and Swartz 1984). Prior to 1988 it was rare to find a stranded whale longer than 9.0 m in the study area, but in 1990, 1991, and 1992, 79.5% of the stranded whales were 9.6 m long or longer (Table 1). The predominance of larger whales during this period follows an event during the 1989 winter in which an unusually large number of gray whales was observed inside the Gulf of California and as many as 54 whales, including a calf, were seen in Bahia de La Paz, Baja California Sur (Fleischer and Maravilla 1990).

Differences in the average lengths between female and male neonates and yearlings (Table 2) were not statistically significant (t-test; α = 0.05). For whales estimated to be two years and older, females were significantly longer (34 cm on average). This supports the conclusions of Rice and Wolman (1971) who found that female gray whales overall are longer than males.

The 1:1.3 ratio (61 to 84) of stranded females to males suggests that females have a higher probability of surviving in these areas or that males were more abundant than females in certain years, as was found in 1990, 1991, and 1992 (22 females, 55 males). This difference is particularly noticeable for stranded whales of the third size category ($\leq$ 9.6 m), where the female to male ratio was 1:2.1 (25 to 52).

Table 1. Annual distribution of stranded gray whales by age class.

Year	Calves 3.4–6.5 m	Yearlings 6.6–9.5 m	Two years and older >9.6 m	Total
1984	4	3	3	10
1985	4	2	1	7
1986[a]	3	3	0	(6)
1987	7	3	1	11
1988	4	6	2	12
1989	7	8	6	21
1990	0	2	14	16
1991	6	2	37	45
1992	7	0	15	22
1993	8	0	0	8
1994[a]	4	0	1	(5)
1995	7	4	2	13
Total	61	33	82	176

The stomach contents of three stranded adult gray whales were examined. The first was from a whale longer than 7.0 m, believed to be a male. The stomach contained about 3 kg of pebbles averaging 0.6 cm in diameter. Other than a reddish paste, no evidence of animal or plant material was contained in the stomach. The second stomach examined was from a 13.3-m female and was essentially empty except for some fragments of eel grass and a gray-green liquid. The intestines contained a dark gray paste in the anterior portion. The third stomach examined was from a 12.4-m female; it contained only small amounts of a dark greenish paste. These findings are consistent with the conclusion of Rice and Wolman (1971) that feeding does not occur on the winter breeding grounds.

Although it was not possible to determine the exact cause of death for the stranded whales, we observed some activities that could have contributed to their mortality. Calves were often observed being severely struck by adult whales that were involved in mating groups, and these blows could have resulted in fatalities. It is also possible that calves may become separated from their mothers by males, strong currents, or vessels and, once separated, become disoriented, exhausted, and die. In 1985 we observed a probable yearling (8.75 m) in Guerrero Negro Lagoon that appeared to be disoriented and unable to

Table 2. Number and mean length of stranded gray whales by age class and sex.

	Females			Males		
Age class	*n*	$\bar{x}$ (m)	SD (m)	*n*	$\bar{x}$ (m)	SD (m)
Calves	22	4.52	0.50	21	4.65	0.56
Yearlings	14	8.33	0.68	11	8.43	0.67
2 yr and older	25	12.16	1.07	52	11.81	0.64

find the channel to the lagoon entrance. It was observed on several occasions about to strand and was finally found dead along the shore. Five of the stranded whales examined had distinct shark bites, but none of these appeared severe enough to cause injury to vital areas or death. It is more likely that sharks feed on the carcasses before they strand, as suggested by Eberhardt and Norris (1964). With regard to human activities, one stranded whale had propeller cuts deep enough to cause severe bleeding and perhaps death. Three whales exhibited rope scars on their caudal peduncles, and one whale had an entire fishing net wrapped around it.

Three of the stranded calves were discovered alive, but two of these were later found dead from undetermined causes within 5 and 30 h from stranding, respectively. The third was pushed into deep water and was not seen again.

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LONG-TERM ASSOCIATION OF AN INDIVIDUAL LONG-FINNED PILOT WHALE AND ATLANTIC WHITE-SIDED DOLPHINS

Multispecies associations range from congeneric to interordinal and occur across a wide range of taxa. They have been described for numerous mammalian species, including cetaceans (references below). The nature of these associations is not always clear, and they may be of temporal or spatial happenstance without direct interaction, or more dynamic with direct interactions and coordinated activities. Although they typically involve groups of individuals from the associating species, occasionally a single animal will join a group of heterospecifics. Most multispecies associations appear to be relatively brief, and associations across years are quite rare. Bearzi (in press) reported seeing the same common dolphin (*Delphinus delphis*) with bottlenose dolphins (*Tursiops truncatus*) in two different years, and M. Poole (personal communication) has observed an individual spinner dolphin (*Stenella longirostris*) with bottlenose dolphins over four years. There are no other documented accounts of relationships of such duration. The association described here, of an individually identified long-finned pilot whale (*Globicephala melas*) with Atlantic white-sided dolphins (*Lagenorhynchus acutus*) over six consecutive years is thus highly unusual.

On twelve days between 1991 and 1996, a single long-finned pilot whale was observed 16 times with variably sized groups of Atlantic white-sided dolphins. Two of these days (13 June 1992 and 22 September 1993) included multiple sightings over several hours. Fourteen of the sightings were off the Massachusetts coast in the southern Gulf of Maine and one (4 July 1993) was in the northern Gulf of Maine, approximately 20 nautical miles east of Mt. Desert Rock, Maine (Table 1). No other pilot whales were observed in the vicinity of any of these encounters. The pilot whale was photographed in each case. Nicks in the dorsal fin, a prominent white scar on the right side behind

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GRAY WHALES BORN NORTH OF MEXICO: INDICATOR OF RECOVERY OR CONSEQUENCE OF REGIME SHIFT?

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Abstract. Every winter, most gray whales (*Eschrichtius robustus*) of the eastern North Pacific stock migrate from feeding areas in the Arctic to warm, shallow lagoons in Mexico, covering a distance of 15 000–20 000 km roundtrip. It is hypothesized that this migration to warmer climes is undertaken to reduce the whales' thermoregulatory energy requirement during winter when food resources are low. Calves are particularly vulnerable as they have yet to acquire a thick layer of blubber. Prior to the mid-1970s, newborn calves were seen primarily in Mexico's lagoons. However, since 1980, shore-based observers have reported increased numbers of calf sightings north of Mexico. Calves were greatly under-represented in the shore-based records as rarely did more than one independent observer at a time recognize the presence of a calf and a strong nearshore preference was not evident from the aerial data. Although cows with calves were difficult to detect, significant increases in average annual calf counts occurred at two counting stations in California, USA; counts increased in the late 1970s at a station near San Diego (southern California) and in the mid-1980s at a station near Carmel (central California). This trend is probably more than an increased emphasis on reporting calf sightings over the years for two reasons: (1) The first reports of calves stranding north of Mexico during the southbound migration occurred after 1976; and (2) calves were absent during many of the earlier censuses, and when they were seen, most appeared near the end of each migration. In subsequent years, calf sightings spread through the respective seasons, first at the southern stations (sometime after 1969) and then farther north (sometime after 1980). Increased calf counts at the northern stations were strongly correlated with warmer sea surface temperature anomalies. The interannual increase in calf sightings may be related to the increased abundance of the population, to changes in ocean climate, or to both factors. A one-week shift in the timing of the southbound migration since 1980 placed the mean passage date for pregnant females near Carmel at 8 or 9 January, coinciding with earlier estimates of median calving date (10–13 January). Assuming the median parturition date has not changed, this would mean that nearly half of the calving now occurs north of Carmel.

Key words: birth; calf; California; calving lagoons; counting stations; Eschrichtius robustus; *gray whale; Mexico; migration; recovery.*

INTRODUCTION

During late autumn each year, pregnant gray whales (*Eschrichtius robustus*) of the eastern North Pacific stock lead a migration from their feeding grounds in the Arctic south to wintering areas in or near lagoons of Baja California, Mexico (Rice and Wolman 1971, Rugh et al. 2001). Presumably as food resources dwindle, gray whales seek warmer climes where their thermo-energetic needs are minimized (Rice and Wolman 1971). During the winter they only feed opportunistically, relying on fat reserves until the following spring when they return to northern feeding areas (Nerini 1984, Dunham and Duffus 2001). In particular, newborn whales are vulnerable to heat loss because they have yet to acquire a sufficient layer of blubber (Rice and Wolman 1971). Besides providing an escape from the cold arctic seas, the warm, shallow lagoons of Baja California have been described as sites for breeding, calving, and nursing (Norris et al. 1977, Rice et al. 1981, Swartz 1986).

The assumption that gray whale calving does not, or rarely, occurs north of Mexico pervades much of the literature (e.g., Rice and Wolman 1971, Sund 1975, Rice et al. 1981, 1984, Sumich 1983, Swartz and Jones 1983, Sumich and Harvey 1986). Previous studies indicate that calving occurs from the coastal waters of San Diego, California, USA (Gilmore 1960, Hubbs 1960), south to the lagoons of Baja California (Scammon 1874, Hubbs 1959, Rice et al. 1981, Swartz and Jones 1983) and lagoons on the mainland of Mexico (Findley and Vidal 2002). San Diego Bay has been described as the northernmost calving site (Gilmore 1960), although Henderson (1972, 1984) did not believe this was an effective calving area.

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TABLE 1. Sightings of newborn gray whale calves during the southbound migration.

Study period	Location	No. calves	Calves/ whale	Source
Jan–Mar 1976	Southern California Bight	3	0.011	1
Jan–Mar 1977	Southern California Bight	4	0.015	1
Jan–Mar 1978	Southern California Bight	1	0.007	1
22 Jan 1979	Santa Catalina Island	1	—	2
9 Jan 1981	Long Point, CA	1	—	2
1980–1983, biweekly	central and northern California	12	0.004	3
8–21 Jan 1984	Monterey, CA	15	—	4
20–25 Jan 1986	Channel Islands, CA	20†	0.133‡	5, 6
13–15 Jan 1987	Channel Islands, CA	11§	0.080	6, 7

Note: Sources are as follows: 1, Dohl et al. 1981; 2, B. Samaras, *unpublished manuscript*; 3, Dohl et al. 1983; 4, Malme et al. 1984; 5, Jones and Swartz 1987*a*; 6, Jones and Swartz 1990; and 7, Jones and Swartz 1987*b*.

† Seventeen sightings made during strip-transect surveys plus three during nearshore surveys.

‡ Calculated from transect data only.

§ Seven on-transect sightings and four off-transect sightings (including a calf attacked and killed by killer whales).

Prior to the 1990s, there were only a few published accounts of gray whale calf sightings north of Mexico during the southbound migration (Leatherwood and Beach 1975, Sund 1975), and these papers described a single observation of a mother with calf. However, multiple calf sightings have been noted in a number of unpublished reports dating back to the 1970s (Table 1). Often authors of these earlier accounts (e.g., Leatherwood and Beach 1975, Sund 1975) suggested that calves born during the migration were premature because the birth occurred north of what was considered to be the calving grounds. Rice and Wolman (1971) examined gray whales collected near San Francisco during southbound migrations from 1959 to 1969. They found 26 females carrying near-term fetuses, but no recently postpartum females or calves. This seemed to confirm that calving did not occur during the southbound migration, at least not north of San Francisco. The unpublished accounts of large numbers of calves off Monterey and the Channel Islands in the mid-1980s (Table 1) prompted us to review and analyze datasets maintained by the National Marine Mammal Laboratory (NMML) and the American Cetacean Society (ACS) for gray whale calf sightings.

METHODS

Survey sites

Over the last 50 years, gray whale counts have been conducted during the southbound migration from shore stations near San Diego, Los Angeles, and Carmel, California, USA. Data from the following long-term studies were reviewed for gray whale calf sightings:

1) Census operations conducted by the National Marine Mammal Laboratory (NMML) and its predecessors were designed to monitor gray whale abundance from shore-based survey sites. Censuses were conducted near San Diego intermittently from 1952 to 1978 at Point Loma (32°42′ N) on a cliff 130–156 m above sea level and at La Jolla (32°30′ N) from a lookout 23 m above sea level (Fig. 1; Gilmore 1960, Reilly 1984). However, an undetermined number of gray whales migrated beyond the view of observers at the southernmost station at Point Loma, some as far as 200 km offshore from the mainland (Rice 1965). From 1967 to 2002, there were 22 censuses conducted near Carmel, initially at Yankee Point (36°29′30″ N) at a site 23 m above sea level, and then, starting in 1974, at Granite Canyon (36°26′41″ N) from the edge of a cliff 21 m above sea level (Reilly 1984, Rugh et al. 2001). During whale marking cruises conducted near Yankee Point in the 1960s, it was determined that few whales migrated beyond the visual range of observers on shore (Rice and Wolman 1971). This was confirmed in 1973, when five flights were conducted to test the width of the migration corridor (Sund and O'Connor 1974). Results indicated that 96% of the whales passed within 4.8 km of shore (94% within 1.6 km). This offshore distribution was also documented during aerial surveys at the Granite Canyon station, where fewer than 2% of the whales migrate beyond the sighting range of shore observers (Shelden and Laake 2002).

2) The American Cetacean Society (ACS) chapter in Los Angeles has maintained records of all marine mammals seen throughout daylight hours for nearly half of each year since 1979, except for the winters of 1981–1982 and 1982–1983. This project has operated from Long Point or Point Vicente (33°44′ N, 118°24′ W) on the edge of a cliff 38 m above sea level (Fig. 1). During 1984–1987, parallel stations also operated near the west end of Santa Catalina Island (33°28′43″ N, 118°36′18″ W; 206 m elevation) and at Cavern Point on Santa Cruz Island (34°03′13″ N, 119°33′47″ W; 96 m elevation). South of Point Conception (34°27′ N), as gray whales enter the Southern California Bight, the migration route spreads out with many animals going directly south through the Channel Islands, while others continue to follow the coastline (Fig. 1; Jones and Swartz 1987*a*). Because most gray whales use offshore

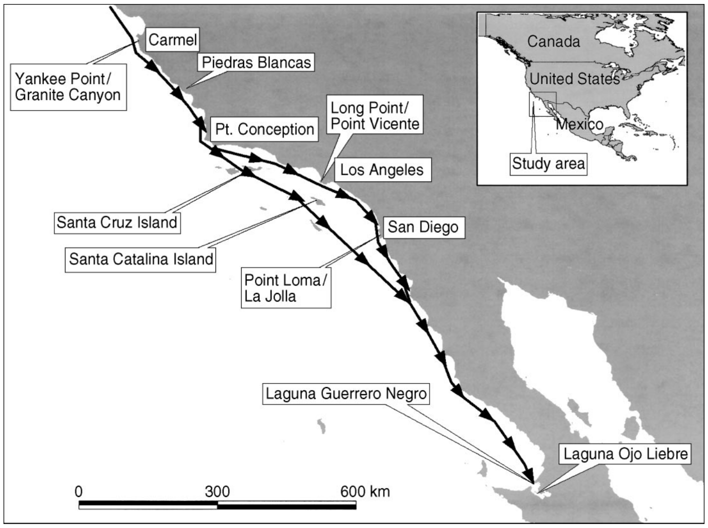

FIG. 1. Map of gray whale census sites located along the California, USA, coast and place names mentioned in the text. Arrows indicate the migration path of southbound whales.

migratory routes through the California Bight, especially on the southbound migration, the ACS project near Los Angeles has focused on ascertaining seasonal usage of the nearshore migratory path and documenting trends over time.

Data collection

Data collection procedures during censuses conducted by NMML and its predecessors have been fairly consistent since shore-based counts began in 1952 (detailed in Rugh et al. 1993). Throughout most daylight hours, observers maintained independent searches for whales, hand recording sighting and related effort and environmental data (referred to as standard watch). Prior to 1987, generally only two observers conducted the census throughout the entire field season (from mid-December to mid-February), each working five hours per day. Observers scanned a 130-degree field of view, confirmed identifications and recorded the number of animals in each pod (using 7 × 50 binoculars), with emphasis on careful and repeated observations. Distances of animals from shore were estimated in increments of 0.25 nautical miles (nmi; 0.463 km). Sightings of calves were recorded, although there were no explicit instructions on calf identification and observation methods.

After 1987, the 9-h daylight period was broken into three 3-h watches in order to minimize fatigue. Replacement observers were rotated into the schedule, so that rarely did any one observer need to stay for the entire survey season. The primary search area was reduced from 130 degrees to 60 degrees to concentrate the effort in a zone near and north of the beamline (Fig. 2). Binoculars (7 × 50) with reticles (marks etched into the binocular optics) were used to measure the angle of a sighting below the horizon, providing a more accurate calculation of distance from shore. Calves were systematically recorded in a dedicated column and described in the comment section of the data form. Starting in 1986, during a portion of each field season, a second observer did a paired, independent search, providing a test of the repeatability of the observational record (Rugh et al. 1990, 1993). Since 1995, tests of the observers were also made by conducting simultaneous watches through fix-mounted, 25× binoculars (Rugh et al. 2002). This provided improved sighting conditions at greater distances and precise records of whale sightings, but within a limited field of view. Aerial surveys were conducted in conjunction with the land-based surveys at Carmel in January of 1979, 1980 (Reilly et al. 1983), 1988, 1993, 1994 (Withrow 1990, Withrow et al. 1993, 1994), and 1996 (Shelden and Laake 2002) to document the offshore distribution of gray whales in the viewing area of the shore-based observers and to circle some whale groups for determining group size as a means of calibrating observer's estimates (Shelden and Laake 2002). These aerial surveys provided a more accurate assessment of the proportion of calves to adults and the distribution of sightings relative to shore.

During the ACS census near Los Angeles, volunteers search for whales each year from 1 December through 15 May throughout all daylight hours, seven days a week. All participants use binoculars (most recently with reticles), and spotting scopes were available to confirm and detail sightings. Weather data, including visibility and sea conditions, are recorded at least hourly. Observers identify and record various marine mammals and their behaviors, focusing on gray whales.

Identifying calves

Often synchronized blows of a pair of whales traveling close together, one distinctly smaller than the other, provided the first cue to shore-based observers. However, blow size alone did not indicate the size of a whale. Even large whales may make small blows at

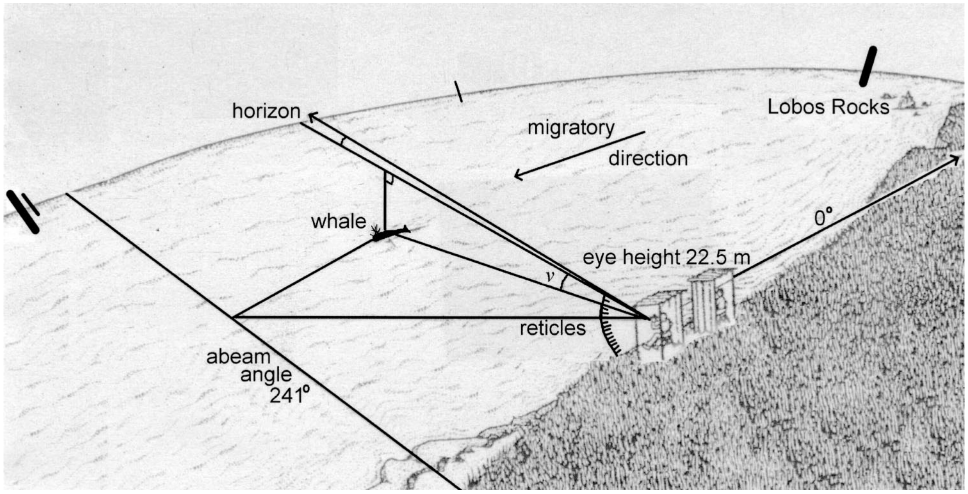

FIG. 2. Diagram of observer field of view at the Granite Canyon station near Carmel, California, where paired observers independently record whale sightings. Vertical angle to a sighting (v) is established relative to the horizon by using reticles in the binoculars (the horizon is 0.15° below true horizontal). Horizontal angles are magnetic bearings; 241° is perpendicular to the shoreline. Small tick marks on the horizon indicate a 60° field of view as used in recent years; broader tick marks represent the 130° field of view used in previous years.

times, and in some instances, the two blowholes of one whale may make different-sized blows. Although cows and calves have more or less synchronized diving intervals, the calves need to surface more often, and they spend less time at the surface than adults.

Calves often swim along the flank of the adult, usually on the left or right, but sometimes changing sides (Fig. 3). Shore-based observers notice the dorsal ridge more than any other part of the calf. The ridge on a calf is extremely narrow compared to an adult's, and the height of the ridge above the water is usually much lower for the calf than for an adult. Although the amount of back exposed during a surfacing changes rapidly through the surfacing, a calf's back is clearly smaller than an adult's. Flukes on a calf are tiny compared to the accompanying adult. Very young calves sometimes lift their entire head out of the water when they surface to breathe, instead of exposing little more than their blowholes as adults do. Gray whale calves do not have the pronounced markings of the adult caused by ectoparasites, especially barnacles; the skin of calves appears relatively clean and dark (Fig. 3a). Even so, calves do have some natural pigment patterns and may appear to have some mottling. Calves were

FIG. 3. Photographs of newborn gray whales observed during the southbound migration: (a) photo by Phillip Colla (Hawaii Whale Research Foundation) and (b) photo by Wayne Perryman (Southwest Fisheries Science Center).

PLATE 1. Kim Shelden (senior author) and Janice Waite track gray whales during the southbound migration past Granite Canyon, in central California (USA), where the gray whale census is conducted. Photo credit: NOAA Fisheries.

identified during NMML aerial surveys based on a combination of three characteristics: their size (usually one-third the length of the companion whale), coloration (pale and lacking barnacle clusters), and position (usually swimming beside the peduncle of the larger whale) (Fig. 3b).

Data analyses

Original data records were not available for shore-based censuses conducted between 1952 and 1956, therefore survey effort and gray whale counts were obtained from Gilmore (1955, 1960). Counts of whales observed during San Diego censuses from 1957 to 1978 were obtained from Rice (1981; National Marine Fisheries Service [NMFS], *unpublished data*). Computer database summaries provided tallies of total number of whales for the Carmel stations (1967 to 2002), but only identified calves in comment entries until 1987 (this meant reviewing the original data forms for calf sightings). Northbound whales were not included in the analyses. Calf counts were tabulated from raw data collected from 1959 to 1986, while computer database summaries provided these numbers for the NMML surveys conducted from 1987 to 2002. A calf sighting was considered valid when three independent reviewers agreed with the identification. A sighting was considered questionable, but still listed as a possible calf sighting, when discrepancies between the reviewers occurred. These questionable sightings were not included in the ratios of calves to whales. Calf counts and total number of whales observed were obtained for the aerial surveys conducted in January 1988, 1993, 1994, and 1996 (no calf sightings were reported in the 1979–1980 surveys).

During shore-based surveys near Los Angeles, the first three seasons (1979–1981) from Long Point and Santa Catalina Island were quite truncated, and though some calves were seen (Table 1), there were no special efforts made to identify and record calves. Since 1984, more attention was given to gray whale calf sightings during both the southbound and northbound migration. The intent was to improve the tracking of trends in calf recruitment. The number of southbound calves and whales was tabulated from the computer database maintained by the ACS-Los Angeles Chapter.

The proportions of calves relative to all gray whale sightings recorded each season at the respective stations was calculated based on raw counts of calves divided by the total count of gray whales, including calves. Census season dates were truncated on figure axes to simplify comparisons across years (e.g., 2001 refers to the 2000/2001 season). Calf counts were graphed and tested for changes in average annual counts over time. Log-transformed counts from each station were tested for potential trends over time using regression analyses. The seasonal distribution of calf sightings was graphed for each research site and compared across decades. Median passage dates were calculated for years with adequate samples (i.e., >2 calf sightings). Correlations between calf numbers and climatic variables were also explored.

Repeatability of calf sightings was tested by comparing records when independent, concurrent shore-based watches occurred at the NMML Granite Canyon station (i.e., paired, independent standard watches; paired searches through two 25× binoculars; and searches through 25× binoculars compared to the standard watch; see Plate 1). Records of individual pods observed during concurrent aerial and shore-based surveys in 1993 and 1994 were reviewed to determine the ability to see calves from shore relative to sightings from the air.

Offshore distances in kilometers were computed from reticle distances (Lerczak and Hobbs 1998) for those years in which binoculars with reticles were used during the standard watch (1987–2002) near Carmel. These distances were compared with the offshore distances of calf sighting made during aerial surveys (obtained by interpolating distances relative to time of sighting on the trackline [dead-reckoning] or global positioning system [GPS] locations) and using 25×

TABLE 2. Censuses of gray whales during the southbound migration from 1952 to 2002 (data from standard watches only).

Census sites and dates	No. southbound whales†	No. calves	Calves/whale
Point Loma			
26 Dec 1952–15 Feb 1953‡	982	0	0
1953/1954§	800	0	0
19 Nov 1954–28 Feb 1955‡	1646	0	0
1955/1956‡§	918	2	0.0022
2 Nov 1956–25 Mar 1957‡	1834	0	0
10 Dec 1959–15 Jan 1960	2344	0	0
27 Dec 1967–16 Feb 1968	1324	0	0
20 Dec 1968–14 Feb 1969	1154	1 (1)	0.0009
15 Dec 1975–11 Feb 1976	2822	8 (3)	0.0028
15 Dec 1976–13 Feb 1977	3648	4 (1)	0.0011
15 Dec 1977–17 Feb 1978	5122	11	0.0021
Yankee Point			
18 Dec 1967–4 Feb 1968	3091	0	0
10 Dec 1968–7 Feb 1969	3270	0	0
8 Dec 1969–9 Feb 1970	3419	1	0.0003
9 Dec 1970–13 Feb 1971	3306	2	0.0006
18 Dec 1971–8 Feb 1972	2745	0	0
16 Dec 1972–17 Feb 1973	4147	0 (2)	0
14 Dec 1973–9 Feb 1974	3901	0	0
Granite Canyon			
10 Dec 1974–7 Feb 1975	3825	0	0
10 Dec 1975–4 Feb 1976	4287	0	0
10 Dec 1976–7 Feb 1977	4657	0	0
10 Dec 1977–5 Feb 1978	3700	0 (1)	0
10 Dec 1978–9 Feb 1979	3887	1	0.0003
10 Dec 1979–7 Feb 1980	4906	1 (1)	0.0002
28 Dec 1984–7 Feb 1985	5343	13	0.0024
10 Dec 1985–7 Feb 1986	5300	23 (1)	0.0043
10 Dec 1987–7 Feb 1988	6072	4	0.0007
10 Dec 1992–7 Feb 1993	3210	10	0.0031
10 Dec 1993–17 Feb 1994	4754	36	0.0076
6–26 Jan 1995	1502	8	0.0053
10 Dec 1995–23 Feb 1996	4324	21	0.0049
9–23 Jan 1997	2035	7	0.0034
13 Dec 1997–24 Feb 1998	4101	60	0.0146
13 Dec 2000–5 Mar 2001	2950	8	0.0027
12 Dec 2001–5 Mar 2002	3137	18	0.0057

Notes: Numbers in parentheses indicate additional questionable calf sightings that were not included in the proportion calculation. The southern census sites are near San Diego (Point Loma/La Jolla), and the northern sites are near Carmel (Yankee Point and Granite Canyon).

† Whale tallies obtained from Gilmore (1960), Rice (1981), and the National Marine Mammal Laboratory gray whale database.

‡ Census site is Point Loma/La Jolla.

§ Survey effort data not available.

binoculars (with reticles etched on the optics). To determine where calves occurred within the migratory corridor, a comparison was made of distance data from the full field season of shore-based counts in 1993/1994 and 1995/1996 to aerial records collected during January 1994 and 1996.

RESULTS

The first calf sightings reported north of lagoons in Mexico occurred during the 1955/1956 census near San Diego (Table 2). There were no other reports until the 1968/1969 census, when a single confirmed and an additional unconfirmed sighting were recorded. However, the last three censuses near San Diego (1975/1976, 1976/1977, and 1977/1978) each reported multiple calf sightings with a peak of 11 sightings during 1977/1978 (Fig. 4). Calf sighting rates ranged from 0.001 to 0.003 calves/whale during these three censuses. In contrast to the increased sighting rates in the late 1970s near San Diego, the initial 13 censuses conducted near Carmel (645 km north of San Diego) from 1967 to 1980 had only five confirmed calf sightings (corresponding to $\leq$0.001 calves/whale), only two of which occurred during the late 1970s (Table 2, Fig. 5). The difference in calf sighting rates at the two sites was significant ($X^2 = 19.9$, df = 3, $P = 0.0002$). During the more recent 11 censuses that were conducted near Carmel from 1985 to 2002, proportions of calves increased to an average of 0.005 calves/whale, ranging up to 0.015 calves/whale (Table 2, Fig. 5), but no comparable re-

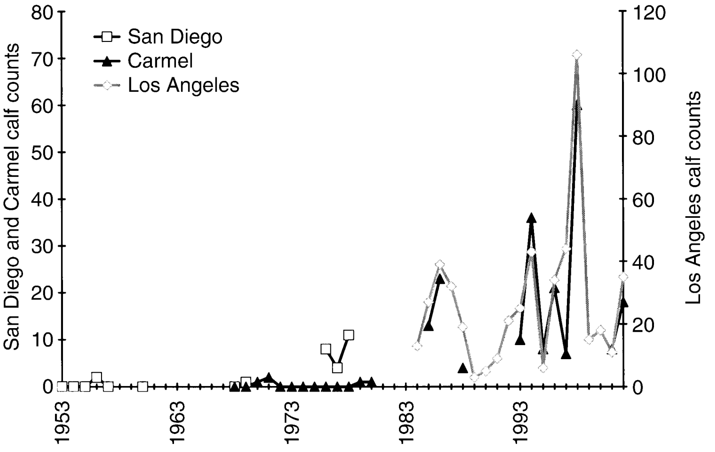

FIG. 4. Counts of gray whale calves observed during the southbound migration at counting stations near San Diego, Los Angeles, and Carmel, California.

cords were available from San Diego after 1978. During the same period, data from Los Angeles showed an average of 0.034 calves/whale, with annual values ranging from 0.005 to 0.086 calves/whale (Table 3, Fig. 5). The last three field seasons (1997/1998, 2000/2001, and 2001/2002) produced the first northbound calf sightings near Carmel (on 22 February 1998, 28 February 2001, 1 March 2001, 26 February 2002, 1 March 2002, and 5 March 2002). Northbound sightings were not included in analyses involving relative numbers of calf sightings.

Seasonal distribution of sightings

At the southernmost counting stations based in San Diego, calves were absent during many of the censuses prior to the 1970s, and when present, were observed only near the end of the southbound migration (Fig. 6). By the late 1970s, calf sightings near San Diego were scattered throughout the season (as early as 17 December and as late as 16 February). However, near Carmel, calves were absent during most of the censuses in the 1970s, and, when calves were observed, sightings were in the middle or the end of the migration (Fig. 7). In the 1980s, calves began appearing several weeks before the peak of the migration off Carmel (median date = 16 January; Rugh et al. 2001). A similar pattern was also observed during the 1990s. By the end of this study, sightings near Carmel were occurring throughout the season, as early as 25 December in the 1997/1998 season and as late as 1 March in 2001/2002 (Fig. 7). Near San Diego, 65% of the sightings occurred in January (26% in December), while at the Los Angeles and Carmel stations, most of the southbound calf sightings occurred in January (90% and 95%, respectively; Figs. 6–8). For these three stations, median calf sighting dates were similar (15–17 January; see asterisk symbols on Figs. 6–8), indicating that, during the southbound migration through the southern half of California, gray whale calves are more likely seen in mid-January.

The distribution of calf sightings at the Carmel station prior to and after the mid-1980s was compared to the median passage dates for all gray whales (Table 4). Before 1980, the few calves that were seen appeared well after the main migration had passed the site. After 1980, observations of calves before the migration peak (which was one week later than the pre-1980 period; Rugh et al. 2001) resulted in a median date of all calf

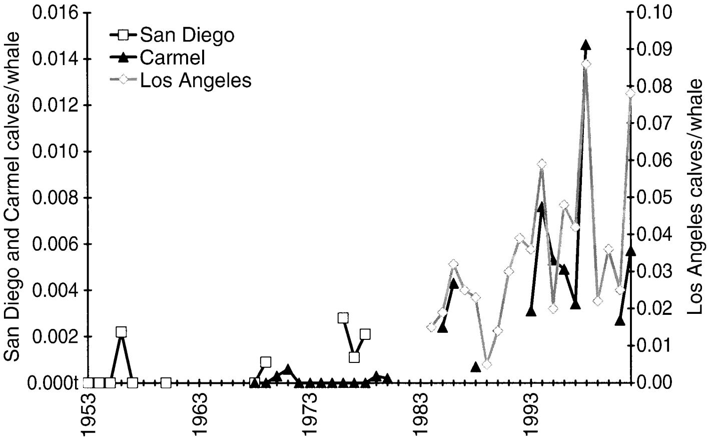

FIG. 5. Proportion of gray whale calves (calves/whale) observed during the southbound migration at counting stations near San Diego, Los Angeles (ACS), and Carmel, California.

TABLE 3. American Cetacean Society, Los Angeles Chapter, counts of gray whales during the southbound migration from 1984 to 2002.

Season	Station	No. southbound whales	No. calves	Calves/whale
1 Jan–31 May 1984	Long Point	898	13	0.015
1 Dec 1984–31 May 1985	Long Point	1001	17	0.017
29 Dec 1984–18 Feb 1985	Santa Catalina Is.	407	10	0.025
1 Dec 1985–17 May 1986	Long Point	903	18	0.020
1 Dec 1985–18 Feb 1986	Point Vicente	990	32	0.032
28 Dec 1985–16 Mar 1986	Santa Catalina Is.	682	7	0.010
1 Dec 1986–11 Feb 1987	Long Point	907	30	0.033
15 Dec 1986–20 Feb 1987	Point Vicente	1288	32	0.025
8 Jan 1987–1 Feb 1987	Santa Cruz Is.	1340	40	0.030
1 Dec 1987–14 May 1988	Point Vicente	831	19	0.023
1 Dec 1988–30 Jun 1989	Point Vicente	589	3	0.005
1 Dec 1989–6 Jun 1990	Point Vicente	361	5	0.014
1 Dec 1990–12 May 1991	Point Vicente	301	9	0.030
1 Dec 1991–3 May 1992	Point Vicente	545	21	0.039
1 Dec 1992–8 May 1993	Point Vicente	703	25	0.036
1 Dec 1993–7 May 1994	Point Vicente	735	43	0.059
1 Dec 1994–5 May 1995	Point Vicente	306	6	0.020
1 Dec 1995–10 May 1996	Point Vicente	706	34	0.048
1 Dec 1996–16 May 1997	Point Vicente	1053	44	0.042
1 Dec 1997–15 May 1998	Point Vicente	1230	106	0.086
1 Dec 1998–15 May 1999	Point Vicente	682	15	0.022
1 Dec 1999–15 May 2000	Long Point	500	18	0.036
1 Dec 2000–15 May 2001	Point Vicente	439	11	0.025
1 Dec 2001–15 May 2002	Point Vicente	449	35	0.078

sightings that was not significantly different from the median passage date for all gray whales ($t = -0.659$, $P = 0.52$).

Unobserved calves

Many calves were missed by shore-based observers. During independent, concurrent standard watches conducted near Carmel, there were 76 instances in which at least one observer recorded a sighting of a cow–calf pair, but 80% of the time the other observer entirely missed the pod or did not see a calf next to the adult. When observers were compared on independent searches through 25× binoculars, 11 calves were seen, but none were seen by more than one observer at a time. Among all of the records from watches through 25× binoculars, whether or not a second, independent search through similar binoculars was underway, there were 28 calves seen, but only four were also seen by observers on the standard watch. During experiments where the aerial crew directed shore-based observers to specific pods to test estimates of pod size, shore-based observers were able to locate only four of eight cows and never saw the associated calf. It was often noted in the sighting record that cows with calves were cryptic (i.e., barely breaking the surface to breathe and exhaling without casting a distinctive V-shaped blow). No corrections for calves missed by observers on the standard watch were included in calf counts in Table 2.

The distance cows with calves traveled from shore may have also contributed to the number of calves missed by the shore-based observers. The median distance calves were detected during a standard watch

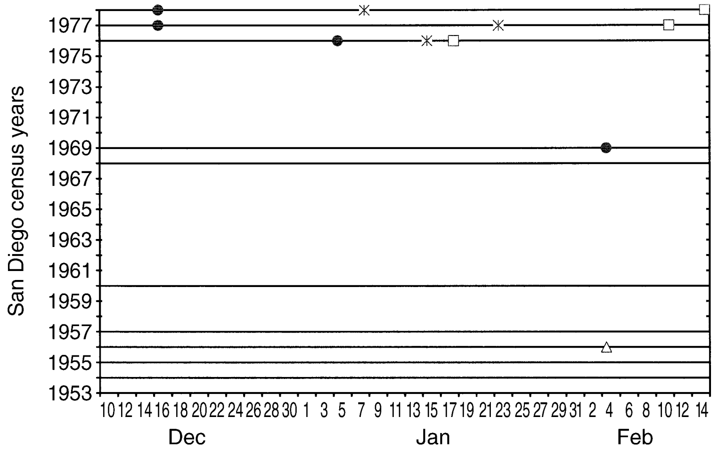

FIG. 6. Seasonal distribution of gray whale calf sightings at the southernmost counting stations near San Diego, California. Solid circles indicate first sighting of the season, stars (⁎) indicate median date, and open squares indicate last sighting. The open triangle in February 1956 represents two calf sightings for which observation dates were not provided (see Gilmore 1960).

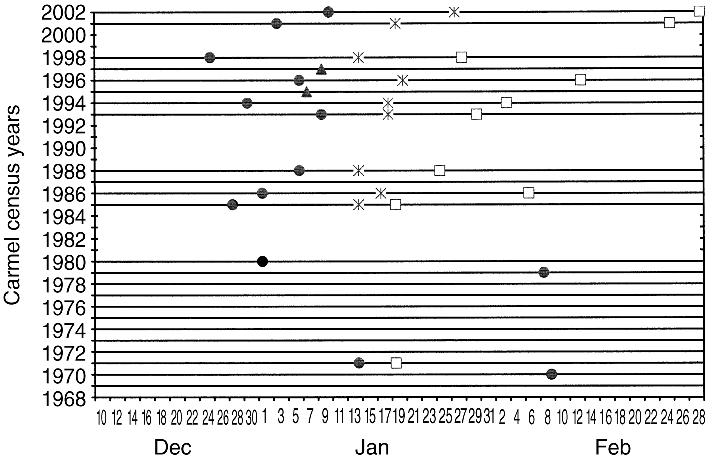

FIG. 7. Seasonal distribution of gray whale calf sightings at the northernmost counting stations near Carmel, California. Solid circles indicate first sighting of the season, stars (✳) indicate median date, and open squares indicate last sighting. Solid triangles in 1995 and 1997 indicate first sighting for a truncated field season.

was, in general, closer to shore than the distances reported using 25× binoculars or during aerial surveys (Table 5). About 99% of the southbound population passes within the shore-based observers' visual range of 5.6 km (Shelden and Laake 2002). Of the 1.28% (n = 18 pods) observed beyond 5.6 km during aerial surveys (Shelden and Laake 2002), only three were cows with calves (at 9.4, 14.3, and 33.9 km), representing ~10% of the calves observed during aerial surveys (n = 29; Table 5). However, if shore-based observers had difficulty identifying cows with calves beyond 2.6 km (the maximum distance calves were seen during the standard watch; Table 5), then 28% of the calves migrating past the site may have been missed due to distance alone based on the aerial survey data.

The proportion of calves to total number of gray whales seen from the air (0.022) was 6.3 times greater than the proportion seen from shore (0.003) when sampled during January (Table 6). The ratio of these proportions for aerial and shore sightings (6.3:1) gave an approximation of how many calves were missed from shore (i.e., shore observers saw only 16% of the calves in the viewing area). Recomputing the aerial ratios (Table 6) using only those sightings where offshore distances were available (n = 29) and excluding sightings beyond the shore-based observers' visual range of 2.6 km (n = 8), resulted in a 3.3:1 ratio between aerial and shore observations. Therefore, shore-based observers were seeing only 30% of the calves within their visual range of 2.6 km. Including calves missed beyond 2.6 km results in a 22% sighting rate.

Although the spatial distribution of cows with calves observed by shore-based observers was significantly different from that of other pods, with increased sightings occurring shoreward of the main migration corridor (Table 7), this distribution was biased because calf detections diminished rapidly with increasing distance, more so than the sightings of adults. Aerial survey data do not show as strong a nearshore preference.

Trends in calf counts

Although detecting calves was difficult, significant increases in average annual calf counts occurred near San Diego in the mid- to late-1970s compared to the 1950s and 1960s, and near Carmel in the mid-1980s through 2002 compared to late-1960s through 1980 (Fig. 4). The difference between averages of these annual calf counts was significant at both San Diego (t

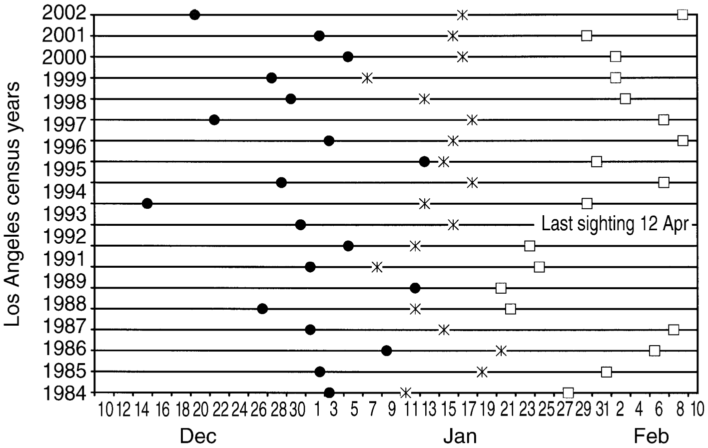

FIG. 8. Seasonal distribution of calf sightings at the ACS counting stations near Los Angeles, California. Solid circles indicate first sightng of the season, stars (✳) indicate median date, and open squares indicate last sighting.

TABLE 4. Median dates on which gray whale calves were seen, and median passage dates for the entire population, off Carmel, California, during the southbound migration.

Calves		
Date	N	All whales
Pre-1980; median of all calf sightings = 29 Jan, median passage date of all whales = 7 Jan		
9 Feb 1970	1	5 Jan 1970
16 Jan 1971	2	8 Jan 1971
8 Feb 1979	1	7 Jan 1979
Post-1980; median of all calf sightings = 17 Jan, median passage date of all whales = 16 Jan		
14 Jan 1985	13	14 Jan 1985
17 Jan 1986	23	14 Jan 1986
14 Jan 1988	4	12 Jan 1988
18 Jan 1993	10	13 Jan 1993
18 Jan 1994	36	18 Jan 1994
20 Jan 1996	21	16 Jan 1996
14 Jan 1998	60	18 Jan 1998
19 Jan 2001	8	25 Jan 2001
27 Jan 2002	18	20 Jan 2002

Note: Calf counts were made during standard watches.

$= 3.566$, $P = 0.035$) and Carmel ($t = 3.157$, $P = 0.003$). This increasing trend in calf counts over time can be modeled as a linear increase in the log-transformed counts near San Diego in the mid-1970s ($R^2 = 0.61$, slope $= 0.03$, $P = 0.004$), then near Carmel in the mid-1980s ($R^2 = 0.73$, slope $= 0.05$, $P << 0.001$). However, key years were not surveyed (i.e., 1969/1970 to 1974/1975 at San Diego and 1980/1981 to 1983/1984 at Carmel), so whether there was a gradual increase or a step-wise ''shift'' is unknown. This increasing trend leveled off after 1984 at Carmel ($R^2 = 0.02$) and is not apparent in the data from the Los Angeles station ($R^2 = 0.04$).

Climate correlates

We explored possible correlations between calf presence and changes in oceanic phenomena (sea surface temperature [SST]). West Coast SST anomaly data were obtained from the National Oceanic and Atmospheric Administration (NOAA), National Weather Service, National Centers for Environmental Prediction, and Climate Prediction Center affiliated web sites.[4,5] A positive correlation between warmer water temperature anomalies and increased numbers of calves was evident at Carmel ($r = 0.48$, $P = 0.008$) and Los Angeles ($r = 0.47$, $P = 0.022$), but not at San Diego ($r = -0.14$, $P = 0.676$).

DISCUSSION

The idea that gray whales birth calves in the ''calving lagoons'' of Baja California pervades the literature. However, the evidence presented in this report shows that many, if not most, of the calves are born during the southbound migration well north of Mexico. The disparity between earlier literature and current records may in part be due to a change in where calving occurs. Calf sightings have increased over a 50-year period of shore-based surveys of gray whales migrating south along the coast of California. Because calf sightings increased first at the southernmost site (San Diego in 1976) and then farther north (at Carmel in 1985), this trend was probably more than an increased emphasis on reporting calf sightings and changes in protocol over the years. There were no reports of calves during many of the earlier censuses and, when observed, most appeared near the end of each migration. The sightings then spread through the respective seasons, first at the southern stations and later farther north.

Adult gray whales are sometimes missed by shore-based observers even during good sighting conditions (19% are missed within the viewing area during standard watches near Carmel; Rugh et al. 1993). The small size of calves makes them even more difficult to see than adults. Although not as pronounced as the pattern observed for the northbound migration (Perryman et al. 2002), southbound cows with calves appear to segregate shoreward of the main migration corridor. However, adults, as well as cows with calves, traveling very close to shore were missed (Rugh et al. 1993). Reduced visibility, especially during fog and elevated sea states, probably affects sightings of calves more than of adults. Overall, calves were greatly under-represented in the shore-based records.

The upward trend in calf sightings may be related to the increased abundance of this stock of whales (rising 2.5% per annum from 1967/1968 to 1995/1996; Buckland and Breiwick 2002) and the concomitant rise in total calf production. However, unless calving rates changed, we would expect the proportion of calves in the population to remain more or less constant given a gray whale population with a stable age structure (Rice and Wolman 1971). Instead, the increase in calf sightings may be more directly related to changes in the location of migrating whales when they give birth, assuming that the timing of parturition is less a function of location (such as in the lagoons) than of date.

Parturition begins in late December and continues through mid-February (Rice and Wolman 1971). Based on observations in the Mexico lagoons, most births occur between 26 December and the beginning of March (Swartz and Jones 1983, Sanchez-Pacheco 1998), with a peak calving date around 27 January (Rice et al. 1981). Perryman and Lynn (2002) found that the median birth date for gray whales passing through the Channel Islands was 13 January (95% confidence interval 12–15 January, based on the proportion of parturient females to those with calves). Rice and Wolman (1971) estimated a mean birth date of 10 January based on the scientific catch of parturient gray whales off San Francisco (Table 4). It seems unlikely that median calving dates have changed given that

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[4] ⟨coastwatch.pfel.noaa.gov⟩

[5] ⟨www.cpc.ncep.noaa.gov⟩

TABLE 5. Distance from shore of gray whale cows with calves seen from Granite Canyon, California.

Survey years	Distance (km) from shore					
	Standard watch		25× binoculars		Aerial surveys	
	Median	Maximum	Median	Maximum	Median	Maximum
1987/1988	0.86 (4)	1.89			0.34 (2)	0.54
1992/1993	0.90 (10)	2.18			1.06 (3)	14.19
1993/1994	0.93 (36)	2.57			1.72 (14)	33.89
1995	0.96 (8)	1.99	2.21 (11)	3.71		
1995/1996	0.79 (21)	1.44	1.04 (3)	1.60	1.66 (10)	4.72
1997	0.62 (7)	1.03				
1997/1998	0.72 (60)	1.45	1.24 (9)	1.83		
2000/2001	0.79 (8)	1.61	0.93 (2)	1.11		
2001/2002	0.84 (18)	2.31	1.39 (3)	1.83		

Note: Numbers in parentheses indicate sample size.

''length of gestation varies greatly among species but is confined within narrow limits in each species'' (Fuchs and Fields 1999). The dramatic increase in calf sightings after 1980 appears to be tied to a one-week delay from 8 January (1968–1980) to 16 January (1985–2002) in the median passage date of the southbound migration (Rugh et al. 2001). Although the median timing of the southbound migration has been consistent prior to and after this shift, any delays in the first part of the migration, when most of the pregnant females pass, may affect where calving occurs.

Over at least a 38-day period, pregnant females (near full-term) passed San Francisco during the southbound migration in the 1960s, with a mean passage date of 31 December (Rice and Wolman 1971). If we allow for a one-week shift in timing, then the mean date could now be close to 7 January. Because Carmel is ~170 km south of San Francisco and the whale route roughly parallels the coast, the mean passage date for pregnant females near Carmel could now be near 8 or 9 January. This is very close to earlier estimates of calving date (10 January, Rice and Wolman 1971; 13 January, Perryman and Lynn 2002), assuming, again, that it has not changed. Theoretically, then, since 1980, nearly half of the calving occurs north of Carmel.

In order to estimate how many gray whale calves were born near or north of Carmel during the southbound migration, we used a ratio of uncorrected counts to total abundance for this whale stock, 0.145:1 (data from Laake et al. 1994, Hobbs and Rugh 1999, Rugh et al. 2002). Calf counts since 1993 (average = 29/yr) corrected by this ratio suggest that on an average year, there are 197 calves born north of Carmel. The northbound migration of adults with calves is monitored from Piedras Blancas, and calf production is estimated from these surveys (Perryman et al. 2002). Based on estimated numbers of calves from three years (1993/1994, 1995/1996, and 1997/1998), when data were available from both Granite Canyon (Carmel) for the southbound count and from Piedras Blancas during northbound counts (Perryman et al. 2002), 23% of the calving occurs north of the Carmel area. Including a factor for the low sightability of calves relative to adults would raise this estimate, while including a factor for mortality would lower it.

The delay in the migration of pregnant females may be due to increased competition for food resources in the northern feeding areas (Stoker 1990, Highsmith and Coyle 1992, Coyle and Highsmith 1994, LeBoeuf et al. 2000) as the population reaches carrying capacity (Moore et al. 2001, Wade 2002). The climatic regime shift that occurred in the North Pacific during the winter of 1976–1977 resulted in unusually warm water temperatures along the North American coast (e.g., Miller et al. 1994, Hare and Mantua 2000). A reduction in percent ice cover anomalies for the Bering and Chukchi

TABLE 6. Number of calves and total number of gray whales observed during concurrent aerial and shore-based surveys of the southbound migration in January off Granite Canyon, California.

Year	Aerial surveys†			Shore-based standard watch		
	No. calves	No. gray whales	Proportion of calves	No. calves	No. gray whales	Proportion of calves
1988	2	822	0.0024	1	2776	0.0004
1993	6	252	0.0238	5	1377	0.0036
1994	20	455	0.0440	14	1980	0.0071
1996	12	325	0.0369	5	1154	0.0043
Total	40	1854	0.0216	25	7287	0.0034

† Aerial surveys include on- and off-effort sightings.

TABLE 7. Chi-square contingency analysis of pooled data from the 1993/1994 and 1995/1996 gray whale censuses at Granite Canyon, California.

	Aerial survey†		Shore-based standard watch‡	
Distance	Cows with calves	Others	Cows with calves	Others
Nearshore	10 (4)	57 (64)	45 (11)	933 (967)
Main	7 (14)	256 (248)	12 (38)	3317 (3291)
Offshore	7 (6)	98 (99)	0 (8)	672 (664)

Notes: Distance offshore is represented by three migratory corridors: nearshore, 0.0–1.4 km; main, 1.4–2.8 km; offshore, >2.8 km. ''Others'' refers to pods without calves. Shore-based data include all sightings collected from December–February. Expected counts for within-survey type analysis are shown in parentheses.

† $X^2 = 15.76$, df = 2, $P < 0.001$.

‡ $X^2 = 129.12$, df = 2, $P < 0.001$.

Seas, formerly primary feeding areas for these whales, also occurred after 1977 (Niebauer 1998). It is important to note that El Niño events have increased in frequency since the regime shift and that there have been very few La Niña events since 1976 (Niebauer 1998, 1999), which may explain the correlations found between calf counts and positive SST anomalies. Because the North Pacific has warmed, calves likely experience reduced thermo-stress when born along the migration route. Gray whales appear to have responded to warmer waters, reduced ice cover, and changes in productivity in primary feeding areas such as the Chirikov Basin by expanding their foraging range (Rugh and Fraker 1981, Miller et al. 1985, Moore et al. 2003). Therefore, as pregnant females disperse farther to find adequate food, their migration south can take longer (assuming that the timing of the onset of the migration does not change; Rugh et al. 2001), and they might be migrating with reduced fat reserves. This may also explain the appearance of calf carcasses along the migration corridor after 1977.

Prior to the late 1990s, strandings of gray whale calves were rare north of Mexico. Stranding reports compiled from 1952 to 1981 document 50 calf strandings in Mexican lagoons and 17 along the migration route (Sumich and Harvey 1986). All of the strandings north of Mexico have been since 1977. Heyning and Dahlheim (1990) report 204 calf strandings between 1975 and 1989, mostly in Mexico, but some as far north as northwestern Alaska. However, there is no evidence that any of these calf strandings occurred during the southbound migration. Monthly surveys of a 14.5 km section of the central California coastline from 1980 to 1986 to determine deposition patterns of seabird and marine mammal carcasses yielded few cetaceans and no gray whales (Bodkin and Jameson 1991). The first record of a calf stranding during the southbound migration was a live stranding in 1980 in British Columbia, Canada (Baird et al. 2002; Table 8). This is also the northernmost stranding of a southbound calf. The majority of calf strandings occurred in early 1998 (Table 8), which coincides with the highest calf counts on record at the census stations.

The appearance of northbound calves near Carmel is of interest because northbound migrants usually do not appear in California waters until after mid-March (Perryman et al. 2002). Sightings of northbound calves during the census of the southbound migration may be a function of longer survey seasons in recent years. Prior to 1994, the census was usually terminated by the end of the first week of February, but since then the census has been extended to cover an increasingly prolonged southbound migration (Rugh et al. 2001). It is possible that these northbound calves did not migrate as far south as Mexico as may be the case for many of the southbound calves observed near Carmel and Los Angeles. A one-week (6.8-day) delay in the migration timing (Rugh et al. 2002) without a change in birthing dates would mean that calving would occur 1000 km further north, assuming a constant travel rate of 147 km/day (Swartz et al. 1987). Therefore, a whale that might have calved just as it arrived at the northernmost lagoon in Mexico prior to 1980 would now calve near Point Conception, which is roughly halfway between Carmel and Los Angeles. If, in the past, whales migrated directly to a location somewhere south of the northernmost lagoon to calve, sufficient deviation or delay in the migration would mean that calving would occur farther north of Point Conception. This, indeed, is evident after 1980. Similarly, assuming that the one-week shift in migration timing has been the only significant change in the gray whale migration over the past five decades, recent observations of newborn calves near Carmel imply that prior to 1980 some or many calves were born north of the lagoons, given the rate of travel of migrating gray whales and the distance between Carmel and the lagoons. Furthermore, given the documented difficulty in seeing calves from shore, it is possible that calves were near Carmel during the 1970s, but went unobserved until their numbers were high enough to raise the probability of some being noticed.

TABLE 8. Gray whale newborn strandings reported during the southbound migration from 1980 to 2002.

			Distance from Mexico lagoons		
Date	Location	Disposition	km	d	Source
1980					
29 Dec	Bonilla Island, BC, Canada	found alive, died (4.42 m)	3385	23	1
1985					
27 Jan	Camp Pendleton, CA	dead, entangled in monofilament (5-m male)	725	5	2
1986					
29 Feb	Point Loma, CA	found alive wrapped in gillnet, died (neonate)	625	4	2
1993					
16 Jan	Del Mar, CA	found alive, died (4.22 m)	650	4.5	3
30 Jan	Santa Cruz Is., CA	dead (4.22 m)	850	6	3
1994					
25 Jan	San Nicholas Is., CA	dead (4.27 m)	780	5	3
26 Jan	Coronado, CA	dead (3.98 m)	625	4	3
1995					
25 Jan	Gardiner, OR	euthanized (5-m female)	2195	15	4, 5
1996					
10 Jan	Brookings, OR	advanced decomposition (3-m female fetus)	1995	13.5	5
29 Jan	San Simeon Beach, CA	found alive, died (4.5-m female)	1155	8	5
30 Jan	Smith River, CA/OR state line	moderate decomposition (4.17-m female)	1980	13.5	5
1 Feb	Cardiff, CA	advanced decomposition (>4.2-m female)	625	4	5
1997					
10 Jan	Marina Del Rey, CA	alive (4.5-m female, rehabilitated at Sea World)	825	6	5
10 Jan	Point Arena, CA	euthanized (3.52-m female)	1620	11	5, 6
20 Jan	Coronado, CA	decomposed, entangled in kelp bed (4.5-m male)	625	4	5
1998					
1 Jan	Morro Bay, CA	found alive, died (4.75-m female)	1120	8	5, 6
7 Jan	Crescent City, CA	found alive, died (4.47-m female)	1960	13	5, 6
14 Jan	Redondo Beach, CA	pushed out to sea, restranded dead 26 Jan (4.45 m)	800	5.5	5
16 Jan	Bolinas, CA	euthanized (4.84-m male)	1460	10	5, 6
16 Jan	Crescent City, CA	found alive, died (5-m male)	1960	13	5, 6
17 Jan	Fort Bragg, CA	found alive, died (4.6-m male, umbilicus attached)	1685	11.5	5
18 Jan	Bolinas, CA	pushed out to sea (4.67 m)	1460	10	5
20 Jan	Monterey, CA	euthanized (4.54-m female)	1300	9	5
29 Jan	Aliso Beach, CA	stranded 30 min, swam out to sea (3.6 m)	750	5	5
3 Feb	Ocean Beach, CA	dead (5 m)	625	4	5
5 Feb	Coronado, CA	dead (5 m)	625	4	5
4 Mar	Redondo Beach, CA	advanced decomposition (4.75-m female)	800	5.5	5

TABLE 8. Continued.

Date	Location	Disposition	Distance from Mexico lagoons		Source
			km	d	
2001					
9 Jan	Montana de Oro State Park, CA	alive swimming ~5 km offshore when it was struck and severely injured by a cable-laying vessel, carcass never recovered (estimated 4.5 m)	1120	8	3
10 Feb	Morro Bay, CA	alive swimming in bay, last seen alive 13 Feb, stranded dead 25 Feb, moderate decomposition (4.9-m male)	1120	8	3, 6

Notes: A gray whale was considered to be a southbound calf if it was ≤5 m in length (Rice and Wolman 1971, Perryman and Lynn 2002) and stranded between late November and early March (i.e., northbound migrants usually do not appear in California waters until after mid-March; Perryman et al. 2002). Distance (km) from Mexico was approximated following the coastal migration route, and travel time (d = days) was derived using an average travel speed of 147 km/d (Rugh et al. 2001). Abbreviations are: BC, British Columbia; CA, California; OR, Oregon. Sources are: 1, Baird et al. 2002; 2, Heyning and Lewis 1990; 3, J. Cordaro, *unpublished database*; 4, J. Hodder, *unpublished manuscript*; 5, Norman et al. 2000; 6, K. Zagzebski, *unpublished data*.

It is possible that female gray whales that reach parturition en route do not complete the migration to Mexico with their calves; instead, they might congregate in the Southern California Bight, near the Channel Islands, until their calves are large enough to return north. Lagoon use and calf production has changed significantly since the 1980s at Ojo de Leibre (one of the northernmost lagoons) and Lopez Mateos (one of the southernmost) (Fleischer and Schweder 2002). At the northern lagoon, a significant decline in peak abundance of calves as well as adults occurred in 1990, while at the southern lagoon a more gradual but highly significant decline occurred from 1981 to 1990. Overall, calf production has not recovered to levels observed in the early 1980s (Fleischer and Schweder 2002). In part, this may be due to high water temperatures during El Niño events (and possibly overall warmer temperatures since the regime shift), which seem to discourage gray whales from migrating to the southernmost lagoons (Gardner and Chávez-Rosales 2000, Urbán et al. 2003*b*). Urbán et al. (2003*a*) noted a 59% decrease in the number of cows with calves at Laguna San Ignacio during the 1982/1983 El Niño and a northward shift to waters off southern California during the 1998 event. What are the implications for survival outside the relatively protected waters of the lagoons? Besides exposure to winter storms, we also found a strong correlation between killer whale presence and calf numbers near Carmel ($R^2 = 0.72$, $P << 0.001$).

If the occurrence of calving north of the lagoons is related to the size of the gray whale population, then it also should have occurred when the population was near carrying capacity prior to commercial whaling. This idea is supported by the Makah Indians' names for the months of the year. The Makah, who live in northwest Washington ~2,500 km north of the lagoons in Mexico, call December *se-hwow-as-put'hl,* or the moon in which the gray whale makes its appearance, and they call January *a-a-kwis-put'hl,* or the moon in which the whale has its young (Swan 1870). This timing and location fits well with what we are now seeing during the southbound migration. Is it coincidental that the earliest and northernmost sighting of an adult with newborn occurred on 18 November 1998 in Discovery Bay, Washington (Shelden et al. 2000)?

In conclusion, it is evident that greater numbers of gray whale calves are born north of Mexico during the southbound migration. Calf sightings have increased across the past five decades, in part due to the increased size of the gray whale population, but the increase may also be related to environmental changes affecting a delay in the migration. Range expansion in northern feeding areas, perhaps because the population is approaching the carrying capacity of its environment, has meant that pregnant females have farther to travel at the start of the southbound migration. Warmer sea surface temperature anomalies were also correlated with increased calf counts at the northern stations as well as declines in counts at the Mexico lagoons. Assuming that parturition timing has not changed, the one-week delay has meant that calving has been occurring farther north. It appears that one-quarter to half of the calving now occurs north of Carmel.

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The Gray Whale

Eschrichtius robustus

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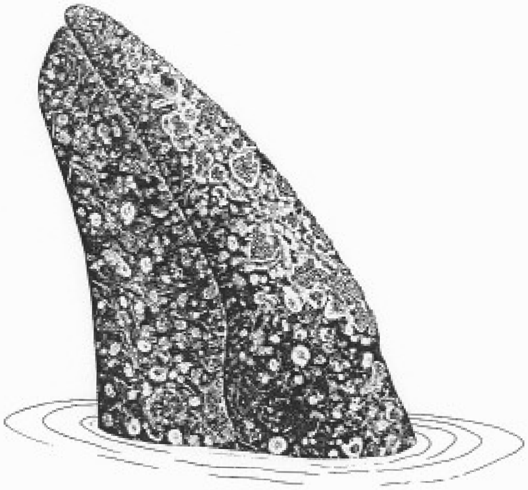

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Soviet Studies on the Distribution and Numbers of the Gray Whale in the Bering and Chukchi Seas from 1968 to 1982

Alfred Antonovich Berzin

Introduction

The main task of Soviet research of the Chukotka–California population of gray whales was to estimate their present abundance. A review and analysis of the literature and material from Soviet scientific research cruises to study the distribution and numbers of gray whales during the period of 1958 to 1964 is presented in the work of Berzin and Rovnin (1966). The present chapter does not intend to present and analyze population estimates for the Chukotka–California gray whale population produced by U.S. researchers during the past few years as this information is presented in numerous publications. At the same time, it is perfectly obvious that an exact determination of gray whale abundance must include a census of all regions the whales inhabit, particularly the summer range. The study of the whale's abundance, especially on the summer grounds, is inseparably linked to the study of their distribution. The scientific colleagues of TINRO (Pacific Research Institute of Fisheries and Oceanography) conducted systematic surveys of gray whale abundance and distribution from aircraft and vessels in the Bering and Chukchi Seas from 1968 to 1982.

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Table I
Summary of Soviet Research Effort for Gray Whales: 1968 to 1982

	Aerial surveys			Marine surveys	
Year	Date	Extent of route (km^2 × 10^3)	Area (km^2 × 10^3)	Date	Area (km^2 × 10^3)
1968	July 10–30	8	108		
1973	Aug. 3–23 Oct. 17–23	40	216		
1974				Sept. 26 Oct. 23	21.5
1975	Sept. 24–25 Oct. 1–9	22	162		
1979				Sept. 28 Oct. 25	37.8
1980				Sept. 17 Nov. 15	33.0
1982				Aug. 23 Oct. 13	90.0

[a] No data available.

Methods

The first aerial surveys of the gray whale's abundance and distribution in the coastal regions of the Bering and Chukchi Seas were conducted in 1968 and 1973 as part of the research program of TINRO. Subsequent surveys were conducted in 1974 and 1975 as part of the Soviet national research program within the framework of the "U.S.S.R.–U.S.A. Agreement for Collaboration in the Field of Environmental Conservation."

In accordance with the joint program, a research plan was formulated in 1975 for a simultaneous aerial census of Soviet and American portions of the Bering and Chukchi Seas for the purpose of surveying the entire summer range of the gray whale population (Table I). Unfortunately, the Americans were unable to conduct their surveys, which significantly decreased the effectiveness of the surveys conducted by Soviet scientists in the Soviet sector. Vessel surveys to estimate gray whale abundance and distribution were conducted jointly by Soviet and American scientists in 1979 to 1982 as part of this same program (Project 02.05-61, "Marine Mammals"). Participants from TINRO who participated in this research included V. V. Zimushko, A. P. Shustov, N. V. Doroshenko, V. N. Kolesnikov, and the author.

Aerial surveys were conducted in a twin-engine aircraft, the IL-14. Survey altitude was dependent upon weather conditions, but the optimum altitude selected was 300 m. Surveys followed parallel tracks separated by 15 km and extended a maximum distance of 250 km from shore. Survey strip width was determined by measuring the time from when a whale was spotted until the aircraft was over the animal and correlating this with the aircraft's ground speed. Maximum strip width was 5 km, but it was frequently less during surveys because of the weather conditions. In 1975 surveys were conducted in a flying "photosurveyor" which had "bubble" windows on both sides. This allowed simultaneous observation from both sides of the aircraft and doubled the effective survey zone. During each meeting with whales, V. V. Zimushko noted visibility, altitude, aircraft speed, etc. From these factors the survey strip width was determined; however, strip width changed relatively rapidly (within 15–20 min) from 270 m to 2 km.

The number of whales observed at any one moment does not reflect their true numbers as individuals may be below the surface; therefore, counts must be corrected for animals missed below the water's surface. In 1973 several systematic surveys were undertaken to determine a correction factor. Control counts were conducted from a vessel while an aircraft circled above the same group of whales. In our experience, this was the first comparison of its kind done for these whales. The counts from these surveys are a bit contradictory and insufficient, but they have the advantage of being actual counts and not estimations. The comparison of counts of the gray whales conducted simultaneously from Soviet vessels and aircraft in the coastal waters of Chukotka suggested that aerial observers detect approximately two-thirds of the whales. A correction factor is dependent upon the behavior of the whales: the group structures, their dive times, and their surface intervals. Weather conditions are not predictable and may affect the visibility of whales profoundly; in our opinion they cannot be introduced into a correction factor as this would produce uncertainties. The following relationship, recommended by Arsen'yev *et al.* (1973), was used to determine the abundance of whales in the survey area:

$$N = kn(1 + t_1/t_2)$$

where N is the general quantity of whales, n is the number of detected whales, t_1 is the time the whale is submerged underwater, t_2 is the time the whale remains at the surface, and k is a function of the aircraft's speed, visibility, and the distance of detection. V. V. Zimushko utilized this relationship in his analysis of the 1973 aerial census and estimated the population at three times the base (raw) count.

The summer distribution of gray whales is very irregular; thus, the survey area was divided into several regions each with different concentrations of whales to increase accuracy. The flight tracks were plotted on charts and the area that had been surveyed was determined, as was the number of whales encountered along a track line. From these data, whale densities in each region were calculated, and the total population was extrapolated region by region. I participated in the aerial observations of gray whales in the Bering and Chukchi Seas in 1973; based on my experience, I consider an aircraft flying at 250–300 km/hr to be a poor platform for observations of this kind. The aircraft passes over areas too rapidly to detect many great whales whose dive times are long, and because of the aircraft's large turning radius, it is difficult to return to whales once they have been detected. One must, however, utilize fixed-wing aircraft in certain conditions, like the Chukchi Sea, when a helicopter cannot be utilized.

When whales were spotted from survey vessels, the vessel followed the whales to obtain a precise count. Sighting information from years of vessel surveys in various regions of the northwest Pacific indicated that while vessels are underway the effective observation zone is up to 10 miles wide (5 miles on each side).

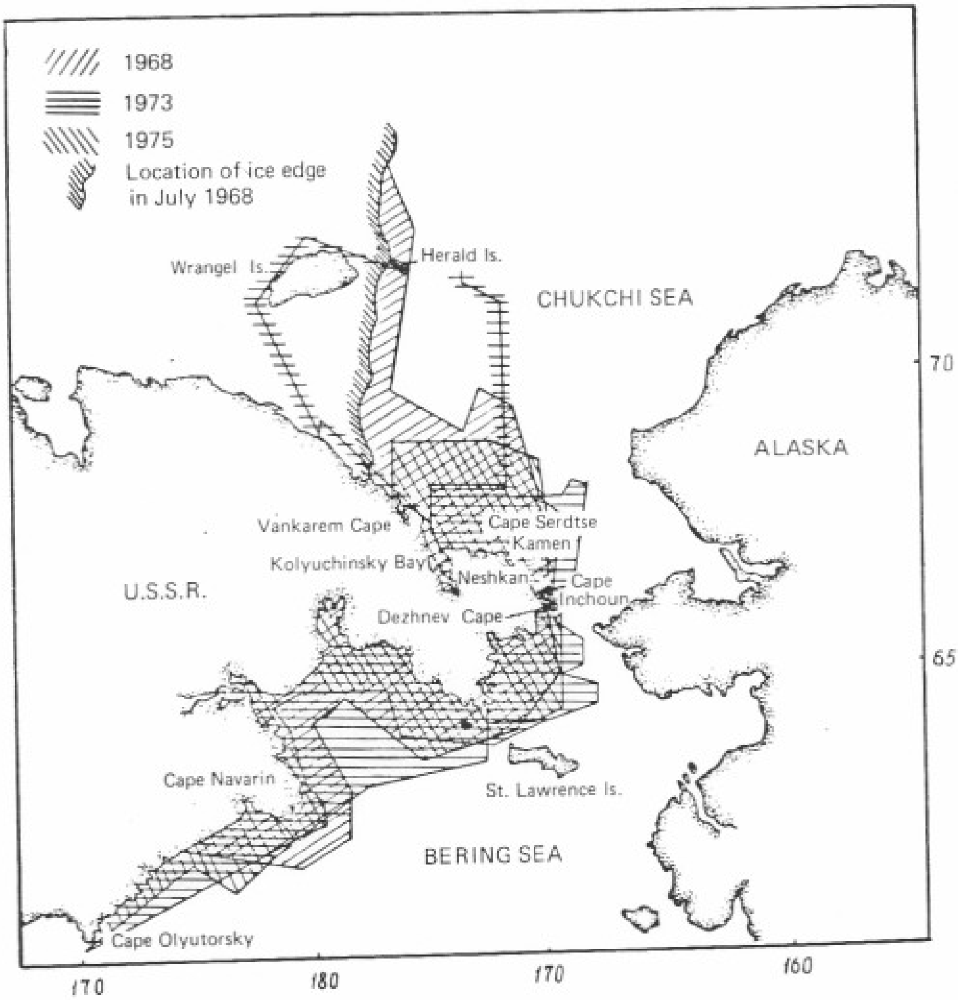

Fig. 1. *Regions of aerial observations during 1968, 1973, and 1975.*

Results

Aerial surveys of the Bering and Chukchi Seas conducted in 1968 included the coast and up to 50 km from shore and the ice-edge zone by Herald Island (Fig. 1). In all, 124 whales were counted. The largest group seen at one time included 17 animals observed in the region of Cape Inchoun (in the Chukchi Sea). The majority of the whales were seen along the coast no more than 35 km offshore. During the 1968 survey, the distribution of gray whales in the open sea was documented: two groups of 3 animals each were counted on a transect off Cape Serdtse Kamen at a distance of 90 km from shore.

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Gray whales were observed in the Chukchi Sea only in the area of Cape Dezhnev (the Bering Strait) to the settlement of Neshkan. No additional whales were counted in the remaining area north from the settlement of Neshkan along the ice edge to the pack ice near Herald Island. Only a few lone whales were observed in the area of Cape Navarin and in the area to the south at Cape Khatyrka (Zimushko, 1970).

In 1973, aerial surveys were conducted of the northwest Bering Sea and the portion of the Chukchi Sea from Cape Dezhnev to Wrangel and Herald Islands (Fig. 1). A total of 290 whales was counted. The greatest density of whales was noted in the Chukchi Sea from Cape Dezhnev to Kolyuchinsky; the density was 0.11 whales/km^2. As in 1968, no whales were observed in the northern area from Cape Kolyuchin along the ice edge to Wrangel and Herald Islands. Five individual whales were counted by Cape Olyutorsky, although no whales were seen in Olyutorsky Bay itself. Whales were seen at Cape Pouten in the Bering Sea. In the Chukchi Sea (68°N, 169°05′W) 44 whales were counted during a 12-km long, 3-min flight. Later, during a 30-min flight along the same track, 132 whales were counted. During that same year whales gathered in significant numbers further offshore, which was explained by a corresponding change in their foraging areas. Sixty-eight percent of the sightings were of whales in groups of 2 to 3 animals. The largest group included 24 animals.

In 1974, the main region of Soviet studies was the Okhotsk Sea; therefore, studies in the Bering and Chukchi Seas were limited to short cruises in a limited area by the R/V *Tamango*. The count of whales along the Koryaksk coast and the Chukotka peninsula was 198 animals. This was extrapolated to a population size of 1800 to 2000 whales as a guide to the whale density in this area (Kuz'min and Berzin, 1975). The general movements of the gray whales confirmed that a massive departure of animals from the Chukchi Sea occurs in mid-October.

In 1975 aerial surveys included the coastal regions of the northwest Bering Sea; in the Chukchi Sea an investigation was conducted from Cape Dezhnev to Cape Vankarem and along the ice edge to 68°40′N (Fig. 1). Some 873 gray whales were counted. As in previous years in the Chukchi Sea, the following traditional regions contained aggregations of gray whales:

1. From 67°30′ to 68°15′N and 171°30′ to 172°00′W.
2. From 68°10′ to 68°30′N and 171°30′ to 172°00′W.
3. From 66°30′N and 169°55′ to 170°10′W.

A dense aggregation of whales usually occurred in the Bering Strait near Cape Pouten, where 50 whales were counted in 1975 during a 3-min flight along a 12-km transect line. One of the main groups of gray whales was located, as in previous years, in the Bering Strait at 64°50′ to 65°00′N and 170°00′ to 170°20′W. Anadyrsky Bay continues to be a region with the lowest density of whales. Solitary whales were observed near Cape Olyutorsky. This same year, no whales were observed beyond the 25-km wide coastal zone.

According to the aerial observations of V. V. Zimushko, gray whales on their feeding grounds are usually observed as single animals or small groups. Out of our 232 sightings of whales, single animals were observed 102 times (44%), groups of 2 to 5 animals were seen 113 times, and groups greater than 5 animals were observed on 17 occasions (7.8%). A group size of 2 to 3 animals was most frequently seen (67.6%). As previously stated, the largest group included 24 whales.

During a Soviet–American cooperative expedition on board the R/V *Avangard* to study the abundance and distribution of gray whales in 1979, large quantities of grays were confirmed up to 100 miles from shore over depths of 50 m (Fig. 2). On October 19 at 67°47′N and 172°72′W, 260 whales were counted. All of these animals were large, and they swam as singles or in groups of 2 to 3 animals as they do in other portions of their summer range. Occasionally (eight observations), compact groups of 5 to 6 animals were observed. The largest group contained 13 whales. Large concentrations of whales (70 animals) were encountered in the region of King Island, and on October 25, 50 whales were counted north of Saint Lawrence Island. A total of 411 whales was counted during this cruise.

The results of the second Soviet–American expedition on the R/V *Razyashchy* contributed substantially to our present-day understanding of the distribution of whales in these regions (Fig. 2). Whales were first encountered in the coastal regions of Long Strait and in the eastern part of the East Siberian Sea. Large groups were encountered in the region of Cape Dvukh Pilotov (Cape of Two Pilots), and a smaller quantity was near Cape Shmidta. At the end of September, gray whales were encountered near the coastal shelf of the East Siberian Sea from Cape Yakan to Cape Billings and further west. The westernmost sighting of gray whales was at 178°30′E. The results of this cruise defined the boundaries of the gray whale distribution and identified locations of aggregations of whales in the Chukchi Sea 100 miles from shore at approximately 67°40′ to 68°15′N and 169°40′ to 172°00′W. The approximate number of whales in this region was ~2000 animals, although undoubtedly these data are only approximate and demand more precise determination. Because 588 gray whales were counted over a 4-day period, it is apparent that gray whales are abundant in this area. During the 1980 cruise 1021 gray whales were counted in this same area.

Information gathered during the 1979 and 1980 cruises confirmed that the gray whale fall migration out of the summer grounds begins in the middle of October and ends with the formation of the ice sheet. Newly pregnant females are the first to enter the summer grounds and the last whales to leave the Chukchi Sea, departing with the polar whales or bowheads (*Balaena mysticetus*).

The program of cruises on board the Soviet vessel R/V *Enthusiast* in 1982, which included American scientists, differed from the 1979 and 1980 cruises in that it started earlier (July 15) and covered a wider area in the Chukchi Sea (to 158°W) (Fig. 3).

The 1982 research may be divided into three stages. During the first stage of the work (from July 23 to August 8), gray whales were encountered in groups of 4 animals on July 25 north of Saint Lawrence Island. Upon entering the Chukchi Sea on July 27 between the settlements of Uelen and Inchoun, groups of 2 to 20 gray whales were encountered. That same day 300 gray whales were counted in an area of approximately 120 square miles north of Cape Serdtse Kamen. The center of this aggregation contained a dense group of 70 to 80 whales, all of which were feeding intensively. The following day, three groups of 40, 20, and 60 animals, respectively, were discovered

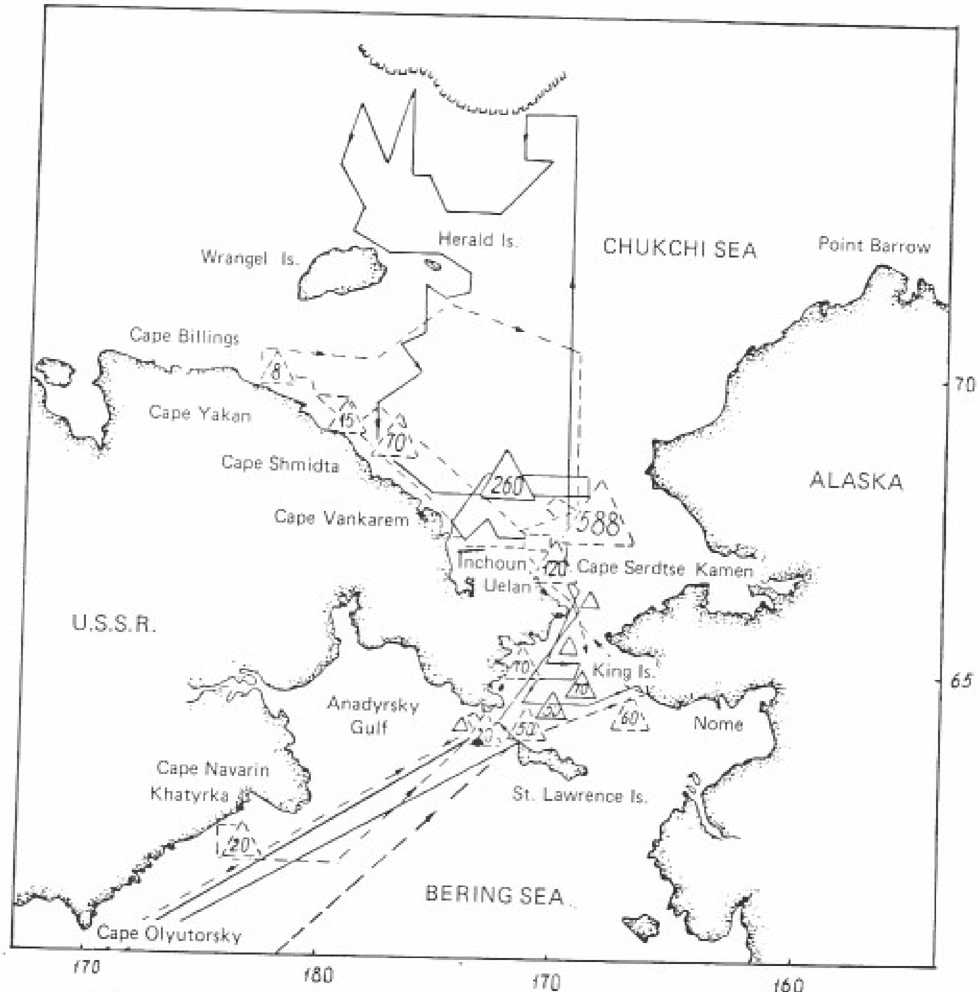

Fig. 2. *The distribution of gray whales and the routes of the R/V Avangard and R/V Razyashchy in 1979 and 1980. Symbols: solid arrow, route of R/V Avangard, 1979; broken arrow, route of R/V Razyashchy, 1980; zigzag area at top, ice edge in October, 1979. Numbers in triangles are counts of whales.*

between Cape Serdtse Kamen and Cape Vankarem. No gray whales were encountered at the ice edge to the west–northwest at Herald Island in the Chukchi Sea. On August 4 near Point Barrow (71°08′N 158°19′W), a group of 40 gray whales was encountered, our easternmost sighting of gray whales. Dense ice forced the ship to turn to the west–southwest where a group of 200 gray whales was encountered.

During the second stage (August 6–25), the ship traveled to the southwest and encountered a group of 60 gray whales in the same region. No large groups of whales were seen while traveling in a southerly direction along the coast of Alaska. Significant numbers of gray whales were again encountered in the same regions of the Chukchi coast visited during the first stage of this cruise: two groups of whales numbering

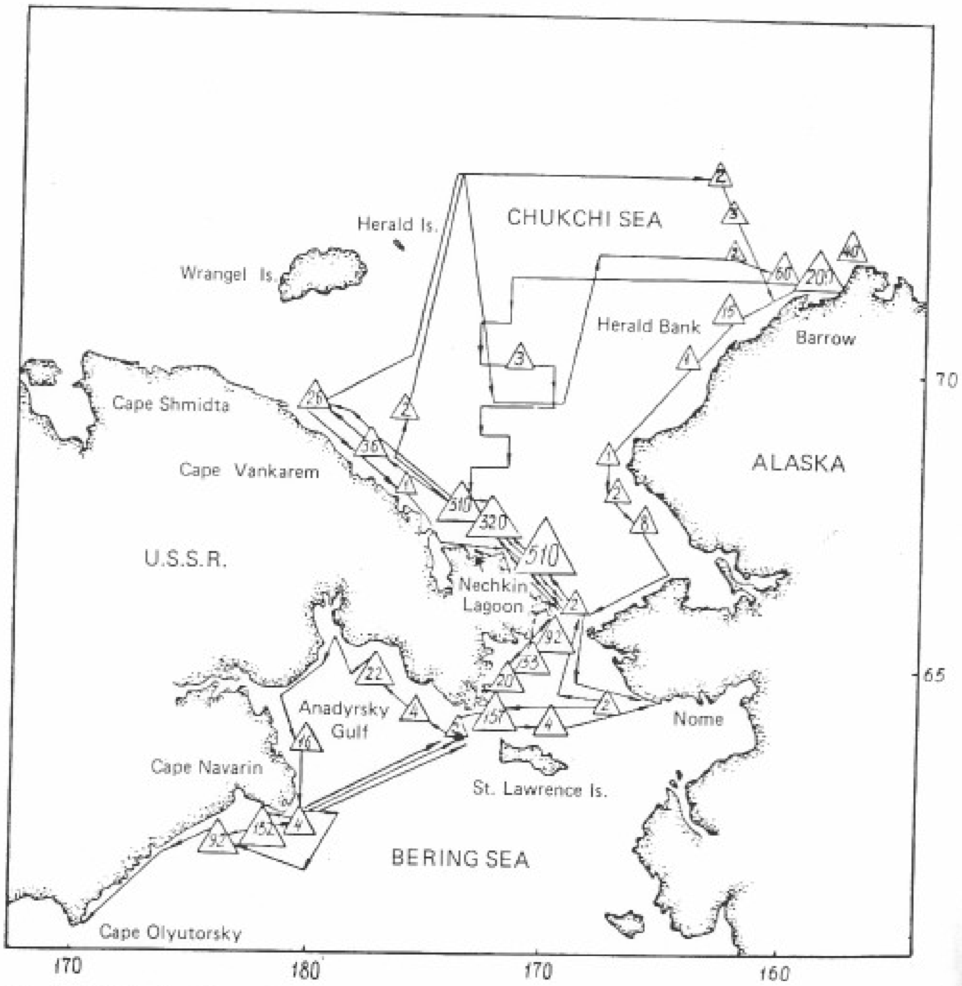

Fig. 3. *Distribution of gray whales and the route of R/V* Enthusiast *in 1982. Numbers in triangles are counts of whales.*

approximately 90 animals each were encountered in the region of Cape Serdtse Kamen. No whales were encountered during a return visit to the ice edge north of the Chukchi Sea. Five animals, a pair and a group of 3, were encountered near the ice edge at 71°56′N and 161°47′W (Fig. 3). Only 3 whales were seen during the vessel's westward track in the central Chukchi Sea; these animals were encountered southeast of Herald Banks on August 20. On August 22–23, 190 whales were counted in an area of 1000–1100 square miles located at 68°24′ to 68°00′N and 172°174′W.

In the third stage (September 2 to October 13), a 12- to 15-mile coastal zone of the Chukchi Sea from the Bering Strait to Long Strait was investigated. Near Cape Shmidta, two groups of 13 and 10 gray whales were sighted. Single whales and groups of 8 to 30 animals were observed in all the traditional areas near Cape Shmidta and Cape Dvukh Pilotov. From Nechkin Lagoon to Cape Shmidta, 259 whales were encountered during a 2-day period. Three whales were encountered at the westernmost point of the survey at the edge of the ice near Long Strait (69°27′N and 179°19′E).

Groups of 2 to 20 gray whales were encountered throughout the northern part of the Bering Sea from Cape Dezhnev to Arakemchechen Island. Near Cape Chaplino, 127 whales were counted in a 120- to 140-square mile area, and approximately 60 whales were encountered in the coastal waters of Anadyrsky Bay. At the end of September near Cape Navarin (in the region of Maino-Pilgyn), a gathering of 130 whales was observed, and in the region of Khatyrka ~90 whales were seen. This cruise confirmed the continuous distribution of gray whales in these areas. In all, 2142 whales were counted during the 1982 cruise.

Discussion and Conclusions

Studies of the Chukotka–California population of gray whales in their summer grounds have been limited basically to the collection and analysis of material generated by the whaling industry and to nearshore observations where these whales were collected. As the result of the systematic study conducted according to the Soviet national plan, as well as the joint Soviet–American program, the morphobiological aspects of the gray whale were significantly investigated and new information was obtained on the summer habits and distribution of these whales.

Analysis of the information collected over the last few years on the abundance and distribution of the Chukotka–California population of gray whales indicates that their summer grounds contain regular aggregations of animals in specific areas determined by their forage (prey) distribution. It has been established that in the Chukchi Sea, a significant part of which is relatively shallow, gray whales form aggregations a great distance from shore (in part up to 180 km) to the north of Cape Serdtse Kamen. Thus, gray whales are not a coastal species of whales in the full sense of the word, but only inasmuch as shallow depths as a rule occur nearshore.

According to Tomilin (1957), gray whales do not go farther west than Cape Serdtse Kamen. According to the latest data, gray whales do form some of their largest aggregations in this area. Our observations indicated that the gray whales westernmost distribution is off the lagoons of Tenkergyn–Pilgyn (177°30′W) and that this defines the western boundary of their range (Berzin and Rovnin, 1966). Recent studies suggest that gray whales begin to be encountered in the Long Strait and the Eastern Siberian Sea along the edge of the pack ice. Our westernmost sighting of a gray whale was 178°30′E. This suggests that the western distribution of the gray whales is limited by the pack ice, and because of the increase in the population the whales have recently expanded westward (Doroshenko, 1981). Studies of the eastern distribution of gray whales in the Chukchi Sea clearly suggest that their eastern distribution is also limited by pack ice. Our easternmost sighting of gray whales was at 158°19′W.

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in Cape Serdtse

The indications in the literature of periodic penetrations of gray whales into the high latitudes near Herald and Wrangell Islands is not supported by contemporary information. Additionally, replicate surveys of the central and northern regions of the Chukchi Sea have demonstrated an absence of whales in a large area of this basin; the only exception was the sighting of a small group of whales in the shoal water to the southeast of Herald Bank in the central Chukchi Sea (Fig. 3). The extreme northernmost sighting of gray whales was in the western area at 69°27′N and on the east at 72°N.

Information on the abundance of gray whales (in groups of 100 or more) in the coastal regions to the south of Cape Navarin (Tomilin, 1957; Berzin and Rovnin, 1966) relate to the period of commercial whaling. Up until the 1970s only a few gray whales were ever encountered in these areas during the summer. Only during the migration were sightings of gray whales indicative of an increase. Gray whales have not been seen south of Glubokaya Bay for the past 20 years, and this latitude (61°12′N) is considered the southern limit of gray whale distribution along the northwest coast of the Bering Sea. Frequent recent observations of large aggregations of gray whales south of Cape Navarin, near the Maino–Pilgyn lagoon, the settlement of Khatyrka, and others, along with the discovery of gray whales near Cape Olyutorsky, is indicative of the increase of the population of whales and the southward expansion of their range to 60°N. The distribution and southern limit of the gray whale's summer grounds on the eastern shelf of the Bering Sea are not known.

The extrapolation of the census counts of gray whales in the areas investigated in 1982 allowed the calculation of the first numbers of whales arriving on the feeding grounds, although these first estimates are undoubtedly imprecise and should be improved. Approximately 10,000 gray whales inhabit an area of 45,000 square miles of the Chukchi Sea during the summer, according to V. N. Kolesnikov, and within a 14,000 square mile area of the northwest and northern part of the Bering Sea there are approximately 3,300 to 3,500 whales. As previously mentioned, we have no data on the numbers of gray whales in the eastern part of the Bering Sea. Previous information suggests the benthic communities in these areas are relatively poor, and it is unlikely that any large quantities of whales live in these areas. If one postulates a minimum number of 1,000 whales, then we may assume that approximately 14,500 to 15,000 gray whales inhabit the northern waters of the Bering and Chukchi Seas to feed during the summer. If this is compared with current American estimates of 17,000 whales in the population (Chapter 10, this volume), then we may assume that approximately 2,000 whales linger in the winter range and along the migratory route.

K statement

The Chukotka–California population of gray whales inhabits a limited and relatively easily studied area and has reestablished its abundance, following its catastrophic decline, to a current population size nearing the present carrying capacity of the ecosystem of the North Pacific. Because most of the biological parameters of the gray whale have been studied more intensively than for any other species of great whale, the gray whale may be considered a model population. Research on the Chukotka–California population of gray whales that inhabit the territorial waters of several nations need to be coordinated by all nations in all portions of its range, from the winter calving grounds, along the migratory route, and in the summer grounds. This is within our present technical capabilities and is in the best interest of the species.

Summary

This chapter presents the results of Soviet studies on the distribution and abundance of the Chukotka–California population of gray whales on their summer grounds between 1968 and 1982. Aerial and vessel observations established that gray whales regularly concentrate in the same general areas of the Bering and Chukchi Seas. The formation of permanent groups was observed at distances up to 100 nautical miles or more from the shallow coastal regions of the Chukchi Sea. Large aggregations of whales were encountered on the area's eastern boundary near the ice at Point Barrow. The area occupied by gray whales has expanded in a westerly direction and they have appeared in the Eastern Siberian Sea. An increase in abundance of a permanent population of gray whales was noted in the coastal zone to the south of Cape Navarin. Gray whales have appeared for the first time in several years near Cape Olyutorsky. These studies have defined more exactly the boundaries of the gray whale's summer habitat. Population estimates of the number of gray whales summering in the Bering and Chukchi Seas are between 14,000 and 15,000 animals, of which 10,000 inhabit the Chukchi Sea. The detailed information available for the Chukotka–California population of gray whales is the result of many years of multidisciplined investigations by Soviet and American specialists and allows us to consider a model for this population of great whales.

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The Gray Whale

Eschrichtius robustus

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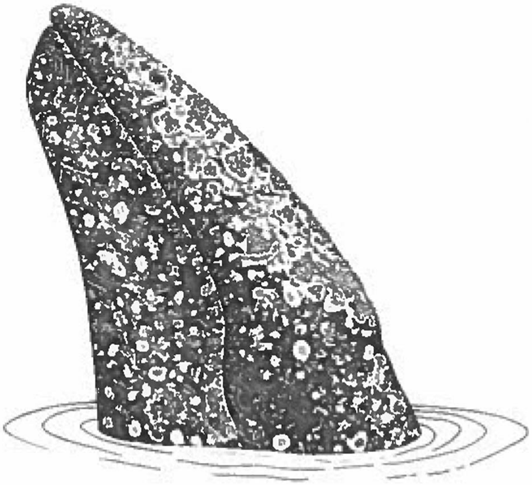

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A Review of Russian Research on the Biology and Commercial Whaling of the Gray Whale

Alexey V. Yablokov and Luydmila S. Bogoslovskaya

Introduction

Scientific study of the gray whale (*Eschrichtius robustus*) in the Asiatic waters of the north Pacific was begun in the eighteenth century by S. P. Krasheninnikov (1755) and was renewed episodically in subsequent years by Ditmar (1890–1900), Vasil'yev (1891), Grebnitskii (1902), and Suvorov (1914). Gray whale research became specialized between 1933 and 1936 during the period of active pelagic whaling in the Bering Sea by the Soviet fleet *Aleut* (Zenkovich, 1934a,b,c, 1935a–d, 1937a,b,c, 1938a,b; Tomilin, 1937a, 1946). The results of research of the whaling industry by Soviet scientists were summa-

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rized in the work of Sleptsov (1952), Zenkovich (1952), Tomilin (1957, 1962), and Klumov (1963).

Following World War II, gray whale research was principally conducted in association with aboriginal whaling in the waters of Chukotka Peninsula, mostly the opportunistic research of Zimushko (1969a,b, 1970a–d, 1972a,b; Zimushko and Lenskaya, 1970; Zimushko and Ivashin, 1980). In recent years, various aspects of gray whale research have been explored by the scientists of TINRO (Pacific Ocean Institute of Fisheries and Oceanography): Berzin (1974, 1978), Berzin and Kuz'min (1975), Berzin and Rovnin (1966), Berzin and Vladimirov (1981), Blokhin (1979, 1981), Blokhin and Pavlyuchkov (1981), and Doroshenko (1981). Additional research has been conducted by members of the Academy of Sciences of the U.S.S.R. and Magadanrybprom: Votrogov and Bogoslovskaya (1980), Bogoslovskaya and Votrogov (1981), Bogoslovskaya *et al.* (1981a,b, 1982), and Bogoslovskaya and Lemberg (1979), Bogoslovskaya et al. (1981b).

The limited volume of this contribution does not allow us to describe in detail the results of Soviet studies on the gray whale, which have been presented in more than 80 scientific publications, or even to mention all of them. Our main goal was to summarize data that is not well known or is mostly lacking in the English scientific literature.

Okhotsk–Korean Population

According to data compiled by earlier researchers, the whales of this population and the humpback whales (*Megaptera novaeangliae*) were very common and even abundant in the coastal waters of the northern part of the Okhotsk Sea and off the western shores of the Kamchatka Peninsula (von Ditmar, 1890–1900; Krasheninnikov, 1755; Vasil'yev (1891) indicated that the main mass of these whales migrated twice each year along the shores of the Far East Seas. Gray whales penetrated into the Okhotsk Sea from the Japanese Sea through the Tartar Strait and probably through Laperuz Strait (Sleptsov, 1961b); relatively recently they have been observed occasionally in Akademiya and Sakhalin Bays (Sleptsov, 1952).

Berzin (1978) summarized all the scattered data on the Okhotsk–Korean population of the gray whale, their wintering grounds with indications of their southern borders, their feeding grounds, and migration. He also commented on the incidental sightings of this animal in the Okhotsk Sea and ascertained the catastrophic condition of the entire population (Berzin, 1974). Solitary gray whales were encountered in 1967 and 1974 in the coastal waters of the Okhotsk Sea (Berzin and Kuz'min, 1975). The gray whales were observed in Peter the Great Bay: in July 1978 near Vladimir's Bay (one whale) and at the end of April, 1979 near Furugelm Island (two whales) (L. M. Votrogov, personal communication). Aerial surveys of the northwest coastal part of the Okhotsk Sea in the summer of 1979 demonstrated an absence of gray whales in the Sakhalin–Shantar region (Berzin and Vladimirov, 1981). Zoologist M. K. Maminov encountered one gray whale near the southeastern tip of the Kamchatka Peninsula at the beginning of October, 1979. Berzin and Vladimirov speculated that this individual was from the Japanese portion of the

Okhotsk–Korean population and possibly part of an independent population that breeds in the inner Sea of Japan. They believed that this population migrates along the eastern shores of the Japanese Islands where sightings of gray whales were previously recorded (see Chapter 3, this volume). The number of whales in the Okhotsk–Korean population prior to the beginning of the whaling industry for this species was estimated to be 1,500–10,000 animals. Contemporary censuses indicate there are no more than 100–200 animals remaining (Berzin and Vladimirov, 1981). According to Berzin (1978), the size of the Okhotsk–Korean population has diminished to its minimum; they are not recovering and their numbers continue to decline. Therefore, any whaling of this population would be catastrophic to their survival and should be banned.

Chukotka–California Population

MIGRATIONS

The spring migration of the gray whale is extended in time (Sleptsov, 1952, 1961a; Berzin and Rovnin, 1966) and is closely related to the ice condition and direction of the ocean currents (Fedoseev, 1981; Votrogov and Bogoslovskaya, 1980; Bogoslovskaya and Votrogov, 1981). These authors believe that there are several independent migratory routes of the gray whales; in the beginning of May the gray whales appear simultaneously and independently in two different regions divided by the vast area covered with ice, one near the coast of Koryak from Cape Khatyrka to Cape Navarin and the other at the southeast tip of Chukotka Peninsula in the waters between the settlement Sireniki, Cape Chaplino, and Saint Lawrence Island. Apparently animals utilize the powerful streams of the Poperechny current for their migratory movements. These streams deviate on the northwest from the Aleutian Islands and flow toward the permanent coastal polynya (an unfrozen patch of water in the midst of ice) which form in these areas (Votrogov and Bogoslovskaya, 1980). Votrogov and Bogoslovskaya (1980) proposed one more, the southernmost migratory route towards the Asian coast, along the Aleutian range and the Commander Islands. This author's opinion on the existence of possible migratory routes is based on the findings by Grebnitskii (1902) and Barabash-Nikiforov (1938) as well as some other results of recent findings (Votrogov and Bogoslovskaya, 1980).

However, the main core of the gray whale population stock moves north along the shores of North America and usually arrives in the Bering Strait by the end of May. Whales are distributed along the cracks of ice throughout the large water areas free of ice packs; one part of the herd begins its movements southward along the Asiatic coast and another part penetrates into the Chukchi Sea where the whales split off into two opposite directions, west and east, towards the Chukotka Peninsula and Alaska (Tomilin, 1937a,b; Berzin and Rovnin, 1966; Fedoseev, 1981; Votrogov and Bogoslovskaya, 1980).

The massive departure of whales from the northern seas during the fall migration begins in the middle of October (Kuz'min and Berzin, 1975; Doroshenko, 1981) to November of some years (Sleptsov, 1961a), when they share these waters with the bowhead whale (*Balaena mysticetus*). In the region of Sireniki polynya, near leads in the ice, and at the entrance to the shore of Providenya Bay, some gray whales hold out until mid-November and sometimes until mid-December. Local natives indicate the gray whale leaves the Koryak Coast by September (Bogoslovskaya *et al.*, 1982). Most of the migratory routes of the gray whales are through coastal waters, and it remains unclear whether the same animals utilize the same routes during the spring and fall migrations.

DISTRIBUTION ON THE FEEDING GROUNDS

Practically all researchers involved in the study of summer distribution of the gray whales were involved in this problem, including Zenkovich (1934a, 1937a) and Tomilin (1937a, 1957). In Soviet waters, the main concentration of the gray whale can be observed in two different regions: the southern area, from Cape Olyutora to Cape Barykov and the Lagoons of Tymne in the Bering Sea, and a northern area, from the Kresta Bay in the Bering Sea to Cape Sertse-Kamen' and the lagoon of Neshkan in the Chukchi Sea (Arsen'yev, 1961; Sleptsov, 1961a; Berzin and Rovnin, 1966; Zimushko, 1970a; Votrogov and Bogoslovskaya, 1980). Based on the data of Berzin and Rovnin, the gray whales in the Chukchi Sea do not go further west than the lagoon of Nutang'ye and Mayino-Pylgyn or further north than 69° latitude, although Sleptsov (1952) indicated that in some years the gray whales may move along the ice leads and drifting ice as far as Wrangel Island (Ostrova Vrangelya).

Recently, Doroshenko (1981) encountered gray whales for the first time in the coastal waters of the Long Strait and the eastern portion of the Eastern Siberian Sea, from Point Yakan to Point Billings. In addition, he discovered in the Chukchi Sea a large concentration (approximately 2000 whales) of animals about 160 km offshore. This concentration was located between 67°40′ and 68°15′N and 169°40′ and 172°W. The author believes that gray whales have expanded their distribution to the west as a result of the continued increase of the Chukotka–California population.

As a rule, gray whales distribute themselves in shallow waters near the shore and rarely go beyond 35 to 50 km offshore (Zimushko, 1970a; Votrogov and Bogoslovskaya, 1980). They choose to frequent areas where the salinity of the water is somewhat lower than 30%, where the wind turbulence reaches to the bottom, and the oxygen content is near 150% (Kuz'min and Berzin, 1975). They congregate and remain in areas where the concentration of benthic organisms is not less 100 g/m^2 (Berzin and Povnin, 1966). In the summer feeding grounds, the whales are unevenly distributed along the Asian coast (Fig. 1). The whales are constantly moving; their distribution in areas 3-21 varies not only from year to year, but even from month to month within the same season, as a result of constant local migrations of the gray whales between the feeding grounds (Votrogov and Bogoslovskaya, 1980; Bogoslovskaya *et al.*, 1981a, 1982).

One can assume that at the present time the populations of California and Korean gray whales do not overlap (Zenkovich, 1937a; Zimushko, 1972b; Zimushko and Ivashin, 1980); however, the question remains open whether or not these two populations were

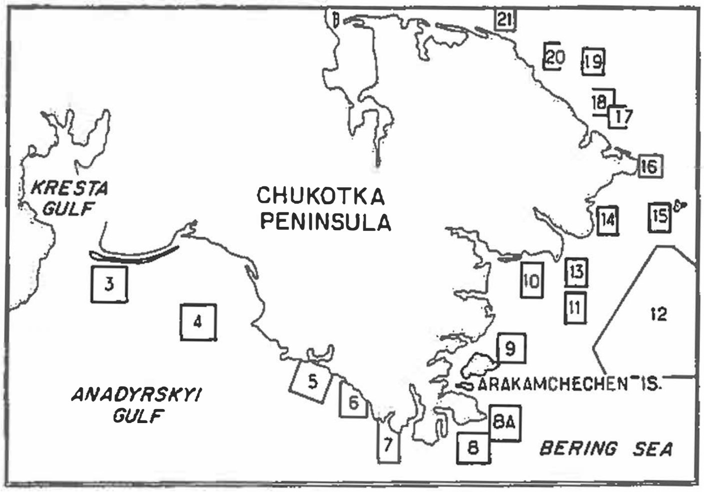

Fig. 1. *Feeding grounds of the Chukotka–California gray whales in Soviet waters, summer to early autumn. From whaling cruises 1964–1980, concentrations of whales have been discovered in areas 3–21 while other regions remain "empty."*

mixed in the past; the data of earlier studies indicated that the gray whales were usually common in the waters around Kamchatka Peninsula and the Commander Islands (Krasheninnikov, 1755; von Ditmar, 1890–1900; Grebnitskii, 1902).

There is a great deal of opinion in the literature that the gray whales of all ages, including both males and females, spend their summer in the Bering Sea. At the same time a great age differentiation of the stocks is also observed: young animals, as a rule, congregate around the Koryak coastline, from the Glubokiy Bay to Cape Navarin, but the adult groupings are in more northern waters, around Chukotka Peninsula (Zenkovich, 1934a, 1937a; Tomilin, 1937a; Sleptsov, 1952). However, working with the results obtained from the whaling industry from 1969 to 1981, as well as from direct observations, predominantly females and young whales distribute themselves mainly in the shallow coastal waters, but the large whales are found further offshore in waters up to 50–60 m deep (Votrogov and Bogoslovskaya, 1980). Moreover, there are four regions where the small animals are predominant in numbers: near Achechen lagoon, and at the mouth of Kurupka River (regions 5 and 6 on Fig. 1), near Cape Kygynin of the Arakamchechen Island (region 9 on Fig. 1), and the west portion of the Mechigmen Bay, including region 10 and the adjacent portion of the Mechigmen Inlet as well as the northern area from Cape Nunyamo, near Cape Chaplino (Bogoslovskaya *et al.*, 1981; Bogoslovskaya *et al.*, 1982). Out of 514 adult gray whales taken from the needs of the aboriginal population of Chukotka Peninsula, 69.8% were females and 30.2% were males (Rezvanov, 1981).

It is important to mention that Zenkovich (1954, 1969) reported two sightings of gray whales around the Chilean–Peruvian coastal waters of South America. This observation may support the hypothesis that some part of the gray whale population may cross the equator in the search for suitable feeding grounds.

ABUNDANCE

In 1942 the Soviet whaling vessels sighted 1197 gray whales within 46 days in the area of Anadyr Gulf and the Bering Strait (Vadivasov, 1947). In August and September of the same year, P. G. Nikulin counted 1154 whales from shore stations in the same regions, although it was known that only in August 1012 animals were observed. According to Vadivasov's data (1947) during the period between 1932 and 1941, whalers would sight every year on the average about 466 gray whales in 46 to 53 days of observations. Apparently, all animals observed belonged to the Chukotka–California population. We want to call attention to observations conducted by Zenkovich (1937a, 1954); on September 3, 1936 he encountered in the Chukchi Sea a herd of 200 gray whales, which formed five or seven different groups. Later, in one of the fijords of the Koryak coastline he counted more than 60 gray whales cleaning themselves of their ectoparasites in the brackish water.

Sleptsov (1961a) believed that by 1946 there were not less than 1500 gray whales in the Chukchi Sea and in the northwestern part of the Bering Sea. In this very same region, the author observed about 1200 gray whales from August 21 until September 11 of 1948 while aboard the whaling vessel *Purga*. He believes that the population of gray whales doubled by the beginning of 1960 and that their numbers reached 2500–3000 individuals. In 1962, 1033 gray whales were sighted in the coastal waters of the Chukotka Peninsula (Berzin and Rovnin, 1966).

V. V. Zimushko conducted three aerial surveys of the Chukotka–California population of gray whales. From July 10 to July 30, 1968, he observed 124 whales in 107,900 km^2 with an average distance from the Koryak shore and Chukotka Peninsula of 35 km; from these counts the population was estimated to be 4800–5000 whales (Zimushko, 1970a). During 159 hours of aerial surveys between August 3 and 23 and October 17 to 27 they surveyed an area of 215,932 km^2 within 240 km offshore and calculated a population estimate of 7700–7800 whales. From September 24 to 25 and October 1–9, 1975, V. V. Zimushko counted only 2000 gray whales during 89 hours of aerial surveys over 162,000 km^2 as much as 250 km from shore. The author correlated these counts with the migration of the whales during this period (Zimushko and Ivashin, 1980).

Zimushko's last population estimates agreed with the recent counts conducted during scientific expeditions in September and October, 1974, when the total number of gray whales estimated in Soviet waters was 1800–2000 (Kuz'min and Berzin, 1975). In the spring of 1978, Fedoseev (1981) conducted aerial surveys from an elevation of 100 m at different locations along the Koryak coast. He counted 30 gray whales, which, when extrapolated from these aerial surveys, suggested that not less than 1200 gray whales occupied the areas in the Bering Sea clear of ice at the end of May.

Surveying from the vessel *Zvezdnyi*, I. M. Votrogov counted 2200 gray whales between the end of June and the beginning of November, 1980 and 1438 whales from the second half of August until November 9, 1981 (Bogoslovskaya *et al.*, 1982).

Comparison of all these data obtained during aerial and vessel surveys allowed us to assume that from the time of the complete abolishing of commercial boat whaling, that is, by 1946, the numbers of the Chukotka–California population were not so low as was suggested by the majority of researchers, and accordingly, the increase of numbers of animals within the period of 1940 to 1960 was not as significant as believed. For example, Blokhin (1979) estimated a rate of increase of 18% per year.

MORPHOLOGY

The average measurements of the gray whale body are summarized in Table I. In spite of some scatter in the data, we may assume that on the average an adult female whale is approximately 0.3 m longer than a male.

Zimushko (1972b) compared pecularities of the external morphology of Chukotka–California and Okhotsk–Korean (data by Andrews, 1914) populations of gray whales. This comparison raises some doubts in the previous conclusion that the whales of the Okhotsk–Korean population are generally larger than individuals of the Chukotka–California population. On the other hand, the distance from the tip of the rostrum to the base of the pectoral fins, from the tip of the rostrum to the eye, the maximum width of the pectoral fin, and the length of the baleen plates were statistically greater in the Okhotsk–Korea whales than similar measurements in Chukotka–California whales. Also, the whales from the waters of Chukotka Peninsula have smaller numbers of baleen plates and on the average fewer throat grooves. The authors at present believe that these differences may indicate the existence of two distinctive groups of gray whales in the northern Pacific, which may allow them to be designated as subspecies.

Zimushko (1972b) revealed that male gray whales differed from females in the relative size of the body and head. In addition, females have significantly longer tail sections in relation to the smaller width of the flukes. The average number of baleen plates in both sexes was practically the same: 323 ± SE 4.9 in females ($n = 111$) and 322 ± SE 3.4 in males ($n = 70$).

The vibrissae of the gray whale embryos are distributed almost equally on upper

Table I
Average Length of Gray Whales Taken in the North Pacific[a]

Males (m)	Females (m)	Comments
11.3 (8.5–14.3) $n = 88$	11.9 (8.6–15.0) $n = 104$	Pelagic whaling in the Bering Sea, 1933–1936
11.5 (8.2–13.0) $n = 39$	12.2 (7.7–14.2) $n = 55$	Coastal (in-shore) whaling off the Chukotka Peninsula, 1965
12.2 (9.3–14.1) $n = 26$	12.2 (8.8–13.8) $n = 15$	Same as above, 1966
12.6 ± SE 0.09 $n = 70$	12.9 ± SE 0.07 $n = 111$	Same as above, 1965–1971

[a] From Zenkovich (1937a) and Zimushko (1969b, 1972a).

Table II
Average Number of Vibrissae on the Head of the Fetus of the Gray Whale[a]

	Upper jaw	Lower jaw
Males	131	141 (117–165)
Females	155	131 (100–172)

[a] From Zimushko (1972b) and Zimushko and Ivashin (1980).

and lower jaws (Table II). It was learned that the total number of vibrissae is slightly less in near-term fetuses, and their number is significantly less on the upper jaw of the adult whales. Thus, Tomilin (1937c) counted just 60 vibrissae on the upper jaw and 120 vibrissae on the lower jaw of an adult female.

Bogoslovskaya and Lemberg (1979) showed that the structure of the gray whale brain is typical of that of other baleen whales; except for the more simplified picture of the arched convolutions, the brain of the gray whale resembles the brain of the sei whale (*Balaenoptera borealis*).

Zimushko (1970d) examined the reproductive system of the gray whale, including 70 ovaries collected during 1965–1968 in the waters of Chukotka Peninsula. He describes in detail the morphology of the ovaries (ovaries of sexually mature females weighed from 318 to 1830 g, but together with the corpora lutea were up to 4820 g) and also the stages of development of follicles and the corpora lutea. Zimushko concluded

Table III
Dimensions of Some Internal Organs of the Gray Whale[a]

Organ	Size	Comments
Heart	131 ± 16 SE (90–166) kg	Sexually mature males and females
	172 kg	Pregnant female 13.4 m
Liver	519 (455–580) kg	Sexually mature males and females
Spleen	3.2 (2.5–4.3) kg	Same
Lungs	333 kg	Same
Testes	23 (14–27) kg	Sexually mature
	50–74 cm length	
	43 kg	Both testes, 12.1 m
	54 kg	Both testes, 13.6 m
Brain	4376 kg	Pregnant female, 13.4 m
	4200 kg	Unknown sex, 11.0 m
	4300 kg	Unknown sex, 12.0 m
Intestine (total length)	177.3 m	Pregnant female, 13.4 m
Urinary bladder (maximum volume)	12.0 liters	Adult male and female

[a] From Bogoslovskaya and Lemberg (1979), Zenkovich (1937b), Zimushko (1972b), and Zimushko and Ivashin (1980).

that the atrophied follicles remain in the ovary for a relatively short time compared to the traces of the corpora lutea and scars from ovulation; between these, there is a distinct histological difference.

There is only one known instance of the complete weighing of a gray whale by Soviet researchers (Zenkovich, 1937b). This pregnant female, carrying a fetus 207 cm long and weighing 126 kg, was caught on August 19, 1936 in the Bering Sea. The female's length was 13.35 m and she weighed 31,460 kg not including the weight of the blood; the blubber weighed 9,100 kg; the muscles, 6,729 kg; the head, 1,692 kg; the lower jaw, 1,265 kg; the tongue, 1,278 kg; the vertebral column plus the ribs and scapulae (with remnants of the muscles), 6,163 kg; the pectoral flippers, 612 kg; and the internal organs, 4,493 kg. Zenkovich concluded that the approximate weight of a gray whale may be determined by $V = (L D^2)/3$ where L = the body length and D = its maximum height. Some measurements of the internal organs of the gray whale are presented in Table III.

In conclusion, on the morphological peculiarities of the gray whale we wish to note that according to Tomilin's data (1937a, 1957) the depigmented white spots, some of which develop from the attachment of parasitic barnacles (*Cryptolepas rhachianecti*) can be repigmented following the removal of the barnacles. As this process continues on different parts of the body at different times, the general color of the whale's skin is mottled with some dark and some light areas. In 1957 Tomilin reported sighting a partially albino gray whale in the Bering Sea. The anterior part of the body of this whale was completely white.

GROWTH AND AGE

Among the gray whales studied by the Soviet researchers in the waters of the North Pacific, they came across whales ranging from 7.7 to 14.3 m long. After comparing whale

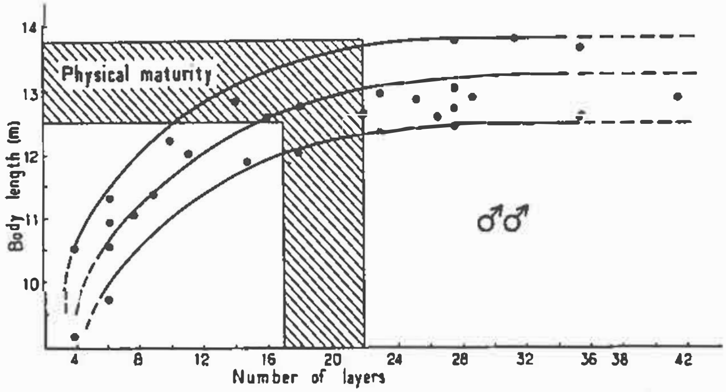

Fig. 2. *Correlation between the body length and the number of ear plug layers (1 layer = 1 year) of male gray whales (n = 29), which allows the determination of the age of physical maturity. (Data by Zimushko (1970b) and Zimushko and Ivashin (1980).) Lines are theoretical curves fit to the mean values (middle line), largest values (upper line), and smallest values (lower line). Hatched area indicates the range of absolute values for body length and number of ear plug layers for the onset of physical maturity.*

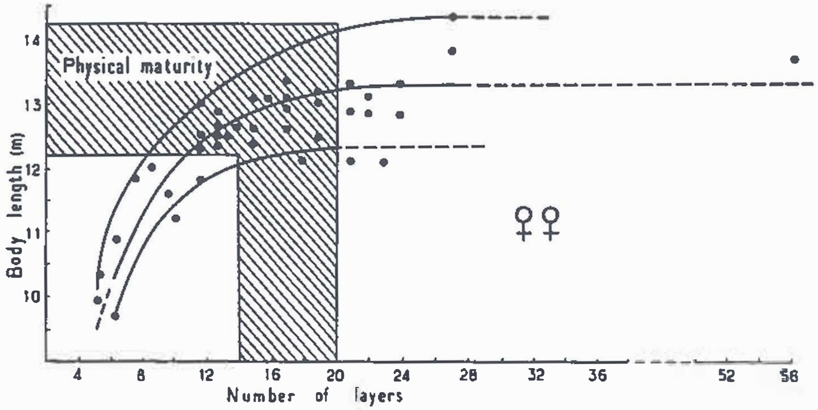

Fig. 3. *Correlation between the body length and the number of ear plug layers (1 layer = 1 year) of female gray whales (n = 41), which allows the determination of the age of physical maturity [Data by Zimushko (1970b) and Zimushko and Ivashin (1980).] See Fig. 2 for symbol designation.*

body size to the number of layers in the wax ear plugs of whales (one layer comprises one light and one dark lamina), Zimushko (1970b) concluded there is no significant difference in the rate of growth between male and female whales under 12.2 m; the average body length of males and females at the age of 1 year is 8.9 meters (range 8–9.5 m), and at 2 years it is 10.4 m (range 9.5–10.7 m). Further growth of both males and females is slower (Fig. 2), without considering the slightly larger dimensions of the females (sexually mature females on the average are larger than males by 0.3–0.4 m). The 3-year-old whales average about 11 m (range 10.7–11.6 m).

The analysis of relatively large amounts of data, obtained by Zimushko in the Chukotka Peninsula coastal waters in 1965–1976 and summarized in Figs. 2 and 3, allow us to estimate the age of physical maturity of the gray whale. It is determined by the cessation of the growth rate of the body and occurs in males when they reach an average length of 13.2 m; in the case of some smaller animals, it occurs when they reach a length of 12.5 m. This occurs when the animals reach an average age of 19 years (range, 17–22 years), when one considers that each layer of the ear plug is equivalent to 1 year of a whale's life. In females, physical maturity on the average occurs at a body size of 13.2 m, but apparently with a greater range among individuals (the smallest mature female was 12.2 m in length). The data indicated that the age of attaining physical maturity for females encompasses a range of 14 to 20 years, averaging 17 years. We want to add that the maximum number of layers in the ear plug of the gray whale was shown by Zimushko (1970b) to be 56 layers for a female 13.8 m long and 42 layers for a male of 12.9 m.

The data on the length of gray whale embryos and young whales, when presented as a circular graph, demonstrate the range of the size during embryonic growth and during the first year of life (Fig. 4).

Measurements conducted by Zimushko (1972b) on 12 skulls of the gray whale showed that with age the length of the rostrum increased relative to the length of the lower jaw.

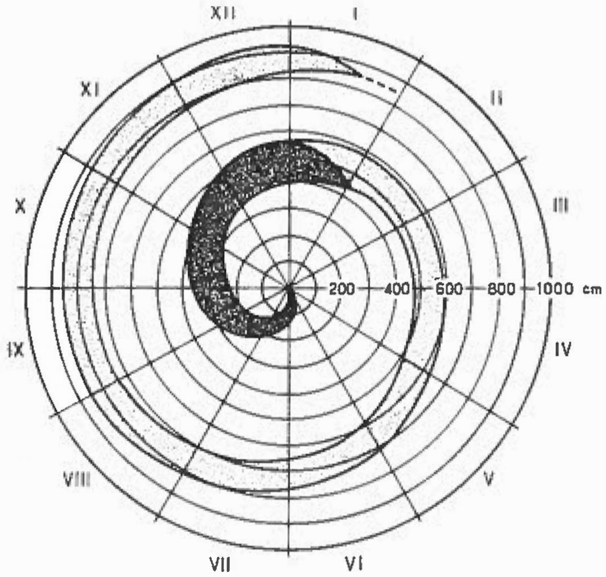

Fig. 4. *Growth of gray whale embryos and neonates according to combined data by Tomilin, 1937c; Zenkovich, 1937a; Rice and Wolman, 1971; and Zimushko and Ivashin, 1980. HEAVY STIPPLING indicates embryo length during pregnancy; embryos 25–140 mm long (not shown) can be found in whales taken in the second half of February (Rice and Wolman, 1971). LIGHT STIPPLING shows observed dimensions of body length during the first year of life. Roman numerals are months from Jan.–Dec.; Arabic numerals are body length in centimeters.*

REPRODUCTION

Attainment of sexual maturity occurs at different ages in female and male gray whales. Sexual maturity in females was determined by the presence of an embryo, corpus luteum, corpus albicans, or evidence of ovulation. Age of sexual maturity of females varied from 8 to 12 years (8–11 layers in the earplugs) when they reached a length of approximately 12 m (Zimushko, 1969b; Zimushko and Ivashin, 1980). The smallest female with a corpus of pregnancy was 11.3 m long although one 12.5 m female had no corpora. The largest number of corpora (11) was found in a 13.2 m female, and the average number of corpora for mature females was 5.1 (Blokhin, 1982). Males aged 6 to 7 years were found to be either immature or mature whereas those males aged 8 years (not less than 8 layers in the earplugs) with lengths of 11.5 m were usually mature (Zimushko, 1969b; Zimushko and Ivashin, 1980). There was a considerable increase in size and weight of the testes when the body length reached almost 11 m (Zimushko, 1969a). The investigation of mature male whales collected from July to October revealed that males had no spermatozoids in their epididymides, indicating a marked seasonality of the mating condition in male gray whales (Zimushko, 1969a).

The sexual cycle in female gray whales is believed to last 2 years and includes copulation, pregnancy, lactation, and a resting period after reproduction. The duration of pregnancy is nearly a year (Tomilin, 1957). Bogoslovskaya *et al.* (1981) found that pregnant females are the first to arrive off Chukotka and they are the first to leave, which corresponds with the findings of Rice and Wolman (1971) that pregnant females were the first to begin the northerly spring migration to the summer range, and they were the first to arrive at the breeding grounds after the fall southerly migration. This migratory timetable is supported by the findings of Blokhin (1982) who reported that the percentage of pregnant females in the 1980 catches was highest in the summer (July) and steadily declined during the 4-month fishing season and was lowest in autumn (October).

Analysis of the correlation between the number of corpora lutea and ovulation in females of reproductive age showed that the average biennial rate of ovulation in physically mature females was 1.4 (Blokhin, 1981). It also was shown that the first ovulation in the young females results in pregnancy, since there were some females whose ovaries showed some signs of pregnancies but no signs of ovulation. On the other hand, there were ovaries that indicated multiple ovulations, but no signs of pregnancy. The overall ratio of pregnant to nonpregnant female whales was 1:1 and supports the 2-year reproductive cycle proposed by Rice and Wolman (1971). On the average, according to Zimushko (1972a) and Zimushko and Ivashin (1980), in females 12.0–12.5 m long the ratio between signs of ovulation and signs of pregnancy was 1:1; in females 13.0–13.5 m long the ratio was 2.5:1. If this finding can be confirmed in the future it may indicate that with maturity (age) the intervals between pregnancies increase.

It is very important to note that some lactating females could also be pregnant at the same time. Zimushko (1969b) encountered seven such females. The occurrence of females simultaneously pregnant and lactating may serve as an indirect confirmation that some females give birth yearly. Determining the exact number of these females is difficult because of the ban on whaling females with calves; collection of this material can only be accidental. However, during observations in the waters of Chukotka Peninsula from 1965 to 1968 about 20% of such females were encountered; this may indicate a relatively widely distributed phenomenon of simultaneous lactation and pregnancy among female gray whales.

In his work, Zenkovich (1938a) described the composition of the milk in lactating gray whale females taken in September (the time when lactation has usually ceased). The milk had a fat content of 53%, a water content of 40.6%, and a dry content of 6.4%. Based on Tomilin's (1946) calculation, during the period of nursing the calf consumes 36.6 kg of milk per day on the average; for the total lactation period this would be approximately 5000 kg of milk. In July to September 1965 to 1970 some nonpregnant females were found to be lactating and others had recently finished lactating (Zimushko and Ivashin, 1980). Blokhin (1982) reports that many of the nonpregnant females taken in October 1980 had large corpora and well developed mammaries, indicating that they had recently weaned their calves. From these data it appears that lactation lasts approximately 7 months and that gray whale calves are weaned when their body length is about 7 m (Zimushko and Ivashin, 1980). Examination of the stomachs of whales from 7.7 to 9.0 m long showed that they were feeding on amphipods. Ascidians, polychaetes, algae, and mud were also found in their stomachs (Zimushko and Ivashin, 1980).

FEEDING

Zenkovich (1934c, 1937a,b) and Tomilin (1937a) were the first researchers who determined that along the Asian coast the main food source of the California gray whales is benthic amphipods; while in the Bering Strait and the Chukchi Sea, they feed predominantly on *Ampelisca macrocephala* but near the Koryak shore they feed on *Pontoporeia* sp. Further study of gray whale feeding by Sleptsov (1952) determined the maximum volume of the stomach of the gray whale was 350 liters; Klumov (1963) compiled the first list of the food species of the gray whale which consisted of 17 different species of invertebrates.

Furthermore, a detailed study of the differences in the aspects of feeding by gray whales off the coast of Chukotka Peninsula was done by Zimushko and Lenskaya (1970) from the analysis of 70 stomach-content samples of gray whales between 1965 and 1969. Blokhin (1981) and Blokhin and Pavlynchkov (1981, 1983) collected stomach samples from 38 whales and Bogoslovskaya and Votrogov (1981, 1982) also sampled 230 stomach contents from whales taken between 1979 and 1980 by the whaling vessel *Zvezdnyi*.

The list of the prey species of the gray whale, based on the data from all authors, consists of 60 species of amphipods and 80–90 other species of invertebrates, as well as algae and significant amounts of sand or pebbles which are present in the stomachs of these whales at all times. According to data by Bogoslovskaya *et al.* (1981a, 1982) the primary prey species of gray whales are 18 species of amphipods from the 12 families of the suborder Gammaridae. No age or sex difference of these prey species has been determined (Zimushko and Lenskaya, 1970; Blokhin and Pavlynchkov, 1981, 1983), but there is a clear difference between the southern (from the Island of Kosa Meechken up to the Providenya Bay in the Bering Sea) and the northern (from the Cape Nunyamo in the Bering Sea up to the Cape Serdtse-Kamen' in the Chukchi Sea) regions of feeding according to the dominant species of amphipods (Fig. 1) (Bogoslovskaya *et al.*, 1981a, 1982). The same authors showed that the aquatic region between Providenya Bay and Cape Nunyamo is characterized mostly by the variety of composition of invertebrates; *Pontoporeia femorata* as a dominating species in the southern regions is gradually replaced by *Ampelisca macrocephala* in the northern regions.

Gray whales congregate in "feeding spots," regions where amphipods accumulate. These areas probably provide a main food resource for other marine mammals and other species as well. For instance, in the aquatic region near the walrus (*Odobenus rosmarus*) hauling-out ground on the Arakamchechen Island gray whales and walruses graze in close association (Bogoslovskaya *et al.*, 1981b, 1982).

Tomilin (1946) calculated that a single fully grown gray whale would consume between 379 and 2496 kg of benthic organisms within a 24-hr period. Recently Zimushko and Lenskaya (1970) determined a 24-hr feeding bout would result in the ingestion of 1200 kg of the food species, 300 kg of which would be freshly ingested. These same authors came to the conclusion that the Chukotka–California population would consume 850,000 tons of food species on their feeding grounds during one season. According to the type of feeding, Tomilin (1954) separated gray whales into absolutely specific groups of benthic foragers and provided a description of morphological characteristics indicative of their benthic feeding habits (head, oral cavity, filtering apparatus, etc.).

GROUPING AND SOCIAL BEHAVIOR

Many aspects of the behavior of whales are touched upon in the works of Zenkovich (1934a, 1937a, 1954), Tomilin (1937a,b,c, 1954, 1957), Sleptsov (1952, 1961a), Zimushko and Ivashin (1980), Bogoslovskaya *et al.* (1981a, 1982), and Bogoslovskaya and Votrogov (1981). These investigators reported that gray whales feed in small groups of 2–4 whales, or more often as single whales (commonly pregnant females). It is not unusual for a herd to consist of 30–40 animals and sometimes 100–400. During the times of such large congregations, lasting from 1–4 days, strange and unexplained behavior is observed which is presumed to be connected with courting and mating behavior, as has been suggested by Tomilin (1937a) and the whalers of the Chukchi Sea.

Zimushko stated (Zimushko and Ivashin, 1980) that in 1973, of 232 whales encountered 44% were single, 24% were in pairs and 13% were in threes; 13 groups of 4 and 12 groups of 5 were also sighted. Groups of 7 and 8 animals were encountered three times each; the largest congregation included 24 whales. In 1980 Bogoslovskaya and Votrogov (1982) encountered 2447 whales of which singles were 47%; pairs, 31%; threes, 13%; and other groupings 9%; correspondingly in 1981 from 1595 whales, singles included 65%, pairs, 25%, threes, 6%; and others, 4%. These observations were conducted from whaling vessels, small motor boats, and Eskimo kayaks.

Among the groupings, the pairs are the most frequent associations. Adult animals are very often strongly attracted to each other during grazing and migrating when they are constantly together and very close; they observe the same breathing regime, surfacing synchronously or with a slight difference in breathing rhythm. The adult animals help each other, often reaching self-sacrificing measures; also there is a mutual attachment between paired females as strong as between male and female (Bogoslovskaya *et al.*, 1982). Groups of larger than three animals are usually unstable. Sex composition of the groups varies: there are different types of pairs, female and male, two females, and two males. Trios include two females and one male (or vice versa), and in the groups of five animals there were two males (Zimushko and Ivashin, 1980; Bogoslovskaya *et al.*, 1982).

It is important to describe the relationship between the mother and the calf. Nursing apparently ceases when the calf reaches a length of 8.5 m, but 9.6-m juveniles were observed swimming with their presumed mothers although they (the juveniles) had been feeding on benthic organisms (Tomilin, 1937a). Bogoslovskaya et al. (1982) assumed that the majority of the young whales separated from their mothers in July to August and congregated in certain areas, usually shallow waters and lagoons. Zenkovich (1937a) pointed out an example when the mother whale attacked the whale boat of the *Uelen* whalers after they wounded her calf. The same authors indicated that when the mother whale is killed, the juvenile whale usually leaves; therefore, in the gray whales at this stage in the calf's life, there is a one-sided attachment of the mother to the calf.

Tomilin (1937a,b) and Zenkovich (1937a,b, 1954) described in detail [after von

Ditmar (1890–1900) and apparently Krasheninnikov (1755)} a specific migration of whales with heavy infestations of skin parasites into the freshwater lagoons and shallow waters off the Koryak coast. The whales entered the lagoons, and dozens of them filled the shallow lakes connected with the sea. Some whales were just lying on the sand bars; with the tide they would move out to sea, and begin to feed as if nothing had happened. Some whales would lie immobile at the surface not paying attention to the approaching boats or even prods of the oars, as if they were sleeping (Zenkovich, 1954).

According to the observations of the Eskimos of Naukan the gray whale is capable of getting off the sand bars if next to a deep channel. He then arches, pushing with the rostrum and tail into the ground, which is possible because of the free neck vertebrae (Sleptsov, 1952).

Many whalers consider the gray whale the most intelligent of all large whales. He knows how to leave when pursued, changing his course drastically or surfacing at the same place where he dove, zig-zagging, entering shallow waters to escape, or surfacing without blowing although revealing only their blowholes (Zenkovich, 1934a, 1954). While being pursued, the gray whales increase their usual speed from 3–4 knots to 7–8 knots (Tomilin, 1937c). They can hold on in the unfrozen patches of water among the pack ice and shallow ice fields and at the very edge of the Arctic ice (Sleptsov, 1961b; L. S. Bogoslovskaya and T. N. Votrogov, unpublished notes). Gray whales coexist peacefully with the other mammals inhabiting the Chukchi Sea. On the feeding grounds they are found with the humpback whales and walruses. For example, in region 9 near the largest hauling ground of the walrus on Arakamchechen Island, whales and walrus graze in very close proximity to each other. Observers never recorded any aggressive behavior between these two species (Bogoslovskaya *et al.*, 1981b). Some authors indicated that the gray whales feeding near the entrance to Providenya Bay do not react to or feel threatened by the passing of nearby boats. They ceased to feed and demonstrated evasive behavior after persistent pursuit by vessels, however.

The behavior of gray whales suggests a plasticity or flexibility which allows them to utilize successfully the entire variety of coastal resources, from subtropical to polar regions.

POSITION OF THE SPECIES IN THE ECOSYSTEM

The position of the gray whale in the North Pacific ecosystem is determined by its interrelationships with food organisms (see above), parasites, enemies, and commensals. Some of these relationships were studied by Soviet researchers for the Chukotka–California population.

Practically all whales observed in the wild or killed by commercial whaling are covered with parasites such as *Cryptolepas rhachianecti* and whale lice (*Cyamus scammoni, C. ceti, and C. kessleri*) (Tomilin, 1937b; Zenkovich, 1935a; Zimushko and Ivashin, 1980). All authors noticed that the majority of the parasites accumulated on the head, around the blowhole, on the jaws, in the regions of the anal and genital orifices, and on the fins. Gray whales enter (brackish) water in coastal lagoons and the mouths of rivers to get rid of these parasites. Apparently this cleaning procedure is very successful. In

1978, a great number of of large black whales (body length between 12.5 and 13.5 m) approached the Chukotka Peninsula coast; all of them were free of parasites (Votrogov and Bogoslovskaya, 1980).

Soviet helminthologists found new species of endoparasites of the gray whale, which included helminths, acanthocephalans, and trematodes (Treshchev *et al.*, 1969; Zimushko and Ivashin, 1980). Most of these helminths were found only in the intestines of the gray whale. Of all the whales studied by Zimushko, 68.3% were infested by the cestode *Priapocephalus eschrichtii*, 58.7% by the trematode *Ogmogaster pentalineatus* (up to 1000 organisms in one whale), and by the acanthocephalans *Corynosoma semerne* and *C. septentrionalis* (29.9%), *C. validum* (24.4%), and *C. strumosum* (9.7%); the trematodes *Orthosplanchus pigmaeus* and *O. plicatus* were found only once. There is a similarity between the helminth fauna of the gray whales and pinnipeds, especially between the walrus and the bearded seal (*Erignathus barbatus*) who also feed on benthic organisms.

Apparently the gray whale has no other enemies than the killer whale (*Orcinus orca*), which pursue the gray whale and attack by grasping them by the pectoral flippers and the flukes and trying to open the whales' mouths to bite into the tongue (Zenkovich, 1934a, 1954). Gray whales escape from killer whales by swimming into shallow water, often inside the surf zone (Zenkovich, 1934a, 1954).

Many researchers commented on the strong correlation between feeding gray whales and large congregations of sea birds, including *Fulmarus glacialis*, *Larus hyperboreus*, *Rissa tridactyla*, *Aethia pusilla*, *Fratercula corniculata*, and *Puffinus tenuirostris*, which often landed on the whales' backs before they dove (Tomilin, 1937b; Zenkovich, 1954; Bogoslovskaya *et al.*, 1981a). Apparently whale feeding is responsible for bringing to the surface benthic invertebrates which then are easy prey for these birds.

WHALING

From ancient times, the gray whale was the object of aboriginal hunting by the native inhabitants of Kamchatka, the Koryak region, and the Chukotka Peninsula (von Ditmar, 1890–1900; Krasheninnikov, 1755). The most intensive whaling of young gray whales was common on the coast of Mechigmensky Bay, as indicated by many hundreds of the skulls of these animals that were discovered in the ruins of the ancient settlements (Bogoslovskaya *et al.*, 1981b; Bogoslovskaya and Votrogov, 1982a; Chapter 5, this volume). Species identification of the skulls was conducted by L. S. Bogoslovskaya with the assistance of A. G. Tomilin. The history and specific characteristics of the different aboriginal whaling tribes was described by I. I. Krupnik (Chapter 5, this volume).

From 1932 until the complete ban on whaling for gray whales in 1946, the Soviet whalers conducted the hunt on the Chukotka–California population in the Bering and Chukchi Seas (Zenkovich, 1947; Vadivasov, 1947). Whales from the Okhotsk–Korean population were hunted very sporadically during World War II in the region of Peter the Great Bay (Sleptsov, 1961b). In 1969, the aboriginal hunt of the gray whale ceased as a result of a large number of "struck-and-lost" whales. Aboriginal whaling in the Chukotka Peninsula was replaced by the modern whaling vessel *Zvezdnyi*. Statistics of aboriginal and vessel catches of gray whales from 1932 to 1980 are shown in Table IV.

Table IV
Whaling Statistics for the Gray Whale
from the Chukotka–California Population[a]

Year	Number taken	Year	Number taken
1932[b]	—	1957	56
1933	2	1958	145
1934	54	1959	187
1935	34	1960	156
1936	102	1961	207
1937	14	1962	147
1938	54	1963	179
1939	29	1964	188
1940	47	1965	175
1941	57	1966	194
1942	101	1967	125
1943	99	1968	135
1944	—	1969[d]	199
1945	30	1970	146
1946	22	1971	150
1947	1	1972	181
1948[c]	19	1973	173
1949	26	1974	181
1950	10	1975	171
1951	12	1976	163
1952	42	1977	186
1953	37	1978	182
1954	36	1979	178
1955	59	1980	179
1956	121		

[a] From Zenkovich (1947), Sleptsov (1952), Ivashin *et al.* (1972), Ivashin and Mineev (1978), and Ivashin and Mineev (1981).

[b] From 1932 until 1946; data is only from whaling groups.

[c] From 1948 until 1968; data only on aboriginal whaling from small boats.

[d] Catch data from the whaling vessel *Zvezdnyi*.

PROTECTION

All Soviet researchers recognize the critical condition of the Okhotsk–Korean population of the gray whale, which they feel is on the brink of extinction. The status of the Chukotka–California population is satisfactory; however, its existence is threatened by disturbance in the breeding grounds, by pollution along the migration route, and by extensive fisheries along the migratory route and the summer and fall feeding grounds (Bogoslovskaya *et al.*, 1982). Thus, beginning in 1974 the whaling vessel *Zvezdnyi* took one or two whales each year that bore marks of civilization on their bodies; remnants of synthetic ropes, fishing nets, etc. (L. M. Votrogov and L. S. Bogoslovskaya, unpublished notes). Fishing nets that became attached to the peduncles of the whales were probably acquired during the migration along the North American coast, and from their condition these wounds appeared to be 3–5 months old. We wish to emphasize that all the whales seen with fishing gear remnants on their bodies were adult, large animals, which were able to free themselves from the gear. Young animals and yearling calves are probably not as successful.

In conclusion, we wish to call attention to the intensive utilization by man of the natural resources in Alaska and Far Northeastern Asia. The utilization of natural resources along the coastal shelf and coastline jeopardizes the benthic communities and marine fauna in which the gray whale is playing a very visible role. In this regard, it has been proposed that a portion of the Bering Strait, which is important to gray whales as a feeding area, should be set aside as a protected area (Bogoslovskaya *et al.*, 1982).

Conclusions

The present short survey could not include many current observations of the biology of the gray whale contained in numerous Russian research publications. We have not included here any statistical data of the whaling industry, most of which has been made available due to the International Whaling Commission. The authors tried to illuminate those areas of research on gray whales that are known to a lesser degree in the English-speaking scientific community.

Summary

This article provides information on observations of the Okhotsk–Korean population of gray whales. Also, fundamental results of studies of the migration, summer–fall distribution, abundance, morphology, growth, reproduction, feeding, parasites, and behavior of the Chukotka–California population of the gray whale are summarized. Position of the gray whale in the ecosystem of the North Pacific is considered, as are problems associated with commercial whaling and protective measures of these two populations of this species.

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A note on observations of gray whales in the southern Chukchi and northern Bering Seas, August-November, 1980-89

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ABSTRACT

A total of 176 sightings of 488 gray whales (*Eschrichtius robustus*) were made during 85.6 hours of aerial surveys in the southern Chukchi Sea and northern Bering Sea, east of the International Date Line, from August to early November 1980-1989. Surveys were flown infrequently and effort varied considerably between years and geographic areas. Gray whales were sighted in all areas where surveys were flown, with the exceptions of Kotzebue Sound and Norton Sound. Abundance indices of whales per unit effort (WPUE) in the northern Bering Sea were higher than those in the southern Chukchi Sea during every month except September, when survey coverage was inadequate for abundance calculations, indicating comparatively higher overall use of that area or suggesting the onset of the southbound migration. Most gray whales were feeding (57%, $n = 276$). Incidental sightings of gray whales observed in and near the study area by other researchers were reviewed to better assess gray whale activity and migration patterns.

KEYWORDS: GRAY WHALES; SURVEYS-AERIAL; BERING SEA; NORTH PACIFIC; DISTRIBUTION; MIGRATION

INTRODUCTION

The distribution and migration of the California-Chukotka stock of gray whales is well-documented for most of its range (Swartz, 1986). However, information is still limited for some regions, including the northernmost summering areas in Alaskan waters. Distribution, migration timing and observed behaviours have been described for gray whales in the northern Bering and eastern Chukchi Seas in the summer (Moore and Ljungblad, 1984; Moore *et al*., 1986b; Würsig *et al*., 1986), the northeastern Chukchi Sea in the autumn (Moore *et al*., 1986a; Clarke *et al*., 1989) and the eastern Alaskan Beaufort Sea in the autumn (Rugh and Fraker, 1981; Würsig *et al*., 1983). These reports are augmented by reviews of opportunistic sightings in Alaskan waters (Maher, 1980; Marquette and Braham, 1982; Braham, 1984). However, specific information on gray whales in the southern Chukchi Sea and northern Bering Sea east of the International Date Line (IDL) between late summer and autumn is particularly scarce. Aerial surveys have occasionally been conducted in this area since 1980 as one component of a larger survey effort for endangered whales in the Beaufort, Chukchi and Bering Seas. This paper summarises the sightings of gray whales reported during these surveys and reviews other relevant information from the literature.

METHODS

The study area included coastal and offshore regions of the southern Chukchi Sea and the northern Bering Sea (63° to 69°N) east of the IDL (Fig. 1) which was divided into survey blocks. The area approximates the boundaries of the Hope and Norton Basin Outer Continental Shelf (OCS) Planning Areas, as designated by the US Department of the Interior, Minerals Management Service (MMS) for decision-making regarding offshore oil and gas activities. Two types of aerial surveys were flown: transect surveys along randomly selected east-west transect lines in survey blocks; and search surveys while transiting to offshore survey blocks (Moore *et al*., 1986b). Surveys were flown in a *Grumman Turbo Goose* model G21G at 152-458m altitude and speeds of 222-296km per hour.

Data routinely collected at each sighting included aircraft altitude, time, latitude, longitude, ice conditions, sea state, visibility, species, number of animals at the surface, number of visible calves, orientation of individual(s) at first sighting, behaviour and inclinometer angle. Whale behaviour classifications included swimming, diving, resting, milling, feeding, mating, cow-calf interaction and displaying. Survey effort and gray whale distribution were analysed for each month. Temporal (by month) and spatial (by survey block) abundance were derived as number of whales per survey hour (WPUE, whales per unit effort).

RESULTS

A total of 85.6 survey hours was flown, with 47.3 hours in the southern Chukchi Sea and 38.3 hours in the northern Bering Sea between August and November 1980-1989[1] (Fig. 2; Table 1). Survey effort was not consistent between years (Fig. 3): there were no surveys in the study area in 1982, 1984, 1985 or 1988. Flight effort in September was limited to the northernmost section of the study area near Point Hope, while survey coverage was most widespread in October. Total flight effort per month varied from 6.4hrs in September to 34.9hrs in October, with 70% (50.9hrs) of total survey effort in October and November.

There were 176 sightings of 488 gray whales in the study area (Fig. 4; Table 2). Gray whales were sighted in all areas where surveys were flown with the exception of Kotzebue Sound (blocks 30 and 31) and Norton Sound (block 29). In August, whales were seen just south of St Lawrence Island and in offshore waters between the Bering Strait and St Lawrence Island, with a single sighting of three animals north of Bering Strait in the southern Chukchi Sea. In September, gray whales were nearshore south of Point Hope

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[1] Limited aerial survey effort continued in the study area in November 1990 and 1991 (Clarke and Moore, 1993); no gray whales were seen and the survey effort is not incorporated here.

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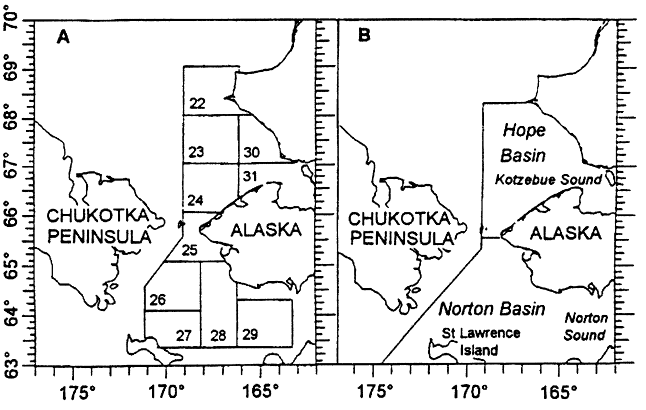

Fig. 1. Study area depicting survey blocks (A) and Hope Basin and Norton Basin OCS Planning Areas (B).

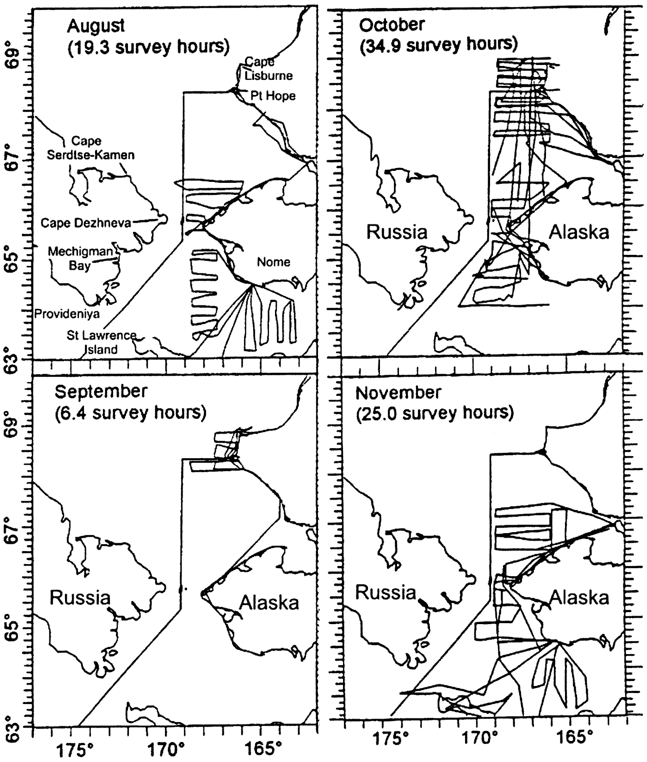

Fig. 2. Monthly composite flight tracks, 1980-89.

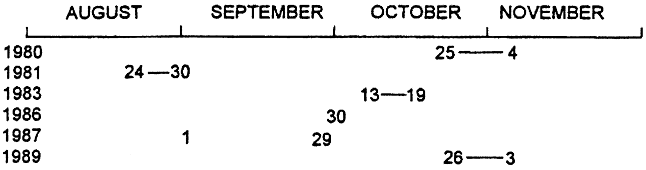

Fig. 3. Breakdown of monthly survey effort, 1980-89, showing dates on which flights occurred.

peninsula. The October sightings were offshore in the south-central Chukchi Sea and north-central Bering Sea, with scattered sightings along the coast. In November, gray whales were seen west of St Lawrence Island and in offshore areas south of Bering Strait, with one whale north of Bering Strait.

Monthly abundance indices (WPUE) for the southern Chukchi Sea (Table 1) were highest in October (5.3) and September (5.0) and negligible in August and November (< 0.5). WPUE in the southern Chukchi Sea was highest in block 23 (12.3) in October and block 22 (6.4) in September. In the northern Bering Sea, WPUE values were highest in October (11.3) and November (10.8) and considerably lower in August (3.0). The highest WPUE value was in block 26 in November (32.1). Comparing the two regions, WPUE was higher in the northern Bering Sea during every month except September, when survey coverage (0.8 hours) was inadequate. The indices were probably influenced by the sporadic survey effort, but may indicate comparatively greater use of the northern Bering Sea region or be an indicator of the onset of the autumn southbound migration from the Chukchi Sea.

The majority of whales seen were feeding (57%, $n = 276$), as evidenced by mud streaming from the whale's mouth or by the presence of conspicuous mud plumes, which are large billows of sediment brought to the surface by bottom feeding whales. For a significant proportion (25%, $n = 124$) of whales, no behaviour was recorded. Other behaviour observed included swimming (16%, $n = 78$), diving (1%, $n = 7$) and displaying (1%, $n = 3$). Feeding whales often changed swim direction while at the surface and generally

Table 1

Relative abundance of gray whales by survey block, August-November 1980-89 (does not include 12 whales seen in unblocked areas in August 1981 and November 1980). WPUE = whales per unit of effort (i.e. per hour).

	August			September			October			November			Total		
Survey block	Hrs	No.	WPUE	Hrs	No.	WPUE	Hrs	No.	WPUE	Hrs	No.	WPUE	Hrs	No.	WPUE
Southern Chukchi															
22	0.5	0	0	4.4	28	6.4	11.1	61	5.5	0	-	-	16.0	89	5.6
23	0	-	-	0	-	-	5.3	65	12.3	1.1	0	0	6.4	65	10.2
24	2.4	3	1.3	0.2	0	0	4.2	2	0.5	4.8	1	0.2	11.6	6	0.5
30	1.5	0	0	0.7	0	0	2.9	0	0	0.8	0	0	5.9	0	0
31	2.9	0	0	0.3	0	0	0.5	0	0	3.7	0	0	7.4	0	0
Total	7.3	3	0.4	5.6	28	5.0	24.0	128	5.3	10.4	1	0.1	47.3	160	3.4
Northern Bering															
25	3.6	12	3.3	0.7	0	0	4.0	38	9.5	3.5	44	12.6	11.8	94	8.0
26	0.9	17	18.9	0	-	-	4.9	83	16.9	3.3	106	32.1	9.1	206	22.6
27	0.6	1	1.7	0	-	-	0	-	-	1.3	3	2.3	1.9	4	2.1
28	3.5	6	1.7	0.1	0	0	2.0	2	1.0	4.1	4	1.0	9.7	12	1.2
29	3.4	0	0	0	-	-	0	-	-	2.4	0	0	5.8	0	0
Total	12.0	36	3.0	0.8	0	0	10.9	123	11.3	14.6	157	10.8	38.3	316	8.3

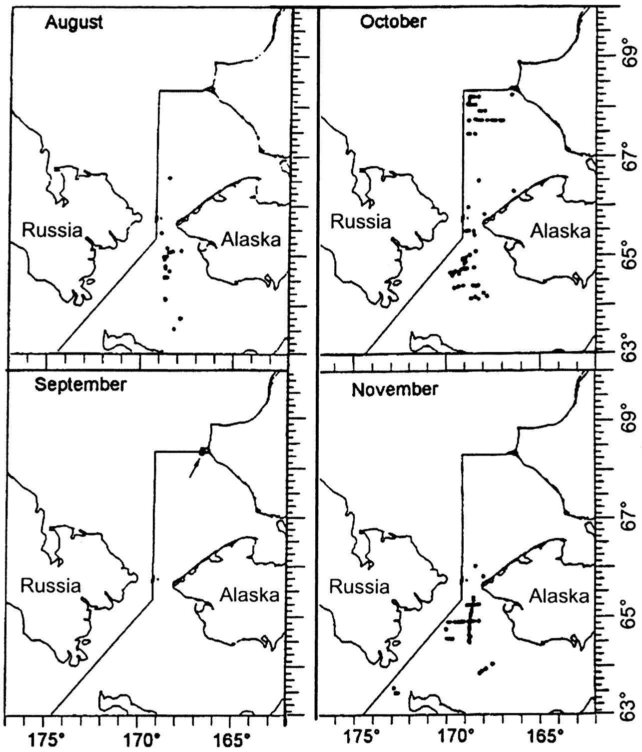

Fig. 4. Distribution scattergram depicting 176 sightings of 488 gray whales, 1980-1989: 28 sightings of 46 whales in August; 6 sightings of 28 whales in September (denoted by arrow); 82 sightings of 251 whales in October; 60 sightings of 163 whales in November. Each symbol represents one sighting of one or more whales. There were two sightings in August to the southeast of St. Lawrence Island (*ca* 63°N, 169°W).

Table 2

Monthly summary of gray whale sightings per number of whales August-November 1980-1989. * = no survey effort during this time period.

Year	August	September	October	November	Total
1980	*	*	44/125	60/163	104/288
1981	28/46	*	*	*	28/46
1983	*	*	3/7	*	3/7
1986	*	0	*	*	0
1987	*	6/28	*	*	6/28
1989	*	*	35/119	*	35/119
Total	28/46	6/28	82/251	60/163	176/488

did not show any concerted movement in any one direction. Therefore, whales seen feeding were not considered to be actively migrating and swim direction analyses excluded feeding whales. Consequently, there were insufficient data on swim direction collected to warrant analysis. One calf was seen in the study area, south of Point Hope in September 1987 (Clarke *et al.*, 1989).

DISCUSSION

Gray whales in the southern Chukchi Sea and northern Bering Sea of Alaska in late summer and early autumn have not been extensively studied for several reasons. The southern Chukchi and northern Bering seas are not important areas of offshore oil exploration and development, a factor greatly influencing the degree of interest and funding available for biological studies in the region. Additionally, unlike bowhead whales (*Balaena mysticetus*) which are actively hunted by Alaskan Eskimos, gray whales make only a minor contribution to native subsistence in a few US communities (Marquette and Braham, 1982; Krupnik, 1987). Thus, the incentive in the USA to support research on sustainable yields for gray whales is not as great as for bowhead whales. Finally, the California-Chukotka gray whale stock was removed from the Endangered Species List in June 1995 after having recovered to, or bypassed, pre-exploitation size (Breiwick *et al.*, 1988). Gray whales therefore do not receive the same scientific and financial consideration shown to other, more critically endangered, whale populations such as the bowhead whale or the North Atlantic right whale (*Eubalaena glacialis*).

Consequently, most information available concerning gray whales in and adjacent to the study area comes from incidental sightings made during research targeting other species. The data suggest that the southern Chukchi Sea supports relatively high gray whale densities throughout the late summer and autumn. Large gray whale aggregations were described from aerial and shipboard surveys both along the northern coast and offshore of the Chukotka Peninsula (Fig. 5). Soviet researchers conducting aerial surveys in August and October 1973 reported the highest densities of gray whales nearshore north of the Chukotka Peninsula between Cape Dezhneva (East Cape) and *ca* 175°W. Large aggregations were also located offshore at 68°N, 169°05’W (Zimushko and Ivashin, 1980; Berzin, 1984). Likewise, in late September and early October 1975, aggregations were located offshore north of Cape Serdtse-Kamen and north of Cape Dezhneva. During joint Soviet-American research cruises, large groups of gray whales were seen in October 1979 (>250) and October 1980 (>580) north of Cape Serdtse-Kamen (Berzin, 1984) as well as nearshore along the northern Chukotka coast (Miller *et al.*, 1985). Large aggregations were again reported along the coast and north of the Chukotka Peninsula in August and September 1982, with scattered sightings near Point Hope (Berzin, 1984; Miller *et al.*, 1985). Similarly, Blokhin (2003) counted 1,450 gray whales in a broad area north of the Chukotka Peninsula in August 1986. Joint Japanese-Russian-American oceanographic cruises in September-early October 1992-1994 documented gray whale aggregations north of the Strait and nearshore along the northern Chukotka coast (George, 1992; Moore, 1993). These data, combined with the gray whale sightings reported here in the southern Chukchi Sea in October 1989, indicate that the southern Chukchi Sea is an important gray whale habitat throughout late summer and autumn.

Incidental sightings data for the northern Bering Sea lead to more ambiguous conclusions. Gray whale aggregations are routinely reported along the southern Chukotka coast between Cape Dezhneva and Provideniya in association with Soviet whaling (Fig. 5; Zimushko and Ivashin, 1980; Berzin, 1984; Miller *et al.*, 1986; Blokhin, 2003). Whales were seen there as late as November in 1984 and 1987 (Blokhin, 1990). In addition, Blokhin (1990) noted that large numbers of gray whales occupy Mechigmen Bay (Mechigmenskiy Zaliv) from August to October in some years. Aggregations of gray whales were also reported offshore between St Lawrence Island and Bering Strait in September-October 1975 (Zimushko and Ivashin, 1980) and in November 1980 (Fig. 4), but these waters have rarely been surveyed in the autumn. Additional incidental data include five sightings of an unspecified number of whales near St Lawrence Island in September-October 1958-1981 (Braham, 1984), two gray whales in northwest Norton Sound in September 1982 (Leatherwood *et al.*, 1983) and scattered sightings of a few gray whales north of St Lawrence Island in December 1984 (Kibal’chich *et al.*, 1986). Gray whales were observed

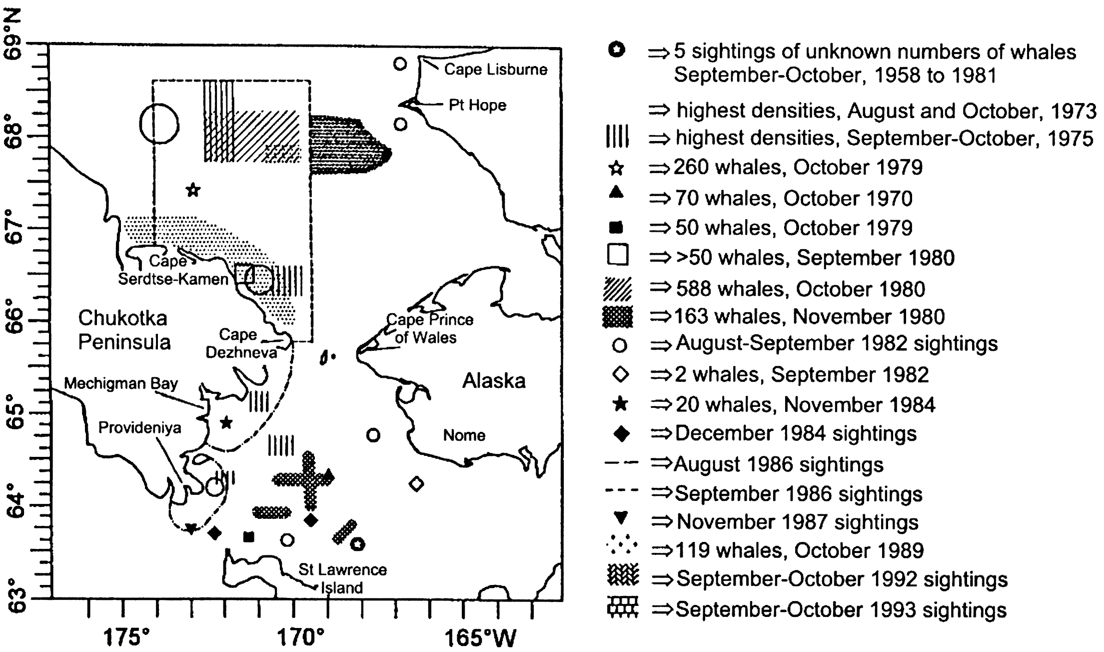

Fig. 5. Gray whale sightings and high density areas in or adjacent to the study area, 1958-93.

during the joint Japanese-Russian-American oceanographic cruises in late September and early October 1992 and early October 1993 south of the Strait (George, 1992; Moore, 1993).

Describing patterns of gray whale abundance and migration based on the available data is difficult owing to the lack of consistent and comparable survey effort, but some trends are worth noting. Gray whales have been seen in the northern Bering Sea as late as November and December (see Figs 4 and 5), by which time others will have reached the coasts of Oregon and California on their southbound migration (Herzing and Mate, 1984; Graham, 1990). The onset of the southbound migration from the southern Chukchi and northern Bering Seas is probably influenced by ice conditions. Rugh (1984) noted that the 1977 southbound migration past Unimak Pass was 10-11 days earlier than that in 1978, when ice conditions were far lighter and the ice front was much further north. Overall, ice front advances could be correlated with differences in median whale migration dates during 1977-9, although year-to-year variations in ice conditions were far greater than in whale migration dates (Rugh, 1984). Likewise, Graham (1990) estimated the peak migration date past San Clemente Island during the 1988/1989 southbound migration (14 January) to be six days earlier than that of the 1986/1987 migration (20 January) and five days later than that of the 1987/1988 migration (9 January); 1986 and 1987 were both considered light ice years, while 1988 was a heavy ice year in the Alaskan Arctic (Moore and Clarke, 1990). Blokhin (1990) also suggested that gray whales are probably present along the coastline of the Russian Far East, including the Chukotka Peninsula, into December, depending on the prevailing ice conditions. Therefore, while ice cover probably influences gray whale distribution and migration timing in the southern Chukchi and northern Bering Seas, the extent of the influence is unknown.

Gray whales return annually to particular regions in the southern Chukchi and northern Bering Seas which are apparently rich feeding grounds for adult whales (Clarke *et al.*, 1989; Blokhin, 2003) and/or weaning areas (Yablokov and Bogoslovskaya, 1984; Moore *et al.*, 1986b). The size segregation observed off Chukotka may be related to differential prey availability. Stoker (1990) suggests that smaller whales feed on smaller amphipods commonly found inshore, while larger whales feed further offshore on larger amphipods. Estimates of standing benthic stocks in various regions of the northern Bering and Chukchi Seas indicate that gray whales take advantage of those areas where the benthic community biomass is most dense, such as the Chirikov basin south of St Lawrence Island. Areas where gray whales are usually not seen feeding, such as north of St Lawrence Island, are often characterised by benthic communities dominated by species not preferred by gray whales (Stoker, 1990). Blokhin (2003) reported that preliminary hydrobiological results indicated that the area between Cape Serdtse-Kamen and Cape Dezhneva had the highest measured biomass of prey preferred by gray whales (62% of the total measured benthic biomass). This area was where the greatest proportion of whales (57%) was seen. However, it was pointed out that the occurrence of whales did not always coincide with areas of high benthic concentration and it was consequently suggested that gray whales probably graze from area to area. The lack of gray whale sightings in Kotzebue and Norton sounds may be due to the lack of preferred prey in those areas. Such sounds typically contain brackish water, which support prey species ingested by anadromous fishes rather than mysticete whales (Cooney, 1981). Additionally, Frost and Lowry (1988) report that crangonid shrimp, a preferred food for spotted seals and white whales but not gray whales (Nerini, 1984), are abundant in Kotzebue Sound.

The information presented here is of limited significance due to the circumstances under which it was collected, as it does not lend itself to the testing of hypotheses on gray whale abundance, migration patterns and behaviour. There has been no additional dedicated research on gray whales in the northern Bering and southern Chukchi Seas since 1989. Aerial surveys dedicated to determining gray whale distribution and relative abundance in this area were flown for one week in summer 2002 (Moore *et al.*, 2002). Results from that limited effort suggest that the northern Bering Sea may no longer be a primary feeding ground. Information on gray whales in this area will probably continue to result from incidental sightings by researchers on projects targeting other species or with other primary interests. Despite this, the material presented here provides some additional insights into gray whale natural history in a geographic area that is not well known.

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GRAY WHALE FORAGING HABITAT IN THE NORTHERN BERING SEA: A GIS-BASED RETROSPECTIVE SUMMARY

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ABSTRACT

A retrospective summary of gray whale and benthic fauna distribution and abundance in the 1980s was undertaken to provide a baseline for comparison to present conditions. As reported in previous studies, the central Chirikov Basin was the area of highest relative abundance of both whales and benthic fauna. Ampelicid amphipods were the dominant benthos (70%) in the area where gray whale distribution was clustered and relative abundance was highest. The Eastern North Pacific (ENP) gray whale population grew at an estimated 3.29% between 1967/68 and 1987/88, with population size in 1987/88 estimated at 21,296 (CV=6.05%) whales. A 30% decline in benthic biomass was reported for the Chirikov Basin from 1986 to 1988, but estimates of gray whale numbers continued to climb to an estimate of 26,635 (CV = 10.06%) in 1997/98. While the reason for the recent very high mortalities of ENP gray whales is unknown, a reduction in available prey leading to starvation has been suggested as a possibility. Available measurements of benthic community biomass and faunal structure in the northern Bering and southern Chukchi seas indicates a downturn in productivity and shift in prey species in the 1990s. While studying the situation at one feeding location is inadequate for an assessment of prey availability, the Chirikov Basin may provide a key index to the response by the ENP gray whale population to changing conditions on their sub-Arctic and Arctic feeding grounds.

INTRODUCTION

Gray whales (*Eschrichtius robustus*) are opportunistic foragers. While all other mysticetes filter or scoop prey from the water column, gray whales suction mud, epi- and infauna from the seafloor (Nerini, 1984) and, when prey densities are high enough, zooplankton from the sea surface (Darling *et al.*, 1998). Suction feeding is highly disruptive to the benthos (Oliver and Slattery, 1985), directly effects the local distribution of seabirds by bringing benthic prey to the surface (Grebmeier and Harrison, 1992), and may be considered a specialized type of niche construction (Odling-Smee *et al.*, 1996). Gray whales feed extensively in the northern Bering Sea, especially in the Chirikov Basin between St. Lawrence Island and Bering Strait (Moore *et al.*, 1986; Moore and DeMaster, 1997). Whales feed there on comparatively dense populations of ampeliscid amphipods, which dominated benthic samples obtained in the late 1970s through the mid-1980s (Stoker, 1981; Grebmeier *et al.*, 1989). In the mid-1980s, the

Chirikov Basin was reported to have the highest secondary production rates for any extensive benthic community (Highsmith and Coyle, 1990), although the abundance and biomass of the amphipod community appeared to be in decline by the end of that decade (Highsmith and Coyle, 1992).

The recent increase in documented mortalities of gray whales from the Eastern North Pacific (ENP) stock (Norman *et al.*, 2000), and the emaciated condition of several of those whales, generated speculation that starvation was the primary cause of death. Unfortunately, there is no simple way to test this hypothesis, due to the extensive range and prey plasticity of the species. Gray whales are foraging opportunists; that is, they seem to eat whenever they can. Although benthic amphipods dominated in stomach samples from gray whales taken by Soviet whalers in the Chirikov Basin, Nerini (1984) listed prey items from 19 genera, including sponges, polychaete worms, a wide variety of crustacea, and molluscs. Whales feed from the lagoons of Baja California, Mexico, all along their migration route to Alaska, even when localized sampling indicates low (potential) prey densities (Oliver *et al.*, 1983; Nerini, 1984). Furthermore, it is clear that some whales feed extensively in the summer offshore Vancouver Island (Darling *et al.*, 1998; Kvitek and Oliver, 1986), as well as other areas far south of Chirikov Basin. Most recently, feeding gray whales were reported in Ugak Bay, off the eastern coast of Kodiak Island, Alaska, from mid-August 1999 through March 2000 (K. Wynne, pers. comm., University of Alaska-Fairbanks, 118 Trident Way, Kodiak, AK 99615 USA).

Although prey availability can not be assessed over the full range of the gray whale, a review of habitat features associated with gray whale feeding aggregations reported for the 1980s may be an important first step towards understanding the conditions conducive to robust foraging. Here, we summarize gray whale distribution and relative abundance in Chirikov Basin from aerial surveys conducted from 1980 through 1984. Benthic biomass and abundance data, previously reported in Grebmeier *et al.* (1989), is incorporated via Geographic Information System (GIS) mapping to provide a direct comparison of relative abundance measures for predator and prey in this prime gray whale feeding area.

METHODS

Gray whale distribution and relative abundance were derived from aerial surveys conducted in autumn 1980 and during summer 1981-84. Both search and line transect surveys were flown in a fixed-wing aircraft. Details of survey protocol were previously described in Moore *et al.* (1986). The aerial survey study area was post-stratified to three regions (Fig. 1), focused on the Chirikov Basin south of Bering Strait (regions 1 and 2) and waters around St. Lawrence Island (region 3) in the northern Bering Sea. Relative abundance was calculated as the number of whales seen per survey kilometer, using all survey effort; and as number of whales per transect-kilometer (t-km), which excludes counts of whales made while circling overhead and searching along coastal areas. The calculation using only t-km is considered a less-biased index of abundance, but it excludes most of the survey effort in region 3. Density estimates for sub-blocks of the three regions, calculated for July 1980-83 using strip transect techniques, can be found in Moore *et al.* (1986).

Water column and benthic sampling stations were occupied, both north and south of Bering Strait, from July to September 1984-86. Details of sampling protocol are given in Grebmeier *et al.* (1989). In brief, benthic samples (0.1m^2 van Veen grabs) were washed on 1mm sieve screens and animals were identified to family level and then counted and weighed to determine wet weight biomass and abundance. Highly mobile epifauna, such as crabs and sea stars, were excluded from the analysis, while relatively sessile epifauna and infauna were included. Abundance data were then used in a numerical clustering program, which grouped sampling stations according to faunal similarities, as developed by Stoker (1981) and Feder *et al.* (1985). Surface sediments (to 1cm) were sectioned, dried, homogenized and sampled for grain size, then correlations between animal abundance and sediment parameters were investigated using various correlation tests.

Results of aerial survey sampling of whale distribution and relative abundance, relative to benthic sampling for faunal composition abundance and biomass, were subsequently compared via Geographic Information System (GIS) mapping. This provided a unique integrative approach for a retrospective comparison of predator and prey domains in the Chirikov Basin, a prime gray whale feeding area.

RESULTS

A total of 37,519km of aerial survey was flown in spring, summer and autumn 1980-84 (Table 1). Gray whales were never seen during April surveys and never in region 1 in May (Table 2). Comparatively high counts of gray whales were made in region 2 in May and most regions during the other months. Relative abundance indices suggest substantial intra- and inter-annual variability in gray whale occurrence. For example, in October 1980 relative abundance indices were similar in regions 1 and 2, but by November abundance in region 1 was nearly twice that of region 2, suggesting whales aggregated in the more northern region late in the feeding season that year. Perhaps more suggestive of intra-annual shifts among regions is the 1981 data where highest abundance indices moved from region 2 in May, northward to region 1 in June, back to region 2 in July and south to region 3 in August. Among years, 1983 stood out as a year of peak gray whale abundance in the Chirikov Basin; perhaps this coincided with or was related to a strong El Niño condition.

A total of 10,658km of line transect survey was conducted, with comparatively uniform effort in 1981-84 (Table 3). Relative abundance for each month in which whales were seen again suggest clear inter- and intra-annual variability in gray whale habitat use (Table 4). For example, relative abundance in region 1 was particularly high in November 1980 and again in June 1981 and July 1983. Indeed, with few exceptions, the pattern reflected by relative abundance indices derived from transect-only effort (Table 4) is not demonstrably different from that calculated from cumulative survey data (Table 2). Both are shown in this report to reinforce the sense of whale movements and aggregation indicated by the variability in indices over time.

July was the only month in which surveys were flown over four consecutive years and corresponds best with the period when benthic data were sampled. Combined July survey effort consisted of 12,281km overall (Fig. 2A), including 5,489km of line transect survey (Fig. 2B). Gray whale distribution was clustered in mid-regions 1 and 2 (Fig. 3). This distribution corresponds fairly well with measures of benthic biomass (Fig. 4A) and abundance (Fig. 4B). Biomass was especially high in mid-region 1, where stations showing 23-32gC/m^2 were common. Biomass at stations in regions 2 and 3 ranged from 14-32gC/m^2.

Abundance indices were high in mid-regions 1 and 2, with multiple stations where individuals numbered >10,000/m^2. In region 3, abundance was particularly high at a station southeast of the island; unfortunately, there were no stations near the northwest and southeast coast of the islands where most of the whales were seen.

Abundance data from each station (Fig. 4B) were clustered on the basis of similarities in relative percent of faunal composition, resulting in the description of seven faunal communities in the study area (Fig 5). These communities were identified as faunal group I, II, III, IV, VIII, X and XI in Grebmeier *et al.* (1989). Four of the seven communities were associated with the comparatively cold, saline, nutrient-rich Bering Shelf-Anadyr Water (BSAW), but not with warm, fresh and nutrient-poor Alaska Coastal Water (ACW). A summary of abundance, biomass and sediment composition at these stations shows that faunal groups 1 and 3 represent communities where abundance and biomass were exceptionally high (Table 5). Not surprisingly, these faunal groups correspond with areas where gray whale sightings show the densest clusters (ref. Fig. 3). Indeed, gray whale relative abundance, derived from aerial survey data pooled from July 1981-84, was from two to nearly six times higher in regions 1 and 2 than in region 3 (Fig. 6). Regions 1 and 2 clearly correspond with faunal communities I and III, where abundance and biomass was at least twice as high as at other stations in the study area. While ampeliscid amphipods comprised 70% of the faunal abundance in group I communities, they were only 21% of the abundance in group III communities. Notably, faunal community III was also identified in the area southeast of St. Lawrence Island, near where gray whales sightings were clustered (ref. Fig. 3).

Finally, although it is outside the bounds of our designated study area, benthic sampling southwest of St. Lawrence Island (*i.e.* region 3) suggests that a decline in productivity and a change in dominant benthic fauna occurred in the 1990s. Biomass from samples collected southwest of St. Lawrence Island in June 1990, June/July 1993 and May/June 1994 indicate a drop in benthic biomass from over 45gC/m^2 in 1990 to about 20gC/m^2 in 1993-94 (Fig. 7). Although there is considerable inter-annual variability in benthic biomass measures, recent studies indicate this drop continued through 1998 and 1999 (summarized in Grebmeier and Dunton, 2000).

DISCUSSION

This retrospective analysis of gray whale and benthic fauna distribution and abundance in the Chirikov Basin is meant to provide a baseline for comparison between a period when gray whales fed in what was considered a prime foraging habitat (*i.e.* the early 1980s) and a period when habitat may be less than optimal. The Eastern North Pacific (ENP) gray whale population was estimated to number 16,555 (SE = 690) in 1979/80, increasing to 20,348 (SE=726) by 1985/86 (Buckland and Breiwick, in press). In the three years following (1986-88), Highsmith and Coyle (1992) noted a 30% decline in the abundance and biomass of the amphipod community in Chirikov Basin, yet the gray whale population continued to grow. In 1987/88, gray whales were estimated to number 21,296 (CV = 6.05%), increasing to 23,109 (CV = 5.42%) individuals by 1993/94 (Buckland *et al.,* 1993; Rugh *et al.*, 1999). The most recent (1997/98) estimate of 26,635 (CV = 10.1%) whales is coincident with further declines in benthic biomass reported for sampling stations south of St. Lawrence Island (Grebmeier and Dunton, 2000). Collectively, these data suggest a decline in the gray whale prey base (*i.e.* carrying capacity), starting in the mid-1980s, that had no immediate affect on ENP gray whale recruitment.

But are we seeing the effects of a decline in prey on the ENP gray whale stock now? Because gray whales feed at so many locations along their migration route (Nerini, 1984; Darling *et al.*, 1998), offshore Alaska (Braham, 1984; Moore *et al.*, 1986) and the Chukotka Peninsula (Blohkin, 1984), it is simplistic to equate the current spate of high mortalities (Norman *et al.*, 2000) with a decline in prey biomass and abundance in the Chirikov Basin. However, this formerly-prime feeding area may be a bellwether for the state of gray whale foraging habitat, if either prey abundance or quality has changed significantly. For example, Grebmeier and Dunton (2000) note that while benthic biomass north of Bering Strait has remained high, there has been a change in dominant fauna that is likely the result of changing hydrographic conditions. This is important to note because gray whale prey quality varies with species composition. For example, large *Ampelisca macrocephala* are especially lipid rich, as compared to other common amphipod prey (e.g. *Byblis* spp.), so conditions that favor *Bybliss* spp. over *A. macrocephala* will result in a poorer diet for gray whales. Further, prey species size is influenced by organic matter flux, with the density of small amphipods (e.g. *A. birulai*) favored when organic flux is low (Coyle and Highsmith, 1994). Finally, warming seas will elevate amphipod food requirements which may lead to elevated predation rates, both factors selecting for smaller prey species (Coyle and Highsmith, 1994). Thus physical forcing, which directly effects current strength and flow, is key to any assessment of gray whale prey availability.

The Chirikov Basin and areas southwest of St. Lawrence Island and north of Bering Strait are the downstream end of the productive current that runs along the Aleutian chain, sometimes called the 'Green Belt' (Fig. 8). These productive zones are the result of carbon and nutrient transfer to the shallow shelves of the northern Bering and Chukchi seas (Grebmeier and Barry, 1991). Productivity along the 'Green Belt' is largely determined by the Pacific Decadal Oscillation (PDO), which reflects the relative position and strength of the Aleutian Low (Francis *et al.*, 1998). Overall, a decline in seabird and marine mammal populations in the North Pacific has been found to correlate with the PDO, although linking mechanisms remain very poorly understood (Springer, 1999). Recent evidence points to a weakening of current flow in the Gulf of Anadyr and through Bering Strait (Roach *et al.*, 1995), which may be a driving factor in the amount and type of food available to gray whales in a portion of their range historically considered their primary feeding habitat. Only focused research, integrating scales from atmospheric oscillations to gray whale distribution and body condition, will elucidate this possible connection.

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Table 1. Cumulative aerial survey effort (km) in the northern Bering Sea, by region and month.

		REGION			
YEAR	MONTH	1	2	3	Grand Total
1980	APR	560			560
	MAY	990	328	259	1577
	OCT	1128	529		1657
	NOV	788	683	508	1979
1980 Total		3466	1540	767	5773
1981	APR	1593	4027	1006	6626
	MAY	320	1011	274	1605
	JUN	1104	519	940	2563
	JUL	890	744	289	1923
	AUG	772	520	181	1473
1981 Total		4679	6821	2690	14190
1982	APR	1109	1310	629	3048
	MAY	458	489	270	1217
	JUL	1856	3005	675	5536
1982 Total		3423	4804	1574	9801
1983	APR	238	467		705
	JUL	1681	2477	326	4484
	OCT	73			73
1983 Total		1992	2944	326	5262
1984	APR	1011	1009	69	2089
	MAY	66			66
	JUL	113	225		338
1984 Total		1190	1234	69	2493
Grand Total		14750	17343	5426	37519

Table 2. Number and (relative abundance) of gray whales seen during cumulative survey effort, by region and month. Relative abundance = total number of whales/10 km of survey effort. Gray whales were never seen in April; – = no survey effort.

YEAR	MONTH	REGION 1		2		3		Total	
1980	OCT	91	(0.81)	28	(0.53)	–		119	(0.72)
	NOV	144	(1.83)	14	(0.20)	0	(0)	158	(0.80)
1981	MAY	0	(0)	115	(1.14)	15	(0.55)	130	(0.81)
	JUNE	124	(1.12)	20	(0.39)	3	(0.03)	147	(0.57)
	JULY	14	(0.16)	74	(0.99)	2	(0.07)	90	(0.47)
	AUG	28	(0.36)	10	(0.19)	10	(0.55)	48	(0.33)
1982	MAY	0	(0)	2	(0.04)	0	(0)	2	(0.02)
	JULY	68	(0.37)	80	(0.27)	42	(0.62)	190	(0.34)
1983	JULY	479	(2.85)	526	(2.12)	0	(0)	1005	(2.24)
1984	JULY	0	(0)	38	(1.69)	–		38	(1.12)

Table 3. Line transect aerial survey effort (km) in the northern Bering Sea, by region and month.

YEAR	MONTH	REGION 1	2	3	Grand Total
1980	OCT	35			35
	NOV	306	2		308
1980 Total		341	2		343
1981	APR		228		228
	MAY	33	325	205	563
	JUN	488	310	362	1160
	JUL	299	249	113	661
	AUG	380	363	12	755
1981 Total		1200	1475	692	3367
1982	MAY		342	227	569
	JUL	728	863	72	1663
1982 Total		728	1205	299	2232
1983	JUL	1173	1533	266	2972
1983 Total		1173	1533	266	2972
1984	APR	657	839	55	1551
	JUL	82	111		193
1984 Total		739	950	55	1744
Grand Total		4181	5165	1312	10658

Table 4. Number and (relative abundance) of gray whales seen during transect surveys in the northern Bering Sea, by region and month. Relative abundance = total number of whales/10 km of line transect survey effort; *not calculated for t-km < 50 km. Gray whales were never seen in April; – = no transect survey effort.

YEAR	MONTH	REGION 1		2		3		Total	
1980	OCT	1	(*)	–		–		1	(*)
	NOV	90	(2.94)	3	(*)	–		93	(3.02)
1981	MAY	0	(*)	31	(0.95)	15	(0.73)	46	(0.82)
	JUNE	110	(2.25)	14	(0.45)	1	(0.03)	125	(1.08)

	JULY	2	(0.07)	23	(0.92)	0	(0)	25	(0.38)
	AUG	17	(0.45)	6	(0.17)	0	(*)	23	(0.30)
1982	MAY	--		0	(0)	0	(0)	0	(0)
	JULY	23	(0.32)	32	(0.37)	0	(0)	55	(0.33)
1983	JULY	423	(3.61)	443	(2.89)	0	(0)	866	(2.91)
1984	JULY	0	(0)	7	(0.63)	–		7	(0.36)

Table 5. Mean benthic abundance, biomass and sediment composition for benthic station groups located in Bering Shelf-Anadyr Water (BSAW) and Alaska Coastal Water (ACW). Modified from Table 5 in Grebmeier *et al.* (1989); – = no data.

GROUP	WATER TYPE	MEAN ABUNDANCE (No./m^2)	MEAN BIOMASS (gC/m^2)	SEDIMENT COMPOSITION (%)					
				S/C	VFS	FS	MS	CS	GR
I	BSAW	6940	22.2	6.9	31.7	53.8	5.9	1.0	0.0
II	Both	2529	8.3	–	–	–	–	–	–
III	BSAW	5365	24.2	50.9	25.3	13.7	9.5	0.6	0.0
IV	BSAW	2048	11.3	34.3	40.5	25.0	0.0	0.3	0.0
VIII	ACW	1367	15.4	15.8	7.0	29.2	30.7	14.4	3.3
X	ACW	718	2.0	1.1	0.7	28.6	56.7	11.9	0.0
XI	BSAW	1684	12.5	–	–	–	–	–	–

FIGURE CAPTIONS

Figure 1. Study area in the northern Bering Sea, post stratified to three regions: regions 1 and 2 correspond to Chirikov Basin; and region 3 to waters south and east of St. Lawrence Island.

Figure 2. Aerial survey effort flown in July 1981-84: all survey effort (A); and line transect survey effort only (B).

Figure 3. Distribution of gray whales from surveys flown in July 1981-84.

Figure 4. Biomass in: (A) grams of carbon per square meter (gC/m^2); and (B) number of individuals per square meter (No./m^2).

Figure 5. Distribution of faunal communities based on cluster group analysis, from Grebmeier *et al.* (1989: Figure 6), with boundaries of study area regions included. Dotted line indicates approximate position of the front between Bering Shelf-Anadyr Water (BSAW) and Alaska Coastal Water (ACW).

Figure 6. Relative abundance of gray whales from surveys flown in July 1984 as: number of whales/all survey effort (A); and number of whales seen during line transect surveys/transect survey effort (B).

Figure 7. Benthic community structure (encircled in black; based on faunal abundance) in regions south of St. Lawrence Island for: June 1990 (a); June/July 1993 (b); May/June 1994

(c); and bar graph of inter-annual variation at one site. Reproduced from Grebmeier and Dunton (2000: Figure 5).

Figure 8. General surface circulation and areas with high water column primary productivity (up to 800 gC/m^2 /y) in the Bering and southern Chukchi Seas. Figure modified from Springer *et al.* (1996); reproduced here courtesy of Lee Cooper.

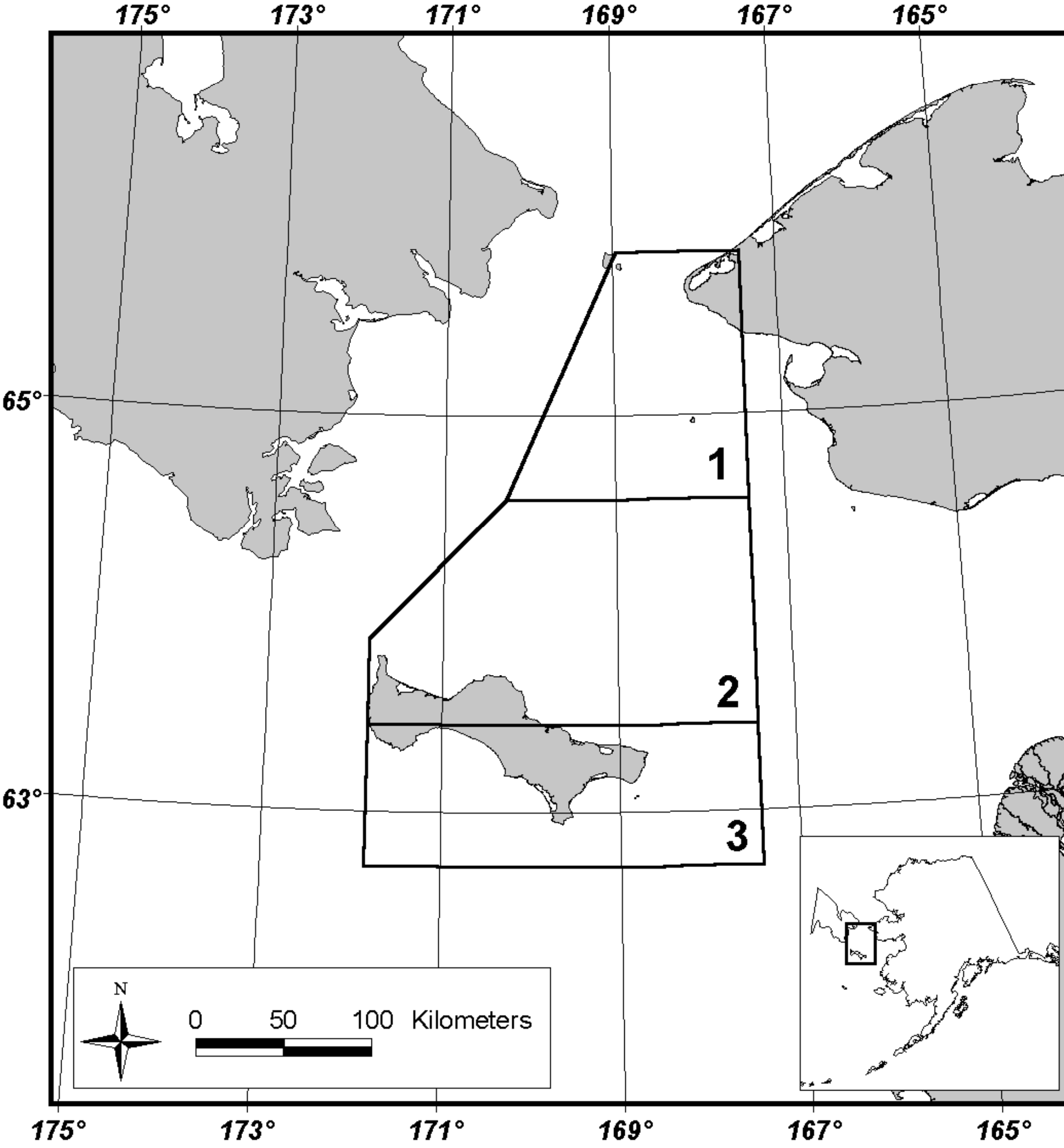

Figure 1.

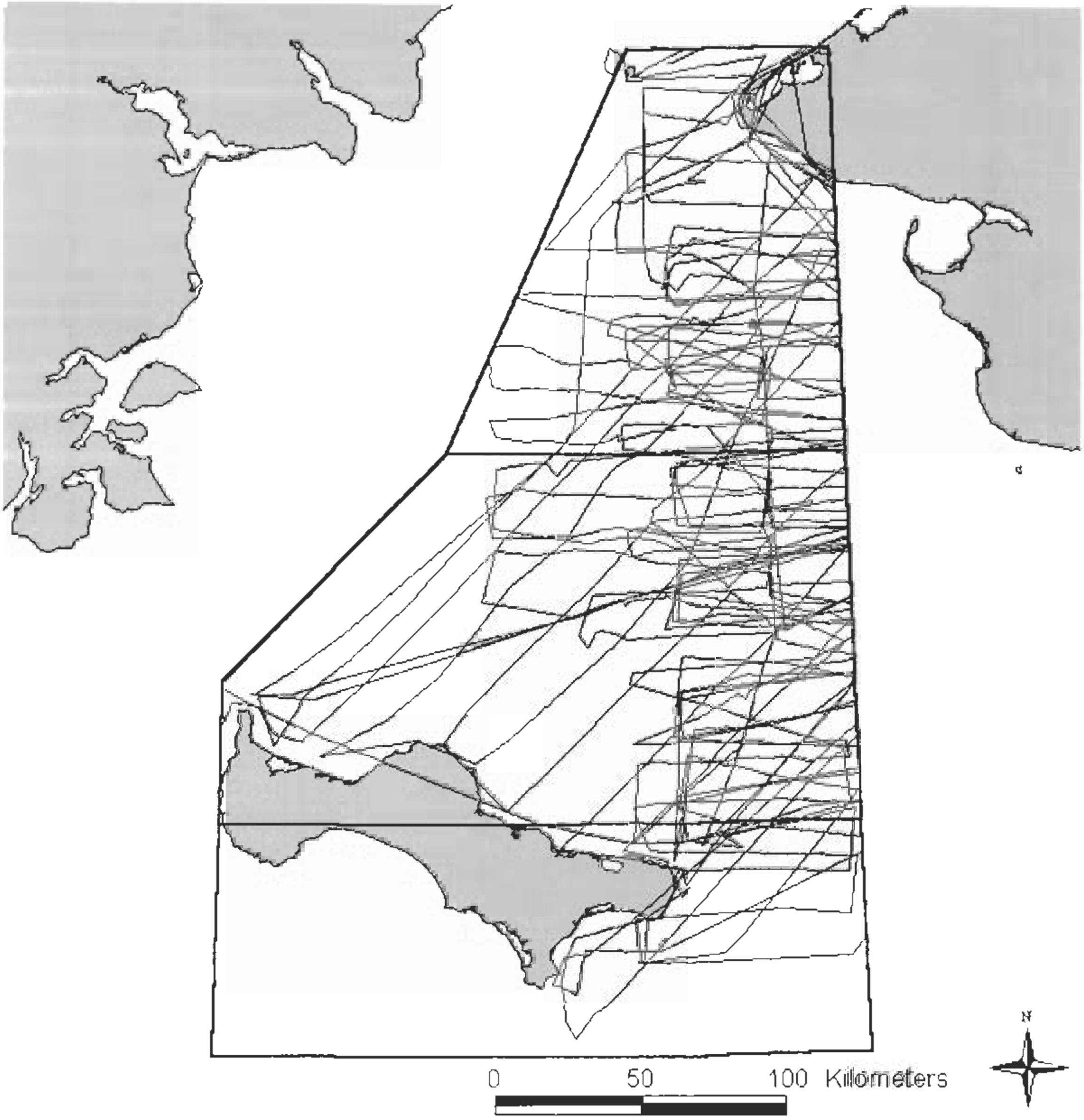

Figure 2A.

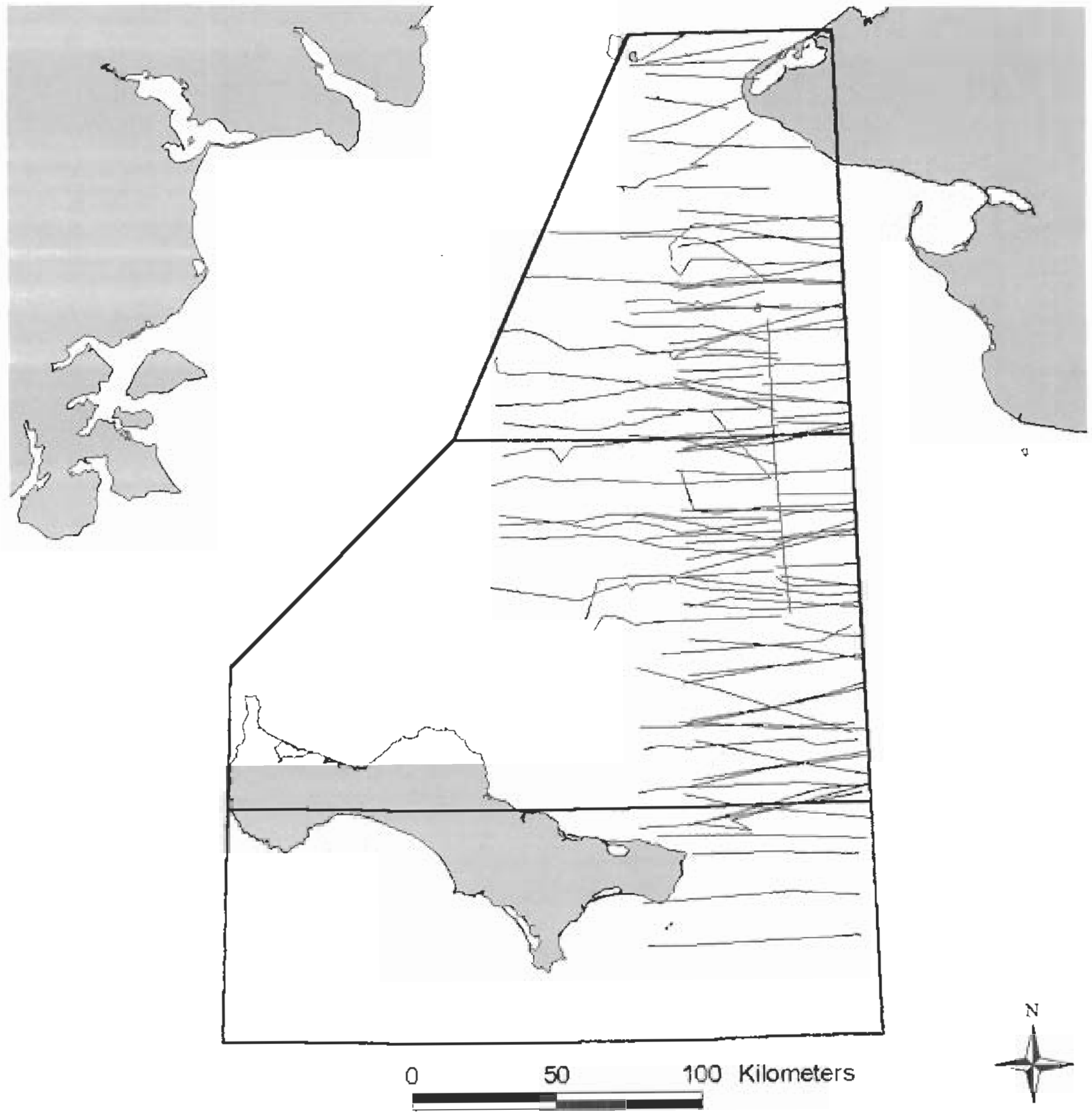

Figure 2B.

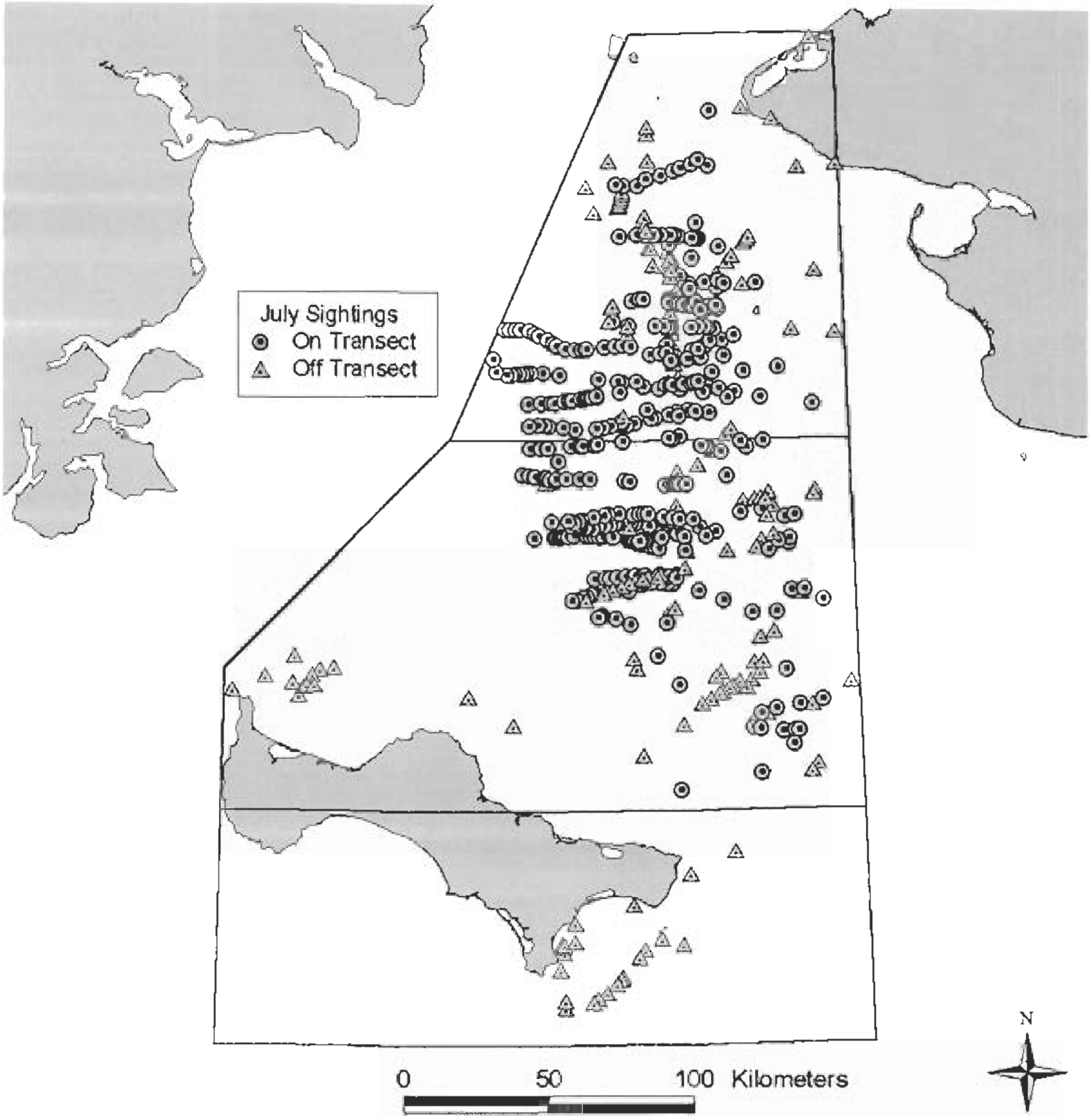
July Sightings
● On Transect
▲ Off Transect
0
50
100 Kilometers
N

Figure 3.

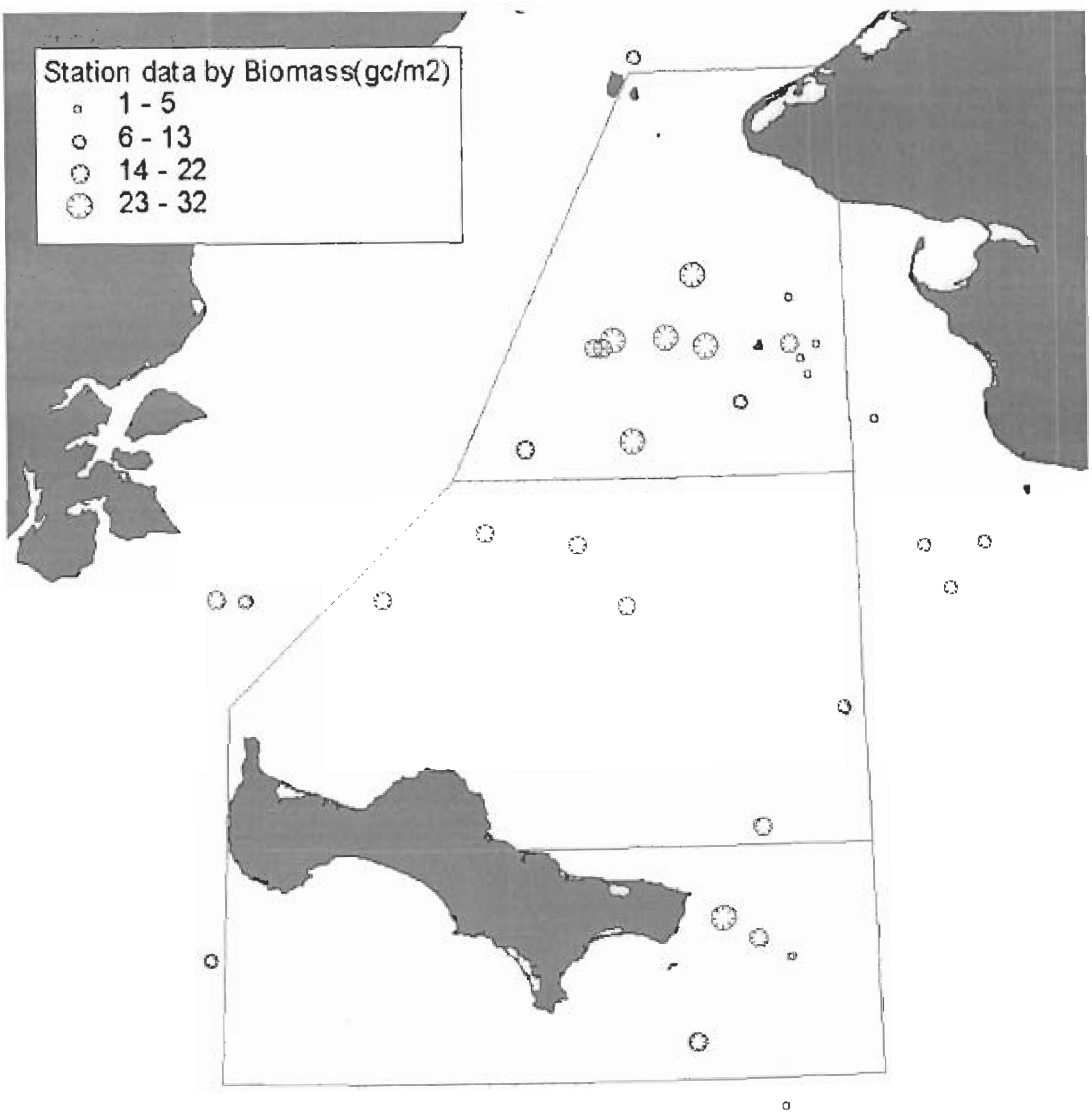

Figure 4A.

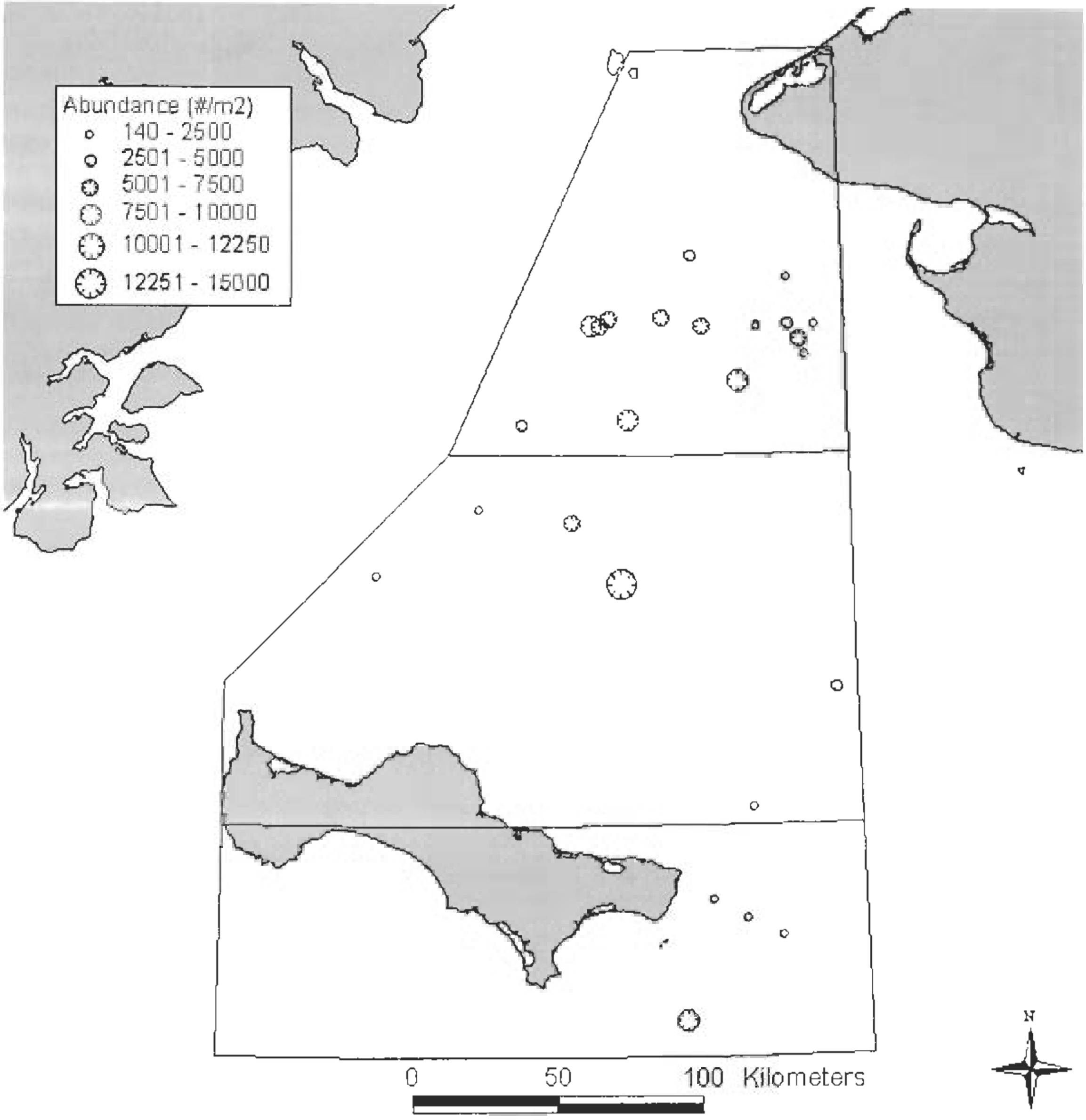
Abundance (#/m2)
○ 140 - 2500
○ 2501 - 5000
○ 5001 - 7500
○ 7501 - 10000
○ 10001 - 12250
○ 12251 - 15000
0
50
100 Kilometers
N

Figure 4B.

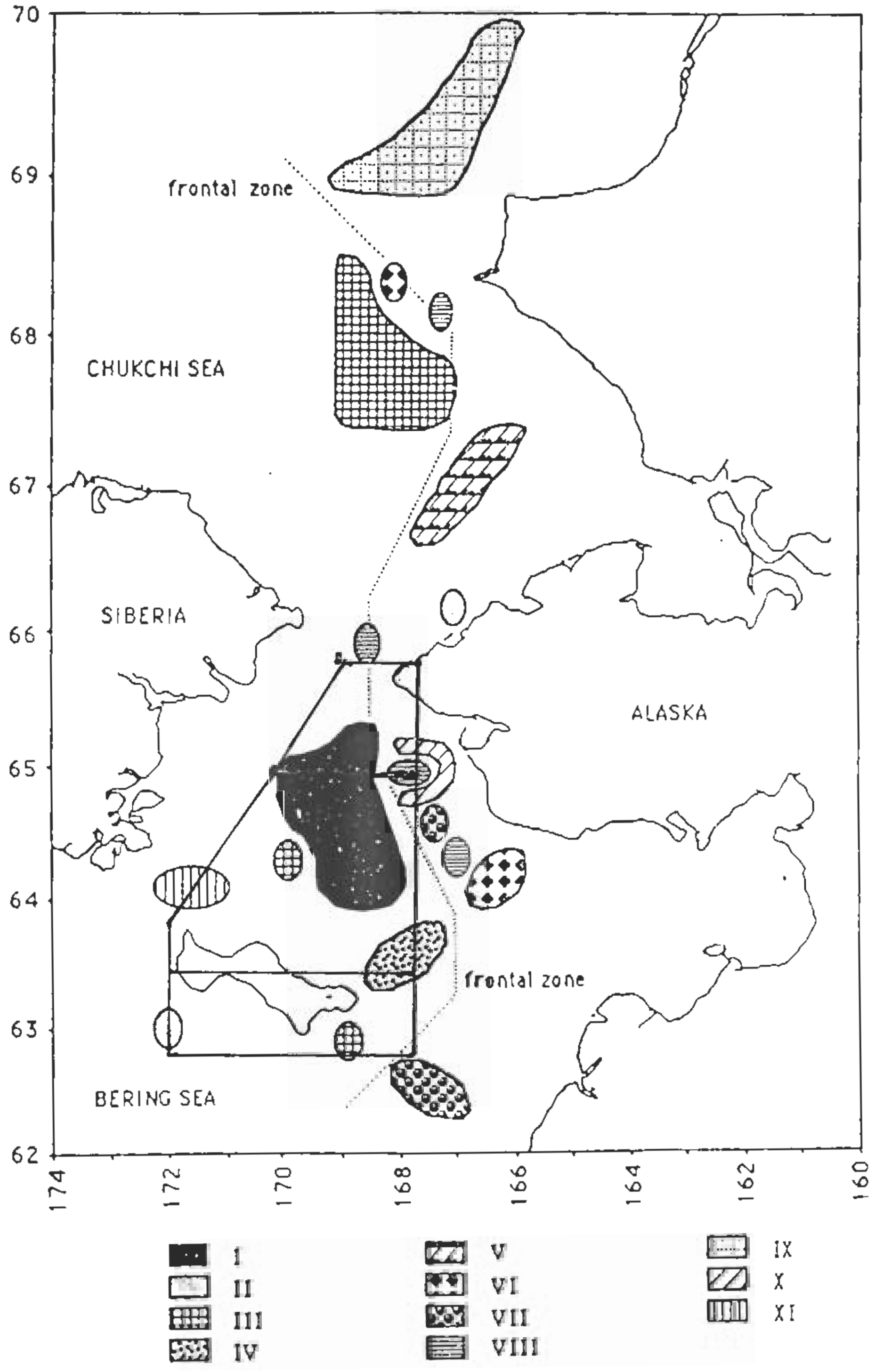
70
69
68
67
66
65
64
63
62
174
172
170
168
166
164
162
160
frontal zone
CHUKCHI SEA
SIBERIA
ALASKA
frontal zone
BERING SEA
I
II
III
IV
V
VI
VII
VIII
IX
X
XI

Figure 5.

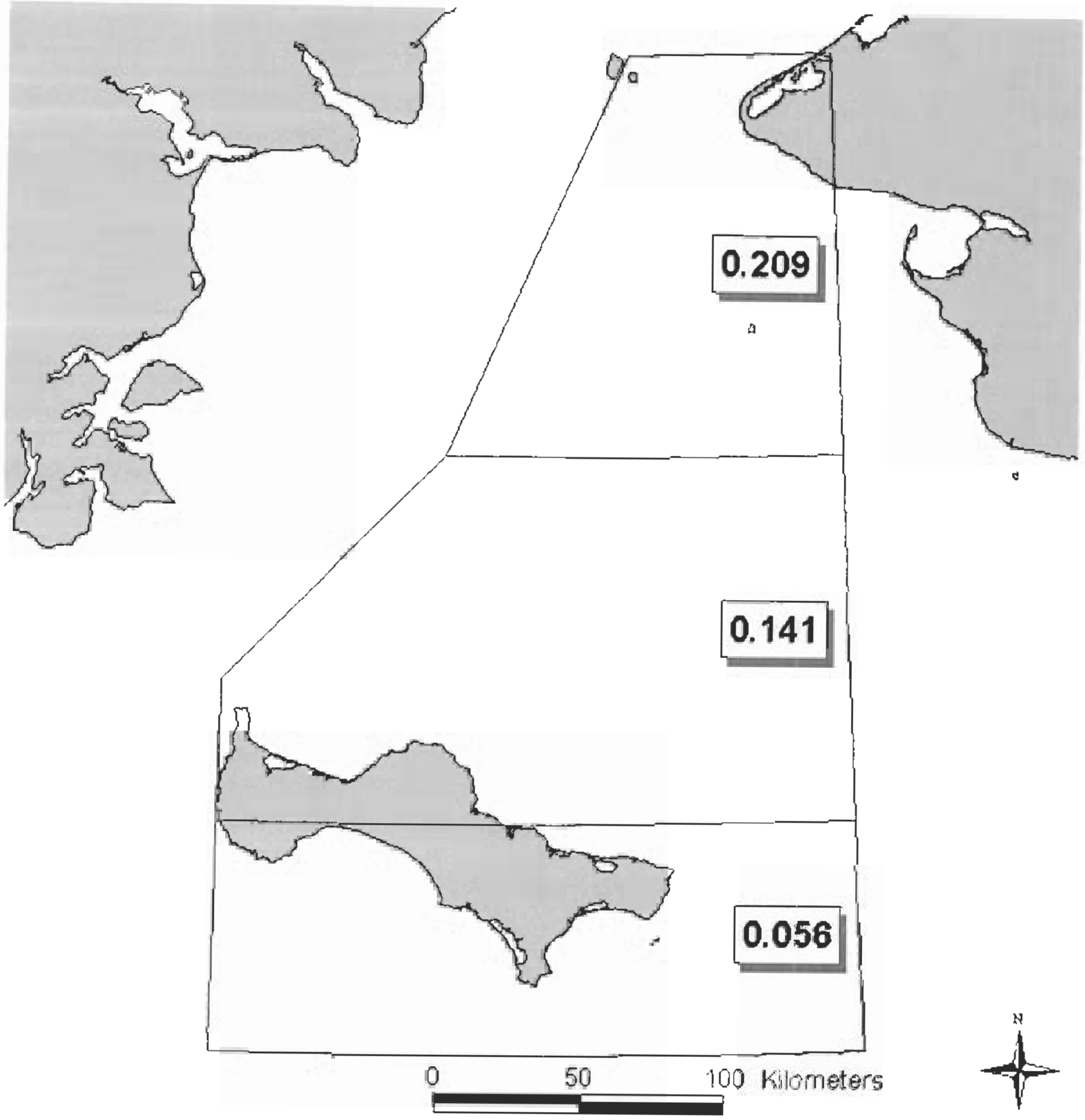

Figure 6A.

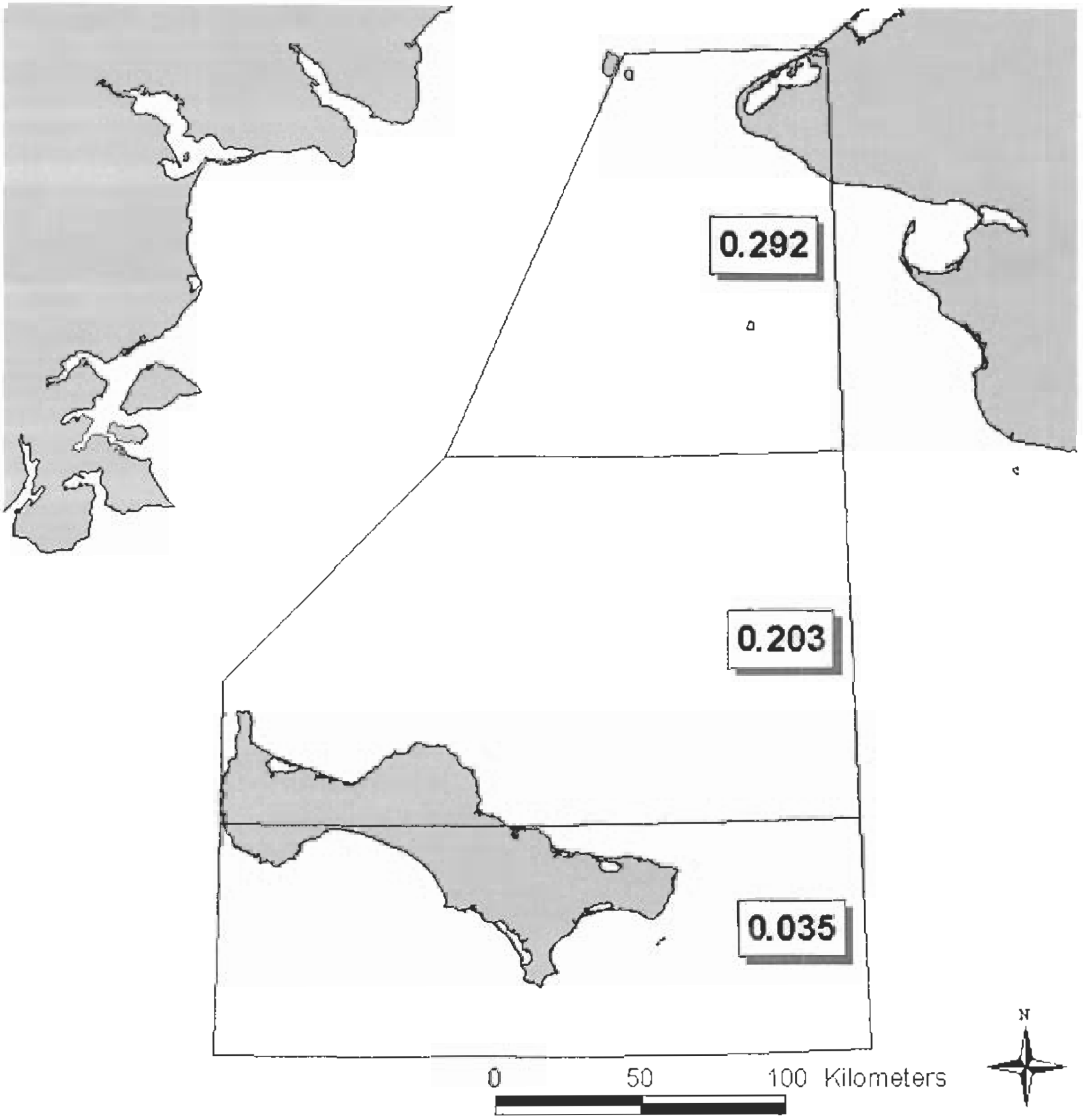

Figure 6B.

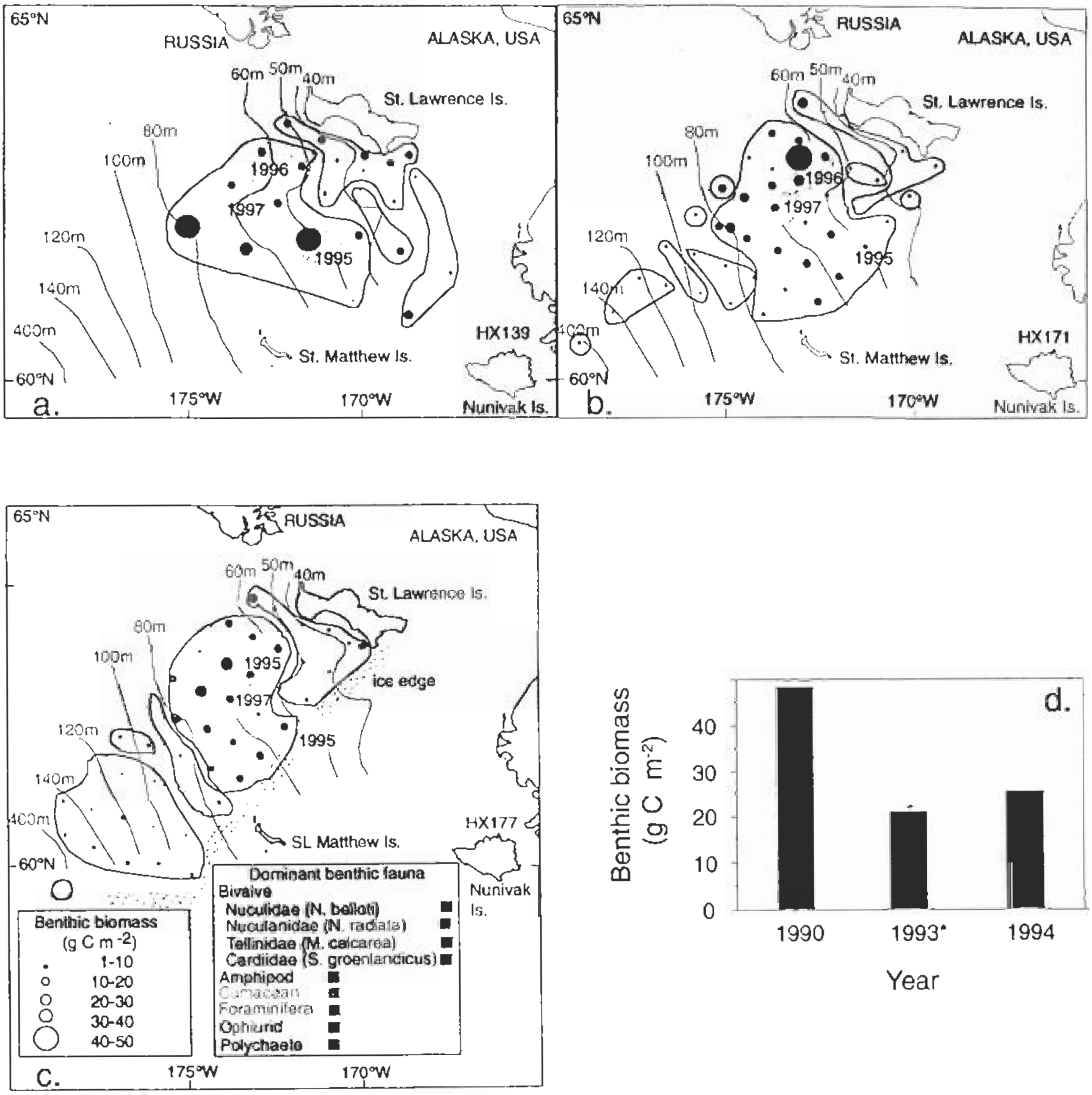
65°N
RUSSIA
ALASKA, USA
60m 50m 40m
St. Lawrence Is.
80m
100m
120m
140m
400m
1996
1997
1995
St. Matthew Is.
HX139
60°N
a.
175°W
170°W
Nunivak Is.
65°N
RUSSIA
ALASKA, USA
60m 50m 40m
St. Lawrence Is.
80m
100m
120m
140m
400m
1996
1997
1995
St. Matthew Is.
HX171
60°N
b.
175°W
170°W
Nunivak Is.
65°N
RUSSIA
ALASKA, USA
60m 50m 40m
St. Lawrence Is.
80m
100m
120m
140m
400m
1995
1997
1995
ice edge
SL Matthew Is.
HX177
60°N
Nunivak Is.
Benthic biomass
(g C m -2)
1-10
10-20
20-30
30-40
40-50
Dominant benthic fauna
Bivalve
Nuculidae (N. belloti)
Nuculanidae (N. radiata)
Tellinidae (M. calcarea)
Cardiidae (S. groenlandicus)
Amphipod
Cumacean
Foraminifera
Ophiurid
Polychaete
c.
175°W
170°W
d.
Benthic biomass (g C m-2)
0
10
20
30
40
1990
1993*
1994
Year

Figure 7.

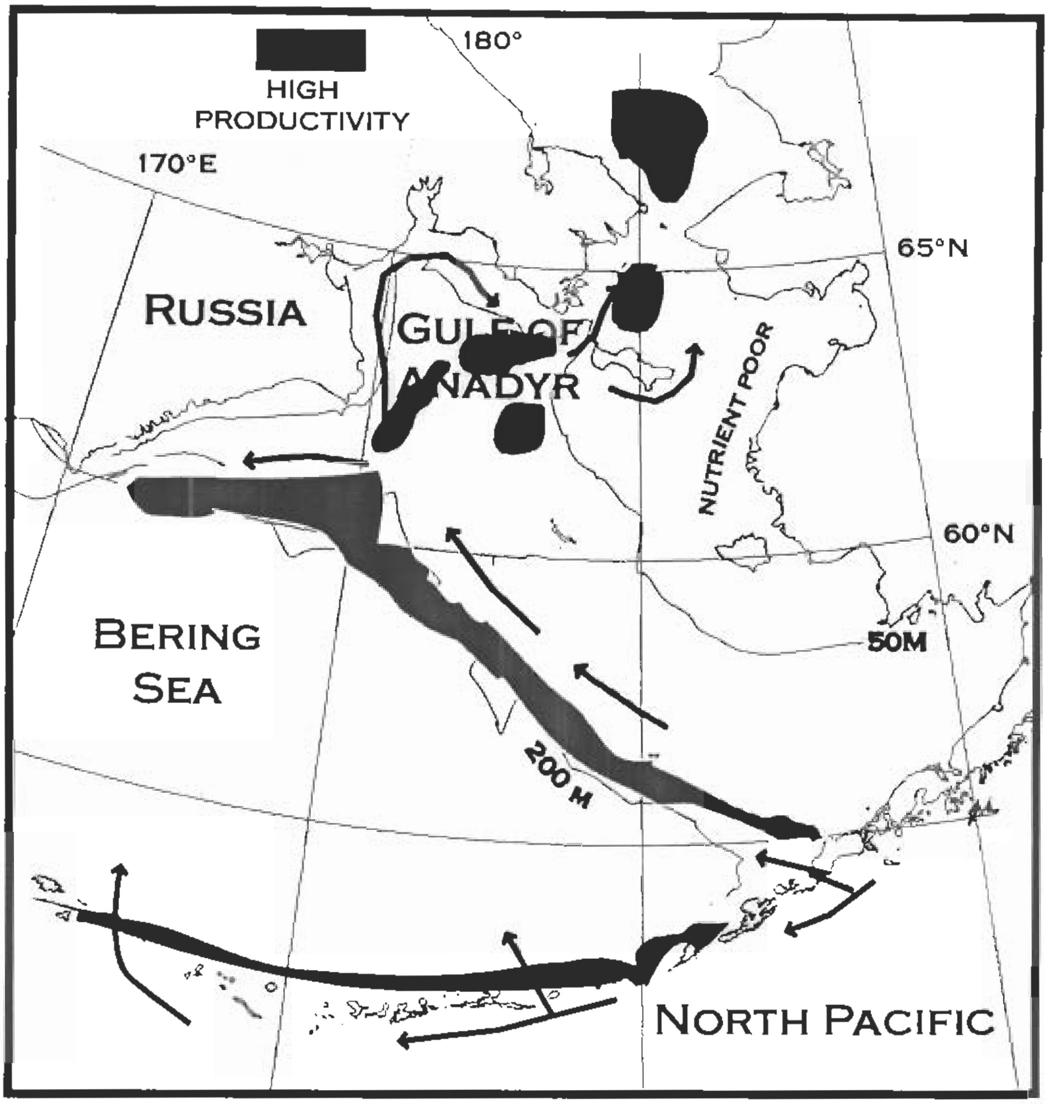

Figure 1. General surface circulation and areas with high water column primary productivity (up to 800 g C m^{-2} y^{-1}) in the Bering and southern Chukchi Seas. High production on the northern shelf is restricted to waters influenced by the Anadyr Current; Alaska Coastal Waters are typically nutrient-poor. Prevailing currents transport particulate organic carbon northward through Bering Strait onto the Chukchi Sea continental shelf. Modified from Walsh et al. (1989) and Springer et al. (1996).

Figure 8.

Gray whale distribution relative to forage habitat in the northern Bering Sea: current conditions and retrospective summary

Sue E. Moore, Jacqueline M. Grebmeier, and Jeremy R. Davies

Abstract: Hundreds of gray whales (*Eschrichtius robustus*) stranded dead along beaches from Mexico to Alaska in 1999 and 2000. The cause of the mortalities remains unknown, but starvation resulting from a reduction in prey, especially in the Chirikov Basin, was suggested as the cause. In the 1980s, the Chirikov Basin was considered a prime gray whale feeding area, but there has been no recent comprehensive assessment of whale or prey distribution and abundance. In 2002, a 5-day survey for gray whales revealed restricted distribution in the basin and a 3- to 17-fold decline in sighting rates. To put these data in context, a retrospective summary of gray whale and benthic fauna distribution and abundance was undertaken. During the 1980s, gray whale sighting rates in the Chirikov Basin were highly variable. Ampeliscid amphipods dominated the benthos where gray whale sighting rates were highest. Available measures of biomass suggest a downturn in amphipod productivity from 1983 to 2000, when estimates of gray whale population size were increasing, suggesting that the whales simply expanded their foraging range. We encourage long-term study of the Chirikov Basin as a location where predator–prey responses to changing ocean climate can be researched, because decadal time series data are available.

Résumé : En 1999 et 2000, des centaines de baleines grises (*Eschrichtius robustus*) se sont échouées mortes sur les plages, depuis le Mexique jusqu'en Alaska. La cause de cette mortalité est inconnue, mais on a suggéré qu'elle pouvait être due à la famine, à cause d'une réduction de la densité des proies, particulièrement dans le bassin de Chirikov. Durant les années 1980, le bassin de Chirikov était considéré comme un site d'alimentation de premier choix pour les baleines grises, mais il n'y a pas eu d'évaluation détaillée récente de la répartition ou de la densité des baleines et de leurs proies. En 2002, un inventaire de 5 jours a révélé que la répartition des baleines grises était restreinte dans le bassin et que le taux de repérage avait diminué de 3 à 17 fois. Pour mettre ces données dans leur contexte, nous avons entrepris une revue des répartitions et des densités des baleines grises et de la faune benthique au cours des années. Durant les années 1980, les taux de repérage des baleines grises dans le bassin de Chirikov étaient très variables et ils atteignaient leur maximum lorsque les amphipodes ampéliscidés dominaient le benthos. Les données de biomasse disponibles montrent un déclin de la productivité des amphipodes de 1983 à 2000, au moment où la taille estimée de la population de baleines s'accroissait, ce qui laisse croire que les baleines ont simplement étendu leur aire de recherche de nourriture. Nous favorisons l'établissement d'études à long terme dans le bassin de Chirikov pour suivre les réactions des systèmes prédateurs–proies aux changements climatiques de l'océan, car il existe déjà des séries de données temporelles à l'échelle des décennies.

[Traduit par la Rédaction]

Introduction

Two populations of gray whales (*Eschrichtius robustus*) occur in the North Pacific, nominally called Eastern and Western stocks (LeDuc et al. 2002). The Eastern North Pacific (ENP) population was removed from the list of endangered and threatened species in 1994, after three decades of research supported the conclusion that it had recovered from removals during commercial whaling (Buckland and Breiwick 2002). In March 1999, a scientific panel convened to conduct a review of population status 5 years after the delisting also concluded that the population was healthy and not in need of legislative protection (Rugh et al. 1999). That same year, the counts of dead gray whales stranded on beaches along their migration route skyrocketed to 273, an order of magnitude higher than in any prior year. In 2000, 354 dead gray whales

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were reported. This dramatic increase in documented mortalities and the emaciated condition of many of the whales, generated speculation that starvation linked to a downturn in benthic productivity in the Chirikov Basin was the primary cause of death (LeBoeuf et al. 2000). Unfortunately, there is no simple way to test this hypothesis, owing to the prey plasticity and extensive foraging range of gray whales (Moore et al. 2001).

Gray whales feed on a broad range of invertebrates. Nerini (1984) listed prey of 19 genera reported from gray whale stomachs, including a wide variety of amphipods (e.g., *Anonyx*, *Atylus*, *Lembos*, *Pontoporeia*), decapods (e.g., *Chionoecetes*, *Nectocrangdon*, *Nephrops*), and other invertebrates, such as molluscs, polychaete worms, and even sponges. While all other mysticetes filter or scoop prey from the water column, gray whales suction sediment and epi- and in-fauna from the sea floor (Nerini 1984) in addition to filtering zooplankton from the sea surface and water column where prey densities are high (Darling et al. 1998; Dunham and Duffus 2001, 2002). Suction feeding is highly disruptive to the benthos (Oliver and Slattery 1985) and may be considered a specialized type of niche construction (Odling-Smee et al. 1996). In the 1980s, gray whales fed extensively in the Bering Sea, especially in the Chirikov Basin between St. Lawrence Island and Bering Strait (Braham 1984; Moore et al. 1986, 2000). In the basin, the whales' primary prey were ampeliscid amphipods (Yablokov and Bogoslovskaya 1984), which dominated benthic samples obtained from the late 1970s through the mid-1980s (Stoker 1981; Grebmeier et al. 1989). In the mid-1980s, the Chirikov Basin was reported to have the highest secondary production rates of any extensive benthic community (Highsmith and Coyle 1990). However, the abundance and biomass of the amphipod community appeared to be in decline by the end of that decade (Highsmith and Coyle 1992; Sirenko and Koltun 1992).

Gray whales feed opportunistically from the lagoons of Baja California, Mexico, all along their migration route along the west coast of North America to Alaska (Nerini 1984). Furthermore, it is clear that some whales spend the summer feeding offshore Vancouver Island (Kvitek and Oliver 1986; Darling et al. 1998; Dunham and Duffus 2001, 2002), off the southeastern coast of Kodiak Island, Alaska (K. Wynne, personal communication), along the north and south coasts of the Chukotka Peninsula (Berzin 1984; Miller et al. 1985), at shoals in the northeastern Chukchi Sea (Moore et al. 2000), and in some years, as far east as the Canadian Beaufort Sea (Rugh and Fraker 1981). While this extensive foraging range begs the question of the relative importance of the Chirikov Basin as a prey source, when combined with prey plasticity it may suggest why this species has recovered from whaling in the ENP.

Our interest in gray whales focuses on their potential role as conspicuous bio-indicators of environmental variability. Because gray whales forage where prey densities are high, they can reflect local areas of very high secondary productivity (hereinafter "hotspots") and indicate when conditions that support that productivity change. The spike in gray whale mortalities, observation of emaciated whales, and reported decline in benthic biomass in the northern Bering Sea set the stage for inquiry into the current status of gray whale distribution and relative abundance in the Chirikov Basin. Thus, in 2002, we conducted an abbreviated aerial survey to determine gray whale distribution and relative abundance to compare with data from the 1980s. The dramatic changes seen led us to prepare a fine-scale retrospective analysis to compare the distribution and relative abundance of gray whales with that of the benthic-community distribution in the early to mid-1980s. This is the first direct collation of relative-abundance measures for predator and prey in this formerly prime gray whale feeding area and provides a baseline for future comparisons. This type of retrospective approach is fundamental to climate-change models that seek to include apex predators as indicators of environmental variability.

Methods

Gray whale distribution and relative abundance were derived from sightings made during aerial surveys conducted in autumn 1980 and during the summers of 1981–1985 and 2002. Survey protocols used during the 1980s were adopted for the 2002 surveys, to allow direct comparison of results. Line-transect surveys, with randomly derived start and end points, were flown in a fixed-wing aircraft at altitudes of 150–450 m. Two observers maintained a continuous watch for whales, while a third observer–recorder entered data on a portable computer that was linked to the aircraft avionics. Search surveys were conducted to and from the start and end points of transect lines and the aircraft occasionally deviated from the trackline to circle a sighting, to allow observers to make certain species identification and obtain an accurate count. Additional details of this protocol are described in Moore et al. (1986).

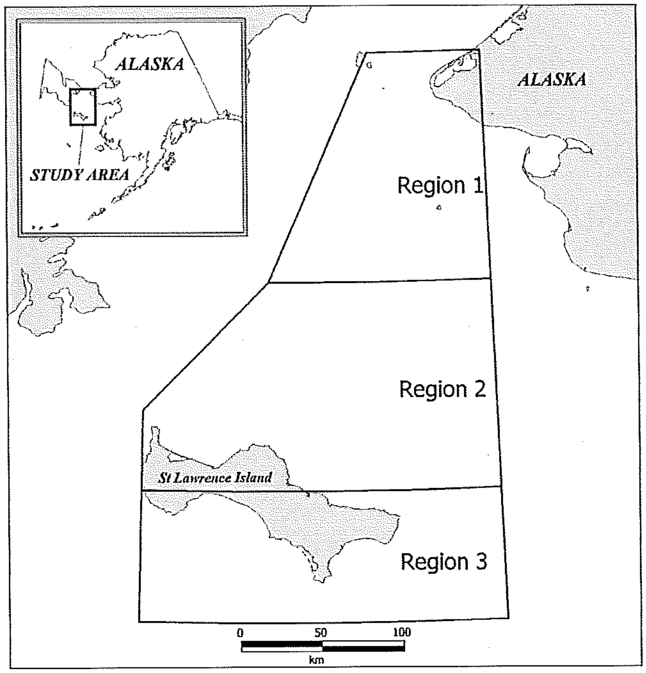
The survey area was post stratified to three regions (Fig. 1), focused on the Chirikov Basin (regions 1 and 2) and waters south and east of St. Lawrence Island (region 3). Whale distribution was plotted and an index of relative abundance calculated as the number of whales seen per survey kilometre. This index was uncorrected for whales missed owing to visibility bias (i.e., observer fatigue) or availability bias (i.e., submergence; see Marsh and Sinclair 1989).

A grid of water column and benthic sampling stations were occupied, both north and south of Bering Strait, from July to September 1984–1986, with four stations occupied opportunistically through 2000. Details of sampling protocol are given in Grebmeier et al. (1989). In brief, benthic samples (0.1 m^2 van Veen grabs) were washed on 1 mm sieve screens; then, to determine abundance and wet-mass (wet-weight as used in Grebmeier et al. (1989)) biomass, animals were identified to family level, counted, and weighed. Highly mobile epifauna, such as crabs and sea stars, were excluded from the analysis, while relatively sessile epifauna and infauna were included. Abundance data were then entered into a numerical clustering program, which grouped sampling stations according to faunal similarities, as developed by Stoker (1981) and Feder et al. (1985).

Results

Aerial surveys (a total of 39 462 km) were flown in spring, summer, and autumn from 1980 to 1985 (Table 1). Gray whales were never seen during April surveys, nor in 2

Fig. 1. Study area in the northern Bering Sea post stratified to three regions: regions 1 and 2 correspond to Chirikov Basin and region 3 to waters south and east of St. Lawrence Island.



of the 4 years when surveys were conducted in May (Table 2). Comparatively high counts of gray whales were recorded in October and November 1980 (the only year of substantive survey effort in autumn), May and June 1981, and July 1983. Differences in sighting rates indicate substantial intra- and inter-annual variability in gray whale distribution. For example, in October 1980, sighting rates were similar in regions 1 and 2 but, by November, the sighting rate in region 1 was nearly twice that in region 2. This suggests that either whales aggregated in the more northern region late in the feeding season that year or that whales migrating south from the Chukchi Sea moved into region 1, while whales in region 2 had already migrated south. Intra-annual shifts among regions are also evident in 1981, in which highest sighting rates jumped from region 2 in May, northward to region 1 in June, back to region 2 in July, and south to region 3 in August. Among years, 1983 stood out as a year of peak gray whale abundance in the Chirikov Basin, coincident with a strong El Niño condition in the ENP. Conversely, 1982 and 1984 were low-abundance years, although this may in part reflect low survey effort, especially in 1984.

July was the *only* month in which surveys were flown over 5 consecutive years and corresponds best with the timing of benthic sampling. Combined July survey effort consisted of 14 224 km (Fig. 2A). Gray whale distribution was clustered along a central axis in regions 1 and 2, off the northwest coast of St. Lawrence Island in region 2, and off the southeast coast of the island in region 3 (Fig. 2B). Fine-scale sighting rates were highest in regions 1 and 2 and southeast of St. Lawrence Island in region 3 (Fig. 3A) and provide a pattern of whale distribution for scaled comparison with benthic-community sampling stations.

Table 1. Cumulative aerial survey effort (km) in the northern Bering Sea, by region and month.

	Region			
	1	2	3	Grand total
1980				
April	560	0	0	560
May	990	328	259	1 577
October	1 128	529	0	1 657
November	788	683	508	1 979
Total	3 466	1 540	767	5 773
1981				
April	1 593	4 027	1 006	6 626
May	320	1 011	274	1 605
June	1 104	519	940	2 563
July	890	744	289	1 923
August	772	520	181	1 473
Total	4 679	6 821	2 690	14 190
1982				
April	1 109	1 310	629	3 048
May	458	489	270	1 217
July	1 856	3 005	675	5 536
Total	3 423	4 804	1 574	9 801
1983				
April	238	467	0	705
July	1 681	2 477	326	4 484
October	73	0	0	73
Total	1 992	2 944	326	5 262
1984				
April	1 011	1 009	69	2 089
May	66	0	0	66
July	113	225	0	338
Total	1 190	1 234	69	2 493
1985				
July	858	176	0	1 034
Total	858	176	0	1 034
2002				
July	1 185	1 449	922	3 556
Total	1 185	1 449	922	3 556
Grand total	16 793	18 968	6 348	42 109

Six benthic communities were identified in the study area, clustered on the basis of similarities in relative percentage of faunal composition (Fig. 3B). Four faunal groups (FGs I, III, IV, and XI) were associated with the comparatively cold, saline, nutrient-rich Bering Shelf – Anadyr Water (BSAW), with two groups (FG VIII and FG X) associated with warm, less saline, and nutrient-poor Alaska Coastal Water (ACW). Biomass of amphipods in FG I was especially high in midregion 1, with one station measuring 30–40 g C/m^2 and numerous stations showing 20–30 g C/m^2 (>10 000 individuals/m^2). Conversely, biomass at most stations in regions 2 and 3 ranged from 10 to 20 g C/m^2, with the highest measure at 20–30 g C/m^2.

Of the six benthic communities characterized, abundance and biomass were exceptionally high in FG I and FG III (Ta-

Table 2. Number and sighting rate of gray whales in the northern Bering Sea study area, by region and month.

	Region							
	1		2		3		Total	
	Number	Sighting rate	Number	Sighting rate	Number	Sighting rate	Number	Sighting rate
1980								
April	0	0	—		—		0	0
October	91	0.81	28	0.53	—		119	0.72
November	144	1.83	14	0.20	0	0	158	0.80
1981								
April	0	0	0	0	0	0	0	0
May	0	0	115	1.14	15	0.55	130	0.81
June	124	1.12	20	0.39	3	0.03	147	0.57
July	14	0.16	74	0.99	2	0.07	90	0.47
August	28	0.36	10	0.19	10	0.55	48	0.33
1982								
April	0	0	0	0	—		0	0
May	0	0	2	0.04	0	0	2	0.02
July	68	0.37	80	0.27	42	0.62	190	0.34
1983								
April								
July	479	2.85	526	2.12	0	0	1005	2.24
October								
1984								
July	0	0	38	1.69	—		38	1.12
1985								
July	397	0.46	81	0.46	—		478	0.46
2002								
July	83	0.70	12	0.08	13	0.14	108	0.30

Note: Sighting rate is the no. of whales/10 km of survey effort; —, no survey effort.

ble 3). Ampeliscid amphipods dominated (70%) the FG I community, but comprised only 21% of the abundance within FG III. The correspondence of feeding whales with FG I, but not with FG III, suggests that the prey abundance threshold was somewhere between 21 and 70% Ampeliscidae. Conversely, some feeding whales occurred in the area of FG IV, where Ampeliscidae comprised only 11% of the community. Sediment composition is key to tube-building benthic organisms, such as *Ampelisca macrocephala*, and it is not surprising that substrate associated with FG I was composed primarily of fine and very fine sand, the type of material required for tube construction. Conversely, sediments associated with FG III and FG IV contained substantial proportions of silt and clay.

At fine scale, the highest gray whale relative abundance (2–5 whales/km; Fig. 3A) was associated almost exclusively with FG I (Fig. 3B). Whale abundance was especially high in the central portions of mid-regions 1 and 2, where benthic biomass was measured at 30–40 g C/m^2 or higher. Conversely, gray whale distribution did not overlap FGs III, VIII, and X, where ampeliscids comprised 21% of the abundance; nor did it overlap FG IV, which was dominated by bivalves. Combined, these results suggest that, at least in the mid-1980s, gray whales were selectively foraging on high-density patches of ampeliscid amphipods, nearly to the exclusion of other possible prey.

After 1986, benthic station 1 (BS1; Fig. 3B) in region 1 was occupied four times, BS2 and BS4 were sampled on three occasions, and BS5 was occupied in 1999 and 2000 (Fig. 4). Dramatic declines in Ampeliscidae biomass (9–15 g C/m^2) were measured at three stations, with some suggestion of recovery at BS1 since 1993 and at BS2 since 1999. Results of the 2002 aerial surveys depict a corresponding decline in gray whale distribution and relative abundance. Although the study area was nearly completely surveyed during the 5-day effort (Fig. 5A), gray whale distribution was restricted to the northern portion of the Chirikov Basin and waters offshore northeast and southwest St. Lawrence Island (Fig. 5B). Sighting rates in the three regions dropped 3- to 17-fold, with the greatest difference between survey periods evident in region 2 (Table 4). While this 1-week survey can be considered only a “snapshot” of gray whale occurrence, it does suggest a marked downturn in whale foraging since the 1980s.

Discussion

This retrospective analysis of gray whale and benthic fauna distribution and relative abundance in the northern Bering Sea provides a baseline for comparing a period when gray whales fed in what was considered a prime foraging

Fig. 2. Combined aerial survey effort (A) and gray whale (*Eschrichtius robustus*) distribution (B) in the study area for July 1981–1985.

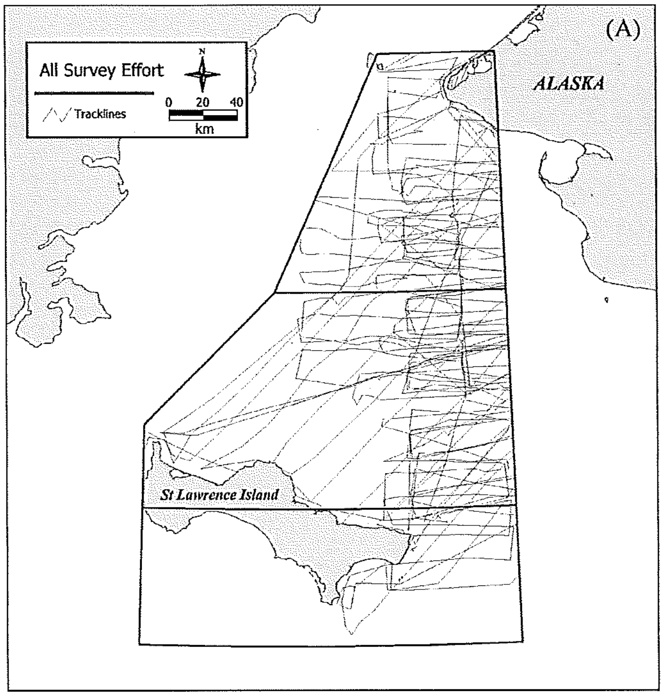
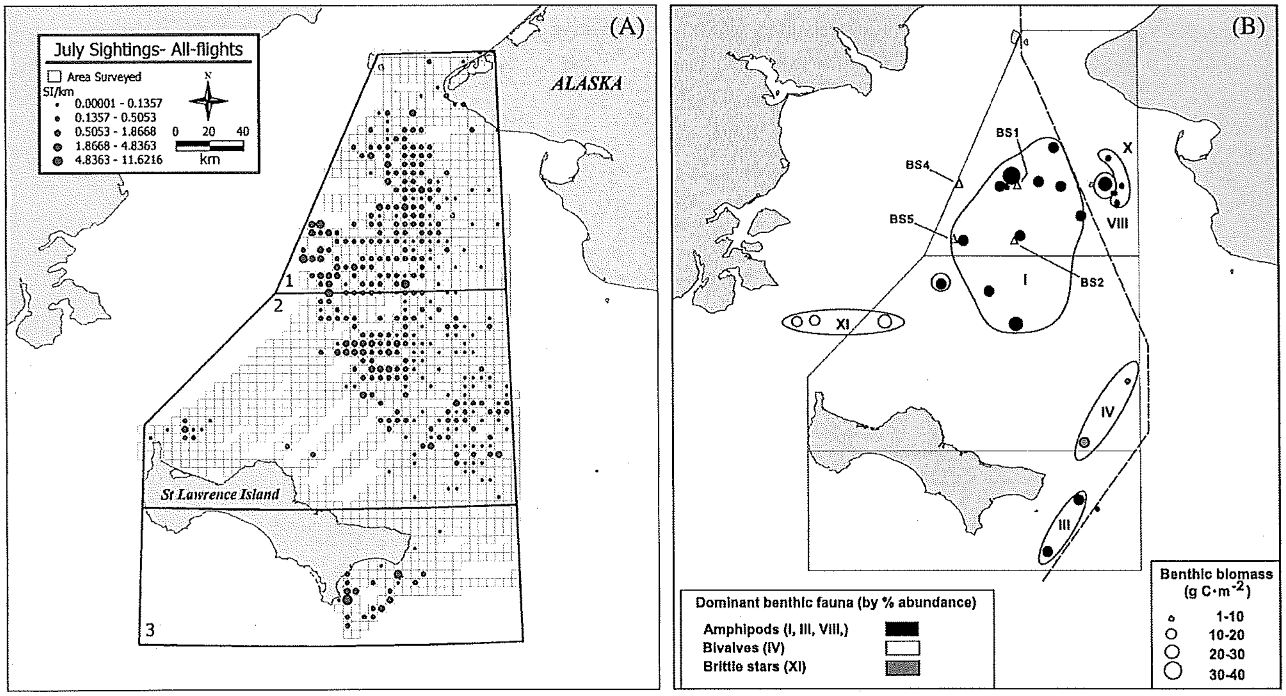


Fig. 3. Sighting rates (no. of whales/km) for gray whales, in 5-km blocks, for July 1981–1985 (A) and the distribution of benthic faunal communities in 1984–1986 (B); modified from Grebmeier et al. (1989). In B, note locations of the benthic stations (BS1, BS2, BS4, BS5), for which time series are shown in Fig. 4.



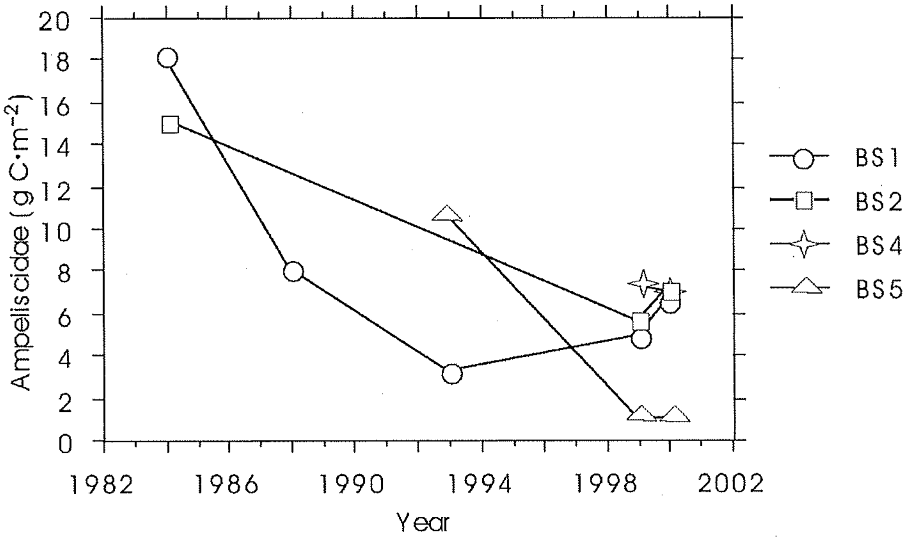
habitat (i.e., the 1980s) with a time when this habitat may be less than optimal. Regional indices of relative abundance show that gray whales were dynamic in their movements through the Chirikov Basin from May through November. In some years, the highest regional indices occurred in autumn, suggesting that whales may have aggregated to feed in the basin prior to initiation of the southbound migration. In July, fine-scale indices of whale abundance were associated with the highest biomass of one particular amphipod-dominated faunal group, suggesting strong prey selection, as shown for

Table 3. Mean benthic abundance, percent Ampeliscidae, biomass, and sediment composition for benthic faunal groups (FGs) located in Bering Shelf – Anadyr Water (BSAW) and Alaska Coastal Water (ACW); modified from Tables 5 and 6 in Grebmeier et al. (1989).

					Sediment composition (%)[a]					
Benthic faunal group	Water type	Mean abundance (no./m^2)	Ampelisci dae (%)	Mean biomass (g C/m^2)	S/C	VFS	FS	MS	CS	GR
I	BSAW	6940	70	22.2	6.9	31.7	53.8	5.9	1.0	0.0
III	BSAW	5365	21	24.2	50.9	25.3	13.7	9.5	0.6	0.0
IV	BSAW	2048	11	11.3	34.3	40.5	25.0	0.0	0.3	0.0
VIII	ACW	1367	9	15.4	15.8	7.0	29.2	30.7	14.4	3.3
X	ACW	718	0	2.0	1.1	0.7	28.6	56.7	11.9	0.0
XI	BSAW	1684	0	12.5	—	—	—	—	—	—

[a] SC, silt and clay; VFS, very fine sand; FS, fine sand; MS, medium sand; CS, coarse sand; GR, gravel; —, no data.

Fig. 4. Biomass time series for dominant benthic amphipod at four stations in the northern Chirikov Basin, 1983–2000 (data from Stoker 1981; Grebmeier et al. 1989; Grebmeier 1993; Grebmeier and Dunton 2000; J.M. Grebmeier, unpublished data).



gray whales feeding offshore Vancouver Island (Dunham and Duffus 2001, 2002).

Coyle and Highsmith (1994) predicted that the gray whale foraging rate on the ampeliscid amphipod communities in the Chirikov Basin, as seen in the 1980s, could not be sustained. Yet collective data suggest that the 30% decline in the gray whale prey base reported for 1986–1988 (Highsmith and Coyle 1992) had no immediate measurable effect on whale recruitment. The ENP gray whale population was estimated to number 16 555 (SE = 690) whales in 1979–1980, increasing to 20 348 (SE = 726) whales by 1985–1986 (Buckland and Breiwick 2002). In 1987–1988, when amphipod biomass was dropping, the population was estimated to number 21 113 (SE = 688) whales (Buckland et al. 1993), with the estimate increasing slightly to 23 109 (SE = 1262) individuals by 1993–1994 (Buckland and Breiwick 2002). The highest estimate, 26 635 (SE = 2681) gray whales in 1997–1998 (Rugh et al. 1999), overlapped further declines in the benthic biomass measured at sampling stations in the north-central Chirikov Basin (Fig. 4) and south of St. Lawrence Island (Grebmeier and Dunton 2000). This apparent delay in the response of gray whales to their diminished food resources seems to conflict with the Perryman et al. (2002) model that shows a fairly sensitive positive correlation between gray whale foraging time in the Chirikov Basin (as inferred by ice cover) and calf recruitment.

Because gray whales feed on such a wide variety of prey and at so many locations along their range, it seems an oversimplification to equate the high mortalities in 1999 and 2000 solely to (or to focus recruitment models on) whale foraging opportunities in the Chirikov Basin. However, this formerly prime feeding area may be a bellwether for the state of gray whale foraging habitat, if either prey abundance or quality has changed significantly. Grebmeier and Dunton (2000) note that, while benthic biomass north of Bering Strait has remained high, there has been a change in dominant fauna that is likely the result of changing hydrographic conditions. This is important, because gray whale forage quality varies with species composition. For example, large *A. macrocephala* are especially lipid rich compared with other common amphipod prey (e.g., *Byblis* spp.), so conditions that favor *Byblis* spp. over *A. macrocephala* will result in a poorer diet for gray whales even when biomass remains high. Of note, *Byblis* spp. are the dominant amphipod found in samples from the central southern Chukchi Sea (J.M. Grebmeier, unpublished data). Further, prey species size is

Fig. 5. Aerial survey effort (A) and gray whale distribution (B) in the study area from surveys conducted 29 July – 3 August 2002.

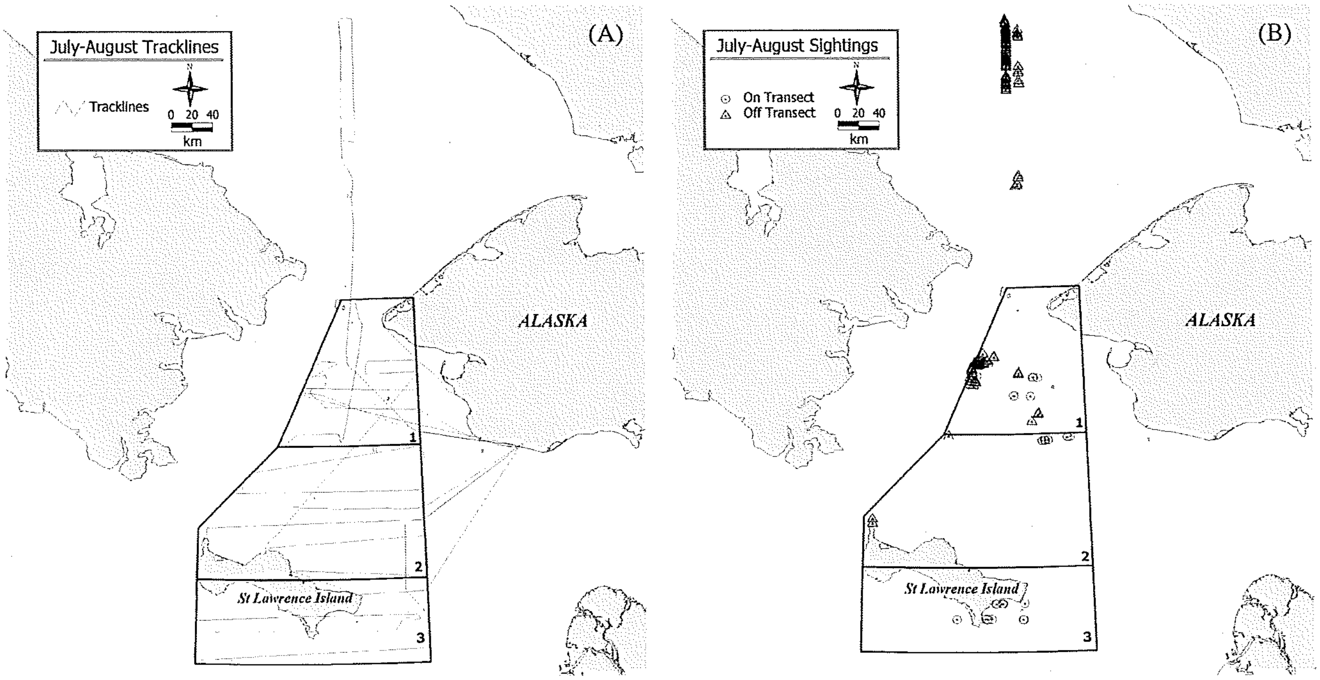


Table 4. Comparison of gray whale sighting rates (no. of whales/km) by region between late July 1981–1985 and late July – early August 2002.

	Region		
Period	1	2	3
1981–1985	0.209	0.141	0.056
2002	0.070	0.008	0.014

influenced by organic-matter flux, with the density of small amphipods (e.g., *Ampelisca birulai*) favored when organic flux is low (Coyle and Highsmith 1994). Finally, warming seas will elevate amphipod food requirements, which may lead to elevated predation rates, both selecting for smaller prey species (Coyle and Highsmith 1994). Thus physical forcing, which directly affects pelagic–benthic coupling of biological processes in the northern Bering and Chukchi Seas (Grebmeier 1993; Grebmeier and Cooper 1995), is key to any assessment of gray whale prey availability.

The Chirikov Basin and areas southwest of St. Lawrence Island and north of Bering Strait are at the downstream end of the productive current that follows the edge of the continental shelf in the Bering Sea called the "Green Belt" (Springer et al. 1996). These productive benthic zones are the result of carbon and nutrient transfer to the shallow shelves of the northern Bering and Chukchi seas (Grebmeier and Barry 1991). Productivity along the "Green Belt" is strongly influenced by the Pacific Decadal Oscillation (PDO), which reflects the relative position and strength of the Aleutian Low (Francis et al. 1998). Overall, a decline in seabird and marine mammal populations in the North Pacific correlates with the PDO, although linking mechanisms remain poorly understood (Springer 1999). Recent reports of an overall decline in carrying capacity in the Bering Sea during the past two decades (e.g., Schell 2000) are countered by observations of increases in concentrations of various species of zooplankton there (e.g., Napp et al. 2002). So, as yet there is no clear picture of marine ecosystem response to atmospheric oscillations, and its affect on benthic environments such as the Chirikov Basin.

Perhaps most important to benthic infauna, sediment grain size is directly related to current strength. Recent evidence points to a weakening in current flow in the Gulf of Anadyr and through Bering Strait (Roach et al. 1995). Changes in current strength and flow directly impact carbon deposition, sediment composition, and benthic-community structure (Grebmeier 1993). Individual species of benthic infauna require specific sediment regimes within which to feed and grow. Over the last decade, the sediment structure in the northern Bering Sea has changed and sediments in the Chirikov Basin have become coarser, suggesting a changing hydrographic regime. Since the dominant ampeliscid amphipod in the FG I group (Fig. 3B) is a tube builder that agglutinates fine sediment into its tubes, coarser sediments could lead to a reduction in amphipod numbers. In addition, a 30% decline in sediment oxygen uptake in the productive areas to the southwest of St. Lawrence Island was observed during the 1990s (Grebmeier and Cooper 1995). This decline in sediment oxygen uptake is another indication of a reduction of carbon supply to the benthos.

As the ENP gray whale population has increased, top-down (predation) and bottom-up (production) effects have acted negatively and synergistically to reduce available prey in the Chirikov Basin. Seemingly, gray whales have responded to this by expanding their foraging range. Still, we encourage long-term study of the Chirikov Basin as the best location to investigate predator–prey responses to changing ocean climate, because decadal time series data are available.

Acknowledgements

Gray whale sighting data from the 1980s were obtained during aerial surveys funded by the U.S. Minerals Management Service (MMS), Alaska Region, and made available for this paper by Dr. Cleve Cowles and Steve Treacy of that office. We thank the pilots at Office of Aircraft Services (OAS), Anchorage Region, for safe and professional flying, as well as the dedicated observers who assisted with the MMS surveys. Janet Clarke was key to "resurrecting" the transect lines from the 1980s for application to the 2002 survey. She also participated in many of the surveys (1980s and 2002) and provided data summaries for all flights. Dave Weintraub and the team at Commander Northwest Ltd. provided professional and safe flying during the 2002 surveys. Kate Wynne (University of Alaska, Sea Grant Program, Kodiak, Alaska) generously shared her recent observations on gray whales feeding near Kodiak Island. Dave Rugh (National Marine Mammal Laboratory (NMML)) provided constructive comments on an early version of the manuscript and Marcia Muto (NMML) provided comprehensive editing assistance. We thank all these people for their help.

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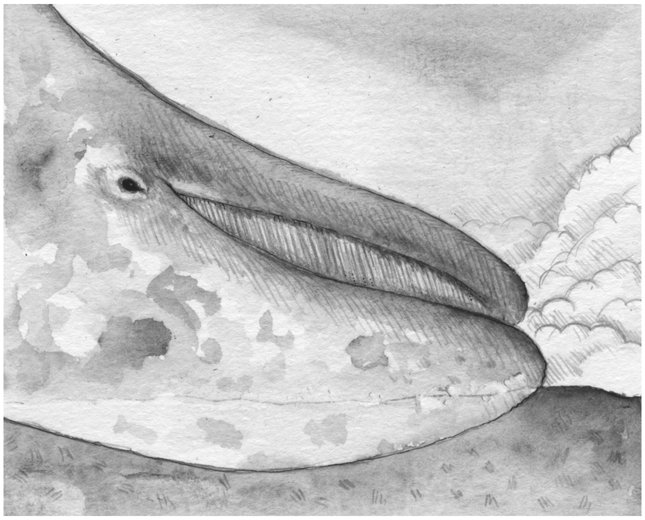
SPECIES CASE STUDIES

TWENTY-THREE

Gray Whales in the Bering and Chukchi Seas

RAYMOND C. HIGHSMITH, KENNETH O. COYLE,
BODIL A. BLUHM, AND BRENDA KONAR



Among the large cetaceans, gray whales *(Eschrichtius robustus)* are unique in three important ways: They are benthic feeders; they undertake one of the longest migrations of any mammal; and they may be fully recovered (at least the eastern Pacific stock) from overharvesting by commercial whaling. The eastern (Chukotka-California) gray whales migrate annually between the mating regions and calving lagoons on the west coast of Baja California to summer feeding grounds in the northern Bering Sea and the Chukchi Sea (Rice and Wolman 1971; Marquette and Braham 1982; Findley and Vidal 2002). The purpose of this chapter is to explore the arctic ecosystem dynamics that justify such a migration and the impacts of the whales upon the system. We will conclude the chapter with an oceanographic production model that both explains the current location of major gray whale feeding sites and can be used for predictive purposes.

Commercial whaling is thought to have reduced the eastern North Pacific gray whale population from 15,000–20,000 to 4,000–5,000 or fewer animals by the late nineteenth or early twentieth century (Rice and Wolman 1971; Reilly 1984; Henderson 1984). Recovery to prewhaling levels had occurred by about 1980 (Reilly 1984), although numbers continued to increase through the 1990s and reached an estimated maximum of 28,000 by 1998 (Rugh et al. 2003). Based on studies of the gray whale prey community, composed of benthic ampeliscid amphipods, in a major feeding site (the Chirikov Basin, B5 in Figure 23.1), it was predicted that the growing gray whale population would not be supportable at the site (Highsmith and Coyle 1992; Coyle and Highsmith 1994), and indeed the eastern population appears to have declined by as many as 11,000 animals by 2000 (LeBoeuf et al. 2000; Moore et al. 2001; Perryman et al. 2002; Rugh et al. 2003).

Northern Feeding Sites

The distribution and relative abundance of gray whales in the Bering and Chukchi seas can be inferred from the results of various aerial and shipboard surveys conducted by Russian and U.S. scientists over the past several decades. The whales are widely dispersed and are usually observed singly or in small groups (Zimushko 1970; Berzin 1984; Table 23.1), not a surprising distribution given the large benthic area needed to support the energy requirements of each whale (Highsmith and Coyle 1992). In the west, consistently large numbers have been seen between Cape Dezhnev (northeastern tip of Chukotka) in Bering Strait to about Cape Schmidt (Table 23.1; C1–C3 in Figure 23.1), with the greatest concentrations off Cape Serdtse Kamen (C1 in Figure 23.1; Berzin 1984). Relatively few whales were observed in or south of the

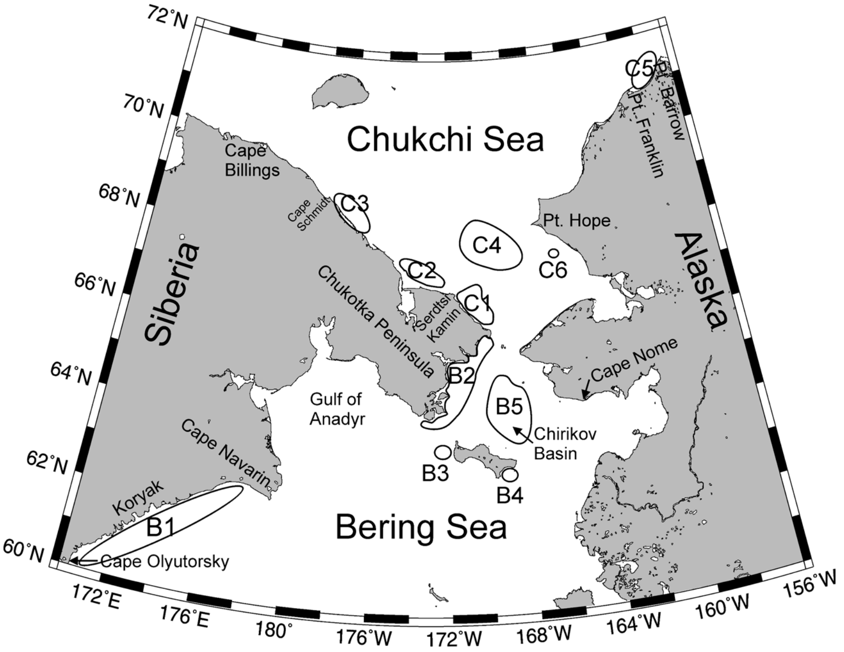


FIGURE 23.1. Map of the northern Bering and Chukchi Seas showing locations of significant gray whale feeding sites. See Table 23.1 for references.

Gulf of Anadyr. The westernmost sighting of gray whales in the Chukchi is 178°30′E (between Cape Schmidt and Cape Billings; Figure 23.1; Berzin and Rovnin 1966; Doroshenko 1981; Berzin 1984). There have been reports of some whales in the C4 area on both sides of the Convention Line (Maher 1960; Wilke and Fiscus 1961; Johnson et al. 1981; Marquette et al. 1982; Braham 1984; Moore and Ljungblad 1984). In the east, gray whales occasionally venture into the western Beaufort Sea (Maher 1960; Rugh and Fraker 1981; Marquette and Braham 1982).

Berzin (1984) suggested that the western (~179°W) and eastern (~157°W) distribution limits of feeding gray whales in the Chukchi Sea are set by the point at which the whales encounter the ice pack. Specific locations vary annually, and with the retreat of the ice pack in recent decades it will be interesting to see whether the whales extend their foraging range. An alternative hypothesis (see the last section of this chapter) is that the western and eastern foraging limits are determined by high benthic production derived from the variable location of the broad (60 km) frontal zone formed off the north Chukotka coast by the intersection of the Siberian Coastal Current and Bering Sea Water (Figure 23.2; Weingartner et al. 1999). This front extends northeastward and intersects the Alaskan coast near the easternmost distribution of significant numbers of feeding gray whales near Point Barrow (C5 in Figure 23.1). The lack of concentrated food may also explain the general absence of gray whales in the north-central Chukchi Sea (Berzin 1984). The southern limit of gray whale foraging in the eastern Bering Sea is off the southeastern coast of St. Lawrence Island at approximately 63°N (B4; Figure 23.1). In the western Bering Sea, after the end of commercial whaling, the southern extent of Chukotka-California gray whale feeding aggregations was at Glubokaya Bay (61°12′N; B1 in Figure 23.1), but as the protected population grew, sightings extended to Cape Olyutorsky (60°N) by the early 1980s (Berzin 1984). These southern distribution limits are presumably determined by the location of soft-bottom depositional habitats with high prey biomass.

Most eastern North Pacific gray whales feed each summer on benthic organisms, especially infaunal amphipods, on the broad continental shelves of the northern Bering Sea and the Chukchi Sea. The majority of foraging activity occurs in water depths of approximately 50 m or less (Rice and Wolman 1971; Berzin 1984; Braham 1984; Nerini 1984; Yablokov and Bogoslovskaya 1984; Highsmith and Coyle 1990, 1992; Moore et al. 2000; Clarke and Moore 2002) and where benthic biomass is very high (Berzin and Rovnin 1966). A variety of foraging sites have been determined (Figure 23.1; Table 23.1). Because gray whales are submerged most of the time (Wursig et al. 1986), the number of whales counted (Table 23.1) is sometimes multiplied by a factor of up to three to obtain an estimate of the actual number of whales at a site (Berzin 1984).

The Chirikov Basin has been identified repeatedly as a major gray whale feeding site (B5 in Figure 23.1; Braham 1984; Moore and Ljungblad 1984). Concentrations of foraging animals occur at both ends of St. Lawrence Island (B3 and B4 in Figure 23.1). Early-arriving whales probably feed in the region until ice conditions allow dispersal farther north (Braham 1984). Thomson and Martin (1986) estimated that 15% of the total whale population remained in the Chirikov

TABLE 23.1

Gray Whale Population Counts and Estimates at Feeding Sites in the Northern Bering and Chukchi Seas

Area	Density	Counted (Estimated)	Survey Type	Survey Date	Reference
B1	Low		Aerial	July 1968	Berzin 1984
	Low	5	Aerial	Aug., Oct. 1973	Berzin 1984
	High		Ship	Sept., Oct. 1974	Berzin 1984
	Low		Aerial	Sept., Oct. 1975	Berzin 1984
	High		Ship	Sept., Oct. 1982	Berzin 1984
		200	Ship	Sept. 1936	Zenkovich 1937a
B2	Few		Aerial	July 1968	Berzin 1984
	High		Ship	Sept., Oct. 1974	Berzin 1984
		4/km	Aerial	Sept., Oct. 1974	Berzin 1984
	High		Aerial	Sept., Oct. 1975	Berzin 1984
	High		Ship	Sept., Oct. 1982	Berzin 1984
		1197	Ship	1942	Vadivasov 1947
		1154	Ship	Aug.–Sept. 1942	Yablokov and Bogoslovskaya 1984
		1033	Ship	1962	Berzin & Rovnin 1966
B3	High		Aerial	1976–1978	Berzin 1984
B4	High		Aerial	1976–1978	Berzin 1984
B5	High		Aerial	Sept., Oct. 1975	Berzin 1984
	High		Ship	Sept., Oct. 1979	Berzin 1984
	High	>500/yr	Aerial	1979–1978	Berzin 1984
	High	299	Aerial	May–June 1981	Moore and Ljungblad 1984
		(3,300–3,500)		1982	Berzin 1984
	High		Aerial	1982–1991	Moore et al. 2000
	Low		Aerial	July 2002	Moore et al. 2003
C1		17	Aerial	July 1968	Berzin 1984
	High	0.11/km²	Aerial	Sept., Oct. 1973	Berzin 1984
	High		Aerial	Sept., Oct. 1975	Berzin 1984
	High	3,000	Ship	July–Aug. 1982	Berzin 1984
	High	180	Ship	Aug. 1982	Berzin 1984
	High		Ship	Sept., Oct. 1982	Berzin 1984
C2	Low		Aerial	July 1968	Berzin 1984
	High		Aerial	Sept., Oct. 1975	Berzin 1984
	High		Ship	July–Aug. 1982	Berzin 1984
C3	Low		Aerial	July 1968	Berzin 1984
	High		Ship	Sept.–Nov. 1980	Berzin 1984
	Medium		Ship	Sept.–Oct. 1982	Berzin 1984
C4	High	44,132	Aerial	Aug., Oct. 1973	Berzin 1984
	High		Aerial	Sept., Oct. 1975	Berzin 1984
	High	260	Ship	Sept., Oct. 1979	Berzin 1984
	High	588 (2,000)	Ship	Sept.–Nov. 1980	Berzin 1984
	High	1,021	Ship	Sept.–Nov. 1980	Berzin 1984
		190	Ship	Aug. 1982	Berzin 1984
		588 (2,000)	Ship	Sept. 1979	Doroshenko 1981
		1,021		Sept. 1980	
		127	Aerial	Oct. 1979	Johnson et al. 1981
		125	Aerial	Sept. 1980	Marquette et al. 1982
		>1,000 (3,000)	Ship	June, Sept. 2003	This chapter
		128	Aerial	Aug.–Nov. 1980–1989	Clarke and Moore 2002
C5		40	Ship	Aug. 1982	Berzin 1984
		60	Ship	Aug. 1982	Berzin 1984
		200	Ship	Aug. 1982	Berzin 1984
	High		Aerial	1982–1991	Moore et al. 2000
C6		(200)	Ship	June, Sept. 2002	This chapter

NOTE: For areas referenced, see Figure 23.1. Total for B1 and B2 was 1,800–2,000; total for C1 and C4 was 873.

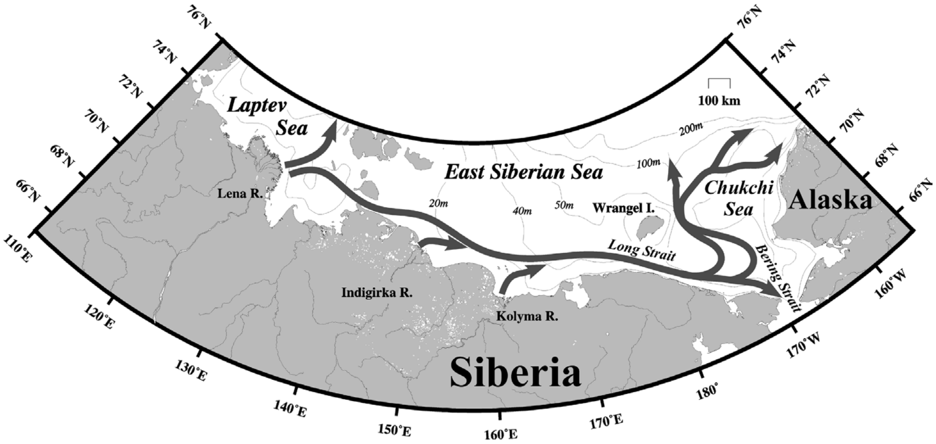


FIGURE 23.2. Map showing the East Siberian Current and region of wide frontal zones established when the northward flowing Bering Sea Water is encountered. From Weingartner et al. 1999.

area to feed during the summer. Soviet scientists estimated that 3,300–3,500 animals were Chirikov residents in the summer of 1982 (Berzin 1984), approximately 19% of the total population (Breiwick et al. 1988). An estimated 70% of the total population (Highsmith and Coyle 1992) feed in the Chirikov while transiting through the area during the spring and fall migration.

In 2003, we made two cruises (June and September) to the C4 region east of the Convention Line. Within an area bounded by 67°00′N to 68°10′N and 168°00′W to 169°00′W (eastern fourth of C4 in Figure 23.1), we counted more than 1,000 gray whales in 4–5 days. Each cruise used a point transect survey. Of those whales observed closely, about half produced mud plumes, an indication of bottom feeding. The whales were arrayed along a broad east-west oceanographic front created by the confluence of the eastward-flowing Siberian Coastal Current (cold, dilute) and northward-flowing Bering Sea Water, which is warmer and saltier (Figure 23.2; Weingartner et al. 1999). It should be noted, however, that the Bering Sea Water includes cold, dense nutrient-laden Anadyr Water, which may underlie the warmer water for tens of kilometers. The highest whale concentrations were observed along the Bering Sea Water (southern) side of the frontal area. We posit that whales observed feeding west of the Convention Line were also orienting to the same frontal system (Figure 23.2).

Animals that are as large and abundant as gray whales and that concentrate most of their feeding during approximately half of the year (Rice and Wolman 1971; Oliver et al. 1983; Perryman and Lynn 2002), need to forage where there is either sustained high primary production or a concentration of production from elsewhere (Moore and DeMaster 1997). Various studies (Walsh et al. 1989; Springer et al. 1996; Weingartner 1999; Figure 23.2) and satellite images (Figure 23.3) show that a plume of production extends from the Gulf of Anadyr through the Bering Strait to the gray whale feeding grounds in the Chukchi Sea (Figure 23.1). The Anadyr Water is upwelled and delivers nutrients as well as phytoplankton to the Chukchi sites. As has been suggested for the Anadyr-fed Chirikov Basin (B5 in Figure 23.1; Hansell 1989; Walsh et al. 1989; Springer et al. 1996), there must be poor coupling between phytoplankton production and zooplankton grazers in areas C1–C5. Thus, much of the diatom biomass settles to the shallow (<50 m) bottom (Grebmeier and McRoy 1989; Fukuchi et al. 1993; Feder et al. 1994) and is consumed by the benthos, which in turn is preyed upon by gray whales and other benthic feeders.

Although the northern feeding grounds are clearly important influences on the distribution and abundance of gray whales, it has become apparent that feeding may occur during the northern migration (Braham 1984) and that tens to a few hundred whales may remain at places, such as Vancouver Island and Kodiak Island, along the migration route during the summer (Darling 1984; Murison et al. 1984; Oliver et al. 1984; Kvitek and Oliver 1986; Calambokidis et al. 2002; Dunham and Duffus 2002; Stelle 2002; Moore et al. 2003). The feeding methods utilized during migration tend to vary, and may include skimming, filter feeding, and benthic feeding in soft-bottom locations. These observations are important for present-day understanding of gray whale ecology and also provide interesting insights into gray whale survival over the millennia. As recently as 10–12 thousand years ago, sea level was roughly 75 m lower than it is today (Hopkins 1967), one consequence being that the areas that are currently the major northern feeding sites utilized by gray whales were emergent. This raises questions about how these animals survived in the absence of required food resources and feeding sites as we presently know them. The ability to utilize alternative feeding modes and locations may have been critical to survival of the species during glacial periods when the continental shelf areas of the northern seas were above sea level.

Benthic Feeding in the North

Gray whale stomach contents collected from the Chirikov Basin and Russian coast indicate that the primary food is infaunal amphipods, primarily the large *Ampelisca macrocephala*

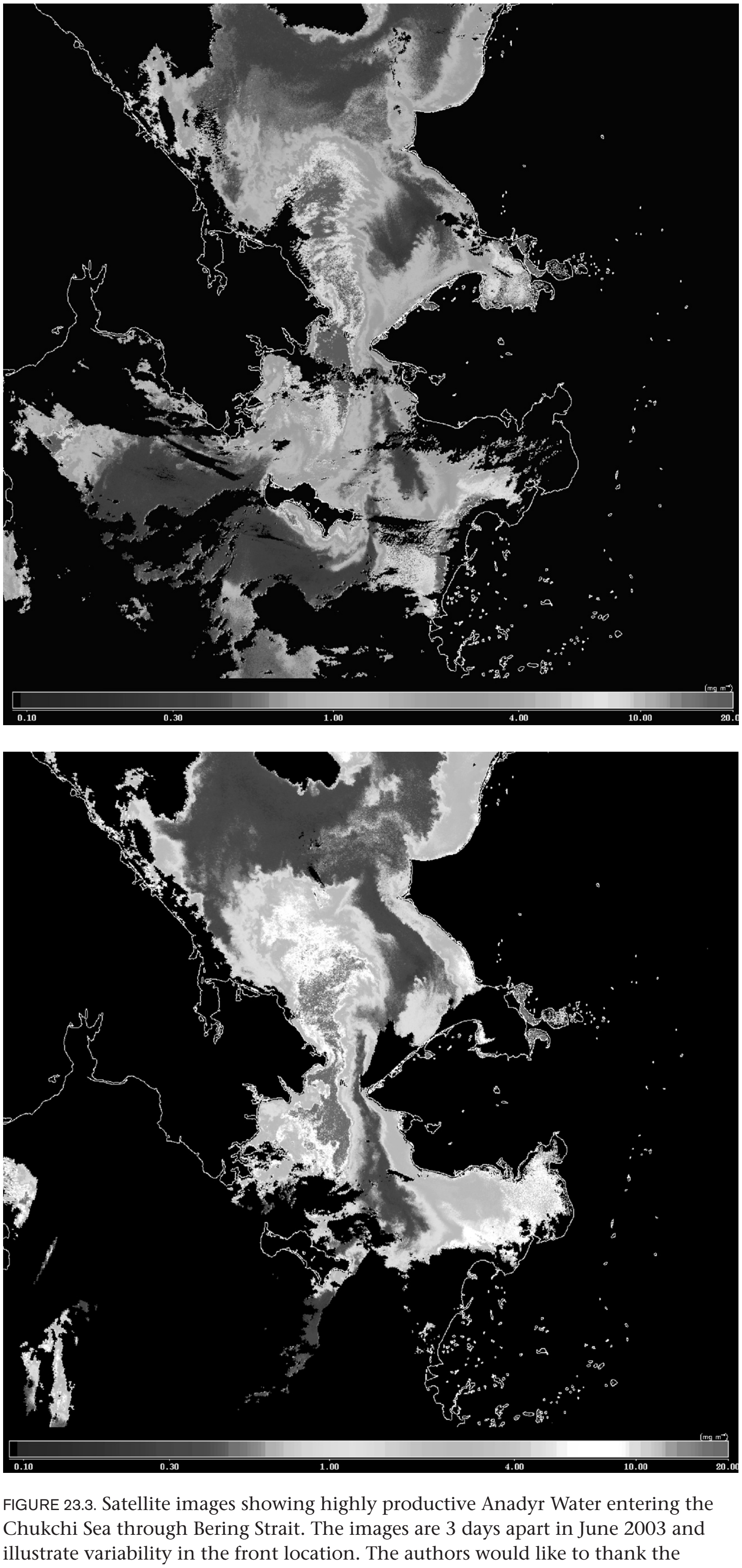


FIGURE 23.3. Satellite images showing highly productive Anadyr Water entering the Chukchi Sea through Bering Strait. The images are 3 days apart in June 2003 and illustrate variability in the front location. The authors would like to thank the SeaWifs Project (Code 970.2) and the Goddard Earth Sciences Data and Information Services Center/Distributed Active Archive Center (Code 902) at the Goddard Space Flight Center, Greenbelt MD 20771, for the production and distribution of these data, respectively. These activities are sponsored by NASA's Earth Sciences Enterprise.

(Nerini 1984; Yablokov and Bogoslovskaya 1984; Highsmith and Coyle 1990, and references therein). The whales prey on the amphipods by placing one side of their mouth on the sandy-mud bottom and sucking out large pits as they swim (Ray and Schevill 1974; Nerini and Oliver 1983; Nerini 1984; Swartz and Jones 1987). Many gray whales produce a mud plume when they surface, which is interpreted to indicate that the whale just made a feeding dive (Scammon 1874; Moore and Ljungblad 1984; Nerini 1984). The distribution of barnacles *(Cryptolepas rhachianecti)* on the whales' heads suggests that they tend to roll on their right side to feed as they work the bottom sediments (Kasuya and Rice 1970; Blohkin 1984). Also, baleen on the right side tends to show greater wear.

In contrast to the Chirikov Basin (B5 in Figure 23.1) and the northern Russian sites (B2 and C1–C3 in Figure 23.1), whales feeding along the Koryak Coast (B1 in Figure 23.1) and on the northeast shore of the Gulf of Anadyr tend to feed on amphipods in the genus *Pontoporeia* (Haustoriidae), particularly *P. femorata* (Nerini 1984; Yablokov and Bogoslovskaya 1984). Stomach contents also included the amphipods *Anonyx* (Lysianassidae) and *Atylus* (Demaxinidae) and polychaetes in the family Oweniidae (Blokhin 1984). Adults of the various amphipod species reach lengths of 13 to 27 mm (Nerini 1984).

The gray whale feeding site in which the prey community has been studied most extensively is the Chirikov Basin (B5 in Figure 23.1; Nerini and Oliver 1983; Braham 1984; Nerini 1984; Nelson and Johnson 1987; Highsmith and Coyle 1990, 1991, 1992; Moore et al. 2003). More than 90% of the stomach contents from this area were *A. macrocephala* (Bogoslovskaya et al. 1981), which requires a soft-sediment habitat. The Chirikov seafloor is covered by an approximate 2-m-thick layer of fine sand (0.125 mm), deposited at the end of the last glacial period, about 10,000 years ago (Johnson and Nelson 1984; Nelson and Johnson 1987).

Ampelisca macrocephala is the largest and most abundant of the eight ampeliscid species present in the Chirikov Basin, reaching lengths of 3 cm and mean densities of about 2,500/m^2 (Coyle and Highsmith 1989; Highsmith and Coyle 1990, 1992). This species constructs mucous tubes that extend a few centimeters into the loose sediment. *A. macrocephala* feed by positioning themselves ventral side up at the opening to their tubes and creating a mouthward feeding current with their abdominal appendages (Highsmith and Coyle 1991). Diatoms in the water column near the seafloor are the primary food source for the amphipods, but they are also capable of sweeping the sand surface around their tubes to a distance of about 1 cm with their long second antennae and wafting any food items detected into the feeding current. The latter feeding method was utilized in experiments in which settling larvae and newly metamorphosed juveniles of a potential space competitor, the sand dollar *Echinarachnius parma,* were eaten, suggesting that *A. macrocephala* is also a facultative predator (Highsmith and Coyle 1991). *A. macrocephala* is long-lived with low fecundity (~60 eggs/brood) and a high age (4–5 years) at first reproduction (Highsmith and Coyle 1991; Coyle and Highsmith 1994). *A. macrocephala* appears to dominate smaller amphipod species with higher reproductive rates and shorter life cycles by outcompeting them for space (Coyle and Highsmith 1994).

The population dynamics and life history features of gray whale prey items at other feeding sites have not been studied. Also, there appears to be little stomach content information from other northern areas. The stomach of a first-year male near Cape Lisbourne contained the benthic isopod *Tecticeps alascensis* (Kim and Oliver 1989).

Nerini (1984) proposed that when gray whales forage on the seafloor, they consume the benthic invertebrates susceptible to the sucking mode of feeding in proportion to their abundance in the community, as the whales lack the means to sort prey. Approximately 60 benthic amphipod species and 80–90 other benthic invertebrate species have been recorded in the diets of gray whales (Blokhin 1980, 1984; Zimushko and Ivashin 1980; Bogoslavskaya et al. 1982; Nerini 1984; Yabolokov and Bogoslovskaya 1984), but most of these species are a small proportion of the stomach contents, commensurate with field abundances. In contrast, the pelagic mode of feeding usually reported along the migration route (Nerini 1984; Dunham and Duffus 2002; Stelle 2002) appears to target swarms or schools of a particular species (Kim and Oliver 1989).

Our 2003 work in the Chukchi Sea (the eastern portion of C4 in Figure 23.1) indicates that gray whales feeding there utilize prey other than infaunal amphipods. We collected 105 grab samples in the area where the whales were feeding and found no *A. macrocephala* and few other infaunal amphipods. The surface sediments were light brown and very soft, but at 2–3 cm deep they turned dark and claylike in texture and appeared to be anoxic. Confirming that the surface sediments were unconsolidated, otter trawls collected large numbers of shallow burrowers such as the small sea cucumbers *Cucumaria japonica* and *Chiridota* sp.; the protobranch bivalves *Ennucula bellotii, Nuculana pernula,* and *Yoldia hyperborea*; and the moonsnail *Cryptonatica affinis*. Epifauna was quite abundant as judged by 10-minute otter trawls that typically included numerous snow crabs *(Chionoecetes opilio)*; lyre crabs *(Hyas coarctatus)*; hippolytid, pandalid, and crangonid shrimp; small seastars (*Leptasterias* sp.); brittle stars *(Ophiura sarsi)*; basket stars *(Gorgonocephalus caryi)*; and occasional sea anemones, compound ascidians, flatfish, and sculpins. Acoustic scattering layers over the bottom consisted of krill, *Thysanoessa raschii,* and arctic cod, *Boreogadus saida*. Most of the listed invertebrates previously have been found in gray whale stomachs near the Chukotka Peninsula, where they appear to have been incidentally caught while the whales were targeting the dominant (>90%) infaunal amphipods (Blokhin 1980; Bogoslovskaya et al. 1982; Nerini 1984; Yablokov and Bogoslovskaya 1984). With infaunal amphipods absent at C4, one or more of the locally abundant shallow-infaunal or epifaunal species, or the dense near-bottom crustacean and fish accumulations, or some combination of these groups, must constitute the gray whale's principal prey.

Of the approximately 70 gray whales near the ship that we observed closely, about half produced light-colored mud plumes, similar to the upper 2–3 cm of surface sediment brought up in van Veen grabs. These findings further suggest that the whales are feeding on near-bottom epifauna or skimming shallow-dwelling infauna from the bottom.

Impacts of Gray Whale Feeding

A large, abundant predator is expected to have a strong role in structuring the biological community in which it feeds (Paine, Chapter 2 of this volume; Jackson, Chapter 4 of this volume; Williams, Chapter 15 of this volume). Gray whales in the northern feeding grounds probably exert their strongest impacts through sediment disruption and removal of the spatially dominant prey species (Nerini and Oliver 1983; Oliver and Slattery 1985; Moore and DeMaster 1997).

Biological Impacts

Daily consumption of benthic organisms by large adult gray whales has been estimated at 379–2,496 kg (Tomilin 1946) and at 1,200 kg (Zimushko and Lenskaya 1970). The latter authors also estimated that the gray whale population at that time consumed 773,000 metric tons of food per year on the northern feeding grounds. This estimate is based upon estimated daily food intake, number of feeding days, and population size. For example, using 1,200 kg day^{-1} and 180 feeding days (May–October) translates into a population of about 3,600 whales needed to consume 773,000 mt yr^{-1}. This estimate is probably too low, because the 1980 population estimate of 15,500 whales (Reilly 1984; Rugh 1984) extrapolates to a 1970 population of about 11,000 individuals, based on a growth rate of 3% per year (Reilly et al. 1983). Eleven thousand gray whales would consume about 2,462,400 mt yr^{-1}. Estimates of this type are subject to substantial errors, but the inescapable conclusion must be that a huge invertebrate live-weight biomass is removed from the benthic communities of the northern Bering and Chukchi Seas each year. This underscores the requirement of gray whales for feeding sites with very high secondary production.

In the well-studied Chirikov Basin (B5 in Figure 23.1), ampeliscid production has been estimated at 170–230 kcal m^{-2} yr^{-1}, more than entire community production at other highly productive locations such as Georges Bank and Long Island Sound (Highsmith and Coyle 1990, 1992). Indeed, the amphipod community inhabiting approximately 40,000 km^2 of the Chirikov Basin in the late 1980s was one of the most productive benthic communities in the world. Based on whale energy requirements and population growth and benthic amphipod production, Highsmith and Coyle (1992) and Coyle and Highsmith (1994) predicted that gray whales were at or near the carrying capacity of the Basin and that by 2000 the amphipod community would not be able to support continued whale predation. Research cruises in late June through early July and September of 2002 and 2003, and a National Oceanic and Atmospheric Administration (NOAA) survey in 2002 (Moore et al. 2003), yielded very few sightings of gray whales in the central Chirikov region, supporting that conclusion. Preliminary results of our 2002–2003 field work indicate that amphipods are still present in the Chirikov Basin, but they have a patchier distribution and overall lower densities than in the 1980s. AUQ1

Physical Impacts

The major physical impact of gray whale feeding is the reworking of surface sediments (Johnson and Nelson 1984; Nerini 1984; Nelson and Johnson 1987; Nelson et al. 1987). A variety of information indicates that this is an important ecosystem-level process. Using side-scan sonar, Johnson and Nelson (1984) and Nerini (1984) detected numerous pits in the sandy floor of the Chirikov Basin that they attributed to the benthic feeding activities of gray whales. In shallow, nearshore areas off the Southeast Cape of St. Lawrence Island, pits were also observed by divers (Nerini 1984). Comparisons of fauna in recently made pits (same season) with adjacent areas revealed a reduction in infaunal abundance of up to 50% and a shift in species from tube-building polychaetes and amphipods to free-living amphipods, especially scavengers (Klaus et al. 1990). Feeding pits cover an estimated 1,200 km^2 or 5.6% of the Chirikov feeding area each year. Associated with this process, an estimated 172 million cubic meters of sand is resuspended, with the clay fraction (4.3×10^6 mt) advected by currents to the Chukchi Sea (Nelson and Johnson 1987; Nelson et al. 1987).

Gray Whale Distribution Model: Bering and Chukchi Seas

The data reviewed in this chapter and in recent oceanographic publications suggest a unifying model that incorporates the major ocean currents, pelagic primary production, and subsequent benthic secondary production to explain the distribution of gray whale feeding sites in the Bering and Chukchi Seas (Figure 23.4). Large marine mammals, especially those that migrate annually, are good indicators of ecosystem productivity, because they are forced to feed efficiently and therefore aggregate in areas of plentiful prey (Moore and DeMaster 1997). The most important gray whale feeding locations are B5 in the Chirikov Basin (at least until recently) and C4 in the Hope Basin (Figure 23.4). The next most important feeding locations appear to be B1, B3, B4, C2, and especially C1, where numerous whales are typically observed. The most important foraging location along the Alaskan coast is C5 between Point Franklin and Point Barrow. Areas C3 and C6 each appear to be utilized by 100–200 whales (Berzin 1984; personal observation, respectively). The Chirikov Basin (B5) was not utilized by many whales in 2002 or 2003, but we include it in our model because it has been the most commonly noted gray whale feeding site over the last century and probably has been a major feeding location since the last ice age.

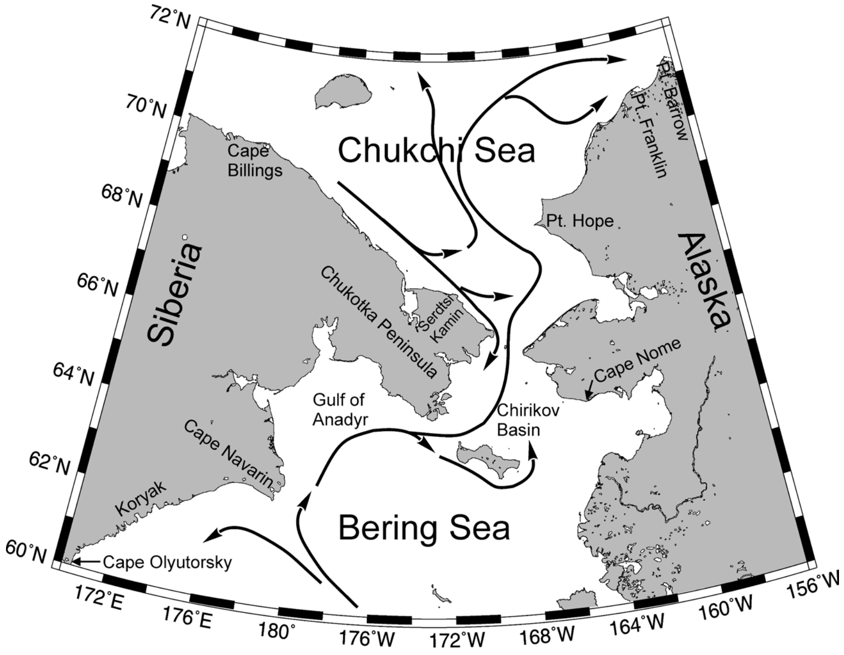


FIGURE 23.4. Model of gray whale distribution in the Bering and Chukchi Seas. Cold, nutrient-rich water upwells near Cape Navarin and the northern Gulf of Anadyr and delivers nutrients and primary production biomass at frontal zones to benthic communities with high secondary production utilized as feeding sites by gray whales.

The Green Belt in the Bering Sea consists of waters running from southeast to northwest along the Bering shelf slope (Hansell et al. 1989; Springer et al. 1996). Deep, nutrient-rich waters of the Green Belt upwell near Cape Navarin and in the Gulf of Anadyr (Figure 23.4). Some of the nutrient-laden water deflects southward along the Koryak coast and fuels high production in feeding area B1. Water deflecting north transits the Gulf of Anadyr, carrying high nutrient concentrations that generate high primary production (Sambrotto et al. 1984), especially by diatoms (Whitledge et al. 1988). The Anadyr Water passes between the Russian coast and St. Lawrence Island to Bering Strait (Walsh et al. 1989), thus enriching feeding area B2 and much of B5 (Grebmeier et al. 1988; Highsmith and Coyle 1990, 1992; Fukuchi et al. 1993). Some of the Anadyr Water also transits around the south side of St. Lawrence Island and then crosses the Chirikov Basin to Bering Strait. The Chirikov Basin appears to be a depositional area as northbound water slows because of the constriction at the Bering Strait (Coachman et al. 1975). Also, the cold, dense Anadyr Water extends along the seafloor many kilometers eastward beneath the warmer Alaska Coastal Water.

Up to one-third of local and advected production, both of which are dominated by diatoms (Whitledge et al. 1988; Highsmith and Coyle 1990, 1992; Fukuchi et al. 1993), settles to the seafloor in the Chirikov Basin and provides food for the ampeliscid amphipods in feeding area B5 (Figure 23.4). Thus, in the Bering Sea this upwelling system provides nutrients and food for benthic amphipods, such as *Pontoporeia femorata* along the Koryak coast (B1) and southern Gulf of Anadyr, and *Ampelisca macrocephala* along the Chukotka Peninsula (B2), the western and eastern ends of St. Lawrence Island (B3, B4; Grebmeier and Cooper 1995), and the Chirikov Basin (B5).

Once through the Bering Strait, the plume of productive Bering Sea Water (Figure 23.3) slows and moves north and west until it encounters the East Siberian Current and forms a front approximately 60 km wide (Figure 23.2), which may occur anywhere from Serdtse Kamen west to the Cape Schmidt area (C1–C3; Figure 23.5; Weingartner et al. 1999). The resulting meander of the front provides an abundant food supply to the benthic communities in the region, especially areas C1, C2, and C4 (Blackburn 1987; Grebmeier et al. 1988; Grebmeier 1993), and to some extent C3. The front is wide in area C4 because the dense Anadyr Water, bearing high phytoplankton concentrations from the Bering Sea, underlies warmer, less productive surface waters for tens of kilometers, and thus delivers considerable production to the benthos. The extension of the bottom front northward along the Hope Valley then swerves northeastward (Weingartner et al. 1999) to Point Franklin on the Alaska coast and provides an energy source for gray whale prey in area C5 (Feder et al. 1994). The only feeding site not presently accounted for by this model is the small feeding area C6, directly east of C4. It is possible that the front with productive Anadyr water on occasion extends that far east to deposit diatoms, but we have no data at present indicating that this occurs.

As gray whales appear to feed on shallow infauna and epifauna, soft sediments are a necessary condition for gray whale bottom feeding. However, sediment grain size may not be as restrictive (Feder et al. 1994) as sometimes has been suggested (Johnson and Nelson 1984; Nelson and Johnson 1987; Moore et al. 2003). For example, fine sand occurs in the Chirikov Basin (Johnson and Nelson 1984), but the bottom in the Hope Basin (C4; Figure 23.4) is dense black silt and clay overlain by 2–3 cm of loose, fine sediments (unpublished observation). We have also observed ampeliscid amphipods in coarser sediments than those in the central Chirikov Basin. Thus, extensive gray whale feeding areas in the Bering and Chukchi seas are soft-sediment habitats with very abundant infaunal or epifaunal prey species supported by high deposition rates of phytoplankton produced by upwelled waters of the Green Belt and Anadyr stream, termed Bering Sea Water in the Chukchi Sea.

The apparent mortality of as many as 11,000 gray whales over a recent three-year period, indicating a food shortage, and the apparent nonuse of much of the Chirikov Basin in 2002 and 2003, suggest that the cause of the population decline is associated with reduced primary or secondary production in area B5 (Figure 23.4). This decline in production could be caused by a reduced flow of nutrient-rich, productive Anadyr Water through the Chirikov Basin or by reduced production of ampeliscid amphipods as a result of overgrazing by the whales. Indeed, if the Green Belt ceases to function, resulting in reduction or loss of upwelled water moving through the northern Bering Sea and setting up a major frontal system in the Chukchi Sea, the known feeding sites would probably not be able to support current levels of gray whale predation.

AUQ2 The gray whale is one of the oldest and more generalized whale lineages (cite). Gray whales have undoubtedly had to respond to changing food supplies over evolutionary time and are known to feed on a variety of pelagic and benthic prey along the northern migration route between Baja California and Alaska (Dunham and Duffus 2002). These observations raise the intriguing question of where and how eastern gray whales fed during the Pleistocene glacial advances, the most recent of which ended just 10,000–12,000 YBP. At that time, all of the present foraging locations in the Bering and Chukchi seas were emergent, and marine access to the Arctic was blocked by the Bering land bridge. Perhaps eastern gray whales in these earlier times mingled with the western stock and fed in the Sea of Okhotsk or spread out in small numbers at various locations along the present migratory route. We may never have a complete understanding of long-past events, but the model we propose accounts for the current feeding ecology of the gray whale. Changes in the upwelled currents and formation of fronts delivering particulate organic carbon to the seafloor have the potential to expand, reduce, or eliminate feeding sites and to create new sites.

Concluding Remarks

Gray whales offer a unique opportunity to advance our knowledge of large whale ecology because they follow well-known, coastal migratory routes (making them countable), feed largely on benthic organisms at well-defined locations, and have profoundly responded to whaling and to management. Indeed, eastern North Pacific gray whales are the only whale stock/species to have recovered to estimated prewhaling numbers following the cessation of industrial whaling. The coastal migration route makes it possible to estimate changes in population size and calving rates. The shallow feeding sites make it possible to study the foraging ecology of the whales and their impacts on the prey community and habitat on a systemwide basis. Gray whale management thus can be viewed as a large experiment that produced interesting and informative results. We have made great progress in our understanding of gray whales, but the species and its associated ecosystem have much more to tell us. The challenge, in our view, is to conduct multidisciplinary research on appropriate scales of space and time.

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AUQ6

AUQ1]: (paragraph before “Physical Impacts”) Please update “Preliminary results of our 2002–2003 field work” if update available.

[AUQ2]: (“Gray Whale Distribution Model: Bering and Chukchi Seas,” seventh paragraph) Please provide citation here, and full reference in Lit. Cited section if not already present.

[AUQ3]: (Lit. Cited, LeBoeuf et al. 2000) Would you happen to know the second part of Ollervides’ surname? Would it be Uribe?

[AUQ4]: (Lit. Cited, Perryman et al. 2002) (answered internally)

[AUQ5]: (Lit. Cited, Walsh, J. et al. 1989) (answered internally)

[AUQ6] (Lit Cited, Zimushko and Lenskaya 1970) Sure the journal title isn’t *Ekologiya* (no *h*)?

Abundance, range and movements of a feeding aggregation of gray whales (*Eschrichtius robustus*) from California to southeastern Alaska in 1998

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ABSTRACT

This study documents the range, abundance and movements of a feeding aggregation of gray whales (*Eschrichtius robustus*) in the Pacific northwest. Identification photographs were collected by eight collaborating organisations between March and November 1998. Surveys extended between northern California and southeastern Alaska. Effort was variable by region and was concentrated off the northern Washington coast and Vancouver Island. Of 1,242 occasions when suitable photographs of gray whales were obtained in 1998, 155 unique whales were identified. Each individual was photographed an average of 8.0 times (SD = 8.4, range 1-42) and the average tenure of whales seen multiple times was 56 days (SD = 41, range 1-170). Whales seen longer than three months generally were seen in multiple regions. Movements among regions in 1998 were documented for 57 whales with the most frequent interchange among three adjacent areas from northern Washington to central Vancouver Island. The overall pattern of movements among regions was complex; whales were not always moving in the same direction at the same time of year. Movements within 1998 among more distant locations did occur but were less frequently observed. Total distances between resighting positions for individual whales ranged from < 1 to 526 n.miles. Most whales photographed in 1998 had been identified in previous years when compared to photographs collected by some of the collaborators. At least 86 (55%) of the whales identified had been seen previously. The rate of inter-year resightings was highest for whales identified off northern Washington and three areas off British Columbia (from southern Vancouver Island to north of Vancouver Island). In these areas, from 70-100% of the whales seen in each region had been photographed previously. Mark-recapture abundance estimates based on comparisons to samples in 1996 and 1997 were 181 and 179, respectively. The management implication for these whales has become controversial due to the resumption of whaling by the Makah tribe in northern Washington, an area used by both migrating and feeding whales. This research shows that there are a few hundred gray whales that range in summer months from at least northern California to southeastern Alaska. The mechanism by which these animals are recruited into this group and the degree to which they should be managed as a separate unit from the overall population is not resolved.

KEYWORDS: GRAY WHALE; PHOTO-ID; PACIFIC OCEAN; FEEDING GROUNDS; MOVEMENTS; SITE FIDELITY; MARK-RECAPTURE; ABUNDANCE ESTIMATE; WHALING-ABORIGINAL

INTRODUCTION

Gray whales make one of the longest migrations of any mammal between their winter breeding grounds off Baja California, Mexico, and their feeding grounds in the Bering and Chukchi Seas. Migrations along the Pacific northwest coast occur in December and January when the animals are southbound and again in the spring when the whales are northbound. Outside these migratory time periods, summer feeding aggregations of gray whales have been reported in a number of areas along the coasts of California, Oregon, Washington and British Columbia (Howell and Huey, 1930; Gilmore, 1960; Rice, 1963; Rice and Wolman, 1971; Patten and Samaras, 1977; Flaherty, 1983; Darling, 1984; Murison *et al.*, 1984; Nerini, 1984; Sumich, 1984; Mallonée, 1991; Avery and Hawkinson, 1992; Calambokidis *et al.*, 1992; 1994; Weitkamp *et al.*, 1992). These animals have been referred to as summer or seasonal residents (Pike, 1962; Darling, 1984; Murison *et al.*, 1984; Weitkamp *et al.*, 1992) and more recently as the 'Pacific Coast Feeding Aggregation' whales (National Marine Fisheries Service [NMFS], 2001).

In the early 1970s, photographic identification research demonstrated that many of the gray whales that would remain off Vancouver Island to feed through late spring and summer were the same individuals that returned to the same area each year (Hatler and Darling, 1974; Darling, 1984). Similarly, gray whales photographically identified off Washington State and northern British Columbia from late spring to autumn were also found to return annually (Calambokidis *et al.*, 1994). These whales appear to be part of the overall eastern gray whale population and generally arrive and depart from these feeding grounds concurrently with the migration to and from the wintering grounds. Gray whales in these regions have been observed feeding on a variety of prey including herring eggs/larvae, crab larvae, amphipods, mysids and ghost shrimp (Murison *et al.*, 1984; Nerini, 1984; Oliver *et al.*, 1984; Weitkamp *et al.*, 1992; Duffus, 1996; Darling *et al.*, 1998). Movements over distances of less than 100km and changes in distribution of

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animals in response to shifting prey types have been documented (Darling, 1984; Darling *et al.*, 1998). Darling (1984) suspected gray whales seen along the coast of British Columbia in summer months were part of a larger 'northwest coast' sub-population that numbered at least 100 animals.

Information on the status, range and movements, and abundance of these whales is crucial in the management of gray whales especially due to the resumption of whaling by the Makah Tribe in northwest Washington State. Although the current management plan for hunting of gray whales calls for targeting migratory animals, it may be difficult to avoid taking whales from this seasonal feeding aggregation (Quan, 2000). It is currently unclear whether the feeding aggregation of gray whales in the Pacific northwest should be treated as a separate population. Genetic differences have not been found to date between these animals and the overall population (Steeves *et al.*, 2001).

This paper examines the range of movements and tenure of individual gray whales between spring and autumn 1998 based on photo-identification research conducted collaboratively in many regions between northern California and southeastern Alaska. With data on these whales from previous years, this paper also examines site fidelity, interchange and estimate of abundance.

MATERIALS AND METHODS

Identification photographs of gray whales were collected by eight collaborating organisations between 12 March and 18 November 1998 from northern California to southeastern Alaska (Table 1). Effort by region was variable with most intensive coverage along the southern and western coast of Vancouver Island. Effort and identifications were grouped into 12 regions (Fig. 1) based on bodies of water and operating areas for surveys.

Photographic identification methods

Although a variety of vessels were used in different areas, most of the effort was conducted using small vessels (< 10m) and photo-identification methods were similar. Whales were approached slowly from the side at a distance of 50-100m. Both left and right sides of the dorsal region around the dorsal hump and the flukes of gray whales were photographed if possible. Most groups used 35mm cameras usually equipped with 300mm lenses and high-speed black and white negative film. Markings used to distinguish whales included pigmentation of the skin, mottling and scarring, which varied among individuals and have provided a reliable means of identifying gray whales over periods of

Table 1

Summary of areas of effort, participating organisations, number of identifications and dates of identifications in 1998.

Region	Region code	Description	Organisations	IDs	Unique IDs	Dates of identifications	
						Begin	End
Northern California	CA	Eureka to Oregon border with most identifications from Patricks Pt. and Pt. St George	Humboldt State Univ. (HSU) Cascadia Research Collective (CRC)	27	15	21 Jul. 1998	10 Oct. 1998
Oregon coast	OR	Primarily central coast near Depoe Bay and Newport, OR	Humboldt State Univ. (HSU) Cascadia Research Collective (CRC)	46	18	29 Jul. 1998	4 Oct. 1998
Grays Harbor and S Washington	GH+	Includes waters inside Grays Harbor and coastal waters along the S Washington coast	Cascadia Research Collective (CRC)	59	7	21 Mar. 1998	11 May 1998
N Washington coast	NWA	Northern outer coast waters with most effort from Cape Alava to Cape Flattery	National Marine Mammal Laboratory (NMML) Cascadia Research Collective (CRC)	46	21	6 Jun. 1998	18 Nov. 1998
US Strait of Juan de Fuca	SJF	US waters east of Cape Flattery extending to Admiralty Inlet (entrance to Puget Sound)	National Marine Mammal Laboratory (NMML) Cascadia Research Collective (CRC)	35	15	17 Aug. 1998	11 Nov. 1998
Northern Puget Sound	NPS	Inside waters and embayments from Edmonds to the Canadian border	Cascadia Research Collective (CRC)	27	6	12 Mar. 1998	20 May 1998
Southern Puget Sound	SPS	Central and southern Puget Sound (S of Edmonds) and Hood Canal	Cascadia Research Collective (CRC)	6	4	18 Mar. 1998	17 Nov. 1998
Boundary Bay	BB	Canadian inside waters in and around Boundary Bay, only a single survey	Vancouver Aquarium	3	3	7 Apr. 1998	7 Apr. 1998
S Vancouver I.	SVI	Canadian waters of the Strait of Juan de Fuca along Vancouver I. from Victoria to Barkley Sound, most effort along the West Coast Trail	West Coast Whale Research Foundation (WCWRF) Juan de Fuca Express Univ. of British Columbia (UBC) National Marine Mammal Laboratory (NMML) Cascadia Research Collective (CRC) Dep't of Fisheries and Oceans (DFO)	487	61	4 May 1998	9 Oct. 1998
Central Vancouver I.	CBC	Central portion of the western coast of Vancouver I. with heaviest effort in and around Clayoquot Sound	West Coast Whale Research Foundation (WCWRF) Univ. of Victoria (UVIC)	401	57	13 Jun. 1998	3 Sep. 1998
N of Vancouver I., BC	NBC	British Columbia waters north of Vancouver I., with principal effort around Cape Caution	Coastal Ecosystems Research Foundation (CERF)	100	22	3 Jul. 1998	11 Sep. 1998
SE Alaska	SEAK	Waters of southeastern Alaska with the only effort in the vicinity of Sitka (single survey)	Cascadia Research Collective (CRC)	4	4	8 Nov. 1998	8 Nov. 1998
All areas				1,241	155	12 Mar. 1998	18 Nov. 1998

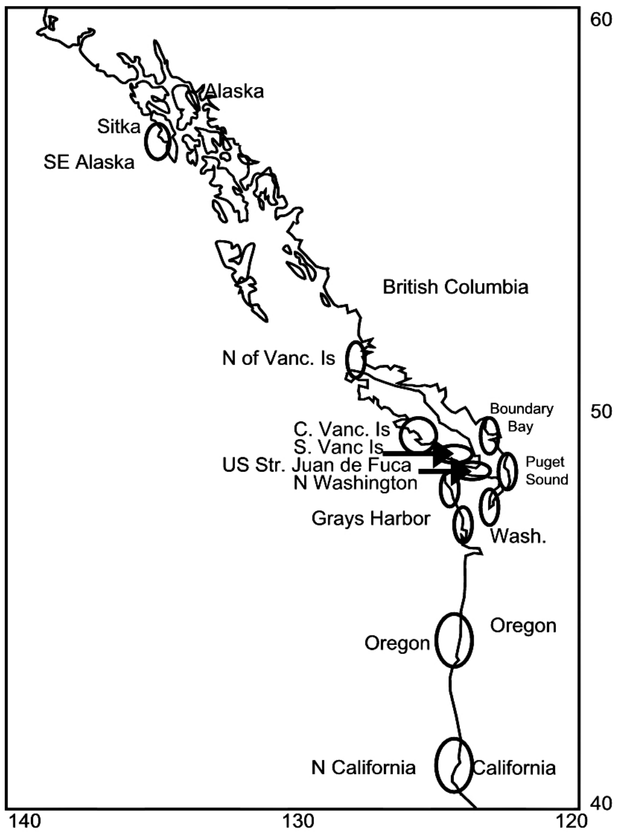

Fig. 1. Study area showing principal areas of effort.

close to 20 years (Darling, 1984; Darling *et al.*, 1998). The relative spacing between the knuckles along the ridge of the back behind the dorsal hump was also used to find photographic matches.

Photographic matching

Comparison of whale photographs to determine matches was made in a series of steps. First, the negatives of gray whales were examined and the best image of the right and left side of each whale (for each sighting) was selected and printed (17.8 × 6.4cm). To determine the number of whales seen during the season, all photographs from 1998 were compared to one another to identify whales seen on multiple days. Finally, a comparison was made between the best photograph in 1998 and Cascadia's catalogue of whales seen in past years (see below). Whale photographs that were deemed of suitable quality but did not match the existing catalogue (compared by two independent matchers) were assigned a new identification number.

Information on sightings from previous years came from two sources. Cascadia's catalogue from past years consisted of 835 records of 171 unique gray whales identified between 1984 and 1997. While most of these identifications were from Washington State, including Puget Sound and inland waters, small samples were also collected off California and southern British Columbia. These photographs were collected by Cascadia Research personnel or other collaborating scientists and naturalists. Additionally, individual research groups participating in the 1998 collaboration provided information on past years' sightings of animals they saw in 1998 (they did not have access to the entire collection of 1998 photographs). Since these groups only compared photographs from their own regions to its past collections, there was not a complete comparison among these collections. The proportions of individuals identified in previous years, therefore, are reported as minimums.

RESULTS

Sighting patterns and movements within 1998

From the 1,241 occasions when suitable photographs of a gray whale were obtained in 1998, 155 were identified as unique whales (Table 1). Each individual was photographed from 1-42 times (mean 8.0, SD = 8.4). The largest number of individuals were identified off the southern coast of Vancouver Island, especially in June and July, and from central Vancouver Island around Clayoquot Sound in July and August (Table 2).

Of the 155 identified whales, 117 (75%) were photographed on more than one day. Time between multiple sightings of individual whales ranged from 1-170 days (average of 56 days, SD = 42). Whales seen with a tenure of over three months generally were seen in multiple regions. The whale (ID# 192) seen over a 170 day period was first seen on 4 May and was resighted 42 times up to 21 October: it was seen from 4 May to 6 July off the West Coast Trail of southern Vancouver Island; 9 to 31 July in the Clayoquot Sound vicinity of central Vancouver Island (with a single resighting off the West Coast Trail on 24 July); 6 to 27 August off the West Coast Trail; and then from 5 September to 21 October, it was seen repeatedly off the northern Washington coast.

Table 2

Number of unique individual gray whales photographed in each region by month in 1998.

	Month									All months
	Mar.	Apr.	May	Jun.	Jul.	Aug.	Sep.	Oct.	Nov.	
Northern California					2	1		13	1	15
Oregon coast					4	17		1		18
Grays Harbor and S Washington	4	7	1							7
N. Washington coast				1	12	6	8	5	1	21
US Strait of Juan de Fuca						1	2	9	7	15
Northern Puget Sound	6	4	1							6
Southern Puget Sound	1							1	2	4
Boundary Bay		3								3
S Vancouver I.			8	40	45	15	30	9		61
Central Vancouver I.				17	40	42	7			57
N of Vancouver I., BC					18	14	3			22
SE Alaska									4	4
All areas	11	14	10	54	88	81	43	37	15	155

Movements among regions in 1998 were documented for 57 whales (Table 3): 38 seen in two regions; 18 in three regions; and 1 in four regions. The most frequent interchange was among three adjacent sites from northern Washington to central Vancouver Island (Table 4a). The overall pattern of movements among regions was complex (Fig. 2). Whales were not always moving in the same direction at the same time of year. Despite the wide variations in movement patterns of different individuals, a few patterns could be discerned. A high concentration of whales identified off southern Vancouver Island in June (40 individuals) and July (45) then appeared to disperse somewhat with 19 transits observed from this area north to Clayoquot Sound in July and, to a lesser degree, August. Some animals also moved south from southern Vancouver Island at this same time with 10 transits to the Washington coast and several more toward Oregon and California (arriving in later months). In August, the number of whales in the Clayoquot Sound area (42 individuals) peaked and a high number of transits were observed late in the month and extending into September from this area back to southern Vancouver Island (14 transits) as well as other areas primarily to the south.

Movements within 1998 among distant locations were rare. Only one whale was found to move from northern California to another location: whale ID# 76 was seen multiple times between 12 June and 9 July off southern Vancouver Island and was not observed again until 10 October when it was seen feeding off Point St George in

Table 3

Summary of identifications and resighting rates of gray whales in 1998 by region.

Region	Unique IDs	No. seen more than once in 1998	No. seen in same region in a previous year	No. seen in another region in 1998	No. seen in any region in a previous year	% seen in any region in a previous year
Northern California	15	6	3	1	7	47
Oregon coast	18	14	0	8	8	44
Grays Harbor and S Washington	7	7	3	0	3	43
N Washington coast	21	19	17	17	17	81
US Strait of Juan de Fuca	15	12	2	6	5	33
Northern Puget Sound	6	4	4	0	4	67
Southern Puget Sound	4	2	0	0	0	0
Boundary Bay	3	0	0	0	0	0
S Vancouver I.	61	60	21	49	45	74
Central Vancouver I.	57	55	20	43	41	72
N of Vancouver I., BC	22	18	10	14	22	100
SE Alaska	4	0	0	0	1	25
All areas	155	119		57	86	55

Table 4a

Matrix of matches between region within 1998. **Bold** numbers along the diagonal show number of animals resighted within the same area.

		Region									
Region	*n*	CA	OR	GH+	NWA	SJF	PS/BB	SVI	CBC	NBC	SEAK
Northern California	15	**5**									
Oregon coast	18		11								
Grays Harbor and S Washington	7			**7**							
N Washington coast	21		1		**8**						
US Strait of Juan de Fuca	15				1	11					
Puget Sound/Boundary Bay	13						**6**				
S Vancouver I.	61	1	6		17	6		**54**			
Central Vancouver I.	57		6		8	3		33	**50**		
N of Vancouver I., BC	22				1			7	9	**16**	
SE Alaska	4										**0**

Table 4b

Matrix of matches for whales sighted in 1998 and other years between regions. Diagonal (**bold**) shows number of whales seen both in 1998 and a previous year in the same region. Columns reflect region seen prior to 1998 and rows show region seen in 1998.

		Region sighted prior to 1998									
Region sighted in 1998	*n* for 1998	CA	OR	GH+	NWA	SJF	PS/BB	SVI	CBC	NBC	SEAK
Northern California	15	**3**		2	1	2					
Oregon coast	18		**0**	2	6	1		3	2	1	
Grays Harbor and S Washington	7			**3**	1						
N Washington coast	21				**16**	9		10	6	5	
US Strait of Juan de Fuca	16					**2**		4	5	4	
Puget Sound/Boundary Bay	13						**4**	1			
S Vancouver I.	61			1	25	16		**21**	20	20	
Central Vancouver I.	57	1		3	17	8		10	**20**	19	
N of Vancouver I., BC	22				2	1		2	3	**21**	
SE Alaska	4				1	1					**0**

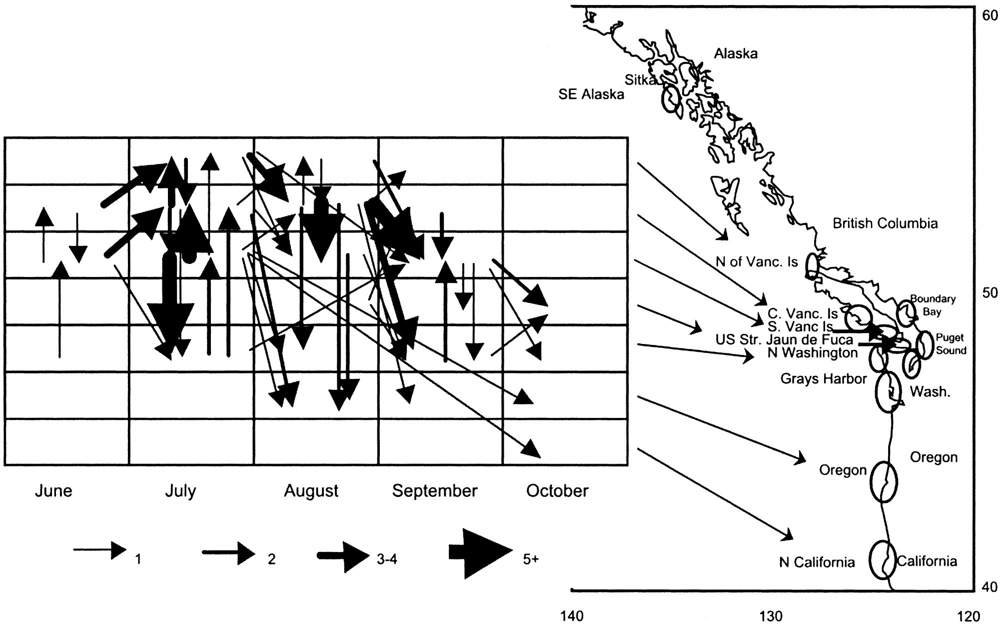

Fig. 2. Movements of gray whales among locations in 1998. Size of arrow indicates number of transits. Movements within a month are shown as vertical lines and movements across months are on diagonals.

northern California. Identifications were primarily made late in the season off Oregon (August) and California (October).

Distance and travel speed were also examined for the 117 whales that were seen on more than one day (Fig. 3). Total distances between resighting positions for individual whales ranged from < 1 to 526 n.miles (great-circle route). The distance a whale was documented travelling through the season averaged 110 n.miles (SD = 137) and was generally directly related to the number of times and span of time over which it was seen. The majority of travel speeds were well under 1 n.mile per hour as would be expected for feeding whales and because the data underestimate the true distance covered (and therefore the speed). Some whales remained in the same area for long periods; for example, ID# 231 was seen 30 times over a 136-day period (23 May to 6 October 1998) off southern Vancouver Island. It accumulated a total distance travelled of only 74 n.miles. The most rapid movement was for an animal (ID# 295) seen seven times from 10-25 August but which moved from central Vancouver Island to Oregon in that period (308 n.miles in less than 10 days). For the eight whales documented moving over 400 n.miles, one transited in one direction from Vancouver Island to California, while the remaining seven made multiple transits in different directions among locations.

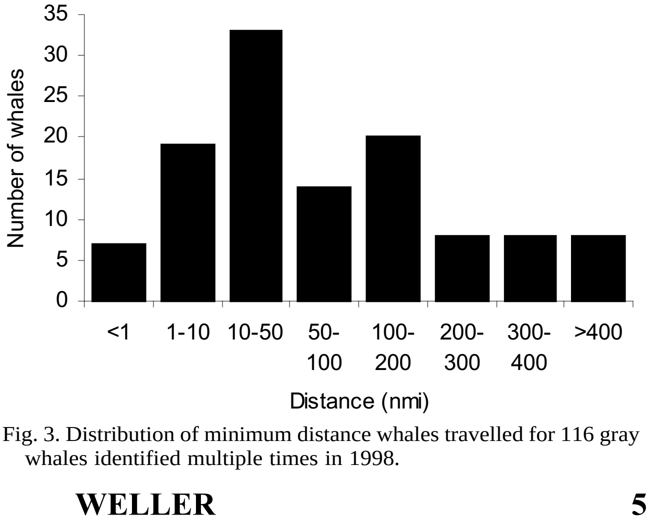

Fig. 3. Distribution of minimum distance whales travelled for 116 gray whales identified multiple times in 1998.

Inter-year resightings

Most of the whales photographed in 1998 had been identified in previous years (Tables 3 and 4b). At least 86 (55%) of the whales identified had been previously identified. This number is a minimum because the matches to past years come from comparison of all 155 of the whales identified in 1998 to the historical catalogue maintained by Cascadia Research of whales primarily seen off Washington. There were also matches to previous years identified by several of the collaborating research groups but these were confined to comparisons of whales identified in the same area (the full 155 whales were not compared to the historical catalogues of the other collaborating research groups). Such a comparison would yield additional documentation of resightings of whales in previous years.

Inter-year resightings were highest for whales identified off northern Washington and the three regions of British Columbia from southern Vancouver Island to north of Vancouver Island. In these areas, from 72-100% of the whales seen in each region had been identified in a previous year. These areas are the regions with the heaviest consistent survey effort in past years.

For some areas, such as Oregon and California, there were few identification photographs available from previous years so inter-year resightings were primarily animals that had been seen in other regions in past years. For Oregon, where no identification photographs were available previously, 8 of 18 (44%) whales identified in 1998 had been seen in six other regions from Grays Harbor to northern British Columbia in the previous years (Table 4b). Whales identified off California in 1998 had been seen previously in the Grays Harbor area, the northern Washington coast and the Strait of Juan de Fuca. Three of the whales identified off California were also seen in the only past sample available: a collection of 13 whales identified in November 1991 in the same location they were photographed in 1998 (off Point St George).

Whales identified in 1998 in southern Puget Sound and Boundary Bay had not been seen in a previous year in any region. This finding from southern Puget Sound is consistent with observations from past years; the presence of gray whales in this area is highly variable each year and whales have not been identified previously (Calambokidis *et al.*, 1994). This is different, however, for whales seen in northern Puget Sound, where four of six whales identified were known from sightings in past years. All four of these whales had been identified multiple times since 1990 or 1991. Whales seen in northern Puget Sound generally have been seen from March through May and then move to other unknown areas.

During 1998, whales that had been identified in previous years were seen more times (mean of 10.6 versus 4.7, $t = 4.73$, $p < 0.001$) over a longer period of time (61 versus 21 days, $t = 6.32$, $p < 0.001$) (starting earlier and extending later) than whales that had not been identified in previous years (Table 5). This was partly a function of the lower proportion of whales known from previous years in areas like California, Oregon and Puget Sound where resightings within 1998 were less common. Even with the elimination of this regional bias, however, this general trend remained within the three best-sampled regions (northern Washington and southern and central Vancouver Island).

Although only four whales were identified in southeastern Alaska in 1998 (and none previously), one of these was seen in past years off Washington. Although it was not seen elsewhere in 1998, it had been sighted 18 times in five of the previous six years off both the Washington outer coast and in the Strait of Juan de Fuca. Despite the small sample size, the movement of this whale suggests either the range of this feeding aggregation extends farther north than the primary effort of this study, or that there are other feeding aggregations with some interchange among them.

Seasonal patterns in resighting rates

Whales were identified from 12 March to 19 November 1998 and whales identified early and late in the season included animals seen over extended periods in 1998 and in previous years. There were, however, seasonal differences in the resighting rates of animals in 1998 (Table 6). Less than 50% of whales identified early (March and April) and late (November) in 1998 were known from previous years compared to 57% to 81% for those seen in previous years for May to October (Table 6). These whales were

Table 5

Summary of sighting rates and parameters for gray whales identified in 1998 for whales identified in previous years and whales not identified in previous years.

	All whales			Seen previous years			Not seen prev. years		
Times seen by region	*n*	Ave	SD	*n*	Ave	SD	*n*	Ave	SD
Northern California	15	1.8	1.3	7	1.9	1.6	8	1.8	1.2
Oregon coast	18	2.6	2.4	8	2.1	2.1	10	3.0	2.6
Grays Harbor and S Washington	7	8.3	3.9	3	6.0	4.0	4	10.0	3.4
N Washington coast	21	2.2	2.5	17	2.3	2.7	4	1.8	1.0
US Strait of Juan de Fuca	15	2.3	1.8	5	1.4	0.5	10	2.8	2.0
Northern Puget Sound	6	4.5	2.8	4	4.8	2.6	2	4.0	4.2
Southern Puget Sound	4	1.5	0.6	0			4	1.5	0.6
Boundary Bay	3	1.0	0.0	0			3	1.0	0.0
S Vancouver I.	61	8.0	7.3	45	8.8	7.3	16	5.6	6.9
Central Vancouver I.	57	7.0	7.0	41	7.4	6.4	16	6.1	8.6
N of Vancouver I., BC	22	4.5	4.6	22	4.5	4.6	0		
SE Alaska	4	1.0	0.0	1	1.0		3	1.0	0.0
All areas	155	8.0	8.3	86	10.6	9.0	69	4.7	6.1
Number of regions seen	155	1.5	0.8	86	1.8	0.8	69	1.2	0.4
First date seen (SD in days)	155	13 Jul.	61.4	86	29 Jun.	47.7	69	30 Jul.	71.7
Last date seen (SD in days)	155	24 Aug.	57.9	86	28 Aug.	49.2	69	19 Aug.	67.3
Tenure (minimum days)	155	42.8	44.0	86	60.6	45.9	69	20.6	29.2

Table 6

Summary of identications and resighting rates of gray whales in 1998 in relation to season.

Season	Unique IDs	No. seen in more than one month/season in 1998	% seen in more than one season in 1998	No. known from a previous year	% known from a previous year
By month					
March	11	8	73	5	45
April	14	9	64	6	43
May	10	9	90	6	60
June	54	54	100	44	81
July	89	80	90	62	70
August	83	69	83	60	72
September	43	41	95	35	81
October	37	21	57	21	57
November	14	5	36	3	21
By season					
Spring (Mar. to May)	25	7	28	13	52
Summer (Jun. to Aug.)	107	45	42	72	67
Fall (Sep. to Nov.)	74	44	59	46	62
All seasons	155	45	29	86	55

disproportionately sampled in Grays Harbor and in Puget Sound so this could partly be the result of regional differences. It also likely reflects the increased probability of sampling migrating whales closer to the time of the migration past the Pacific northwest.

Geographical recruitment

Although it appears that many whales consistently spend most of the feeding season in Pacific northwest waters, it is not known how they are recruited into this group. This is a critical question for evaluating how exploitation would impact this group (Quan, 2000). Some of the sightings in 1998 provide insight into one possible mechanism for the means by which animals adopt this alternate feeding area.

To examine the role that maternally-directed site fidelity plays in whales feeding in the Pacific northwest, some of the sighting history of identified cows and calves was examined. Although females with calves were sighted infrequently, three of the whales sighted in 1997 or 1998 were known reproducing females, plus one was a returning calf. One whale identified off Washington and British Columbia (ID# 43) has been seen in many years since 1984, including every year from 1992-1998. It was documented with a calf in July 1994 (ID# 107) and the calf was seen independently off Washington in three following years, 1995, 1997 and 1998. In the two other cases (ID# 67 and ID# 105), adult females known from multiple years (between 1992 and 1998) had a calf one year (1994 or 1995) that has not been resighted. In at least one of these two cases, the calf photograph was of marginal quality and there is a chance it would not have been recognised even if it had returned.

Estimation of abundance

The sample from 1998 provides a minimum estimate of the total number of whales feeding in summer months from northern California to southeastern Alaska. Although a total of 155 whales were identified, only 137 of these were seen after 1 June, outside the timing of the northern migration (Table 7). Mark-recapture estimates using annual samples from 1998 and either 1996 or 1997 yielded estimates of 181 and 179, respectively (Table 7).

Table 7

Petersen capture-recapture estimates for gray whales identified between June and November 1998 in the Pacific Northwest. See text for explanation of violations of assumptions and biases.

Sample 1		Sample 2				
Year	*n*	Year	*n*	Match	Est.	CV
1997	29	1998	137	22	179	0.09
1996	24	1998	137	18	181	0.10

DISCUSSION

While the presence of gray whales feeding during summer months in the Pacific northwest has been reported, there has been only limited research on the abundance and range of movements of these animals. Darling (1984) reported resightings of whales off Vancouver Island over an eight-year period. He documented movements of animals between different areas of up to 80km in the same season and 150km between seasons and estimated that the Vancouver Island area was occupied by 35-50 whales each summer. There were gaps, however, in the sighting histories of these whales, with some individuals not identified in the study area for several years.

This study shows that these whales inhabit a broad region during the spring, summer and autumn extending from at least northern California to southeastern Alaska. Within this range, gray whales can move widely both within and between years. The use of this broad area by these whales provides one explanation for why many of these individuals would not be seen in specific areas in some years. Even with the broad field effort reported here, only relatively small portions of the potential areas of use by these animals are being searched (Fig. 1). The interval of three months between sightings of one individual during which it moved from northern Vancouver Island to California without being sighted in intermediate areas of British Columbia, Washington and Oregon, demonstrates the limited survey coverage. Animals not seen in a particular year could inhabit neighbouring areas where there was no research coverage.

This sample provides both a minimum estimate of abundance based on the number of identifications and an estimate of total abundance using mark-recapture. The estimates using the Petersen mark-recapture method require several assumptions (e.g. Hammond, 1986) that are not totally satisfied by the current sampling.

1. The population is closed

There would have been some natality and mortality between annual samples, although this should be small. There also may be emigration or immigration of animals with the overall ‘population’ of gray whales.

2. All animals have an equal probability of capture in at least one of the samples

The 1998 sample is the most complete sample obtained and covers a broad geographic area. Even in 1998, however, effort was not systematic and some areas were covered far more thoroughly than others; there was no effort in some portions of the known range of these animals.

3. The two samples are independent of each other such that animals caught or not caught in one sample both have equal probability of being caught in the other sample

The 1996 and 1997 samples are clearly geographically biased and are based on identifications made in a relatively small area (northern Washington, Strait of Juan de Fuca and southern Vancouver Island). Since there is also some bias in the 1998 sample and animals do not appear to redistribute randomly, this would create heterogeneity of capture probabilities.

4. All matches, if present, are found and there are no false matches

There is little probability of false matches because only matches based on photographs showing multiple markings and verified by a second observer were used. Some matches could have been missed although this was kept to a low number by only including good quality photographs and requiring all comparisons to be made by two matchers.

Violations of assumption No. 1 and the probable violation of No. 4 (missed matches) would both bias the estimate upward while the violations of No. 2 and No. 3 would bias the estimate downward. Since violations of No. 1 and No. 4 are likely small, it is possible that the most significant bias would be a downward one caused by the unequal sampling. This would mean the estimates are likely underestimates. Multiple-year samples that more completely and evenly sample the range of this feeding aggregation are needed to refine the estimate.

The gray whales in this feeding aggregation are a relatively small proportion of the overall gray whale population. The total gray whale population was estimated at 26,365 (95%CI 21,800-32,400) in 1997/98 based on censuses conducted on the southbound migration (Hobbs and Rugh, 1999; IWC, 2000). The few hundred animals identified from photographs and based on mark-recapture estimates would make up less than 1% of this population.

The timing of the arrival and departure of the gray whales described in this study coincided with the timing reported for the overall gray whale migration past the Pacific northwest. Initial sightings of these whales that stayed through the season occurred in March, during the peak of the northward migration past the Pacific northwest as determined by Herzing and Mate (1984). Similarly, resightings of whales identified in the summer were made through late November, when the last field effort ended. This is close to the December/January peak of the southward migration (Herzing and Mate, 1984). Since migratory animals could be present through May (Herzing and Mate, 1984), it is hard to distinguish early in the season which whales are migrating through and which would remain in the region. Given this potential overlap, mark-recapture estimates were made excluding animals identified only before 1 June.

Some species of baleen whales show a high degree of maternally-directed site fidelity to specific feeding areas. This has been examined in detail for humpback whales (*Megaptera novaeangliae*) in both the North Pacific and North Atlantic. In the western North Atlantic, humpback whales breed at one primary wintering ground but during the spring disperse to a number of distinct feeding areas in the North Atlantic; interchange among these North Atlantic feeding grounds is limited (IWC, 2002). There are differences in mtDNA among some of these areas (Palsbøll *et al.*, 1997). Similarly, humpback whales in the North Pacific use a number of distinct feeding areas with little interchange among them (Calambokidis *et al.*, 1996; 2001), although interbreeding among these groups does occur to some degree on the wintering grounds (Darling and McSweeney, 1985; Baker *et al.*, 1986; Calambokidis *et al.*, 2001). As in the North Atlantic, maternally directed site fidelity to specific feeding grounds has resulted in pronounced mtDNA differences between these areas (Baker *et al.*, 1990; 1998).

Only limited genetic studies have been done on gray whales. Steeves *et al.* (2001) compared mtDNA from a sample of 16 summer ‘resident’ whales from Clayoquot Sound, Vancouver Island and compared them to whales from the overall population. They detected no significant differences in mtDNA patterns between these two groups. The lack of a difference could result from one or more of the following: small sample size, too short time frame for isolation to develop detectable differences, or lack of isolation of this group. The power to detect differences genetically could be limited as exemplified by comparisons between eastern and western North Pacific gray whales. Despite the generally accepted separation of these two populations, differences in the proportion mtDNA haplotypes, while significant, do not allow reliable separation of individual animals from these two populations (LeDuc *et al.*, 2002).

The degree to which the gray whales in this feeding aggregation should be managed as a unit separate from the overall gray whale population is unclear. Treating two sub-populations as one when dispersal between them is less than several percent per year could result in depleting one of these sub-populations (Taylor, 1997). There is some evidence from whaling data to support the existence of sub-populations of baleen whales on a relatively small geographic scale that were depleted and failed to recover (see discussion in IWC, 2001). The gray whales from the Pacific northwest feeding aggregation appear to migrate to Mexico each winter and therefore are part of the larger breeding population of gray whales. Depending on the stability of this group and how they are recruited, they may represent a unit that should be managed separately. While there are some parallels in the site-fidelity to feeding areas between humpback and gray whales there are some clear differences. The low proportion of gray whale calves documented and the possible evidence for a male bias in this group (Steeves *et al.*, 2001) are different from humpback whale feeding aggregations. Additionally, the overall gray whale population migrates past the Pacific northwest *en route* to their main feeding grounds in the Bering and Chukchi Seas. This would provide a mechanism for animals to encounter productive feeding areas on this migration and potentially adopt this alternate feeding area.

The results also indicate that early in the season it could be difficult to determine with certainty which whales were migrating through the region and which were part of the feeding aggregation that remained in the region. This could be an important management concern related to aboriginal takes of whales in the Pacific northwest. During the migration it would be expected that the overwhelming majority of whales in the migratory corridor would be migrating animals based on the large size of the overall gray whale population and the low numbers of whales estimated in the group that stays in the region. However, some of the gray whales identified in this study as early as March (during the gray whale migration) were animals that had been seen in previous years and stayed through the summer and autumn. The most reliable way to select migratory animals would be based on a combination of season (as close as possible to the time of peak migratory passage), location (in the migratory corridor and away from known feeding areas) and behaviour (animals travelling and not milling in an area).

This paper provides new information on the range, movements and abundance of gray whales utilising the waters of California to southeastern Alaska as a feeding area. While this approach does provide valuable new information, a multi-year effort, currently underway, will provide more accurate estimates of inter-year resighting rates and interchange, and abundance estimates.

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FINAL REPORT

GRAY WHALE PHOTOGRAPHIC IDENTIFICATION IN 1998-2003: COLLABORATIVE RESEARCH IN THE PACIFIC NORTHWEST

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ABSTRACT

A collaborative effort to photographically identify of gray whales in the waters of the Pacific Northwest from California through Alaska from late spring through fall was conducted from 1998-2003. This report summarizes these results and provides new insights about the movements, abundance and survival of gray whales in the Pacific Northwest. Each year between 1,159 and 1,499 photographic identifications of gray whales were obtained. Surveys were most numerous along the south and west coasts of Vancouver Island and just north of Vancouver Island, British Columbia. Using all identification photographs, 600 unique whales were identified. We focused our analysis on 477 gray whales identified after 1 June to exclude whales that were seen during the course of the northward migration to the Bering Sea. Individual whales were commonly photographed in more than one region of the Pacific Northwest during the same year and between years including movements from the southernmost sampled areas of California and northernmost areas around Kodiak, Alaska. Gray whales were most likely to be re-sighted in adjacent regions indicating fidelity at a scale smaller than the entire Pacific Northwest but larger than a single region for most whales. Assessing the degree and scale of site fidelity is further complicated by its dynamic and temporal nature. Whales that were seen in more years were seen in more regions, so our ability to assess fidelity is limited by the timeframe of the observations.

Abundance of gray whales in the Pacific Northwest and sub-regions was estimated with closed and open population capture-recapture models. The well-known Petersen estimator for closed populations was used with adjacent years of photographs. The annual estimates for northern California to SE Alaska ranged from 261 to 298 and for Oregon to British Columbia (excluding Alaska and California), 197 to 256. Analysis of data collected from northern California to northern British Columbia (PCFA – Pacific Coast Feeding Aggregation) using open population models demonstrated a lack of geographic and demographic closure. Most whales seen for the first time were transients and were never seen again probably because they never returned (rather than mortality). Whales were more likely to return in a following year if they stayed for a longer time in their first year as measured by minimum residency tenure (MRT) (*i.e.*, time between first and last dates photographed within a year). MRT was also a useful predictor for the probability that a “returning(resident)” whale would be seen the following year. We propose that the mechanism for these relationships is related to foraging success or failure of whales. Whales visiting this feeding area during and following the migration may join the feeding aggregation depending on the success they have in locating food. The average annual survival rate of resident (returning) whales was 0.97 (SE=0.012). Annual abundance estimates of gray whales in the PCFA ranged from 200 to 225 during 2001-2003. An analysis of data from Oregon to southern Vancouver Island yielded lower estimates of abundance for this smaller region from 137 to 153 during 2001-2003.

INTRODUCTION

The existence of gray whales that spend the spring, summer and fall feeding in coastal waters of the Pacific Northwest has been known for some time. Starting in the 1970s, photographic identification demonstrated that along the west coast of Vancouver Island there was a core group of individual animals returning each year (Darling 1984). The resumption of the aboriginal hunt of gray whales by the Makah Tribe in northern Washington in the 1990s made determination of the status and number of these individuals of greater importance to management.

Beginning in 1998, a collaborative effort among a number of research groups was initiated to conduct a range-wide photographic identification study of gray whales in the Pacific Northwest (Calambokidis et al. 2000, 2002a, 2002b). Findings from 1998 demonstrated there was considerable movement of individual whales from northern California to southeastern Alaska and also provided initial estimates of abundance (Calambokidis et al. 2002a). The ability to look at movements and employ more sophisticated capture-recapture models, however, was restricted by the lack of multiple years of data with broad geographic coverage.

The collaborative effort to collect photographic identifications of gray whales from California through Alaska has continued since 1998 and these data now covers six years (1998-2003). This report summarizes this dataset and the new insights it provides about the movements, abundance and survival of these whales.

METHODS

Gray whales were photographed during small boat surveys conducted from California to Alaska by Cascadia Research, National Marine Mammal Laboratory and collaborating researchers between 1998 and 2003. Details of identifications obtained by the different groups are briefly summarized below and are listed in Tables 1-2. Principal study areas are shown in Figure 1.

- **National Marine Mammal Laboratory**: NMML obtained identification photographs of 754 gray whales representing 235 unique individuals sampling all years from 1998 to 2003 from a variety of locations from northern California to Kodiak, Alaska. Identification photographs were mostly taken while conducting dedicated surveys for gray whales.

- **Cascadia Research:** Cascadia obtained identification photographs of gray whales on 856 occasions representing 285 unique individuals. Surveys were conducted in all years using 5.3m RHIB at a wide range of locations from California to SE Alaska.

- **Humboldt State University**: HSU conducted surveys primarily off northern California from 1998 to 2002 and obtained 316 identifications of 127 unique whales.

- **Brian Gisborne, Juan de Fuca Express**: Brian Gisborne obtained identification photographs every year from 1998 to 2003 along the West Coast trail of southern Vancouver Island during daily trips of this region. He obtained 3,391 identifications of 199 unique whales during the trips from Port Renfrew to Bamfield.

- **Jim Darling, West Coast Whale Research Foundation**: Jim Darling provided identification photographs obtained during surveys along the west coast of Vancouver Island primarily from Clayoquot Sound to Barkley Sound in 1998, 2001, and 2002. These yielded 99 identifications of 59 unique whales.

- **Coastal Ecosystems Research Foundation**: CERF conducted regular surveys from 1998 to 2003 off British Columbia north of Vancouver Island primarily in the vicinity of Cape Caution. Identification photographs were obtained on 1,442 occasions representing 77 unique individuals.

- **University of Victoria:** UVIC obtained identifications photographs from Clayoquot Sound north along the west side of Vancouver Island every year from 1998 to 2003 except 2001. Identification photographs were obtained on 759 occasions of 108 unique individuals.

- **Volker Deeke:** Volker Deeke obtained identification photographs of gray whales from 1998 to 2001 off British Columbia and in SE Alaska. He obtained 64 identification photographs of 39 unique animals.

Each year from 1998 to 2003, between 1,159 and 1,499 identifications were obtained of gray whales totaling 7,743 for the entire period (Table 1). These were conducted from March through November with most effort from June to September. Surveys were most numerous in British Columbia, along the south and west coasts of Vancouver Island and just north of Vancouver Island (Table 2).

Photographic identification procedures

Procedures during surveys by different groups varied somewhat but were similar in identification procedures. When a gray whale was found, the time, position, number of animals, and behaviors were recorded. Whales were generally approached to 40-100 m and followed through several dive sequences until suitable identification photographs could be obtained.

For photographic identification of gray whales, both left and right sides of the dorsal region around the dorsal hump were photographed when possible. Most identification photographs were taken with 35mm cameras and 200-300mm lenses. We also photographed the ventral surface of the flukes for identification when possible. The latter method was not as reliable as the sides of the whale because the gray whales did not always raise their flukes out of the water. Markings used to distinguish whales included pigmentation of the skin, mottling, and scarring, which varied among individuals. These markings have provided a reliable means of identifying gray whales (Darling 1984). We also identified gray whale using the relative spacing between the knuckles along the ridge of the back behind the dorsal hump. The size and spacing of these bumps varies among whales and has not changed over the years we have tracked whales.

Comparisons of whale photographs were made in a series of steps. First, all negatives of gray whales were examined and the best shot of the right and left sides of each whale (for each sighting) were selected and printed (7 x 2.5 inch). To determine the number of whales seen during the season, the prints were then compared to others to identify whales seen multiple days. Finally, a comparison was made to our catalog of whales seen in past years. Whale photographs that were deemed of suitable quality but did not match our existing catalog (compared by two independent matchers) were assigned a new identification number and added to the catalog.

Data analysis

Interchange and tenure of whales

Initially gray whale identifications were grouped into 14 regions representing clusters of areas of effort (Tables1-2, Figure 1). To model some of the intra- and inter-year movements of gray whales, we grouped the range into 6 broader regions dropping some of the peripheral areas with infrequent sampling and low rates of interchange with the core area (Alaska and southern and central California, and some of the inland Washington waters). These six broader areas were: 1) northern California (NCA), 2) Oregon (OR), 3) northern Washington/Strait of Juan de Fuca (NWA), 4) southern Vancouver Island (SVI), 5) western Vancouver Island (WVI), and 6) northern Vancouver Island/British Columbia (NBC). The NWA region corresponds roughly with the Makah usual and accustomed tribal area. In particular, to address the issue of site fidelity and the abundance of gray whales at risk of potential harvest by the Makah, we were interested in the probability a whale would be observed in the NWA region given it was observed in one of the other regions. The interchange probability was estimated for each region within year, between years, and overall (either within or between). The dependent variable was 1/0 (seen/not seen in NWA) given that it was seen in a particular region/year. We used generalized linear modeling for a binomial random variable with a logit link in the R statistical software (R Development Core Team 2003).

For within-year interchange, in addition to region, we examined models with NWA survey effort or survey year, and the number of years a whale was seen as explanatory variables for the probability a whale was seen in NWA. For between-year interchange, we examined models with region, survey year and the number of years a whale was seen as explanatory variables. Survey year represented the year the whale was seen in one of the five other regions. For example, the model would estimate the probability that a whale seen in Oregon in 2000 would be seen at least once in 1998-1999 or 2001-2003. While we were primarily interested in regional differences in interchange, we thought they might also differ in time due to shifts in distribution. We also looked at overall (inter and intra-regional) interchange with NWA. For each whale seen at least once in a region during 1998-2003, we examined the probability it would also be seen at least once in NWA during 1998-2003. For overall interchange, we only considered region and number of years seen. We did not consider survey year because the analysis pooled the 6-year period. In each case, we used AIC (Burnham and Anderson 1998) to select the most parsimonious model. An overall goodness of fit was conducted for the best model using a chi-square test. The data were collapsed into categories as needed to achieve a sufficient expected value in most cells to yield a valid chi-square test.

Abundance/Survival using open population models

Population abundance and survival of gray whales was estimated with open population models for two spatial scales: 1) PCFA- the Pacific coast feeding aggregation from northern California (NCA) to northern Vancouver Island/British Columbia (NBC), and 2) ORSVI- Oregon to southern Vancouver Island. Gray whales photographed and identified anytime during the sampling period between 1 June and 30 November within the defined region were considered to be "captured" or "recaptured". For each unique gray whale photographed in the region, a capture history was constructed using the six years of data from 1998-2003. For example, the capture history 010010 represents a gray whale photographed in 1999 and 2002. The same gray whale may have had a capture history 010000 for the smaller spatial scale ORSVI or may not have been seen at all (000000) in ORSVI and would not be used.

Multiple "detections" of a single whale within the sampling period were not treated differently than a single detection. A "1" in the capture history meant that it was detected on at least one day during the sampling period. However, multiple detections within a region in the same year were used to construct an observed minimum residency time (MRT) for each whale. MRT was defined as the number of days between the earliest and latest date the whale was photographed with a minimum of one day for any whale seen. MRT for a whale seen on only one day was by definition 1 day and a whale not seen was assigned 0.

The capture history data for each region were fitted to a range of models using the POPAN model structure with the computer software MARK (White 2004). The POPAN model structure (Schwarz and Arnason 1996) provided a robust parameterization of the Jolly-Seber model structure in terms of a super population (N), the probability of entry (immigration), capture probability (p), and survival/permanent emigration (S). Models with constant and time-varying S were considered. We also considered models with different survivals for newly seen whales and previously seen whales allowing for the possibility of "transients" (Pradel et al. 1997) which are individuals that pass through (are seen once and then permanently emigrate) and do not return regularly. In addition, MRT for a newly seen whale was considered as a potential explanatory variable for permanent emigration (S) before the next sampling period.

The assumed parameter structure for capture probabilities (p) was important for estimation of abundance (N) particularly due to the limitations of the spatial scale. Clearly whales that typically returned to the PCFA or ORSVI could feed outside of these regions in some years. Thus, a whale may not have been photographed because it did not return to the region (temporary emigration) or it returned to the region at some time during the sampling period but was simply missed. Burnham (1993) has shown that abundance estimation is unbiased if the temporary emigration is random; however, we did not believe it was plausible to assume random temporary emigration for all whales. Instead we assumed that we photographed all whales that were within the defined region at sometime during the sampling period and whales were only missed because they did not return in that year. Thus, all newly seen whales (not seen in a previous year) were considered new immigrants to the "population" in that year and by assumption could not have immigrated in a previous year and been missed. While this assumption may not have been entirely true, it would result in an under-estimate of abundance that would be consistent with a risk-averse strategy in setting a harvest quota for the Makah. This approach was implemented within the POPAN model structure by creating a cohort/group for the newly seen whales in each of the six years. The probability of entry was fixed such that all of the whales in the cohort immigrated immediately prior to the sampling period in which they were seen and their capture probability (p) was fixed for the first occasion to be 1. Thus, the estimate of the initial size of the cohort was the number seen (*i.e.*, by assumption none were missed). Models with constant and time varying capture probabilities beyond the first occasion for each cohort were examined. In addition, we considered models in which the observed MRT for a whale on occasion *t* was used as a predictor variable for capture probability of the whale on occasion *t*+1. The abundance estimate for the population at time *t* was the number of newly seen whales at time *t* and the predicted number of surviving whales from previous cohorts. Surviving meant they were alive and did not permanently emigrate. Thus, the total abundance estimate at time *t* only includes possible transients from the newly seen cohort at time *t*. By excluding the size of the newly seen cohort, we constructed an estimate of abundance of non-transient whales from previous cohorts.

Our analysis could have also been done with the Cormack-Jolly-Seber (CJS) model structure in program MARK by treating each cohort of newly seen whales as a released cohort. However, MARK does not derive estimates of abundance for CJS because it is used primarily for survival estimation. However, we did use Test 2 + Test 3 results from the CJS structure (Lebreton et al. 1992) as a general goodness of fit for the global model and as a measure of possible over-dispersion creating the lack of fit. We used AICc for our model selection criterion (Burnham and Anderson 1998) for selecting the most parsimonious model for estimation. Model averaging was used when two or more models were within a ΔAICc of 4.

RESULTS

Good quality identifications were obtained of gray whales totaling on 7,743 occasions for 1998-2003 and these yielded 600 unique animals (154-254 per year)(Tables 1-3). These included identifications from early in the season during the migration as well as peripheral areas (see following sections).

The proportion of gray whales identified that had been seen in more than one region or more than one year (in any region) varied dramatically by month with whales identified in March through May less likely to have been seen multiple years or in multiple regions than those seen June to November (Table 4). This was expected because the northbound migration of gray whales proceeds past Washington through May making it more likely that gray whales identified early in the season are whales still migrating north. Resighting rates of whales seen after 1 June remained high through November.

Similarly, whales identified at the geographic ends of the sampled range (central and southern California and Alaska) as well as those seen in greater Puget Sound were also less likely to have been seen in multiple years and regions (Table 4). In some of these regions, such as Puget Sound, many of these whales were seen in the spring and may represent migratory animals. Even with exclusion of these early season animals, only a low proportion of the whales seen in Washington inside waters and at the north and south end of our sampled range had been seen multiple years or in more than one region. Gray whales in northern Puget Sound had a higher inter-year resighting rate than those in other parts of Puget Sound, but these whales were seen primarily only in spring and then were generally not resighted, indicating they were moving on to some other area outside where we sampled.

We examined the rate of interchange among regions both within years and overall among years for the 1998-2003 period. Within-year interchange was extensive especially among the outer coast regions from northern California to British Columbia (Figure 2). The low rate of interchange and within-year movements between these areas and those in Puget Sound or at the north and south ranges of our sampling in areas California and Alaska can also be clearly seen (Figure 2). Interchange among specific regions regardless of year, shows that whales seen on one region are most likely to be resighted at regions close to there rather than farther away (Table 5, Figure 3). For each region examined there was a pattern of decreasing interchange with each jump farther to the north or south of that site (Figure 3).

Even though resightings in other regions were less common for the whales identified in the ore geographically peripheral areas like southern and central California and Alaska, some of these animals were resighted in other regions (Table 5). For example, two whales identified off Bodega Head in central California in August 2001 were both seen in 2003 off southern Vancouver Island. Similarly, 5 of 10 whales identified off southeastern Alaska and 8 of 46 whales identified off Kodiak, Alaska had been identified farther south. This includes one animal from each of these Alaska areas that was documented on feeding areas farther south in the same season as when it was identified in Alaska. Directions of movement were opposite, however, with one whale (ID#140) that moved from southeastern Alaska around September 1999 to northern California on 30 October 1999 and another whale (ID#691) seen off southern Vancouver Island from 9 June to 6 July 2003 and then off Kodiak on 9 and 11 August 2003. This latter movement would represent a minimum of 1,104 nmi (by most direct route) in no more than 34 days.

Because of the presence of large number of migrating whales in spring, we restricted our mark-recapture and other analyses to whales that had been identified after 1 June for 1998-2003 each year. This reduced the number of unique individuals identified from 1998 to 2003 from 600 to 477 (Table 3). Unless stated otherwise, all analyses through the rest of this report will only include identifications and effort after 1 June.

Relationships between interchange and tenure of whales

Some simple exploratory plots suggest some interesting relationships regarding tenure and movements of whales. Whales that were seen more frequently (more years) were seen in more regions (Figure 4). Also whales that were seen more frequently had longer minimum residency times in the first year they were seen (Figure 5). Whales with a minimum residency time of three weeks or more were twice as likely to be seen the following year as whales with a shorter minimum residency time (Figure 6).

The most parsimonious model of within year interchange of whales into NWA from the other regions was a function of region, the number of years a whale had been seen and the year (Table 6). The model fit the data reasonably well (χ^2 =94.9, df=78, p=0.09) with the number of years seen collapsed into three groups (1-2, 3-4, 5-6). The next best model replaced year with survey effort in NWA during that year. Observed interchange increased with increasing effort in NWA; thus, many whales may have passed through NWA but were not always seen. However, inclusion of year in the best model suggests that in addition to effort other annually varying factors (*e.g.*, annual variation in movements) influenced the interchange with NWA. As might be expected, regions closest to NWA (SVI, OR, and WVI) had the highest within year interchange with NWA and NCA and NBC on the fringes had much lower within year interchange (Figure 7). Whales seen more frequently were more likely to be seen in NWA and another region during the year (Figure 7) which was most likely associated with longer within-year tenures.

The most parsimonious model of between year interchange of whales into NWA from the other regions was a function of region, the number of years a whale had been seen and the year (Table 6). The model fit the data reasonably well (χ^2 =43.3, df=49, p=0.70) with the number of years seen collapsed into two groups (2-4, 5-6). Again whales seen in the closest regions were more likely to be seen in NWA (Figure 8). As expected, whales seen in more years were more likely to be seen in NWA (Figure 9), which was consistent with whales being seen in more regions (Figure 4).

For overall (within- and between-year) interchange with NWA, the most parsimonious model likewise included region and number of years seen (Table 6). The model fit the data reasonably well (χ^2 =26.3, df=24, p=0.34) using the number of years seen in the six separate groups. The overall interchange was greatest for OR and SVI which are the regions to the south and north of NWA. For whales seen in all 6 years, at least 30% would be expected to be seen in NWA from all regions in the PCFA and more than half were seen in NWA of those seen in SVI and OR.

Population estimates from closed models

Abundance estimates using a simple Petersen mark-recapture model with adjacent years gave fairly consistent estimates of abundance (Table 7). The five estimates from pairs of adjacent years ranged from 261 to 298 for northern California to SE Alaska. Using only sites from Oregon to British Columbia (excluding Alaska and California) lowered the estimates slightly to 197 to 256 (Table 7). These results are very similar to the past inter-year estimate conducted in this manner but using a more limited number of years and not as complete a sample as available for this analysis (Calambokidis *et al.* 2000, 2002a, 2002b). These estimates were consistent from year to year and had a high certainty (Coefficient of Variation of 0.03 to 0.06) reflecting the high recapture rates; estimates were based on up to 206 different individuals identified in a year and up 126 recaptures between years (Table 7).

PCFA open population models

From 1998-2003, 408 unique whales were photographed from 1 June to 30 November within the PCFA (NCA to NBC). Excluding the 24 newly seen whales in 2003, 49% of the whales were seen in only one year and 25% were seen in every year following their first encounter. The latter includes 49 whales that were seen in all 6 years. The minimum residency time in the first year seen was 1 week or less for 46% of the whales and greater than 2 months for 25% of the whales. Of 186 whales with a minimum tenure (MRT) of 1 week or less in their first year, 68% were seen during July-September, the middle of the survey period well outside the migration period.

The goodness of fit results for Test 2 + Test 3 (χ^2=251.6, 11 df, P<0.0001) demonstrated a strong lack of fit for a model with survival and capture probability varying by year but not cohort specific. The lack of fit was predominantly from test component 3.Sr (χ^2=212.0, 4 df, P<0.0001) due to differences between “newly seen” and “previously seen” animals as described by Burnham et al. (1987). We subsequently divided the whales into 3 groups for each survey period: 1) newly seen whales with their first MRT ≤ 3 weeks, 2) newly seen whales with their first MRT > 3 weeks, and 3) previously seen whales. The goodness of fit results for Test 2 + Test 3 (χ^2=28.9, 15 df, P=0.01) suggested some lack of fit for the model group-specific time varying survival and capture probabilities, although most of the lack of fit occurred in one component for occasion 5 (2002), 3.Sr5 (χ^2=13.4, 1 df, P=0.004), which most likely occurred because there was very little survey effort in WVI during 2003. We assumed the lack of fit was structural and there was little or no over-dispersion in the data.

Minimum residency time was an important predictor of “survival” for newly seen whales and capture probability of returning whales (Table 8). Survival of newly seen whales varied by year and was presumably dominated by permanent emigration. Survival of previously seen whales varied by year in the lowest AICc model but was constant in the next closest model (ΔAICc=1.8). In computing estimates we used model-averaging of models 1 and 2.

Estimates of first year survival and their standard errors (SE) were 0.85 (SE=0.04), 0.22 (SE=0.05), 0.57 (SE=0.07), 0.39(SE=0.07), and 0.54(SE=0.12) for cohorts of newly seen whales from 1998-2001 using the mean value of MRT for each year. This first year survival represents both mortality and permanent emigration. The predominance of permanent emigration in these estimates is demonstrated by a comparison of the 1998 cohort to the 1999-2002 cohorts. "Newly" seen whales in 1998 were different than those in other years because many whales first "seen" in 1998 may have regularly returned to the PCFA but were only "first seen" because that was the beginning of the dataset. This was evident in the mean MRT which was significantly greater for whales seen in 1998 (47.6 days, SE=3.7) than the average MRT for newly seen whales in 1999-2002 (24.6 days, SE=2.0) (z=5.44, P<0.0001). The "survival rate" for 1998 was higher because there was less permanent emigration from the 1998 cohort than 1999-2002. Excluding 1998, on average we could reasonably expect about 43% of newly seen whales will return in the following years. The odds of a whale remaining in the PCFA after being first seen nearly doubled (1.92 SE=0.40) for an increase of 30 days in their first MRT.

Annual survival of previously seen whales, presumably true survival, was estimated to be 0.97 (SE=0.012) in model 2. The model-averaged estimates of annual survival were 0.92 (SE=0.04), 0.99 (SE=0.02), 0.97 (SE=0.02), and 0.87 (SE=0.08) for 1999 to 2002.

Estimates of recapture probability were 0.79 (SE=0.04), 0.70(SE=0.05), 0.71(SE=0.04), 0.88(SE=0.03) and 0.74(SE=0.08) for 1999-2003 using the average MRT from the previous year (1998-2002) of whales seen through the previous year. If all whales present in the PCFA each year were observed (as we have assumed), then 12-30% of the regularly returning whales may have temporarily emigrated outside of the PCFA. The odds of a whale being seen in a year doubled (1.90 SE=0.35) for an increase of 30 days in MRT the previous year.

Estimated abundance increased from 129 in 1998 (count of new whales) to a peak of 225 in 2002 (SE=6.6) (Figure 10). By subtracting the newly seen whales, we obtained abundance estimates of returning whales that increased from 102 (SE= 5.7) in 1999 to a peak of 176 (SE=20.5) in 2003. The average annual increase of returning whales was 18.5 from 1999 to 2003.

ORSVI open population models

The patterns observed in this analysis were quite similar to the PCFA analysis because the data were a subset of the PCFA data; however, captures and measures of MRT were restricted to the ORSVI area. A whale newly seen in ORSVI may have been seen previously in the PCFA but not in ORSVI and it was treated as a newly seen whale. From 1998-2003, 260 unique whales were photographed from 1 June to 30 November within ORSVI. Excluding the 28 newly seen whales in 2003, 48% of the whales were seen in only one year and 19% were seen in every year following their first encounter. The latter includes 18 whales that were seen in all 6 years. The minimum residency time within ORSVI in the first year seen was 1 week or less for

41% of the whales and greater than 2 months for 26% of the whales. Of the 107 whales with a minimum tenure (MRT) of 1 week or less in their first year, 69% were seen during July-September, the middle of the survey period, well outside of the northward migration period.

The goodness of fit results for Test 2 + Test 3 (χ^2=106.4, 10 df, P<0.0001) demonstrated a strong lack of fit for the model with survival and capture probability varying by year but not cohort specific. As with the PCFA analysis, the lack of fit was predominantly from test component 3.Sr (χ^2=98.8, 4 df, P<0.0001). As with the PCFA data we divided the whales into 3 groups for each survey period: 1) newly seen whales with first MRT ≤ 3 weeks, 2) newly seen whales with first MRT > 3 weeks, and 3) previously seen whales. The goodness of fit results for Test 2 + Test 3 (χ^2=16.2, 12 df, P=0.18) suggested a reasonable fit for the model with group-specific time varying survival and capture probabilities.

Minimum residency time was an important predictor of "survival" for newly seen whales and capture probability of returning whales (Table 9). Survival of newly seen whales varied by year and was presumably dominated by permanent emigration. Survival of previously seen whales was constant in the lowest AICc model but varied by year in the next closest model ΔAICc=1.4). In computing estimates we used model averaging of models 1 and 2.

Estimates of survival and their standard errors (SE) were 0.82 (SE=0.05), 0.50 (SE=0.11), 0.69 (SE=0.10), 0.26(SE=0.07), and 0.64(SE=0.15) for cohorts of newly seen whales from 1998-2001 using the mean value of MRT for each year. This first year survival is presumably predominated by permanent emigration. This was evident in the mean MRT which was significantly greater for whales seen in 1998 (49.1 days, SE=5.0) than the average MRT for newly seen whales in 1999-2002 (27.5 days, SE=2.6) (z=3.86, P<0.0003). Thus there was less permanent emigration from the 1998 cohort than 1999-2002. Whales that are newly seen in ORSVI may not be new to the PCFA, thus we would expect that permanent emigration would be less as it was. On average we could reasonably expect about 53% of whales newly seen in ORSVI will return in the following years. The odds of a whale not permanently emigrating after being first seen, increased by 2.24 (SE=0.53) for an increase of 30 days in MRT.

Annual survival of previously seen whales was estimated to be 0.97 (SE=0.019) in model 2. The model-averaged estimates of annual survival were 0.95 (SE=0.04), 0.98 (SE=0.02), 0.98 (SE=0.02), and 0.94 (SE=0.09) for 1999 to 2002.

Estimates of recapture probability were 0.70 (SE=0.06), 0.55(SE=0.06), 0.80(SE=0.05, 0.58(SE=0.06) and 0.67(SE=0.10) for 1999-2003 using the average MRT from the previous year (1998-2002) of whales seen through the previous year. If all whales present in the ORSVI each year were observed, that would suggest that 20-45% of returning whales may temporarily emigrate outside of the ORSVI. These percentages were expectedly higher because whales may have returned to the PCFA but outside of ORSVI. The odds of a whale being seen in a year increased by more than 50% (1.56 SE=0.33) for an increase of 30 days in MRT the previous year.

Estimated abundance increased from 84 in 1998 (count of new whales) to a peak of 150 in 2003 (SE=20.5) (Figure 11). By subtracting the newly seen whales, we obtained abundance estimates of returning whales that increased from 61 (SE= 5.0) in 1999 to a peak of 122 (SE=20.5) in 2003. The average annual increase of returning whales was 15.2 from 1999 to 2003.

DISCUSSION

Gray whales annually migrate from their feeding grounds during summer/fall to the breeding grounds in Baja California during winter/spring. Most whales feed in the Bering Sea, but some whales regularly do not complete the migration north and remain in coastal waters along the Pacific coast and in the Gulf of Alaska during the summer/fall to feed. While all whales that migrate north to the Bering Sea pass through the region inhabited by the Pacific Coast Feeding Aggregation (PCFA), most northward migration occurs prior to 1 June.

The northward migration path along the Pacific coast provides a possible natural mechanism for recruitment to the PCFA. Northbound whales have traveled a long distance and may be in search of food to replenish fat stores that have been depleted during the migration. Whales that encounter adequate food along the Pacific coast may choose to remain there and not continue the migration northward. If they are successful in one year, they may continue this in future years. Other whales may not be successful in finding food and may stay a short while before proceeding northward or simply pass through. Whales that typically return regularly may choose to look elsewhere following a year in which they were less successful foraging in the PCFA.

This proposed mechanism for the dynamics of the PCFA whales is supported by the inclusion of minimum residency tenure (MRT) in the models for survival (emigration) and capture probability. It is important to recognize that the observed tenures are minimums and whales may have been within the PCFA longer and not seen because it was in a region that was not surveyed or sampled less frequently. Although whales with short tenures could have been seen as late spring migrants or early fall migrants on their way north or south, more than two-thirds of those with short tenures were seen from July- September.

Lower survival estimates for newly seen whales could reflect permanent emigration (whales passing through) or mortality. Mortality would be more likely in this group if whales in poor physical condition are more likely to stop along the Pacific Coast in search of food. The estimated annual average survival rate (0.97) of PCFA (returning) whales clearly includes very little to no permanent emigration and is consistent with natural survival for a long-lived species. The annual variability in survival of PCFA whales in model 1 may have resulted from some increased mortality in 1999 during the stranding event but also the lack of sampling in WVI during 2003 may have depressed the estimated survival rate for 2002. The evidence for annual variation in survival is equivocal as the model ordering flipped between the two analyses. The support for constant survival in the ORSVI analysis may be due to the smaller sample size, but it may also be a better approximation to reality because it would not have been affected by the lack of sampling in WVI during 2003.

Jolly-Seber capture-recapture models assume that the capture occasion is an instantaneous event. Although a 6 month-long sampling period violates this assumption, it is only practically important if there are losses or gains in the population during the sampling period. Any loss due to natural mortality (0.03) is unlikely to have any importance even if it occurs during the sampling period. And while there will be whales both entering and leaving the region during the sampling period, it should not affect our estimates of population size that conservatively assume that all whales in the region are seen and whales are only missed because they did not return.

We chose a very conservative approach to abundance estimation with the potential for under-estimating abundance. We did so to provide estimates that could be used to set harvest quotas that would be risk-averse. Also, our estimation approach for abundance is consistent with our proposed mechanism for the dynamics of the PCFA whales. We have assumed that whales are only missed because they are not in the PCFA during the year. Thus, the newly seen whales are all of the new immigrants of which some (50-60%) will never return. If they do not permanently emigrate, they may return some years but not others and this is assumed to be random based on the year and their MRT in the previous year as modeled by the capture probability. Thus the estimated abundance is the predicted number of returning whales (did not permanently emigrate) that have survived from each cohort of newly seen whales. This may under-estimate the number of immigrants but newly seen whales have shorter MRTs and thus would be less vulnerable to harvest. Returning whales have longer MRTs and are more vulnerable to harvest.

The abundance estimates from the open population models are lower than the Petersen estimates based on a closed model. There are two reasons for the difference. First, the Petersen estimator treats “newly” seen and “previously” seen the same with each having a capture probability of p. Whereas, we have assumed p=1 for newly seen and estimated p applies only to returning whales. Secondly, the Petersen estimate is only unbiased with an open population if there are only losses or only gains in the population. In this case, there are both and that can create a positive bias because some of the whales seen in year 1 do not return and some of those seen in year 2 were new immigrants that year. Both of these will underestimate p and overestimate abundance.

Selecting a region for estimation is a difficult problem because for any set of boundaries the population size is open to change due to shifts in geographic distribution. We know that even using the PCFA boundaries, some whales that typically return will go to southeastern Alaska or Kodiak or possibly the Bering Sea. There is also considerable interchange within the PCFA so regions within the PCFA will have substantial annual changes when whales shift their distribution in search for food. However, clearly there is some level of fidelity; otherwise the abundance estimates from ORSVI would have been the same as the estimate for the PCFA. We have shown that regions in close proximity have the highest interchange rate thus it is both logical and reasonable to use ORSVI as the region for abundance estimation in setting quotas for a harvest of whales from the NWA/SJF region.

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Table 1. Summary of identifications provided by contributing organizations by year and region.

		Unique	Year						Region													
Contr. Org.	**Records**	**IDs**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**CA**	**NCA**	**SOR**	**OR**	**GH+**	**NWA**	**SJF**	**PS-H(**	**NPS**	**SVI**	**WVI**	**NBC**	**SEAK**	**KAK**
Brian Gisborne	3391	199	373	343	779	586	435	875										3357	34			
Coastal Ecosystem Research Found. (CERF)	1442	77	100	150	251	466	295	180												1442		
Cascadia Research (CRC)	846	285	170	233	117	79	135	112	9	47	138	113	134	86	12	62	138	33		70	4	
Humpboldt State Univ. (HSU)	316	127	21	89	60	75	71			279		37										
Jim Darling	99	59	50			35	14											4	95			
National Marine Mammal Lab (NMML)	754	235	132	194	136	128	88	76		4	2			166	104		22	177	199	13		67
University of Victoria (UVIC)	759	108	351	159	128		121												759			
Volker Deeke	120	64	39	42	28	11										1		72		43	4	
Other *	16	13	3	12		1										8				4	4	
Grand Total	7727	1154	1236	1210	1499	1380	1159	1243	9	330	140	150	134	252	116	63	160	3643	1087	1568	8	67
Unique Ids		600	154	248	178	198	254	172	6	121	57	55	35	113	35	25	42	201	169	82	10	46

*Other includes IDs by G. Ellis and J Ford of DFO, SE AK ids compiled by Jan Straley

Table 2. Summary of effort and identifications by region.

	Days identifications obtained							Identifications of whales																
		Year						Total	Unique	Year						Month								
Region	**Total**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**IDs**	**IDs**	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**
Central and S California	3	0	1	0	2	0	0	9	6		2		7							1	6	2		
N California	70	7	8	20	13	20	2	330	121	27	69	60	78	74	22			2	46	122	35	23	80	22
S Oregon	6	0	0	0	1	4	1	140	57				2	99	39					2	12	88	38	
Central Oregon	27	6	9	5	7	0	0	150	55	47	51	13	39						5	11	85	22	27	
Grays Harbor area	3	0	1	1	1	0	0	134	35	56	40	23	15			12	98	20	1	3				
N Washington coast	63	22	10	7	11	4	9	252	113	45	85	22	53	13	34			79	10	35	42	47	35	4
Str of Juan de Fuca	51	15	8	8	4	1	15	116	35	36	16	23	6	3	32	1	3	7	12	3	10	20	47	13
Other WA inside	17	3	11	3	0	0	0	71	25	9	53	9				3	15	23	21	4		1	1	3
N Puget Sound	1	0	0	1	0	0	0	160	42	27	47	53	13	4	16	34	70	44	12					
S Vancouver Is.	447	91	87	80	55	68	66	3643	201	487	398	833	643	441	841		5	145	709	1241	1035	468	40	
W Vancouver Is.	154	54	46	31	9	11	3	1087	169	401	262	195	57	138	34				95	422	422	131	17	
N British Columbia	248	39	50	53	43	34	29	1572	82	100	192	268	467	327	218				17	480	809	266		
SE Alaska	5	1	3	0	1	0	0	12	10	4	7		1						4		1	3		4
Kodiak, Alaska	6	0	0	0	0	4	2	67	46					60	7						67			
Sum	1101	238	234	209	147	146	127	7743	997	1239	1222	1499	1381	1159	1243	50	191	320	932	2324	2524	1071	285	46

Table 3. (5 pages). Sighting histories of identified gray whales. Only identifications after 1 June of 1998 to 2003 inlcuded.

	Organization									Year						Month						Regions													
ID	BG	CERF	CRC	HSU	JD	NMML	OTH	UVIC	VD	###	###	###	###	###	###	6	7	8	9	10	11	CA	NCA	SOR	OR	GH+	NWA	SJF	PS-H	NPS	SVI	WVI	NBC	SEAI	KAK
6			6	2							1		4	3		1		4	1	2			2	1	5										
14			7		1	1						2	6	1			3	4		2				1	4	2	1					1			
15	44		1		1	7		1	1	20	12	2	7	14		4	32	18	1								1				50	4			
21						1						1				1														1					
22						2						2				2														2					
30	10	15	1			8		6		2	8	4	10	9	7	1	12	20	7									1			10	13	16		
32		34				2			3	2	16			18	3		3	24	12														39		
37	6		1		3	5		2		5	3	4	2	2	1	1	2	7	4	3							1				6	9	1		
41	42	33	3		2	8	1		1	9	7	22	29	14	9	15	35	23	15	1	1							2			47	4	37		
42	61	6	1		4	16		13	1	24	25	9	13	24	7	8	36	38	12	8								8			68	20	6		
43	63		4	2	1	5		1		3	19	18	3	23	10	8	43	14	7	4				1	5		2				66	2			
53						1						1				1														1					
67	2		8			1					5			6				2	3	5	1			5	3		1				2				
68			1						1	1	1					1					1													2	
71	1														1		1														1				
73	5							1				2	3	1			3	3													5	1			
76	16		4		1	3		1	1	7			2	8	9	5	12	5	2	1	1		2	2			2				18	2			
79	10	72	2			2		2	4	13	25	25	19	5	5	6	40	39	7								2				13	2	75		
80	120	11	3			8		8	3	36	13	42	30	8	24	26	55	52	19	1							3				131	8	11		
81	32	13	3		1	9	1	5	1	8	9	11	22	5	10	11	13	25	13	3							3				36	12	14		
83	3	47	9	1	1	5		12		10	9	8	30	13	8	4	27	29	12	6				3	2		6				3	16	48		
84	76		10	2		10		6	2	16	11	39	10	6	24	26	32	34	14					3	9						84	10			
85	11		1	1		3		3		11	8					7	10	1	1						2		2				12	3			
86		1	2			5		3	1	1	4	3		2	2		3	6	3													7	5		
87	75		2		2	9		17	3	24	12	36	18	10	8	26	20	40	19	3			1		1						82	24			
89	75		5		2	1		15	1	20	19	24	9	4	23	26	40	16	14	2	1		1	2	1						78	17			
91	7	31	5		2	2		4		10		15	11	10	5	6	16	17	10	2				5			2				7	6	31		
92	32					14		4	1	17	6	3	7	6	12	4	10	18	13	6							3				38	10			
93	37	7	3	2		8		1	4	10	9	18	13	8	4	19	16	11	13	3			1		1		2				47	3	8		
94	53		3	1		5		20		13	8	31	4	17	9	1	30	38	11	2				2	1						55	24			
98		3	3			1					1			4	2			7															7		
101	43				1	8		6	1	11	4	6	13	17	8	9	20	25	5									1			47	11			
105	16	18	4			3	1	12	3	13	5	7	25	5	2	11	17	25	4						1						20	12	24		
107	58		1	1		6			1	7		34	10	1	15	5	25	19	15	3					1		4				62				
120	8		2	1	1	1							4	9		4	6	2	1				1		2		1				9				
123	55			1		4		3		8	6	9	8	22	10	15	36	8	3	1			1								57	5			
126	6	4	2	1						10			3				4	3	5	1			3								6		4		
127	53		6	2		3				1	3	26	19	1	14	2	14	39	6	3			2	1	5		1				55				
130	30	5	2			7		2	2	13	1	16	6	2	10	4	13	13	17	1				2			2				34	4	5	1	
135	44	5			2	8		22	3	26	7	10	22	6	13	29	22	24	8	1											50	29	5		
136	24			1	2	4		14		9	1	9	7	2	17	8	19	16	1	1			1								24	20			
138	33	47	2		4	4		13	3	28	18	3	30	12	15	16	23	48	19												36	17	53		
140	29		1		2	4	1	8		4	2	17	8	2	12	1	13	11	18	2			1					1			30	12		1	
141	3	17	1		1	5		9	3	16	5		7	8	3	6	6	21	6								1				7	13	18		
143	11	3			1	7		5		8	7	4	4	3	1	3	6	8	10												12	12	3		
144	10	6	2		1	2		11		13	1	2	10	4	2		11	15	6												10	14	8		
145	4		2		5	1		43		37	6	6	6			14	30	8	2	1					2						4	49			
149		16	3		2	3		12		6	3	4	18	2	3	1	5	24	6													17	19		
150	7				1	2		12		21	1					2	3	13	4												9	13			
151								2			2							2														2			
152						3		3			5			1			1	4	1													5			1
153		29	1			1			1		5	14	11	2			11	15	6														32		
154	19				4			9		5		5	9	4	9	14	11	3	2	2											20	12			
164				2									1	1			1	1					2												
166	67		1			9		3	1	9	9	21	18	9	15	16	26	28	10	1							5				73	3			
169	8	1	6			3							3	5	10	2	6	4	3	3				5			3				8		2		
175	51		1		4	11		15	2	14	14	6	18	2	30	20	27	23	11	2	1		1				3				48	32			
177	46				1	8		9	5	17	52					11	17	28	12	1							2				57	10			
178		1				3		15		11	3	4			1	2	6	9	2													18	1		
185	63				2	6		15		6	18	20	14	2	26	19	32	19	13	3								4			58	24			
186	50		4	3		7		6	2	13	11	13	11	6	18	25	22	13	7	5			3		4						55	10			
187	95		2		1	19		1	4	14	21	50	6	4	27	14	41	43	18	5	1						11				107	4			
192	146		3			15		7	4	38	29	35	22	29	22	43	57	55	18	2				1	1		7				159	7			
193	2	1				1		14		11				6	1		8	5	5												2	15	1		
196	9		2			1						2		1	9	4	3	4	1					1	2						9				
202			1							1										1			1												
204	54		12	1		2		1		1	2	45	3	5	14	3	9	28	25	2	3		4	6	3		1				55	1			
205	1				2	14		1			6	1	3	3	5		5	6	5	1	1						14				1	3			
206			6	9		1				3	2	1	3	4	3	1	6	1	3	5			10	6											
209	4					1				5						3	2										1				4				
212	40		2		3	9		1		22	15		15	3		10	18	11	12	4											50	5			
215			4	2		4				1				5	4	2		4	3	1			2	3	1		1	3							
216	16	35				13		1	1	1	2	28	20	2	13	6	30	21	6	3							4	9			16	1	36		
219	100		3			12			3	24	20	33	14	16	11	16	39	34	26	3											116	2			
226	38		2			3			2	6	2	32	3	2		5	16	14	9	1			1	1			1				42				
227	69	3				5	1	5	2	10	2	19	8	31	15	7	39	37	2												72	8	3	2	
228						2				2											2							2							
229	8	26				4		2	1	5	6	3	11	12	4		7	16	18												8	6	27		
231	47		6			9			1	29	30			3	1	6	14	22	19	2				4							59				
232	10		1		1	4		1		6		1	2	2	6	2	10	5													13	2			2
233	4					2				6						1	5														6				
234	32		4			6		4	1	7	5	4	7	9	15	5	16	17	8	1				3							35	9			
236	17	6	2		1	3		2	1	26	6					3	5	22	2						1						20	3	8		
237	2	53	2	1	1			1	1	7	4	15	11	17	7		27	26	7	1					1						3	2	55		
238	23	18	1		1	4		2	5	11	19		16	1	7	10	23	18	3												27	3	24		
239						4				4										4								4							
242	44		3			19		1	2	8	24	12	18	7		18	13	19	10	6	3						3	14			51	1			
243	1					1				2							1		1												2				
244	18	10	2		2	6		6		10	6	9	10	8	1	1	15	12	14	2											21	12	11		
246						1		2		3							1	2													1	2			
247	2	1							1	3				1			4														3		1		
249			1			4				5										5								5							
250						1				1											1							1							
251						1				1							1										1								
252						1				1											1							1							
253						1				1										1								1							
254	10				1	6		13		9	5	12	1	3			9	6	15												12	18			
255						7				7										7								7							

Table 3. (5 pages). Sighting histories of identified gray whales. Only identifications after 1 June of 1998 to 2003 inlcuded.

	Organization									Year						Month						Regions													
ID	BG	CERF	CRC	HSU	JD	NMML	OTH	UVIC	VD	###	###	###	###	###	###	6	7	8	9	10	11	CA	NCA	SOR	OR	GH+	NWA	SJF	PS-H	NPS	SVI	WVI	NBC	SEAI	KAK
256			1							1											1													1	
257			1							1											1													1	
258			1							1										1									1						
259			2							2											2								2						
260			1							1											1								1						
261			1					1		1				1				1			1											1		1	
267			2							2										1	1							2							
268			2							2										1	1							2							
272						1				1								1									1								
274			1	1						1	1							1		1			2												
275			5	13						5		7	1	5		1	4	4	2	7			18												
276			1	1						1	1						1			1			2												
277			4			1				4		1						1		4			4									1			
278			3	4						1			2	2	2	3			2	2			5	2											
279			1							1										1			1												
280			7							3				3	1				2	4	1		4	3											
281	9	6	5	1		5		3	1		9	8	9	3	1	5	10	8	5	2				4	2						9	8	7		
284				6								5	1				3		1	2			6												
286	1		4	8	1			1		2		1	10	2			6	5		4			8		4						1	2			
289				6								1	4	1			1		3	2			6												
290				1						1							1						1												
291	6		5	9		2		2		2	2	1	3	6	10	7	4	2	2	8	1		10	1	3			2			6	2			
292				1						1								1					1												
293			1							1								1							1										
294				1						1										1			1												
295	2		5	1				3		7			1	1	2			8	1	1	1		2	1	3						2	3			
296	33		12	2		8		2		11	5	3	2	24	12		11	37	4	4	1		1		11		8				33	4			
297			7	2		1				2	2		4	1	1		1	5	1	3			1	1	7		1								
298				2						2								2							2										
300	40		2	1	2	4		19		22	4	39			3	7	28	20	12	1					2						43	23			
301	13		7	5		1		2		3	3	9	3	1	9	5	6	9	7	1			2	2	8						13	3			
302	14	2	4	5		1		1		4	4	1		4	14	2	7	15	3						9						14	2	2		
303	8		7	1				1		2	2		4	1	8			14	3						8						8	1			
304						3				3									2	1							3								
306	4	12			2	2		6	1	4	2	3	15	1	2	1	9	14	3												5	9	13		
307								2		2						1	1															2			
308		20	5		1	4		6	1	3	3	6	13	12			12	19	6													11	26		
309	3	1	1	1		1		2		1	2			5	1	3	3	2	1				1		1						3	3	1		
310				1				3		3	1					2	1	1					1									3			
311	8		2		1	3		19		10	2	4	3	3	11	1	11	16	1	2	2		3								8	22			
312	2				1			2		4			1			2	3														2	3			
314	1	52	2					5	1	9	14	12	9	15	2	2	17	36	6												1	5	55		
315	2	75			3	1		4	3	22	14	24	24	4		5	39	35	9												3	6	79		
316					2	2		5		7					2		4	5														7			2
317	22				2	1		63		33	25	5	12	2	11	17	42	26	2	1											22	66			
318								1		1								1														1			
319	8					7		5		2		2	13	2	1	2	9	6	2	1							5				10	5			
320	21	41	2		2	2		64		16	50	23	17	13	13	27	56	43	6												21	68	43		
321		1						5		6						2	2	1	1													5	1		
322	2	14						5		11		9		1			12	5	2	2											2	5	14		
323		25	2					1		12				4	12		14	14														1	27		
324		62							1	14	21	16		8	4	5	23	25	10														63		
325		36								9			13	10	4		13	15	8														36		
326		24					1		1	4	22						8	14	4														26		
327		14	3					4		1		6	11		3		4	15	2													4	17		
328		44	2			3		1		2	4	2	12	15	15		18	20	12													4	46		
329	3	13								1			14	1			5	11													3		13		
330		17								2				15			4	9	4														17		
351						2					2							2														2			
355						1					1						1											1							
356			1								1									1					1										
357			1								1						1												1						
358			1								1						1												1						
359			1								1					1													1						
360			4								4					4													4						
361				2							2						1	1					2												
362				1							1							1					1												
363			1	2							3							2		1			3												
364			6								1	2		3				3		3				3	3										
365			6	6							1	1	3	4	3	1	2		5	2	2		9	3											
366			3					1			1		1	2			1	1		2				1	2							1			
368	2		3								1		1	3		3	1	1						1		2					2				
372	18	3		2		7		1			21	4		1	5	1	17	7	1	5					2		3				22	1	3		
373				2							2						2								2										
374				2							2							2					1		1										
375				2							2						2						2												
376				1							1								1						1										
377				6							6						6						6												
378				2							2						2						2												
379				4							4						4						4												
380				3							3						3						3												
382						3		7			10					3	1	4	2													10			
384						2					2							2														2			
385						2					2							2														2			
392	2		1	5		5		6			10		5	1	3	3	10	6					5	1			1				2	10			
393						2					2							2														2			
396	33		1			12		2			1	4	17	4	22	10	13	19	4	2							8	1	1	1	35	2			
397			1								1					1													1						
399			10								10					10													10						
407				1							1						1						1												
408				1							1									1					1										
410			2								2								2			2													
411			1	15							1	3	8	4		3	4	1	3	5			16												
412				2							2						1	1					2												
419				1							1								1						1										
424						1					1							1														1			
427						1					1							1														1			
428				1							1						1						1												

Table 3. (5 pages). Sighting histories of identified gray whales. Only identifications after 1 June of 1998 to 2003 inlcuded.

	Organization									Year						Month						Regions													
ID	BG	CERF	CRC	HSU	JD	NMML	OTH	UVIC	VD	###	###	###	###	###	###	6	7	8	9	10	11	CA	NCA	SOR	OR	GH+	NWA	SJF	PS-H	NPS	SVI	WVI	NBC	SEAI	KAK
429				4							4							3		1			3		1										
432				1							1						1						1												
433						1					1							1														1			
434						1					1							1														1			
438			4								4					4													4						
439				2							2						2						2												
440				2							2						2						2												
444				3							3						3						3												
448				5							5						5						5												
449				2							2						2						2												
450				1							1							1					1												
451						3		2			1	4					1	2	2													5			
460				1							1								1						1										
464				8								2		6		1	2	3		2			8												
468				2							2							2					2												
470				1							1							1					1												
471				1							1						1						1												
474				1							1						1						1												
476				2							2						2						2												
477						1					1							1														1			
478				1							1						1						1												
480						1					1								1													1			
483						1					1							1														1			
485						2					2							2														2			
489				2							2							1		1			1		1										
490						1					1							1														1			
492								1				1						1														1			
496								2				2					1	1														2			
501						1						1				1														1					
502						2						2							2													2			
503			1									1							1						1										
505						1						1				1														1					
506						1		1				2						1	1													2			
507	19		1			2			1			17	6				4	8	10	1							2				21				
508			2			4						6						1	1	4					1			5							
509						1						1				1														1					
510	9		6			5						2	1	11	6		1	11	6	2				6			5				9				
511	1					1		2				4					2	2													1	3			
514						1						1						1														1			
515	29					3		2				28	4	2		2	9	14	9								2	1			29	2			
516			1			3						4					1			3								4							
518						1						1						1														1			
519			1									1				1															1				
525	1				1	2						1	2	1			1		2	1											1	3			
527			1									1						1													1				
528						1						1						1														1			
529	40		1		2	3		5			5	35	11			8	17	13	11	2											43	8			
532	23				1	2		1				20	1	4	2		5	15	6	1							2				23	2			
536						1						1							1													1			
537			1	2								2			1				1	1	1		2	1											
538		7	4									4	3	4				8	3						4								7		
539						2						2				2														2					
542						2						1		1					2								1					1			
543						1						1				1														1					
546			1			1						2				1	1												1	1					
548			1									1					1												1						
551			2	1								1		2			1			2			1	2											
552				4								3		1			3		1				4												
553				1								1					1						1												
554			4	5								3	2	2	2	1	1			4	3		7	2											
555			5	7		1						6		4	3	1	5	3	1	1	2		9	4											
556				2								2					2						2												
557				3								3					1	2					3												
558				1								1					1						1												
559				2								2				2							2												
560				1								1				1							1												
561	11			2				3				2	2	3	9	2	7	5	2				2								11	3			
562			1	5								2		4		1	1	1	3				6												
563				1								1				1							1												
564				1								1					1						1												
565			2	1								1		2					2		1		1	2											
566				3		1						3		1			3	1					3												1
567	31		1			1		1					7	15	12	2	21	9		2							2				31	1			
569	13												13			4	4	5													13				
570	5					2							7			3	4														7				
571	4												4			2	2														4				
572	20				1	1		1				7	10	1	5	5	8	7	3												19	4			
573	4												4			3	1														4				
574	5					1							6			3	3														6				
575	1												1			1															1				
576	6					1							7			3	3		1								1				6				
577	22					1							14	9		7	5	11													23				
578	2												2			2															2				
580	1												1				1														1				
581	3												3			2	1														3				
582	1												1			1															1				
583	10				1			1					5	1	6	2	3		6	1											4	8			
584	3							1					3	1		2	2														3	1			
586	28												6	22		10	11	7													28				
587	6					2		3					8	3		3	6	1	1												8	3			
588	1												1			1															1				
589	1												1				1														1				
590	6												6			2	4														6				
591	2												2			1	1														2				
592	4					1							5			3	1		1								1				4				
593	3					1							4			1	3														4				
594	6	27	1						1		5	9	13	7	1	3	10	15	7												6		29		
595	1					2							3			3											2				1				

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	Organization									Year						Month						Regions													
ID	BG	CERF	CRC	HSU	JD	NMML	OTH	UVIC	VD	###	###	###	###	###	###	6	7	8	9	10	11	CA	NCA	SOR	OR	GH+	NWA	SJF	PS-H	NPS	SVI	WVI	NBC	SEAI	KAK
596	1					2		2					3	2		3	2										1				2	2			
597	2	34	2					1	1			18	20	1	1		12	22	6												2	1	37		
598	1					1							2				2														1	1			
599	2												2				1		1												2				
600	1												1				1														1				
601	2	4	1			1						1	2		5		4	3	1												2	1	5		
602						1							1			1											1								
603						2							2			1	1										2								
604	18					1							1		18	5	12	2									1				18				
605	11				1	10		2					11	11	2	1	5	11	3	2	2						7	3			11	3			
606					1	1							2				2															2			
607			1	1		2							2	2			1	2		1			1				3								
608						1							1						1								1								
610						3							3							1	2							3							
611	2			1	1								4				3			1			1								2	1			
612	2	47						6	2			22	18	7	10	2	24	25	6												2	6	49		
613	5							2					2	2	3		4	2	1												5	2			
614	1												1					1													1				
615	1			1									1	1					1	1			1								1				
617	1			2									3				2		1				2								1				
618	1												1						1												1				
619				3									3				1		1	1			3												
620	1				1								2				2														1	1			
621			1	6									7			1	6						7												
622				1									1							1			1												
623				2									2				2						2												
624			9										2	4	3	1			6	2				8	1										
625			4					2					4	2				4	1	1					4							2			
626			2										2			1		1							2										
628		31	3				1		1		1	14	16	3	2		10	20	6														35	1	
629		20	1										11	9	1		3	14	4														21		
634			1										1					1				1													
635	22		1										1		22	3	4	13	3			1									22				
637	1		2										2		1			3				2									1				
638			3	2									3		2	1	1	1	2				2	2	1										
639				1		2							1	2				2		1			1												2
640				2									2			1	1						2												
641	12			6		1							3	3	13	2	2	10	5				6				1				12				
642			1	3									3	1			1	1	1	1			3	1											
643			1	1		1		1					1	2	1				2	1	1		2									2			
644				3									2	1						3			3												
645				3									3				3						3												
646				1										1		1							1												
647			1										1				1					1													
648			2										2					2				2													
649					2								2						1	1												2			
651		46	1						3			21	24		5	1	13	30	6														50		
652		3											3				3																3		
653	9	9			1								3	8	8		6	6	7												9	1	9		
654			1											1						1				1											
655	9		1											1	9		4		5	1				1							9				
656			2											1	1				1	1				2											
657			3											2	1			1	2					3											
658			2											2					2					2											
659			2											2					2					2											
660			1											1						1				1											
661			1											1				1						1											
664			1											1				1					1												
665			3											1	2				3					3											
668			5											5					3	2				5											
669			5											3	2			1	2	2				5											
670			1	1										2		1				1			1	1											
671		25	1											9	17		17	5	4														26		
673			1												1			1															1		
674		2	6											5	3		4	4															8		
675		15	2											8	9	1	9	7															17		
676			3											3			2	1															3		
681	2							1						3			3														2	1			
682	25							1						4	22	5	6	10	5												22	4			
683	1							1						2			2														1	1			
684	4					1		1						5	1		4	2													4	1			1
685	4							1						5			4	1													4	1			
686	1							2						3			1	2													1	2			
687	1							1						2			2														1	1			
688	9		1					1						6	5		6	3	2					1							8	2			
689	1													1		1															1				
691	6					3								2	7	3	3	3													6				3
692	12					1								1	12	2	7	4										1			12				
694	4	19	3						2			12		12	4	2	6	14	6												4		24		
695	1													1				1													1				
696	9					10								3	16	2	5	2	8	2							3	7			9				
697	19													19		3	4	8	4												19				
698	10		2											4	8		6	3	3					2							10				
699	2			1										1	2	1	1	1					1								2				
700				1										1		1							1												
701				1										1				1					1												
702				3										3		2	1						3												
703				2										2				1	1				2												
704				1										1		1							1												
705				1										1		1							1												
706				2										2		2							2												
707				1										1		1							1												
708				1										1		1							1												
709	5			2										2	5	3	2	2					2								5				
710				5		1								6		3			2	1			6												
711				2										2		2							2												
712	7				1			1						2	7		1		7	1												9			
713								1						1					1													1			

Table 3. (5 pages). Sighting histories of identified gray whales. Only identifications after 1 June of 1998 to 2003 inlcuded.

	Organization									Year						Month						Regions													
ID	BG	CERF	CRC	HSU	JD	NMML	OTH	UVIC	VD	###	###	###	###	###	###	6	7	8	9	10	11	CA	NCA	SOR	OR	GH+	NWA	SJF	PS-H	NPS	SVI	WVI	NBC	SEAI	KAK
714								1						1			1															1			
715								1						1					1													1			
716								1	1			1		1			1	1														1	1		
717								1						1			1															1			
718	10	1						2					1	2	10	2	4	5	2												10	2	1		
719	10							1						1	10			9	2												10	1			
720	7					3		1						1	10		2	6	3									3			7	1			
721						1								1				1																	1
722						1								1				1																	1
723						3								3				3																	3
724						2								2				2																	2
725						1								1				1																	1
726						1								1				1																	1
727						1								1				1																	1
728						1								1				1																	1
729						3								3				3																	3
730						1								1				1																	1
731						2								2				2																	2
732						1								1				1																	1
733						1								1				1																	1
734						3								3				3																	3
735						1								1				1																	1
736						1								1				1																	1
737						1								1				1																	1
738						1								1				1																	1
739						1								1				1																	1
740						1								1				1																	1
741						2								2				2																	2
742						1								1				1																	1
743						2								2				2																	2
744						1								1				1																	1
745						1								1				1																	1
746						1								1				1																	1
747						2								2				2																	2
748						1								1				1																	1
749						1								1				1																	1
750						2								2				2																	2
751						1								1				1																	1
752						2								2				2																	2
753						1								1				1																	1
754						1								1				1																	1
755						1								1				1																	1
756						2								2				2																	2
757						2								2				2																	2
758						2								2				2																	2
759		24												15	9		8	10	6														24		
760		15	1											7	9		7	5	4														16		
761		19	1											12	8		7	8	5														20		
762		13	1						1		3			9	3		2	6	7														15		
763		11							2			12			1			12	1														13		
764		13										13						7	6														13		
766									1			1							1										1						
767	1										1								1												1				
768	21										21					1	8	11	1												21				
769									1		1							1															1		
772									1		1					1																		1	
773	4										4						1	2	1												4				
776	1											1				1															1				
777	2											2				2															2				
781			1												1				1					1											
782						8									8		2	5		1							3	5							
783						3									3		3										3								
784						1									1			1																	1
785	2					2									4	1		1	2								1	1			2				
786	11														11	1	2	3	5												11				
787	6														6	1	2	3													6				
788	11					1									12	2		8	1	1							1				11				
789	6														6	1	2	2	1												6				
790	11														11	1	2	7	1												11				
791	7														7			2	5												5	2			
792	11														11		5	4	2												11				
793	2														2	2															2				
794	2														2			2													2				
795	5														5	1	3	1													5				
796	3														3		2	1													3				
797	1														1		1														1				
800		7													7	1	5	1															7		
801		8													8		8																8		
802		1													1		1																1		
803		1													1			1															1		
804							1						1					1																1	
805								1			1						1															1			
806								1			1						1															1			
807								1			1					1																1			
808								1			1							1														1			

Table 4. Gray whales seen in more than one region or year by month and region.

	1998-2003 all seasons			1998-2003 after 1 June		
	IDs	**Seen >1yr**	**Seen >1 region**	**IDs**	**Seen >1yr**	**Seen >1 region**
Month						
March	22	14 (64%)	7 (32%)			
April	67	26 (39%)	17 (25%)			
May	142	43 (30%)	41 (29%)			
June	191	124 (65%)	123 (64%)	191	120 (63%)	119 (62%)
July	274	176 (64%)	169 (62%)	274	176 (64%)	165 (60%)
August	294	180 (61%)	169 (57%)	294	179 (61%)	164 (56%)
September	206	163 (79%)	147 (71%)	206	163 (79%)	145 (70%)
October	130	101 (78%)	97 (75%)	130	100 (77%)	96 (74%)
November	33	23 (70%)	22 (67%)	33	23 (70%)	22 (67%)
Region						
Central and S California	6	2 (33%)	2 (33%)	6	2 (33%)	2 (33%)
N California	121	58 (48%)	54 (45%)	120	58 (48%)	53 (44%)
S Oregon	57	49 (86%)	46 (81%)	57	49 (86%)	46 (81%)
Central Oregon	55	42 (76%)	46 (84%)	55	41 (75%)	45 (82%)
Grays Harbor area	35	11 (31%)	6 (17%)	2	2 (100%)	2 (100%)
N Washington coast	113	53 (47%)	60 (53%)	63	49 (78%)	56 (89%)
Str of Juan de Fuca	35	18 (51%)	22 (63%)	31	16 (52%)	19 (61%)
Other WA inside	25	3 (12%)	6 (24%)	14	1 (7%)	2 (14%)
N Puget Sound	42	11 (26%)	8 (19%)	10	1 (10%)	2 (20%)
S Vancouver Is.	201	132 (66%)	149 (74%)	192	132 (69%)	148 (77%)
W Vancouver Is.	169	122 (72%)	133 (79%)	169	122 (72%)	132 (78%)
N British Columbia	82	72 (88%)	57 (70%)	82	72 (88%)	56 (68%)
SE Alaska	10	6 (60%)	5 (50%)	10	6 (60%)	5 (50%)
Kodiak, Alaska	46	8 (17%)	8 (17%)	46	7 (15%)	7 (15%)

Table 5. Sumnary of inter-regional matches of whales among regions. Matrix shows number of different whales that have been identified in both regions sometime between 1998 and 2003.

Region	**IDs**	**CA**	**NCA**	**SOR**	**OR**	**GH+**	**NWA**	**SJF**	**PS-H(**	**NPS**	**SVI**	**WVI**	**NBC**	**SEAK**	**KAK**
All seasons															
Central and S Californi	6														
N California	121	0													
S Oregon	57	0	24												
Central Oregon	55	0	20	22											
Grays Harbor area	35	0	2	3	2										
N Washington coast	113	0	13	16	17	1									
Str of Juan de Fuca	35	0	3	2	3	0	9								
Other WA inside	25	0	0	0	0	0	1	1							
N Puget Sound	42	0	0	0	1	1	1	1	6						
S Vancouver Is.	201	2	29	27	31	1	53	18	1	1					
W Vancouver Is.	169	0	23	19	29	1	39	14	2	2	113				
N British Columbia	82	0	3	5	10	0	14	5	0	0	48	43			
SE Alaska	10	0	1	1	0	0	1	1	0	0	4	4	3		
Kodiak, Alaska	47	0	2	0	0	1	0	0	0	0	4	4	0	0	
Only identifications taken after 1 June of each year															
Central and S Californi	6														
N California	120	0													
S Oregon	57	0	24												
Central Oregon	55	0	20	22											
Grays Harbor area	2	0	0	2	1										
N Washington coast	63	0	13	16	15	1									
Str of Juan de Fuca	31	0	3	2	3	0	9								
Other WA inside	14	0	0	0	0	0	1	1							
N Puget Sound	10	0	0	0	0	0	1	1	2						
S Vancouver Is.	192	2	29	27	31	1	50	16	1	1					
W Vancouver Is.	169	0	23	19	29	1	35	13	1	1	113				
N British Columbia	82	0	3	5	9	0	12	4	0	0	48	43			
SE Alaska	10	0	1	1	0	0	1	1	0	0	4	4	3		
Kodiak, Alaska	47	0	2	0	0	0	0	0	0	0	4	4	0	0	

Table 6. Model selection results of analysis of within year, between year and overall interchange between NWA and the other 5 regions.

Analysis	**Model**	**# of parameters**	**AIC**
Within-year interchange	Region + Year + #Years seen	11	705.7
	Region + Effort + #Years seen	7	706.7
	Region + Effort	6	707.5
	Region + Year	10	707.6
	Region*Year + #Years seen	31	718.2
	Region	5	730.4
Between-year interchange	Region + Year + #Years seen	11	1179.1
	Region + #Years seen	6	1187.0
	Region*Year + #Years seen	31	1205.5
	Region	5	1248.6
	Year	6	1275.0
Overall interchange	Region + Year + #Years seen	11	1179.1
	Region + #Years seen	6	1187.0
	Region*Year + #Years seen	31	1205.5
	Region	5	1248.6
	Year	6	1275.0

Table 7. Petersen capture-recapture abundance estimates for seasonal res
gray whales. Excludes identifications made before 1 June and those from
Sound area.

Sample 1		**Sample 2**				
Year	**n**	**Year**	**n**	**Match**	**Est.**	**CV**
Identifications from N California to SE Alaska						
1998	133	1999	157	80	**260**	0.05
1999	157	2000	140	74	**296**	0.06
2000	140	2001	175	92	**266**	0.04
2001	175	2002	206	121	**298**	0.03
2002	206	2003	160	126	**261**	0.03
Identifications from Oregon to Northern British Columbia only						
1998	115	1999	120	70	**197**	0.05
1999	120	2000	115	66	**208**	0.05
2000	115	2001	151	83	**209**	0.04
2001	151	2002	180	106	**256**	0.03
2002	180	2003	157	119	**237**	0.03

Table 8. Model selection results for open population models fitted to PCFA (N. CA to N. British Columbia) capture history data. Survival for newly seen whales represents survival (and permanent emigration) for the year immediately following their first encounter. It varied by year (t) for all models while some models also included MRT. Survival for previously seen whales was either constant or varied by year (t). Capture probability models with variation by year and MRT in the previous year were considered.

	Survival		Capture Probability	# par	ΔAICc
	Newly seen	Previously seen			
1	t + MRT	T	t + MRT	16	0
2	t + MRT	Constant	t + MRT	13	1.8
3	t + MRT	T	MRT	12	8.5
4	t + MRT	Constant	MRT	9	16.5
5	MRT	Constant	t + MRT	9	43.9
6	t + MRT	Constant	t	12	66.7
7	t	Constant	t+MRT	12	107.3
8	t	Constant	t	11	133.8

Table 9. Model selection results for open population models fitted to ORSVI capture history data. Model numbers in correspond to ordering of models in PCFA analysis (Table 8). The same models were considered in both analyses.

	Survival		Capture Probability	# par	ΔAICc
	Newly seen	Previously seen			
2	t + MRT	Constant	t + MRT	13	0
1	t + MRT	T	t + MRT	16	1.4
3	t + MRT	T	MRT	12	8.6
4	t + MRT	Constant	MRT	9	11.9
5	MRT	Constant	t + MRT	9	14.0
6	t + MRT	Constant	t	12	19.2
7	t	Constant	t+MRT	12	45.3
8	t	Constant	t	11	57.7

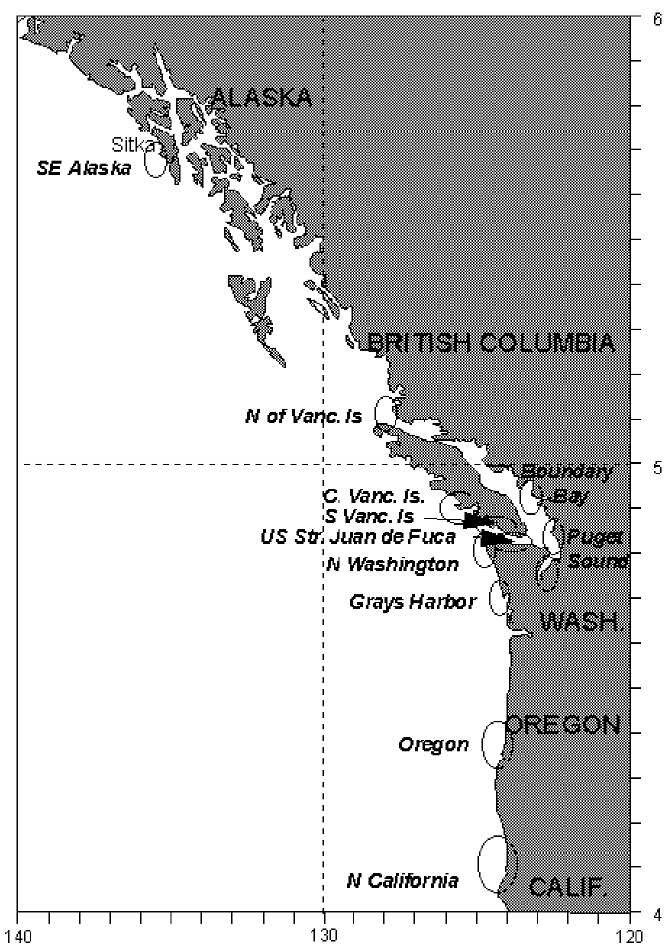

Figure 1. Study areas with principal areas of effort shown by circles.

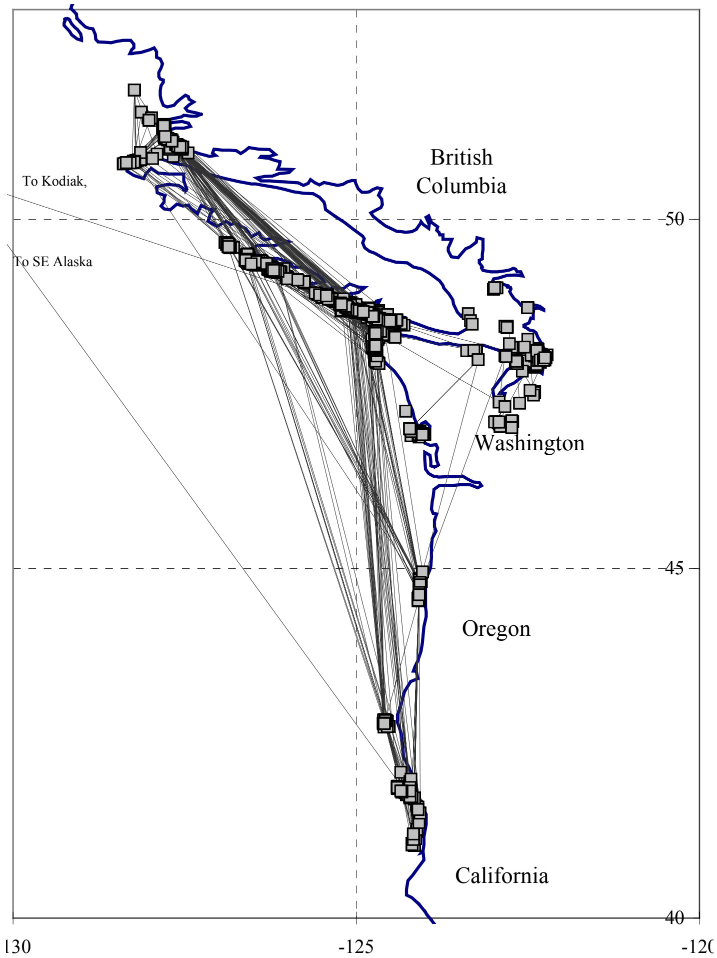

Figure 2. Locations whales were identified in the central study area. Lines connect re-sightings of whales within a year.

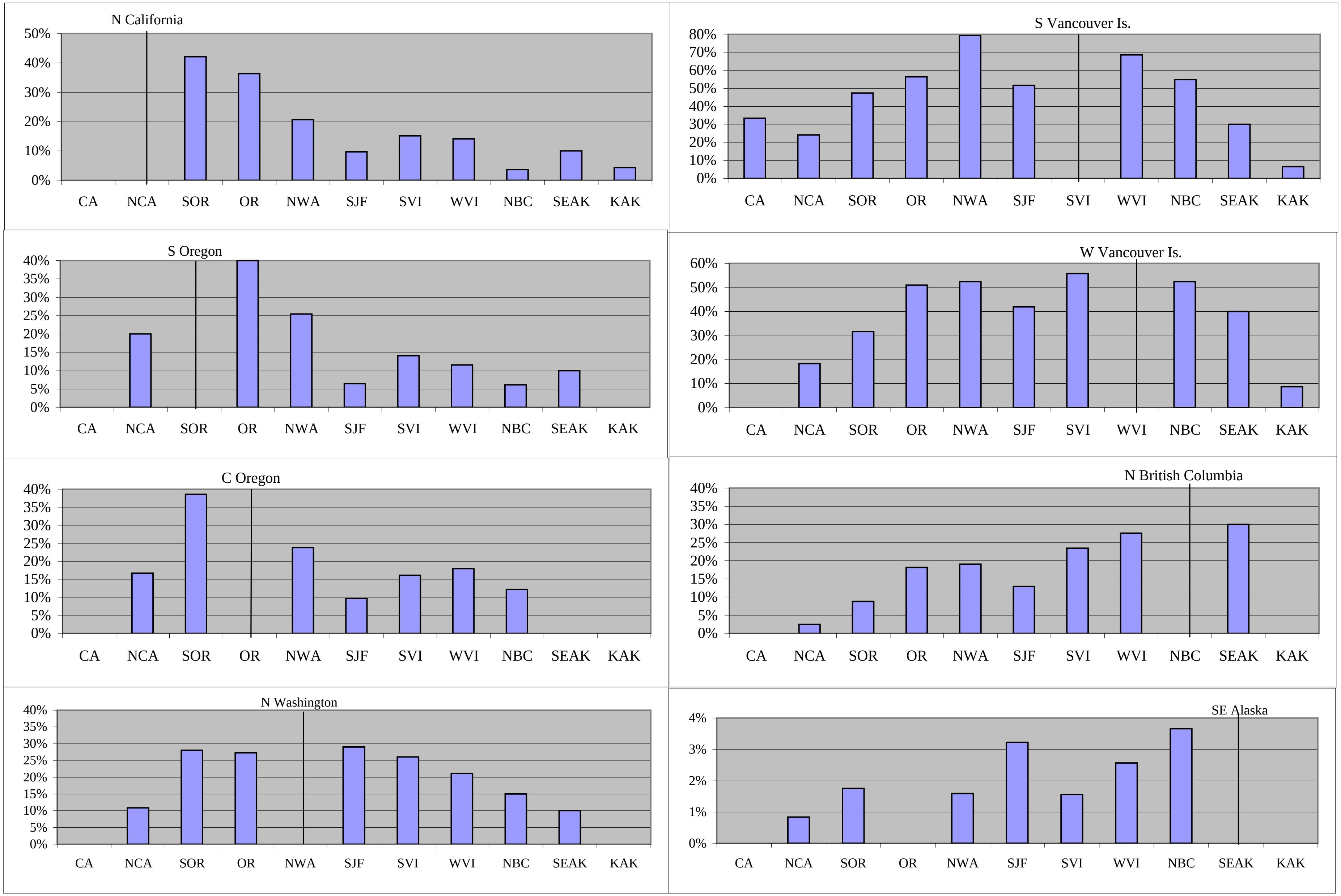

Figure 3. Percent of identified gray whales seen in different regions that match area marked for 1998 to 2003.

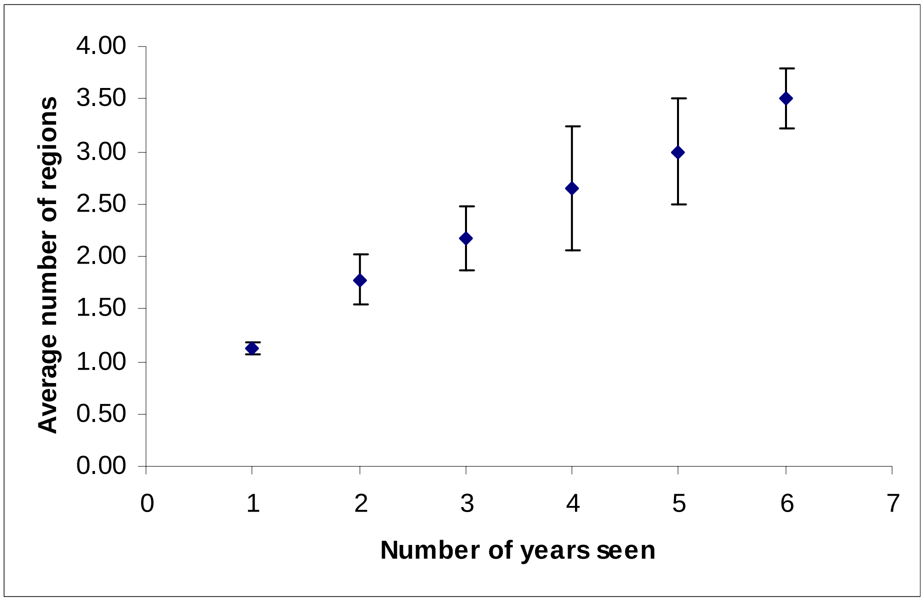

Figure 4. The average number of regions (among the six) in which a whale was seen increases for each year it was seen. Error bars are 95% confidence intervals for means.

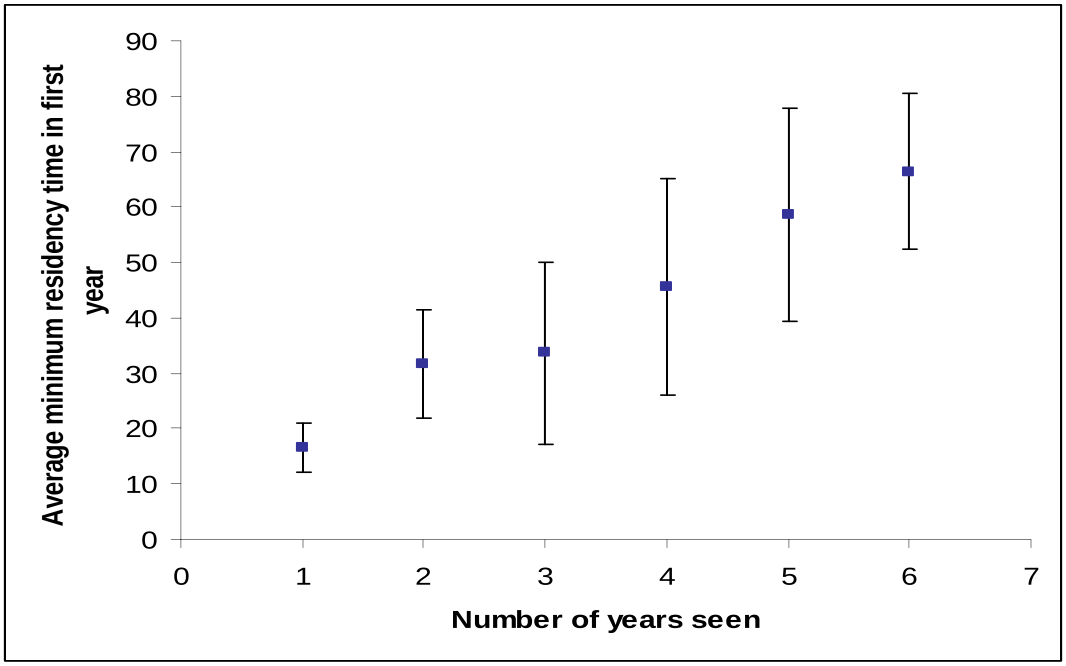

Figure 5. Relationship between number of years seen and the minimum residency time in the first year the whale was seen. Error bars are 95% confidence intervals for means.

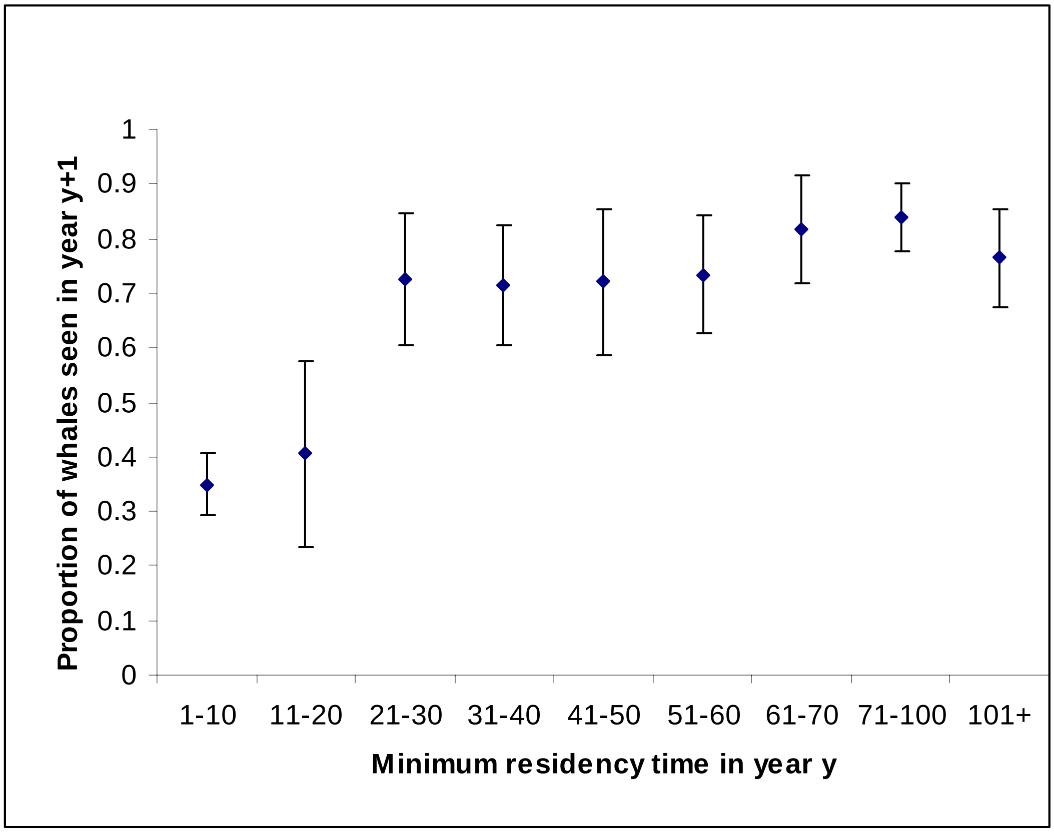

Figure 6. Relationship between minimum residency time in year *y* and the proportion of whales seen in year *y* +1. Error bars are 95% confidence interval based on normal approximation to binomial.

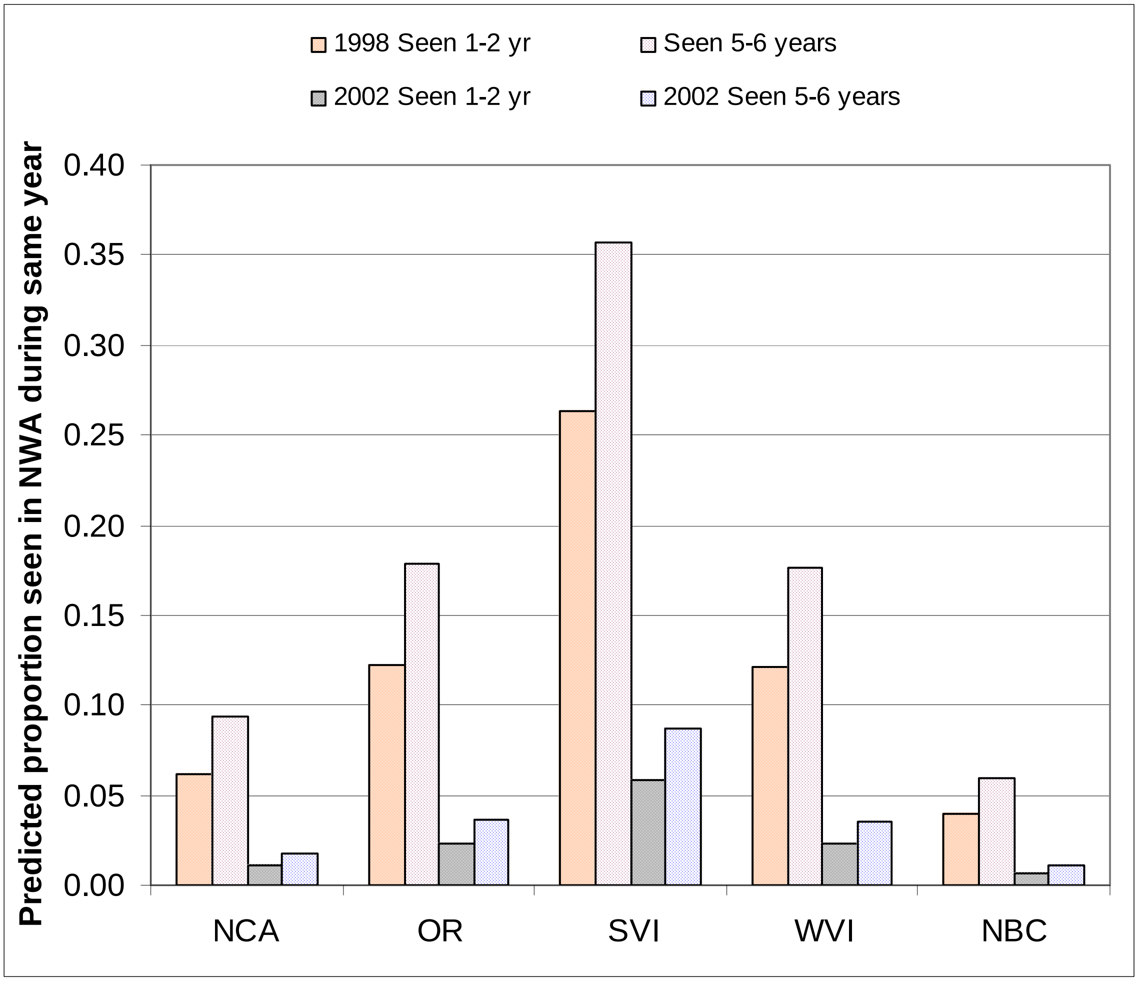

Figure 7. Predicted proportions of within-year interchange with NWA for the highest (1998 - most effort) and lowest (2002 - least effort) years and for whales seen 1-2 years and 5-6 years.

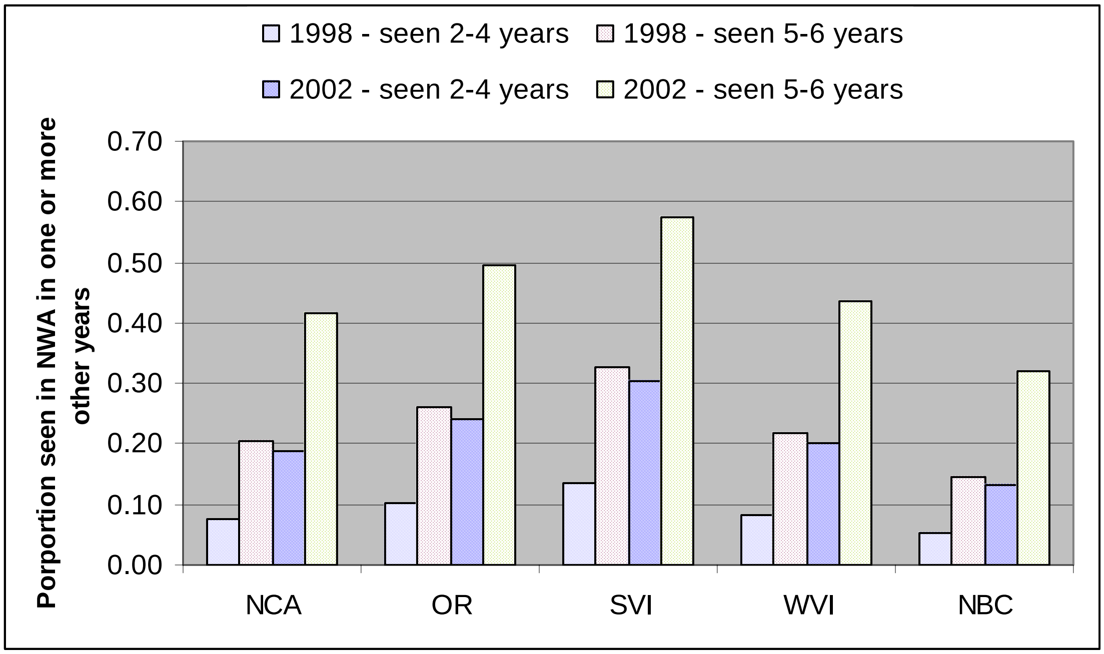

Figure 8. Predicted proportions of between-year interchange with NWA for the highest (2002) and lowest (1998) years and for whales seen 2-4 years and 5-6 years.

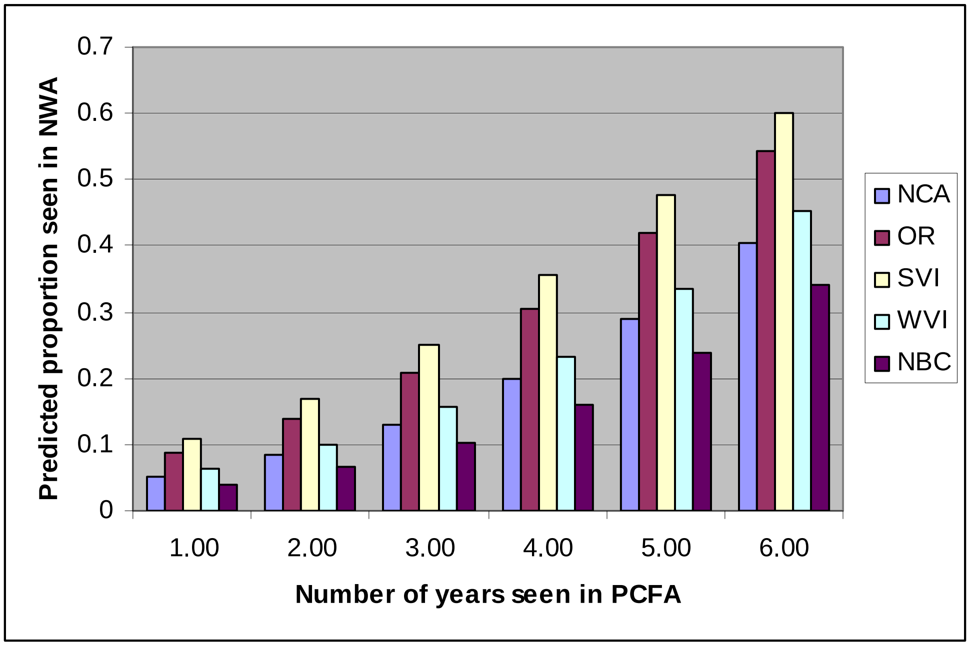

Figure 9. Predicted proportions of overall interchange with NWA for each region and number of years seen.

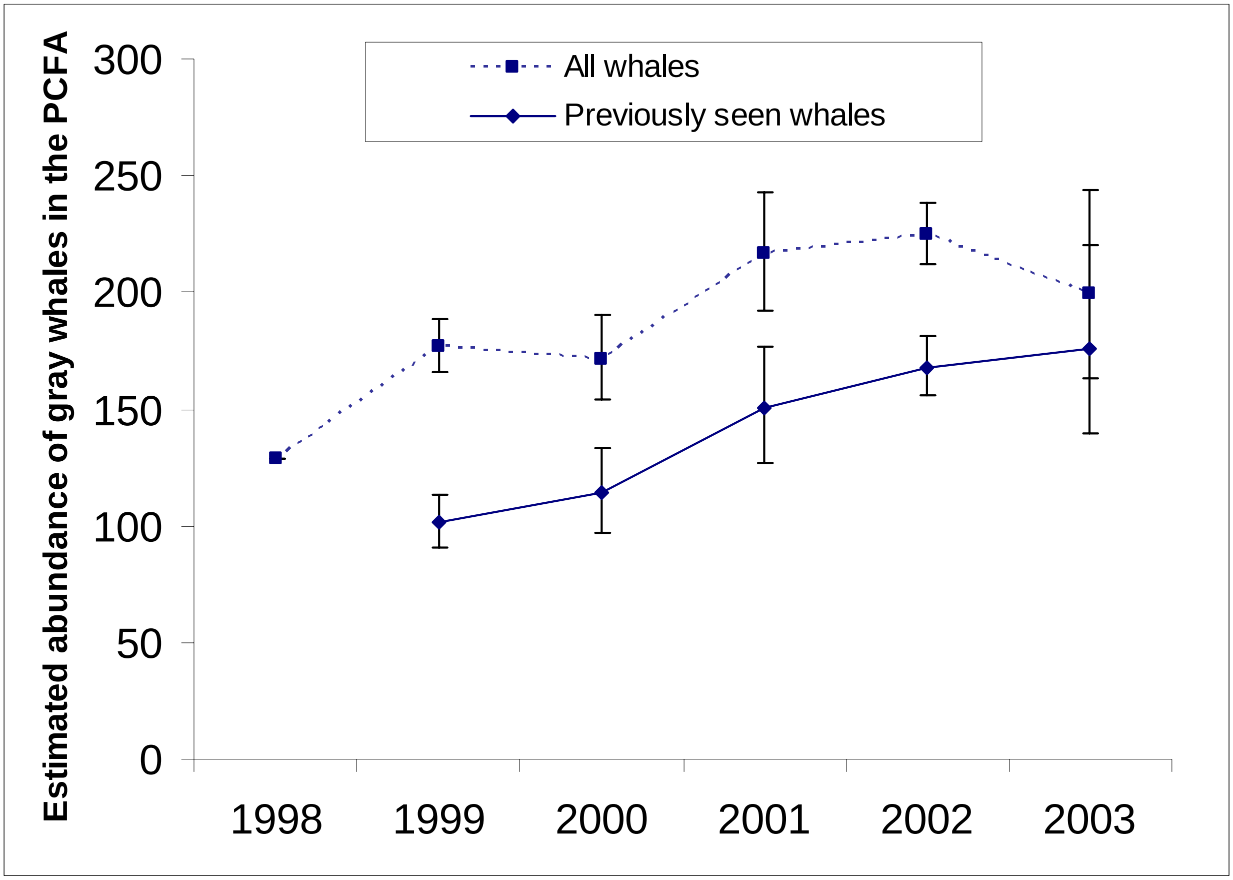

Figure 10. Estimated annual abundance of all whales in the PCFA and returning whales in the PCFA (log-normal 95% confidence intervals shown).

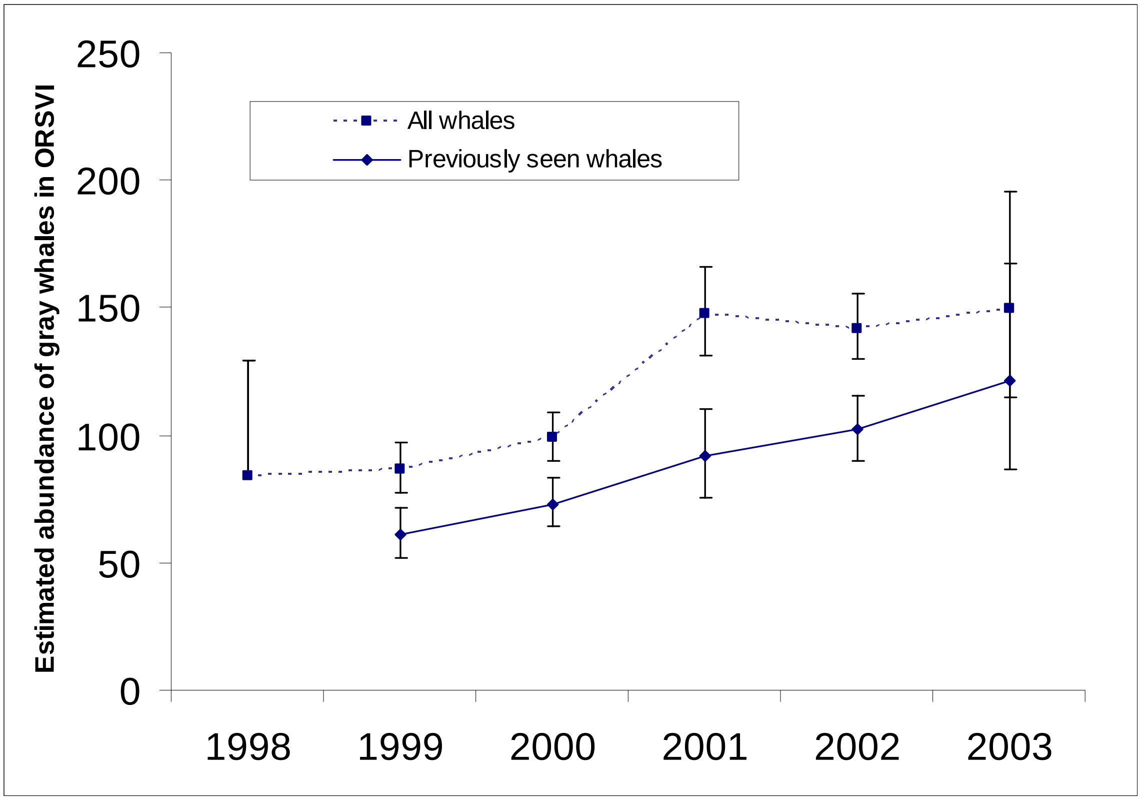

Figure 11. Estimated annual abundance of all whales in ORSVI and returning whales in ORSVI (log-normal 95% confidence intervals shown).

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GRAY WHALE (*ESCHRICHTIUS ROBUSTUS*) HABITAT UTILIZATION AND PREY SPECIES OFF VANCOUVER ISLAND, B.C.

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ABSTRACT

Habitat utilization and prey species of Vancouver Island gray whales were investigated by (1) summarizing 26 yr of distribution and feeding data and (2) conducting intensive observations in Clayoquot Sound, Vancouver Island, from 1989 to 1996. Whale distribution and movements were monitored from March to November through systematic boat surveys and whale-watch sighting programs. Prey species were collected by suction hose and plankton net or determined through analysis of fecal samples. Gray whales utilized virtually all of the southern west coast of Vancouver Island over the 26-yr observation period. Distribution, prey species, and feeding behavior showed marked variability during any one season and between years. Some feeding areas were used on an annual basis, others with >10-yr intervals between use. Feeding occurred in shallow sand or mud bays, eel grass beds, kelp beds, in the open water column, and at the surface. Young whales appeared to utilize habitat and prey species differently than adults. Main prey species included herring eggs/larvae (*Clupea harengus pallasi*), crab larvae (*Cancer magister* megalops, *Pachycheles* spp. zoea), mysids (*Holmesimysis sculpta, Neomysis rayii, Acanthomysis* spp.), amphipods (*Ampelisca* spp., *Atylus borealis*), and ghost shrimp (*Callianassa californiensis*). The definition and relative importance of specific feeding grounds and the study of human impacts on this population are complicated by its broad and variable use of habitat and prey species.

Key words: gray whale, *Eschrichtius robustus*, prey, feeding patterns, habitat, Vancouver Island, oil.

The majority of eastern Pacific gray whales (*Eschrichtius robustus*) migrate annually between winter breeding grounds along the Mexican coast and summer feeding grounds in the Bering and Chuckchi Seas (Scammon 1869, Pike

1962, Rice and Wolman 1971, Rugh 1984). Small populations of gray whales inhabit portions of the North American coast from California to Alaska during the summer (Gilmore 1960*a,b*, Pike 1962, Pike and MacAskie 1969, Rice and Wolman 1971, Darling 1984, Nerini 1984, Calambokidis *et al.* 1991). A gray whale population occupying a summer range along the west coast of Vancouver Island, British Columbia, has been studied since the early 1970s (*e.g.*, Hatler and Darling 1974; Darling 1978, 1984; Oliver *et al.* 1984; Guerrero 1989; Duffus 1996).

The Vancouver Island gray whale population consists of 35–50 whales which occupy the region for 8–9 mo between northern and southern migrations, the period from approximately March to December. During the summer they range and feed over a distance at least the length of the central Vancouver Island coastline. Between the 1970s and the present, a number of individually identified whales returned to this location each year, suggesting that the area may be a "home summer range" of a specific group of animals. Adults were typically identified over multiple years, and small, very young whales were usually present for 1–2 seasons only (Darling 1984).

Several authors have described gray whale feeding behavior off Vancouver Island. They documented benthic feeding on amphipods, ghost shrimp, and possibly polychaete worms (Hatler and Darling 1974, Darling 1978, Oliver *et al.* 1984, Plewes *et al.* 1984, Kvitek and Oliver 1986) and planktonic feeding on mysids (Murison *et al.* 1984, Guerrero 1989). Collectively, these observations indicate gray whales exploit several types of prey off Vancouver Island.

In December 1988 the Nestucca oil spill resulted in substantial amounts of oil being deposited in gray whale feeding grounds off Vancouver Island (Canadian Coast Guard 1989).[1] In the follow-up assessment, JDD was asked by the Department of Fisheries and Oceans to investigate the impact of the spill on the gray whales feeding in the area. Limited knowledge about the patterns of utilization of feeding grounds and specific prey species obscured our understanding of the impacts of the spill. Such information is key to our ability to determine the impacts of human activity or natural phenomena on the whales. The purpose of this study was to document patterns of habitat and prey utilization by gray whales in the Clayoquot Sound region of Vancouver Island.

METHODS

Study Area

Vancouver Island (Fig. 1) is a 480-km long island approximately half-way between gray whale breeding areas in Mexico and northern feeding grounds.

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[1] The spill of 875,000 liters of Number 6 Fuel Oil occurred off Oregon on 28 December 1988, and currents brought oil to Vancouver Island within a few days. Substantial amounts of oil washed onto beaches in gray whale feeding grounds. The majority of gray whales were on their winter migration south of Vancouver Island at the time of the spill.

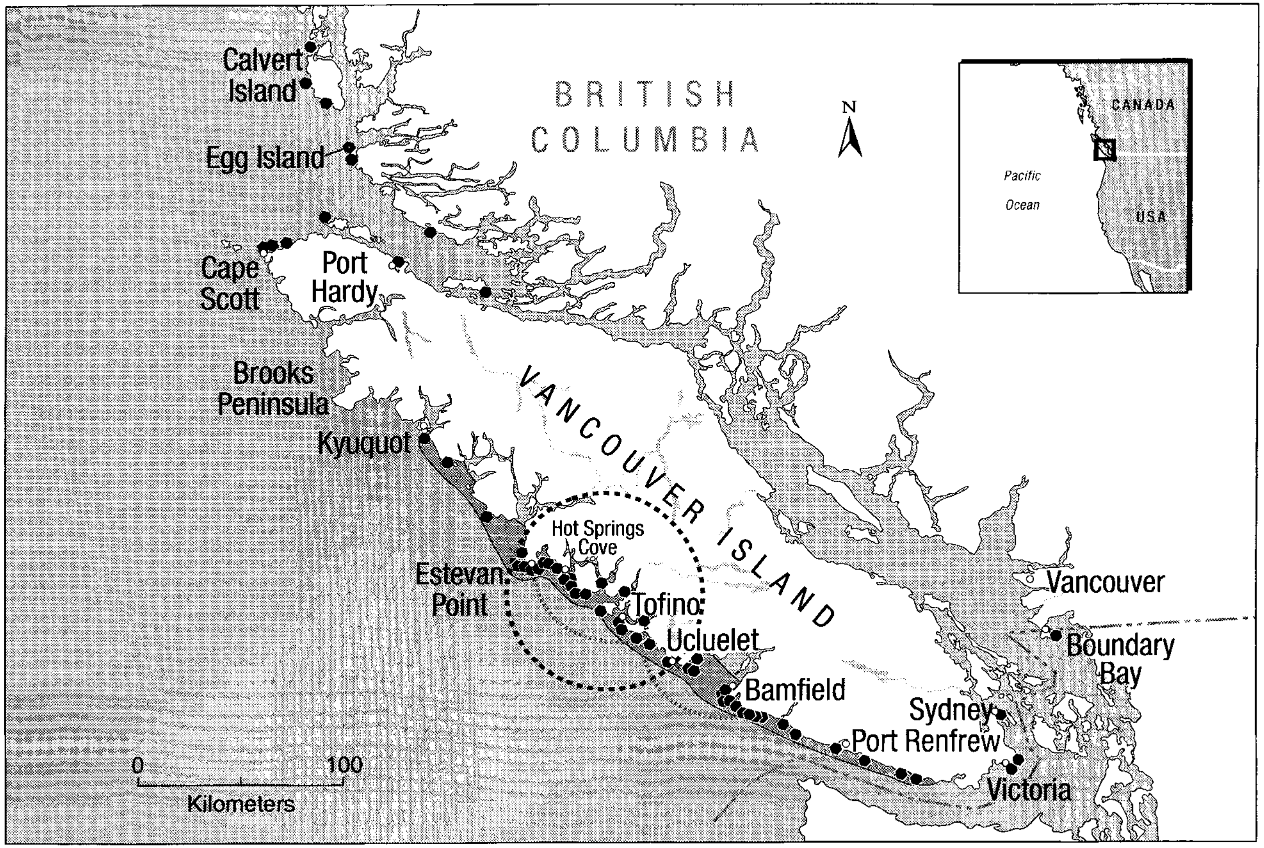


Figure 1. Vancouver Island, study area, and locations of feeding whales, 1971–1996. Primary study area indicated by circle. Dotted lines joining locations indicate actual movements of individuals within one summer and show study area smaller than summer range (Darling 1984).

Between 1971 and 1996, gray whale observations were conducted on the coasts of Vancouver Island between Victoria and Cape Scott and in waters northward on the British Columbia mainland coast. Most of the observations occurred along the 225-km central–southwest coast of Vancouver Island, with the primary study area in the Clayoquot Sound region, extending approximately 80 km from Wickaninnish Bay in the southeast to Estevan Point in the northwest (Fig. 1). Our primary study area is only a portion of the overall summer range of the Vancouver Island population (Darling 1984). This coastline is characterized by open, shallow, sandy bays with surf-swept beaches separated by rocky headlands, coastal islands creating protected inside waterways, and extensive fjords reaching up to 30 km inland.

Vancouver Island and Adjacent B.C Coast Sightings

Sightings were collected along the Vancouver Island and mainland British Columbia coast by JDD and other knowledgeable observers over the 26-yr period, 1971–1996 (Fig. 1). These were recorded in a series of field notebooks, and some have been previously published (Hatler and Darling 1974, Darling 1984).

Clayoquot Sound Observations

The majority of observations that focused on habitat use and prey species were made during an eight-year period from 1989 to 1996. Some of the observations presented originated from earlier work in the region by JDD. Habitat use information was gathered using both research surveys and whale-watch sighting programs. The research effort included systematic small-craft surveys of the study area at least weekly from May through October each year, 1992–1996. Additional surveys were conducted in March–April and November each year as weather allowed. Presence and absence of whales on known feeding grounds were documented. All whales were individually identified by photographs of natural markings on their sides (Darling 1984) and locations, behavior, and associates noted. Photoidentified whales were compared to those in an identification catalog developed over the last 20 yr for sighting histories. Changes in location and habitat use by whales were monitored through these surveys and from the daily whale-watch effort in the region.

Whale watching is a significant industry in the study area and provided an opportunity for an intensive documentation of whale distribution between early March and late October each year. Whale-watch boats searched for whales on a minimum of 175 d between these dates each year, leading to a total of over 1,400 d of observation, 1989–1996. Six–12 boats and one to three planes were involved on any one day, operating from dawn to dusk. A specific marine radio channel allowed all interested to be party to all sightings. Beginning in 1989, whale-watch boats were asked by JDD to record whale sightings. Forms with maps of the region were provided, and boat operators were asked to record trip time, locations, and whale activity (feeding, resting, traveling, rubbing). The majority of the boat operators had at least five years' experience with the whales and were proficient at determining behavior mode. Daily contact between whale-watch operators and researchers conveyed current whale activity, and boat operators contacted a researcher if unusual events occurred. The whale-watch activity amounted to an enormous sighting effort that was difficult to quantify due to variable participation and experience of specific operators. However, we cannot overemphasize the ongoing intensity of this effort, and we are convinced most whale activity in daylight hours in the region was recorded through this program.

The study effort for the years 1992–1996 was nested, with prey collections occurring within regular distribution and abundance surveys occurring within the ongoing whale-watching effort. Combined, these provided an accurate overview of activity in the area.

Prey Collection and Identification

In each feeding location the prey species was determined by collections, or, if needed, fecal analysis. Benthic samples were collected with a suction hose and fine-mesh net. A diver held the collection hose (PVC pipe) on the bottom in the close vicinity of feeding whales and, through use of a scuba tank to create a vacuum, suctioned the sediment/organism mixture into a fine-mesh net. Later, the predominant organisms were sorted and identified. When whales were feeding on deeper plankton or hyperbenthic organisms, collections were made using a plankton net with a cannonball weight attached to drop it to the bottom. It was towed within meters of feeding whales. Patches of prey were usually dense, and the net would often be filled beyond the collection cylinder within a few minutes of tow. When whales were feeding on the surface, the plankton net was used without the weight. If these techniques failed to catch organisms in quantities clearly indicating the prey species, the feces of the whales were collected and examined for body parts identifiable to species.

Once prey organisms were collected from a particular feeding event, the whales were monitored by researchers and whale-watch operators. Any change in behavior or feeding location warranted another collection of prey. Periodic collections were made whether whales had changed behavior or locations or not. This routine was followed throughout the May-November period, 1992–1996. In known benthic-feeding areas in which samples had been repeatedly taken over years (this study and others: *e.g.*, Kvitek and Oliver 1986), collections were made only to confirm prey species. It was presumed that when bottom feeding in these locations the whales were consuming benthic species known to inhabit the region.

Prey organisms were preserved in 5% formalin in seawater and identified by local identification keys such as Kozloff (1983) or by amphipod specialist E. Bousfield at the Royal British Columbia Provincial Museum.

RESULTS

HABITAT UTILIZATION

Vancouver Island and Adjacent B.C. Coast

Observations included both planktonic and benthic feeding activity (Fig. 1). Sightings ranged from Georgia Strait and Victoria on the southern tip of the island to Cape Scott in the north. Whales were also sighted feeding in the Inside Passage, between Vancouver Island and the mainland and along the B.C. mainland coast northwest of Vancouver Island. Research effort was considerably less over the northern half of the Vancouver Island west coast and the mainland coast; the fewer sightings in these regions compared to the southern Vancouver Island west coast, therefore, may reflect effort rather than habitat use. Gray whales occupied a variety of habitats when sighted, ranging from protected, shallow, mud-bottomed bays to exposed surf-swept bays and beaches, to stretches of sandstone shelf, or rugged rocky shoreline with extensive fringing kelp beds. Gray whales were not present in all locations each year, and some locations were more regularly occupied than others. However, the long-term records clearly indicate that virtually all of the central-southern outer Vancouver Island coastline was utilized by gray whales over the 26 yr.

Clayoquot Sound Region

Habitat types included feeding sites, divided into herring, benthic, and plankton feeding locations, and "rubbing" sites (Fig. 2). The whales made use of all of these locations and habitats over time, although not all locations were used each year. Some feeding areas were used regularly, and these are indicated as primary grounds; others were utilized irregularly, and these are shown as secondary feeding grounds (Fig. 2). Primary grounds were those where we observed feeding for at least some portion of the season in most years; secondary grounds included those in which several years separated periods of utilization. The status of sites could change from primary to secondary use over the long term.

Feeding Habitat

Herring sites—These sites could occur wherever herring spawned. Characteristics of herring spawning sites included eel grass or algae beds in semi-protected or protected waters. There was substantial annual variability in the timing, location, and size of the "spawn" and in gray whale use of herring spawn habitat. The most consistent location in the study area was Hesquiat Harbour, at the west end of Clayoquot Sound, a 6 × 10-km shallow bay fringed with eel grass and algae beds and protected from northwesterly seas and weather. Spawning sites within the bay varied somewhat year to year. Other herring spawning habitat utilized by gray whales included sites on the west and east shores of Flores Island and north and east shores of Vargas Island

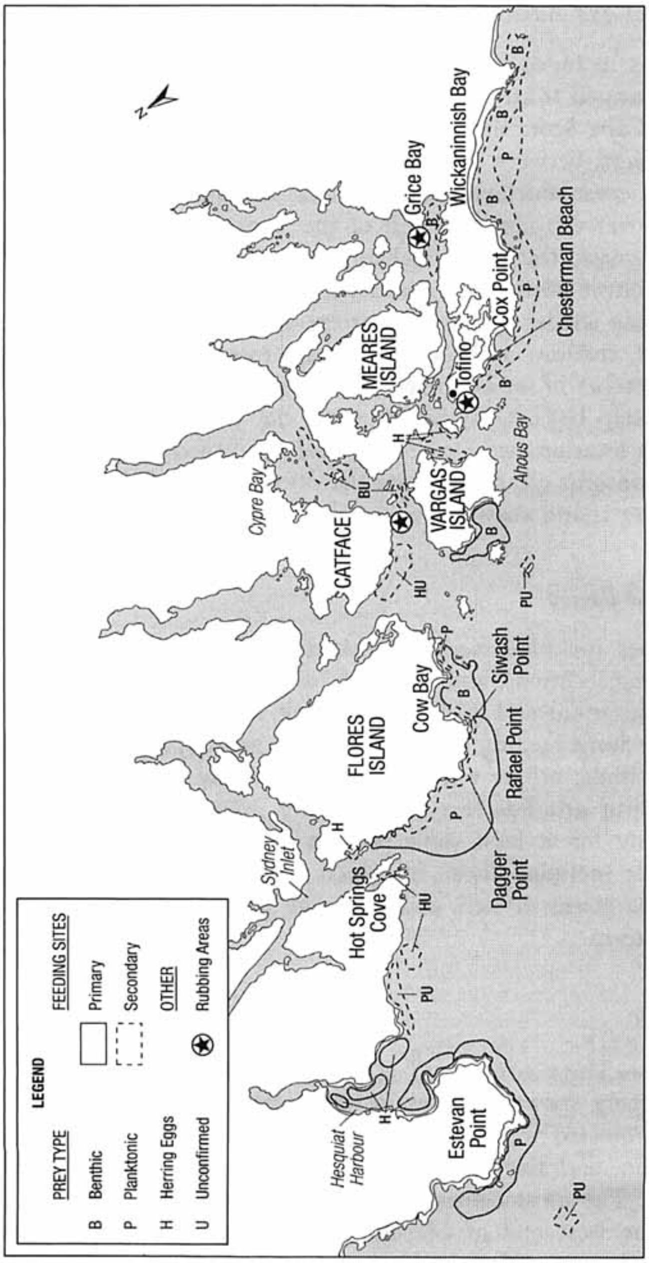


Figure 2. Gray whale habitat use and prey types in Clayoquot Sound, 1971–1996. Primary sites were those used regularly; secondary sites were those used irregularly. Wickaninnish Bay was primary site until early 1980s and now considered secondary site. "U" behind prey type indicates suspected but unconfirmed. Note rubbing areas off Tofino, Catface, and Grice Bay.

and adjacent shorelines (Fig. 2). Gray whale utilization of herring spawn areas occurred also at other locations along the Vancouver Island and Queen Charlotte Island coastlines (JDD, unpublished data).

Benthic feeding sites—Benthic feeding sites were the most definable and predictable of all feeding habitats. The primary sites included Cow Bay on the outside coast of Flores Island and Ahous Bay on the outside of Vargas Island (Fig. 2). Until the late 1970s, Wickanninish Bay and Chesterman Beach, approximately 20 km and 9 km, respectively, to the south of Ahous Bay (Fig. 2) would also have been considered primary benthic feeding sites. However, this has changed in recent years (discussed below). These are all relatively large, shallow, sand-bottom bays with feeding activity ranging from the intertidal zone to approximately 30 m of depth. Many smaller sandy bays in the region were used on occasion. An example of a secondary site was Cypre Bay, a protected passage between Meares Island and the Catface Range (Fig. 2). Several years passed without any extended gray whale use, but in some years this region was occupied by 6–8 whales for weeks at a time. Another important secondary site was Grice Bay, a protected mud-bottom bay so shallow that the majority of it is dry at low tide. It is reached through a 10-km long, narrow, inland passage from the entrance to the open sea at Tofino.

Plankton feeding sites—The plankton feeding sites most consistent over the period of this study were the section of coastline from Wickaninnish Bay to Chestermans Beach near Tofino, the entire outer Flores Island coast from its southern point around to the Sydney Inlet entrance, and the outer coast of Estevan Point (Fig. 2). Different sites within these larger regions were occupied for utilization of different prey species. The boundaries of these sites were quite flexible, with the prey and whales shifting with tide and current. Depending on prey species, the whales were found within and along kelp beds and in the surf zones of rocks (mysids) or slightly farther offshore in open water (crab larvae). Plankton feeding often occurred at locations distinct from benthic feeding sites, but overlap did occur.

Young Whale Habitat

Young whales generally tended to be separated from adult animals and were sometimes found together in small groups. This separation was subtle at times, with the younger animal(s) just several hundred meters away from adult assemblages, often inshore or in a kelp bed; or it was quite marked, when young animals occupied physically separate habitat with nearest adults 10+ km distant. The latter case is exemplified with the utilization of Grice Bay habitat. All sightings in this location over a period of 26 yr were of young whales. Between one and five whales spent months and in some cases a year or more in the bay, feeding benthically.

Sand Bar (Rubbing) Activity

Gray whales used specific habitat in Clayoquot Sound presumably for rubbing purposes. The whales regularly moved to sand bars and gravel spits in

Table 1. Prey species collected in Clayoquot Sound, 1989–1996.

Crab larva	*Cancer magister* (megalops) *Pachycheles* spp. (zoea)
Amphipods	
benthic	*Ampelisca* spp.
swimming	*Atylus borealis*
Mysids	*Holmesimysis sculpta* *Neomysis rayii* *Acanthomysis* spp.
Shrimp	*Callianassa californiensis*
Herring eggs/larvae	*Clupea harengus* pallasi

the region where they rubbed their bodies and "stood" on their tails with heads lunging above the water. This behavior occurred regularly at a sand bar in Templar Channel off Tonquin Beach at the south entrance to Tofino harbor and on a sand bar off Catface Mountain in Calmus Passage (Fig. 2). Whales moved into the area from feeding grounds, or from the migratory route, rubbed for a few minutes to several hours, then moved away again (Darling 1978). Some local observers have suggested that feeding occurs at these sites; however, we have no evidence either way. Whales periodically inhabiting Grice Bay were observed similarly rubbing on the gravel spit off Indian Island. It is possible this activity also occurred regularly on the bottom.

PREY SPECIES

Benthic species (Table 1) included amphipods (*Ampelisca* spp.) and ghost shrimp (*Callianassa californiensis*); planktonic or mobile species included mysids (*Holemsimysis sculpta, Neomysis rayii, Acanthomysis* spp.), crab larvae (*Cancer magister* megalops, *Pachycheles* spp. zoea), and mobile amphipods (*Atylus borealis*). Herring eggs and larvae (*Clupea harengus pallasi*) were also prey for gray whales off Vancouver island.

Appendix 1 gives the prey collection record from 1984 to 1996, including date, locations (Fig. 2), method of collection, and prey species. A total of 43 collections were made. The numbers of collections by species generally reflect only our need to confirm prey during ongoing monitoring and not the relative utilization of the different species.

The leveling off of the graph of "new" species (Fig. 3) indicates that the later collections produced species already documented as prey items. The last 16 collections in 1995 and 1996 and 27 of the last 28 collections since 1994 produced no previously unknown prey species. This suggests that the nine species identified to date made up the predominant prey species of gray whales in the study area during the period of observation. However, we do not wish to imply that this is a complete list. For example, highly suggestive but unconfirmed observations of gray whales feeding on juvenile rockfish and needlefish or sandlance have been made in the region.

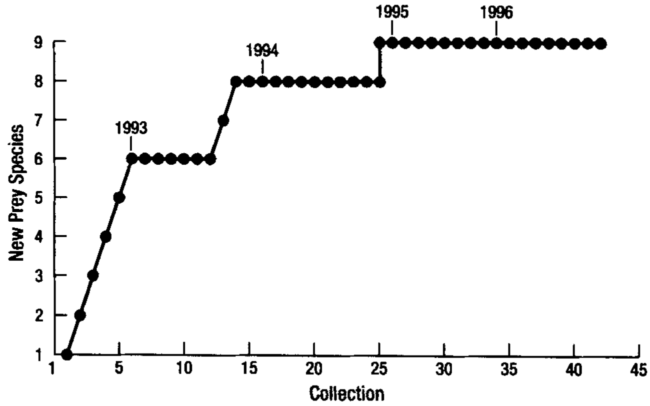


Figure 3. Discovery of prey species, 1984–1996. Leveling off indicates no new species found.

We observed several different feeding techniques and behavior patterns depending on type of prey, including feeding on the bottom, in the water column, and at the surface. Bottom-feeding activity, characterized by whales diving for several minutes and surfacing in approximately the same location streaming sediments from the baleen, and mysid feeding characterized by short dives and more random movements in kelp beds and within the surf zone of rock and islets, have been described by several authors (*e.g.*, Rice and Wolman 1971, Nerini 1984, Murison *et al.* 1984, Guerrero 1989). Feeding on crab larvae included skim feeding, with the whales moving along the surface, the upper jaw above the water, repeatedly "biting" down on the plankton streams along tide lines. When the crab larvae were deeper, the surface activity was similar to benthic feeding, except that the whales generally moved over a greater distance during dives. Feeding on herring eggs often occurred in water several meters deep, the whales on their sides with a flipper and half fluke above the surface. We presume that the whales used suction to engulf the egg masses but this has not been confirmed. A whale that died in the area in April 1997 was found to have its stomach filled with herring eggs (JDD, field notes).

FEEDING PATTERNS IN CLAYOQUOT SOUND

Early Season Herring Spawn Events

Each spring gray whales left the northward migration to feed on herring eggs recently deposited on eel grass and algae beds (Fig. 2). The location, time, and intensity of this activity varied substantially from year to year depending on the timing and abundance of herring. Hesquiat Harbour was the only site in Clayoquot Sound where this feeding occurred on an annual basis throughout the period of study. At Hesquiat the spawn and feeding activity occurred between mid-February and early April and usually lasted two to three weeks, with several separate spawns in some years extending this time considerably. During this period dozens to hundreds of whales utilized the site. It appeared the whales fed until the eggs hatched, which occurs approximately 10 d after spawning (Hart 1973), although we suspect they may also feed on the larvae in some circumstances. There can be an enormous volume of eggs, with egg drifts on beaches a meter or more high. Several other locations in the study area had smaller herring-related feeding events during one or two of the years between 1989 and 1996 (Fig. 2). When this occurred, whales moved into the area for a week or two, then departed. It is likely that herring provided the first food of the season to a portion of the migrating herd. Herring spawn times occurred progressively later along the coastal migratory route of the whales, just ahead of the migration itself. Herring-egg-feeding locations were not included in the annual feeding maps discussed below, as there is no confirmation at this stage that summer resident whales were involved in these events—although there is also no reason to believe they are not.

Summer Feeding Patterns

From observations conducted between 1989 and 1996, we have chosen four years to illustrate feeding patterns in detail: 1992, 1993, 1994, and 1995 (Fig. 4A–D). Observations from other years are referred to in relation to these examples. The terms early-season, mid-season, and late-season are used to generally designate the periods May–June, July–August, and September–November, respectively; and the terms "short-lived" and "extended", "minor," and "major" are arbitrary and used to describe the relative duration and number of whales participating in feeding events. A short-lived event was less than seven days; a major event involved more than ten whales.

1992 (Fig. 4A)—During the early- and mid-season there were several short-lived plankton-feeding events, including: (1) off Cox Point for one week in May (*A. borealis*), (2) north of Rafael Point in late June (*Pachycheles* spp.), and (3) off Estevan Point in mid-July (*Pachycheles* spp.). Beyond these events and through much of the summer, there were few whale sightings in Clayoquot Sound. There were occasional sightings of whales passing through or staying just a few days. On 18 August whales moved into Cow Bay and Ahous Bay and began feeding on benthic amphipods (*Ampelisca* spp.). This activity continued through the rest of the season. Numbers ranged from two to seven whales in Cow Bay through October and one to four in Ahous Bay through November. Noteworthy for this year is that sightings occurred over the period, 8–11 September, in the Cypre Bay region, a secondary ground with the last extended period of use in July–September 1982.

1993 (Fig. 4B)—An extended plankton-feeding event (*A. borealis*) occurred during the period from early May to early June along the coastline from Wickaninnish Bay to Chesterman Beach near Tofino, with up to seven to eight whales involved. During this time, and throughout most of the summer, whales were present in Ahous Bay and Cow Bay feeding on benthic prey (*Ampelisca* spp.). From June to October, one to six whales were periodically present in Ahous Bay. From May to November, one to eleven whales were present in Cow Bay. In the latter an obvious increase in numbers occurred in mid-August, leading to a constant seven to eight whales present through September. Whales also fed on mysids: (*N. rayii*) off Estevan Point in July and (*H. sculpta*) off Rafael Point for a period in July and August.

1994 (Fig. 4C)—This was primarily a plankton-feeding year. Whales were present for a week in early May in Wickanninish Bay (food unknown). From mid-May through late June up to 14 whales were involved in a major mysid-feeding event (*H. sculpta*) in the south Cow Bay area. By July most had moved to Rafael Point, where as many as eight whales fed on crab larva (*Pachycheles* spp.) through the end of August, although the number of whales present declined after 20 August. Whales were present off the Rafael Point–Siwash Point region feeding on plankton through September and October, but the prey species was not confirmed until 2 November: mysids (*N. rayii* and *Acanthomysis* spp.). The whales apparently shifted from crab larvae to mysid prey sometime during this period. Benthic feeding was not observed in the region until 2 November in Ahous Bay.

1995 (Fig. 4D)—Sporadic bottom feeding occurred in Ahous Bay from May to July, with one or two whales present for one or two days at a time. Similarly, sporadic bottom feeding occurred in Cow Bay in June, July, and early August, with one to four whales moving in and out of the area. In Ahous Bay, one to two whales were present continually by mid-September, five to six by early October, and seven to eight by late October. In Cow Bay from mid-August through September whale numbers were steady at three to four, and none were present in October. Through periods of July and August, two to five whales were present in the Rafael Point–Sydney Inlet area feeding on crab larvae (*Pachycheles* spp.), and in September a major feeding event occurred off Estevan Point with 10–15 whales also feeding on crab larvae. The Grice Bay secondary ground was utilized throughout the season, as described below.

Grice Bay utilization—During 1995, one to five young whales occupied the Grice Bay secondary ground from March through August feeding on ghost shrimp (*C. californiensis*). One of the same individuals was also present in the same area in June, July, and September 1996, also feeding on ghost shrimp. This feeding ground had been last utilized extensively in 1984–1985 by one or two young whales, and prior to that, in 1971, by one whale (Fig. 5; Hatler and Darling 1974). During the three documented periods of extended sightings since 1971, at least eight individual whales utilized this habitat for periods up to one year or more. The individual whale present in 1985 was one of the two animals present in 1984 and stayed the winter (JDD, unpublished data). No adults were sighted in the vicinity.

Between-Year Comparisons

It is clear that the differences between years are more striking than any repetitive patterns of occupancy or prey type (Fig. 6). For example, benthic feeding occurred throughout the season in 1993, was virtually non-existent in

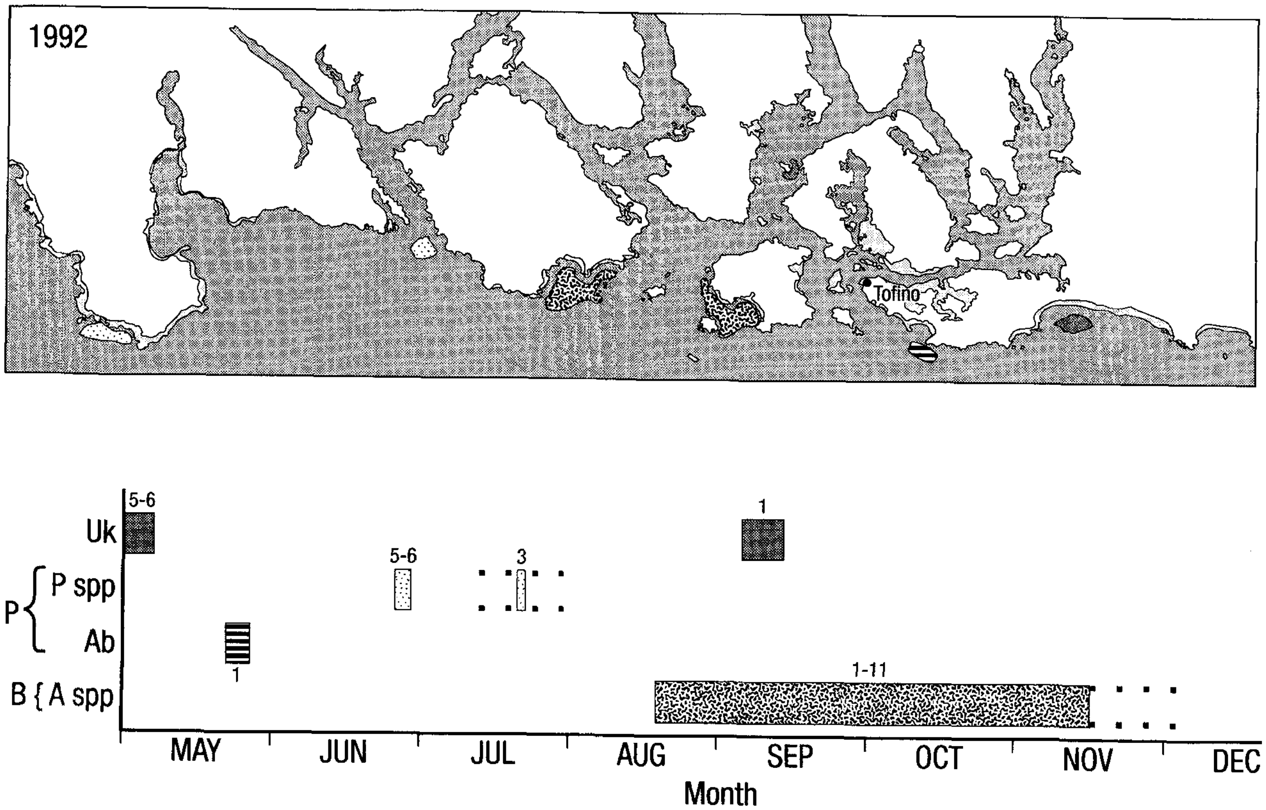
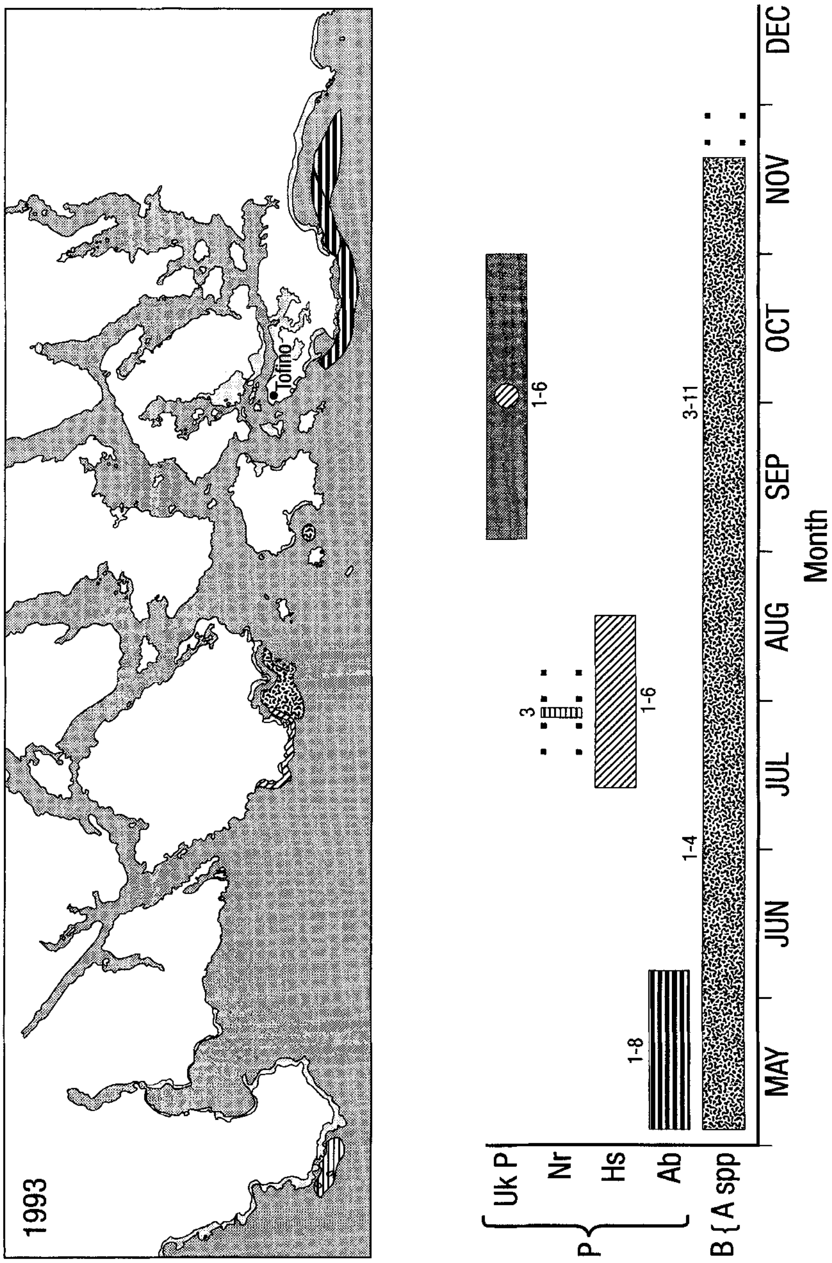


Figure 4. Patterns of habitat and prey utilization: (A) 1992, (B) 1993, (C) 1994, (D) 1995. P = plankton; B = benthic; Uk = unknown; Uk P = unknown plankton; Uk B = unknown benthic; A spp = *Ampleliscа* spp; Ab = *Atylus boralis*; Hs = *Holmesimysis sculpta*; Nr = *Neomysis rayii*; P spp= *Pachycheles* spp; Cc = *Callianassa californiensis*. Numerals indicate approximate number of whales involved in feeding event (determined by individual identification). Patterned circles inside "unknown" designation indicates likely prey (*e.g.*, 1993, 1994). Prey collections made within shaded areas.



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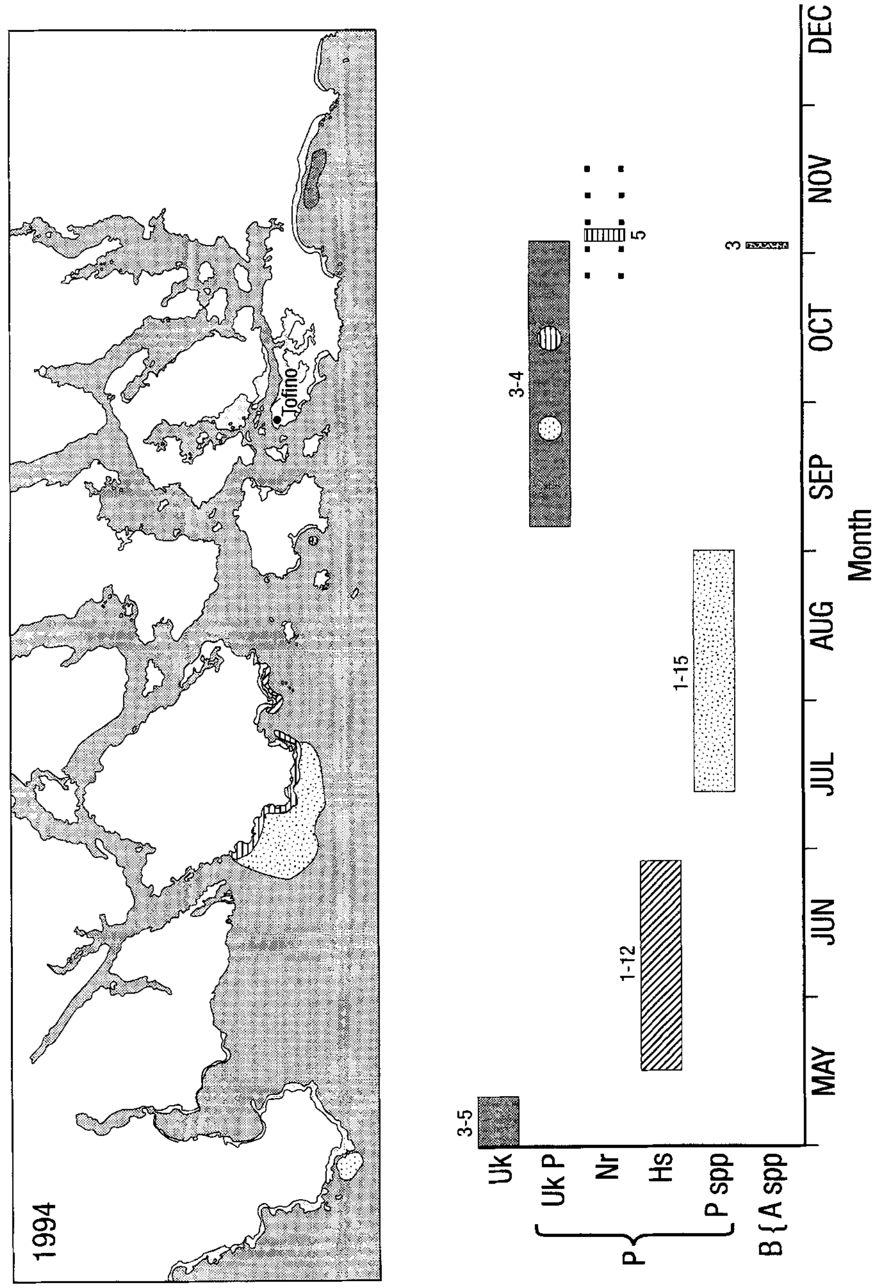

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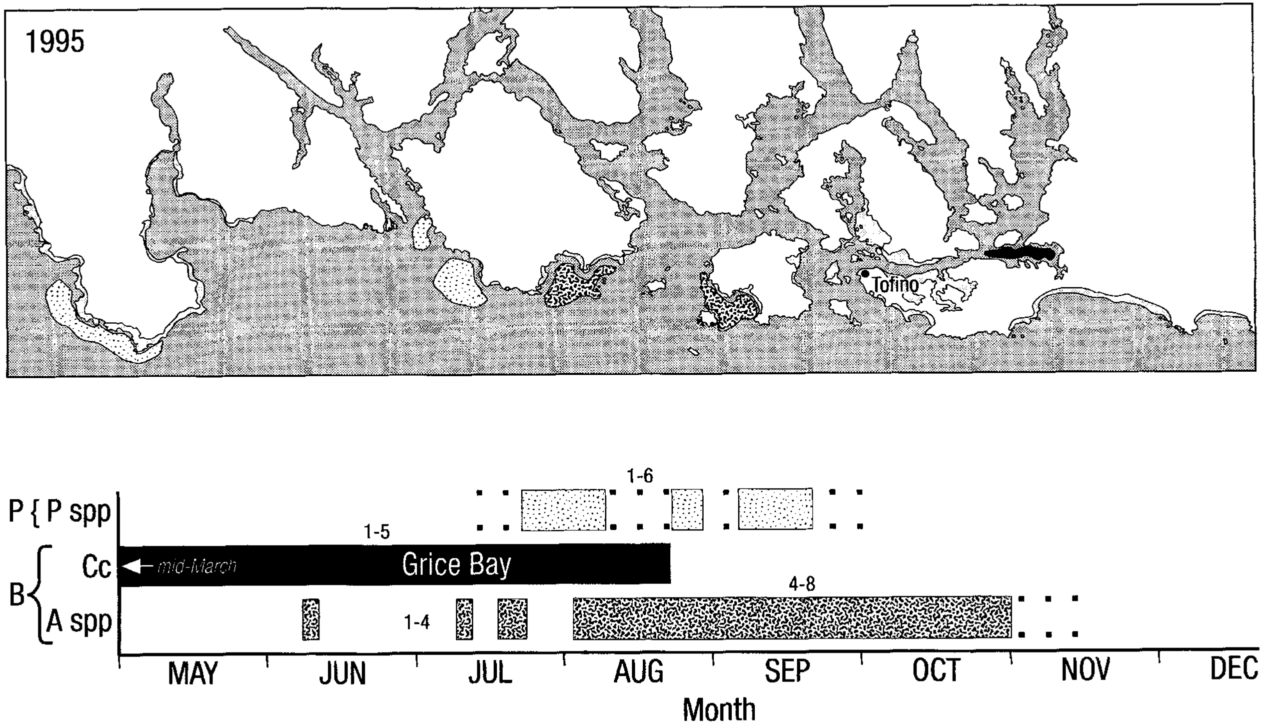

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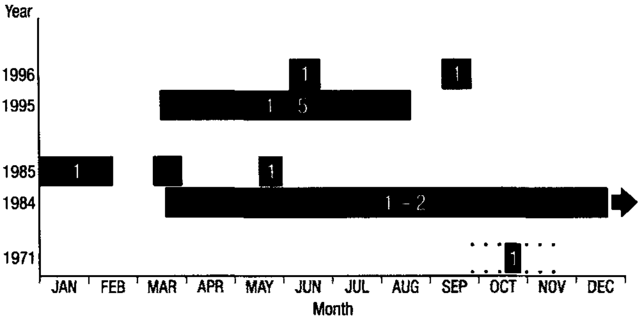

Figure 5. Utilization of Grice Bay, 1971–1996. Only young whales were found in this site in each occupation over 26-yr period, feeding on ghost shrimp (*Callianassa californiensis*). Whale present in 1985 was one of individuals present in 1984 and apparently stayed through winter. Whale present in 1996 was one of five present in 1995.

1994, and occurred for part of the summer in the other two years. Whales were present throughout the entire summer in 1994 due to successive plankton events, whereas in 1992 whales were rare for the first half of the season except for isolated, short-lived plankton events. Mysids were an important part of the prey for two years (1993 and 1994) but were not recorded as prey in the other two years. Early season mobile-amphipod-feeding occurred in essentially the same location for two years (1992, 1993) but over different lengths of time, then was absent in the following two years. Year-to-year variability in timing, prey type, and feeding location is the key feature of observations to date.

Several very generalized patterns may be emerging; these may or may not prove to be significant over the longer term. They are (1) a greater likelihood of feeding on benthic amphipods in the latter half of the season, (2) if there is steady whale-feeding activity in early and mid-season, it is more likely to be on plankton than benthic species, and (3) the Grice Bay ground may be

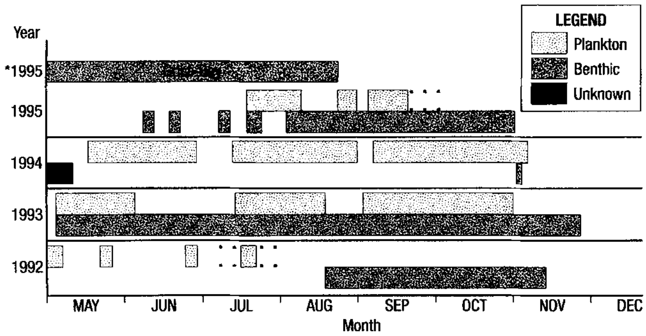

Figure 6. Comparison of gray whale presence and prey types between years, 1992–1995. All locations, except Grice Bay, combined; prey divided only into plankton and benthic types.

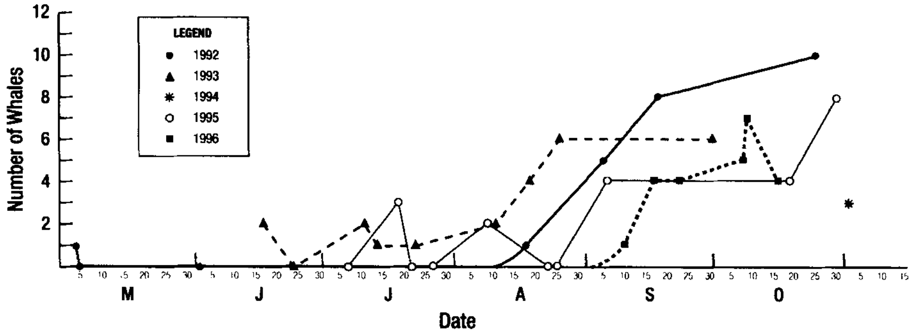

Figure 7. Number of benthic feeding whales in Ahous and Cow Bay combined, through seasons, 1992–1996. Note that in 1994 there was just one sighting of benthic feeding.

utilized by young whales steadily for one- to two-year periods separated by extended periods of non-use.

Our observations (Fig. 4) suggest that the predominant prey species for adult whales were crab larvae and benthic amphipods in 1992, swarming amphipods and benthic amphipods in 1993, mysids and crab larvae in 1994, and crab larva and benthic amphipods in 1995. It should be noted that our study area is only a portion of the animals' overall summer range.

Different Prey Species Utilized Simultaneously

On several occasions adult whales a few km from each other were observed feeding on different prey species. Examples are (1) on 11 August 1993 two whales were feeding on mysids (*H. sculpta*) in kelp off Rafael Point, and two whales were feeding on benthic amphipods (*Ampelisca* spp.) in Cow Bay, 4–5 km distant; (2) on 5 September 1996 two whales were feeding on mysids (*H. sculpta*) off Siwash Point and four to five whales were feeding on crab larvae (*Pachycheles* spp.) of Dagger Point 4 km distant; (3) on 19 October 1996 two to four whales were feeding on mysids between Siwash and Rafael Points, and two to eight whales were feeding on benthic amphipods (*Ampelisca* spp.) in Cow Bay, 3–4 km distant.

Changes in Density of Feeding Whales

The numbers of whales involved in each feeding event could vary substantially in a 24-h period (Fig. 4 A–D). Over the study period (1989–1996), at any one time and location, 1–14 whales were observed preying on mysids, 1–15+ on crab larvae, and 1–12 on benthic amphipods. Changing prey density could have been a factor but was not measured in this study.

A pattern repeated in several of the years was an increase in numbers of benthic feeding whales in late season (mid-August and later; Fig. 7). The numbers clearly increased after mid-August and remained high through the fall. An example of this increase in numbers occurred in 1995 in Ahous Bay. No whales were present through most of the year; then numbers increased from one or two in mid-September to seven to eight by the end of October. In 1994, the "odd" year in terms of benthic feeding, the only record of such feeding occurred in early November.

Longterm Change in Use of a Feeding Ground

Wickaninnish Bay is a 12-km-long open bay, with shallow sandy bottom at the eastern end of the Clayoquot Sound study area (Fig. 2). Sighting effort varied over the 30-yr period, ranging from intensive to sporadic in any one year (Table 2).

A change in use of Wickaninnish Bay as a feeding ground has clearly occurred over the last 30 yr. During the first decade of reports, from 1966–1977, whales were present throughout most summers. The period of most consistent observation was from 1972 to 1976, due to a whale-watch operation operating in the bay and Darling's (1978) observation that whales consistently used the area from May to September. From 1977 to 1979, whale presence became less consistent. From 1980 to 1996, gray whale utilization in summer was sporadic to absent. In some of these later years, whales utilized the area in May and early June. Since 1989 the whales in this region were observed feeding on plankton (crab larvae) or swarming amphipods more often than on benthic amphipods. Occasional bouts of benthic feeding occurred throughout this time, such as in April 1996, when several well-known resident whales (one of which was present in the 1970s when the site was used regularly) were observed in Wickaninnish Bay clearly bottom feeding. Nonetheless, consistent, season-long use has not occurred in the last 20 yr.

DISCUSSION

Broad Utilization of Coastal Habitat

Hatler and Darling (1974) speculated that "pockets" of gray whale habitat occur along the North American coast, and Votrogov and Bogoslovskaya (1980) and Bogoslovskaya *et al.* (1981) discussed "divisions" of gray whale habitat on the Asian coast, separated by empty areas through which whales passed rapidly. These terms were not defined or given scale and so may inadvertently leave the impression of discrete gray whale habitat within a section of coastline, say the length of Vancouver Island. Kvitek and Oliver (1986) described benthic feeding grounds of Vancouver Island as "discrete isolated habitats . . . separated by many kilometers of coast," leaving a specific impression of uneven coastal use. Our review of feeding locations over a 26-yr period questions the perception of an uneven use of coastal habitat by gray whales. At any one time, whales utilized discrete pockets of habitat depending on prey availability, but over the extended period virtually *all* of the southern half of the Vancouver Island west coast was used by feeding gray whales. We

Table 2. Utilization of Wickaninnish Bay by feeding gray whales, 1965–1996.

Years	Type of survey effort	Remarks
1965–1973	Park naturalist and whale watch reports	Present throughout summer in all years except 1966 and 1967 (Darling 1973, Hatler and Darling 1974)
1974–1976	Ongoing monitoring, regular surveys	Present throughout summer; no surveys without sightings (1–14) in May–September 1975–1976 (J. Darling, unpublished data; Darling 1978)
1977–1979	Regular surveys	Presence more sporadic: In 1977 present from May to September except for 6-wk period from July to mid-August. Long periods without sightings in 1978 until August. At least one sighting each summer month, but long periods of absence (J. Darling, unpublished data).
1980–1988	Sporadic surveys	Whales generally not present. In some years (1985, 1986) present in May and not thereafter. Occasional sightings in summer (J. Darling, unpublished data)
1989–1996	Present study	Whales present in May in most years but sightings rare throughout summer season.

suggest that the idea of a "foraging route or range" that covers extended sections of coastline provides a more accurate view of gray whale habitat utilization than the concept of discrete pockets of habitat.

Clayoquot Sound may provide a representative sample of the Vancouver Island gray whale foraging range. Virtually all of the outer Sound was used by gray whales over the study period. Different areas and habitat were used for different purposes, such as herring-egg feeding, benthic feeding, plankton feeding, and "rubbing." In one case, the use was by young whales only. Some habitats were used on a regular basis, often annually, others on some irregular basis that may have included ten or more years between use. Whales likely traveled between different habitats as prey availability and abundance, social behavior, or rubbing activity dictated. The specific function and importance of presumed rubbing behavior and hence habitat has not been investigated. The activity is common in specific areas and may serve a "grooming" or "recreation" function (Hatler and Darling 1974; Darling 1978, 1984).

Variety of Prey Resources: Benthic and Planktonic

Nerini (1984), in a definitive review of gray whale prey and feeding behavior, concluded that "the most extraordinary aspect of the gray whale's feeding ecology is its apparent dietary flexibility" and noted that with three modes of feeding (benthic suction, engulfing, and skimming) the gray whale has perhaps a greater range of foraging techniques than any other great whale. Benthic amphipods are generally considered the predominant prey species in northern seas, but numerous observations of gray whales feeding on fish and planktonic crustaceans exist throughout their range (Pike 1962, Rice and Wolman 1971, Nerini 1984, Kim and Oliver 1989). A review of examinations of gray whale stomach contents since 1874 indicated a broad array of some 70 genera of both benthic and pelagic organisms (Nereni 1984).

The most striking feature of our observations, consistent with Nerini's (1984) review, was the variety of prey and foraging techniques utilized by the whales. Since collections began, at least nine prey species supported the gray whale population in this region. Previous reports of gray whales feeding on benthic amphipods (Oliver *et al.* 1984, Kivetek and Oliver 1986), mysids (Murrison *et al.* 1984, Guererro 1989), and ghost shrimp (Plewes *et al.* 1984) are confirmed in this study. In addition, one species of mobile amphipod (*A. borealis*), at least two species of crab larvae (*C. magister* megalops and *Pachycheles* spp. zoea), and herring eggs and larva (*Clupea harengus* pallasi) were added to the list of Vancouver Island prey species. All three feeding techniques described by Nerini (1984) were utilized by the Vancouver Island whales to exploit these prey.

The polychaete worm, *Onuphis elegans*, has been discussed as a prey species off Vancouver Island in several reports (Darling 1977, 1978; Oliver *et al.* 1984; Kvitek and Oliver 1986; Kim and Oliver 1989; Weitkamp *et al.* 1992), but we do not believe this has been confirmed and therefore leave it in the unconfirmed category with juvenile rockfish and sand lance at this time. All of the prey species reported for Vancouver Island have been reported previously as prey of gray whales somewhere in their range, albeit in some cases from a single observation (Nerini 1984).

The current importance of planktonic prey off Vancouver Island *vs.* earlier observations of extensive bottom feeding (*e.g.*, Hatler and Darling 1974, Darling 1978) raises the question whether a change in prey species has occurred over the last 20 yr, or whether observations have simply become more complete. We lean towards the latter explanation for several reasons: most observations in 1960s and 1970s were in Wickaninnish or Ahous Bay, now well known as bottom-feeding grounds, and whales were documented in locations along the West Coast Trail (now known as a plankton-feeding area) as early as 1972 (Darling 1973). However, two points make us hesitant to entirely discount the idea that predominant prey species may have changed. These are (1) the virtual abandonment of Wickaninnish Bay and adjacent waters as a primary benthic feeding area by the early 1980s, and (2) Highsmith and Coyles' (1992) suggestion of the potential for long-term loss of amphipod habitat, and alterations of ecosystem structure, caused by feeding gray whales.

Overall, the literature has emphasized the benthic feeding behavior and prey of gray whales (Scammon 1869, Nemoto 1959, Pike 1962, Walker 1971, Rice and Wolman 1971). Nerini (1984) revisited this view and noted that observations of feeding in the water column were concentrated in southern regions, whereas whales feeding while migrating or summering along the northern half of the migration route were nearly always consuming benthic resources—that is to say, prey types could be region-specific. Kim and Oliver (1988) furthered this idea and proposed primary, secondary, and tertiary feeding grounds defined by location and predominant prey, with more planktonic prey species farther south in the range. Our Vancouver Island work suggests another view of gray whale feeding behavior. Rather than a region-specific prey regime (Nerini 1984, Kim and Oliver 1988), the whales utilize a variety of prey resources, both benthic and pelagic, within a feeding range. We propose they exploit the most suitable prey species at any one time, on a cyclic or otherwise recurring basis. In this view, pelagic feeding and prey may have equal importance to benthic feeding and prey overall. This clearly was the case on Vancouver Island during this study. Further, it may account for the numerous observations of plankton feeding and the variety of prey species found in gray whale stomachs in other parts of their range (Nerini 1984).

In related discussions, several authors have indicated that one or another prey species was the "most important" for gray whales. Benthic or near-benthic amphipods were often listed as the primary prey (Pike 1962, Rice and Wolman 1971, Nerini 1984) at least in northern seas, and Kivitek and Oliver (1986) and Kim and Oliver (1988) stated that mysids are the major prey along the coast of British Columbia. The species noted may well have been the predominant or most important prey at the time of collection or observation, but our study strongly suggests that such results should not be generalized over time and place. We propose that rather than a single species, it is an assemblage of species that is important to the whale. We speculate that the whales are attuned to natural patterns of abundance and absence occurring within this prey assemblage, and that different species play equal roles over a season or several years.

Variable Patterns of Utilization of Resources and Habitat

Gray whale feeding has been proposed as a major source of physical disturbance to the benthic community, with the activity being part of a cycle of exploitation, recolonization, succession, and maturing of the prey community (Nerini 1984, Oliver *et al.* 1984, Oliver and Slattery 1985). Periods of nonuse by whales are presumed to correspond to recovery and maturing of the prey species. Highsmith and Coyle (1992) and Weitkamp *et al.* (1992) raised the possibility that gray whale exploitation may, in some circumstances, be a one-way street and lead to permanent loss of the amphipod or other prey communities and, hence, changing feeding patterns. The virtual abandonment of Wickaninnish Bay as a primary benthic feeding area since the 1980s may be such an example, although it should be noted that the current status of prey species there has not been investigated.

An additional explanation for variable use of benthic grounds arises from the idea that an assemblage of prey species is potentially available and utilized over a season. A whale may change location and habitat to exploit the "optimum" prey species at any one time. The optimum prey is probably determined by factors such as abundance, density, size, caloric content, and predation pressure, all which may vary throughout the season and year to year, depending on environmental factors and life cycles. This study suggests that a progression from one prey species to the next may occur through the season. A generalized progression of gray whale prey in Clayoquot Sound from spring to fall was seen (herring eggs, mobile amphipods, mysids, porcilid crab larvae, and benthic amphipods), as each presumably became the optimum species to "harvest." A shift from one habitat and prey species to another may not necessarily reflect the loss of the initial prey, only that a better option has developed.

Several authors have noted differences in caloric content among gray whale prey species and within species at different times of their life cycles, especially in relation to reproductive condition. This information combined with bioenergetic considerations in foraging effort may well explain variable use of resources (Guerrero 1989, Highsmith and Coyle 1992, Weitkamp *et al.* 1992). For example, in the Bering Sea, the dry weight, energy content per unit weight, and caloric content of the benthic amphipod, *Ampelisca macrocephala,* increased significantly throughout the summer, with highest values in September–November (Highsmith and Coyle 1992). If the *Ampelisca* spp. in the study area grow similarly, this may explain the later-season progression to this prey species in Clayoquot Sound.

Our observation that patterns of utilization of resources and habitat were highly variable refers to utilization of a specific prey species and its habitat. However, if the assemblage of prey species is considered as a whole, the observation changes substantially. Utilization of the prey assemblage and its overall habitat was remarkably consistent and resulted in the highly predictable presence of gray whales in the region each summer. We speculate that it is the assemblage of prey species that allows the ongoing use of a specific feeding range over time.

Whale Age a Factor in Habitat or Prey Use

Very young whales, apparently ranging from several months in age and recently weaned to a 1-yr-old, made up a portion of the Vancouver Island population each year (Hatler and Darling 1974; Darling 1978, 1984; Oliver 1984; Rice and Wolman 1971; JDD, unpublished data.) The relationship of these whales with other adults in the area is yet to be determined. Darling (1978) noted "small whale characteristics" off Vancouver Island, including occupation of areas not frequented by larger feeding whales and an apparent affinity for kelp beds. Since then, some degree of separation of young whales from adults has been a recurring observation each year (JDD, unpublished data). The periodic use of Grice Bay by young whales best illustrates the apparent age-specific utilization of habitat (Hatler and Darling 1974, Plewes *et al.* 1984, this study).

Zenkovich (1937) suggested that specific areas along the Russian coast may be permanent feeding grounds for younger, apparently recently weaned, animals. Almost all whales captured in these areas were less than two years old, an observation from which he concluded that young gray whales form separate schools at weaning. Bogoslovskaya *et al.* (1981), from investigations in the same region, suggested that such separation does exist but may not be so well defined. Our observations of separation of adults and young, at times very distinct and at other times subtle, are consistent with these reports.

The reason for different habitat utilization patterns by young animals is not known. The Grice Bay young whales were feeding primarily on ghost shrimp at the same time that adults were feeding on other prey species in other parts of the study area. Weitkamp *et al.* (1992) suggested from a study of gray whale predation on ghost shrimp in Puget Sound that, due to density of this species, less foraging time was necessary than with benthic amphipods to obtain comparable bioenergetic gain. If true, this may be of significant benefit to young whales that are possibly learning how to feed and which may have high energy requirements. However, to complicate this view, young whales were commonly sighted in kelp beds in the general vicinity of adult whales feeding on mysids and in benthic grounds near whales feeding on benthic amphipods, and were observed to skim feed crab larvae (JDD, unpublished data). Oliver *et al.* (1984) reported that the small whale he observed was feeding on the benthic *Ampelisca* community. Apparent attributes of Grice Bay are shallow water, protection from storms, and possibly increased protection from predators, as well as abundant food supply. This is also true of kelp beds. Perhaps young whales seek out these relatively protective and productive habitats after weaning.

Management Considerations

1. The determination of the relative importance of specific locations and habitat to gray whales is complex. It is confounded by the whales utilizing different locations and habitat at different times within one season and from year to year. A coastal foraging route extending over hundreds of kilometers may be the appropriate view of gray whale habitat use. Certainly some locations are utilized more regularly than others, but at any one time or season the lesser-used locations may be critical to the survival of the whales, when food in the prime area is less abundant or if used for other purposes such as young whale care. Therefore, efforts to designate priority gray whale habitat within the overall coastline for management purposes may not be meaningful.
2. Determination of impacts of pollution or other human activity on gray whales is complicated by the highly variable patterns of specific habitat and prey utilization. The apparent potentially high natural variability in prey status due to normal environmental and biological fluctuations will likely lead to a corresponding variability in the distribution and behavior of the whales. The separation of natural and human impacts on the whales' distribution and behavior with current knowledge will be difficult below the lethal stage.
3. The ability of gray whales to exploit a variety of prey species, combined with a feeding range that may extend over hundreds of kilometers, may enhance the population's chances of surviving temporary catastrophic impacts on specific prey species or highly localized and contained pollution events or other disturbances. However this "enhancement" relies on the chance that the species or habitat affected is not critical at the time of impact.
4. The variable utilization of habitat and prey resources by gray whales over a large section of coastline strongly indicates that information from partial-season and single-site research projects must be taken in context. Such studies may well determine what is occurring at the particular time or place, or in a specific age class, but they may not be adequate to draw general conclusions about the entire population over time. These limitations should be noted when considering some of the inferences and conclusions in Oliver *et al.* 1984, Kivetek and Oliver (1986), and Duffus (1996).[2]
5. The information presented provides a broad-stroke, preliminary outline of feeding patterns in Clayoquot Sound. Several avenues of research would significantly further our insight into gray whale behavior in the region. These include (1) studies of factors influencing prey life cycles, distribution, and abundance; (2) quantitative studies of prey density and quality (in terms of caloric content) in relation to whale utilization patterns; (3) studies of the means by which whales locate prey, including potential communication between animals; and (4) investigation as to how social factors such as age, status and genetic relatedness may govern feeding distribution and behavior.

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[2] Duffus (1996) studied gray whales in Clayoquot Sound and reported on "shifts" in whale distribution and prey from 1992–1994. He then proposed a pattern of whales moving away from Tofino and the center of "commercial" activity. His observations were limited in time and area and led to different interpretations than would occur with a broader database.

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Appendix 1. Prey Collection Record in Clayoquot Sound, 1984–1996. All collections were made by plankton net except where noted: (D) = low tide digs; (S) = suction hose; (F) = fecal sample. An asterisk * indicates a series of collections on that date, treated as one collection in the analysis.

Year	Date	Location	Prey species
1984	Summer* (D)	Grice Bay	*C. californiensis*
1989	6 April	Hesquiat Harbour	*C. harengus* pallasi (eggs)
	1 June	Wickanninish Bay	*C. magister* megalops
	15 July* (S)	Cow & Ahous Bay	*Ampelisca* spp.
1992	22 May	Cox Point	*A. borealis*
	7 June	Dagger Point	*Pachycheles* spp. zoea
	21 July	Estevan Point	*Pachycheles* spp. zoea
1993	10 March	Hesquiat Harbour	*C. harengus* pallasi (eggs)
	13 March	Hesquiat Harbour	*C. harengus* pallasi (eggs/larvae)
	12 May	Wickaninnish Bay	*A. borealis*
	23 May	Gowland Rocks	*A. borealis*
	2 June	Gowland Rocks	*A. borealis*
	28 July	Estevan Point	*N. rayii*
	11 August	Dagger Point	*H. sculpta*
	19 August* (S)	Cow & Ahous Bay	*Ampelisca* spp.
1994	18 May	Cow Bay	*H. sculpta*
	3 June	Cow Bay	*H. sculpta*
	7 June	Cow Bay	*H. sculpta*
	22 June	Cow Bay	*H. sculpta*
	13 July	Dagger Point	*Pachycheles* spp. zoea
	6 August (F)	Rafael Point	*Pachycheles* spp. zoea & "mysids"
	11 August (F)	Rafael Point	mysids
	15 August	Rafael Point	*Pachycheles* spp. zoea
	30 August	Rafael Point	*Pachycheles* spp. zoea
	2 Nov.	Siwash Point	*N. rayii & Acanthomysis* spp.
	2 Nov.	Ahous Bay	*Ampelisca* spp.

Appendix 1. Continued.

Year	Date	Location	Prey species
1995	21 April (D)	Grice Bay	*C. californiensis*
	20 June (D)	Grice Bay	*C. californiensis*
	22 July	Dagger Point	*Pachycheles* spp. zoea
	9 August	Dagger Point	*Pachycheles* spp. zoea
	23 August	Dagger Point	*Pachycheles* spp. zoea
	25 August	Rafael Point	*Pachycheles* spp. zoea
	6 Sept.	Estevan Point	*Pachycheles* spp. zoea
	19 Sept.	Estevan Point	*Pachycheles* spp. zoea
1996	7 June (D)	Grice Bay	*C. californiensis*
	2 July	Cow Bay	*H. sculpta*
	11 July	Cow Bay	*H. sculpta*
	17 August	Dagger Point	*H. sculpta*
	20 August	Dagger Point	*Pachycheles* spp. zoea
	22 August	Dagger Point	*Pachycheles* spp. zoea
	4 Sept.	Siwash Point	*H. sculpta*
	5 Sept.	Dagger Point	*Pachycheles* spp. zoea
	10 Sept.	West Dagger Point	*H. sculpta*

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GRAY WHALE OCCURRENCE AND FORAGE SOUTHEAST OF KODIAK, ISLAND, ALASKA

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Although the Bering and Chukchi seas are commonly cited as the principal summer feeding grounds of Eastern North Pacific (ENP) gray whales (*e.g.*, Highsmith *et al.* in press, Swartz *et al.* 2006), records indicate that this population actually feeds opportunistically throughout its range from the lagoons of Baja California, Mexico, to Alaskan waters (Nerini 1984). Specifically, recent reports suggest that whales may routinely feed in the Gulf of California (Sánchez-Pacheco *et al.* 2001) and Bahia Magdalena, Baja California Sur (Caraveo-Patino and Soto 2005), whereas Clapham *et al.* (1997) noted that feeding gray whales occurred offshore California even in the 1920s when population numbers were very low. The dynamic nature of foraging in this population is best described from coastal study sites along the southeastern shore of Vancouver Island, Canada, where whales shift among pelagic, epi-benthic, and benthic prey within and between years (Darling *et al.* 1998; Dunham and Duffus 2001, 2002).

In the 1980s the southern Chukchi Sea and the Chirikov Basin in the northern Bering Sea were considered the primary feeding grounds for ENP gray whales, based on reported high densities of both whales (Braham 1984, Kim and Oliver 1989, Moore *et al.* 2000) and their ampelicid amphipod prey (Grebmeier *et al.* 1989, Highsmith and Coyle 1990). However, by 2002, benthic productivity in the Chirikov Basin had declined precipitously, due to either whale foraging (Highsmith *et al.* 2006), ecosystem change (Grebmeier *et al.* 2006), or both, and only the southern Chukchi Sea supported dense aggregations of gray whales (Moore *et al.* 2003). Indeed, the

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decline in benthic biomass in the Chirikov Basin (Highsmith and Coyle 1992) was suggested as causal to the 1999–2000 gray whale mortality event (Le Boeuf *et al.* 2000), although other factors, such as disease, could not be ruled out (Moore *et al.* 2001).

Since 1999 gray whales have been observed feeding year-round near Ugak Bay, Kodiak Island, Alaska, in the course of surveys for pinnipeds (Wynne 2005). These "Kodiak" gray whales have not been described in terms of distribution, relative abundance, behavior, or diet. One reason for this oversight is that waters southeast of Kodiak Island have long been considered simply a portion of the migration corridor for gray whales passing to and from northern seas (*e.g.*, Braham 1984) and not a part of the feeding or overwintering range. Conversely, the distribution and feeding behavior of the Pacific Coast Feeding Aggregation (PCFA; formerly called "summer resident" whales) have been investigated offshore Vancouver Island, British Columbia since 1984 (Darling *et al.* 1998; Calambokidis *et al.* 1999; Dunham and Duffus 2001, 2002). The PCFA has been the focus of photo identification surveys extending from northern California to southeastern Alaska, with mark-recapture estimates of 261–298 whales from photos taken from 1998 to 2003 (Calambokidis *et al.* 2004).

Here we present a compilation of opportunistic gray whale sightings noted between 1999 and 2005 in waters southeast of Kodiak Island, Alaska, accompanied by results from 6 days of benthic sampling conducted in 2002 near feeding whales at the entrance of Ugak Bay. Although these data are limited in scope, they provide evidence of year-round occurrence and a noteworthy feeding area for ENP gray whales in the northern Gulf of Alaska. Building a record of seasonal distribution, relative abundance, and feeding areas is key to interpreting the response of this population to environmental variability and carrying capacity.

Gray whale sightings were recorded opportunistically during aerial surveys for Steller sea lions (*Eumetopias jubatus*) and harbor seals (*Phoca vitulina*) conducted in the Kodiak Island archipelago (Fig. 1: inset). Monthly surveys of Steller sea lion haul-outs were conducted throughout the archipelago from September 1999 through July 2005, whereas surveys of harbor seal haul-outs focused on the east and south side of Kodiak Island and were conducted only in late August each year from 1993 to 2002 and in 2004. Although the sea lion and seal survey routes differed somewhat, both included waters between Long Island and Cape Barnabas along Kodiak's southeast coast, including the entrance to Ugak Bay. In addition, on 25 July 2000, a single aerial survey was conducted along a transect southwest and roughly parallel to Kodiak Island (Fig. 1: inset) to search for North Pacific right whales (*Eubalaena japonica*). This survey was flown in a high-wing aircraft with two primary observers seated at bubble windows and a downward looking high-format camera aboard to photograph whales (for details, see Perryman *et al.* 2002).

All pinniped surveys were conducted from a fixed-wing aircraft at altitudes between 220 and 472 m (700 and 1,500 ft) and speeds of 165–200 km/h (90–110 km). One to three observers (plus the pilot) scanned for blows and whales at the surface ahead of and on either side of the aircraft. When whales were seen, the plane was diverted to (1) confirm species identity; (2) mark the location, either *via* a global positioning system or a position relative to coastal landmarks; (3) estimate number

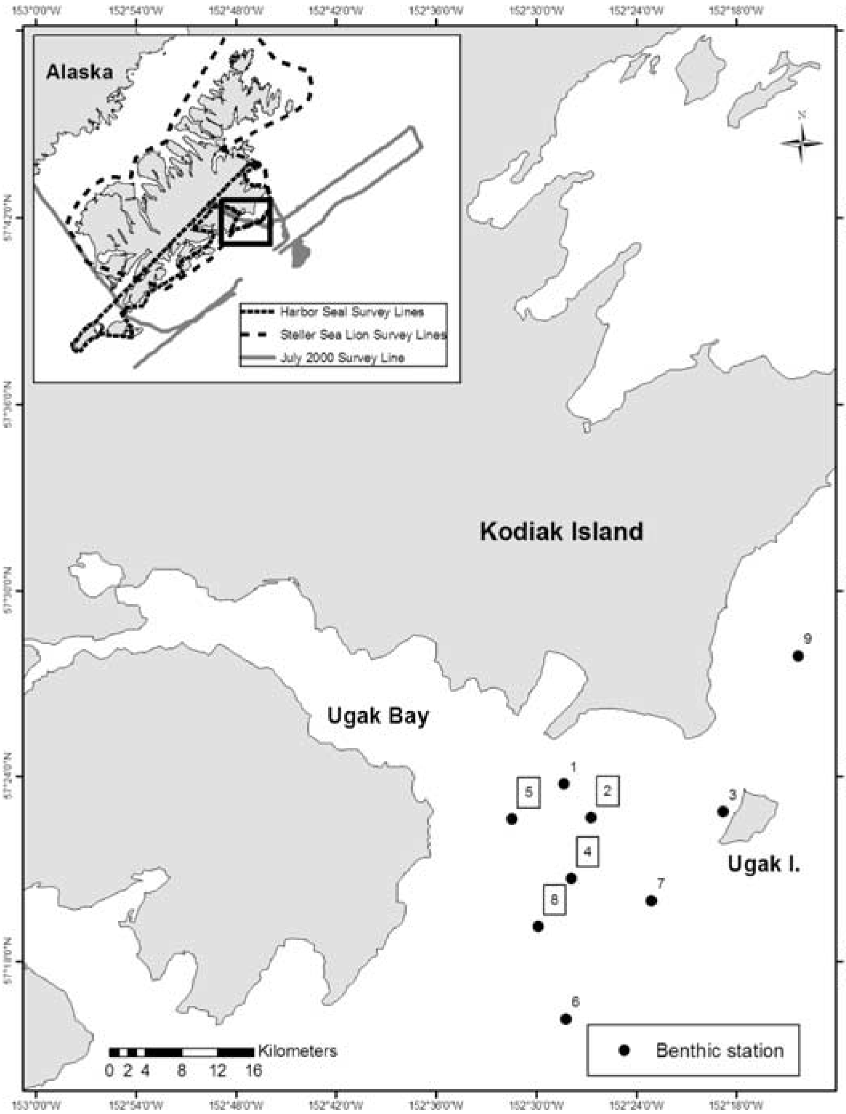

Figure 1. Benthic sampling stations near the entrance to Ugak Bay. Boxes indicate stations with extremely high cumacean densities (see Table 1). Inset: Routes for aerial surveys for pinnipeds around Kodiak Island (Wynne 2005), and trackline for the July 2000 aerial survey offshore the southeastern coast of Kodiak Island, Alaska. Gray whale sightings were recorded opportunistically during surveys for Steller sea lions (dashed line) and harbor seals (solid line) from September 1999 through July 2005.

of whales; and (4) determine general behavior—feeding was recorded whenever mud plumes were seen near whales. Sighting locations were subsequently plotted by season: winter (December–February), spring (March–May), summer (June–August), and autumn (September–November) and "rough-order" sighting rates (number of sightings/survey hour) calculated by dividing the number of gray whale sightings by the average time spent surveying between Long Island and Cape Barnabas on the pinniped surveys. These indices must be considered provisional, as there was no attempt to account for variable survey conditions, nor counts of individual whales in the derivation of sighting rates. In addition, due to the opportunistic nature of these surveys, no effort was made to delineate the full extent of gray whale distribution, detail behavioral interactions, or to derive population estimates from the sightings.

Gray whales were seen year-round along the east side of the Kodiak Island archipelago, most frequently and in greatest numbers near the entrance to Ugak Bay (Fig. 2). Whales were seen with mud plumes in each month, suggesting year-round feeding. Seasonal sighting rates were highest from September to November, declined during December to February and March to May periods, and reached lowest levels during the June to August period. Monthly sighting rates exceeded 100 sightings/h in January, June, September, and November, with >20 sightings/h in all other months except March (Fig. 3A). Annual sighting rates were highest in 2000 and 2001 (>70 sightings/h), lowest in 2003 (<20 sightings/h), with rates >30 sightings/h in 2002 and 2004 (Fig. 3B).

Roughly 350–400 gray whales were counted along the aerial survey transect flown on 25 July 2000. Distribution extended from the mouth of Ugak Bay, where 40–50 whales were seen, to roughly 100 km east-southeast of Ugak Island (Fig. 2: June–August). Overall, the feeding aggregation covered roughly 240 km^2 (*ca.* 80 km × 30 km); actual limits to the distribution were difficult to determine due to low fog over portions of the survey area. Whales were clustered in groups of 10–20 animals, with most associated with conspicuous mud plumes and surface feces trails indicative of active feeding. Most whales appeared to be large adults, with one trio involved in sexual behavior; no small juvenile whales or calves were noted.

To investigate gray whale prey availability, benthic samples were collected at nine stations where whales were seen feeding near the entrance to Ugak Bay (Fig. 1), from 15 to 20 August 2002. Four grab samples were collected at each station using a 0.1-m^2 van Veen grab weighing 88.7 kg (including a 32-kg lead weight), except for station 3 where only one sample was collected due to very large sediment grain size. Each sample was placed on a screen with mesh size of 1 mm and washed with seawater to remove sediment. Samples were preserved in 10% seawater buffered formalin for post-cruise laboratory analysis. To investigate gray whale prey selection, ten fecal samples were collected using a modified small-mesh plankton net with a cod end, attached to a fishing dip net by an extended handle. Samples were collected from the benthic sampling vessel by trolling through water where whales had deposited fecal plumes. One additional fecal sample was collected using a plastic bucket.

Thirty-six benthic samples were collected (Table 1), with potential gray whale prey summarized by station as abundance (individuals/m^2) and carbon biomass (g C/m^2). Cumaceans (*Crustacea: Diastylidae*) were the dominant fauna (93.6%–98.4% of the sampled abundance) at stations 2, 4, 5, and 8 (Fig 1: boxed stations), where biomass ranged from 31 to 67 g C/m^2. Abundance and carbon biomass measures were roughly an order of magnitude lower at stations 1, 6, 7, and 9 (Table 1). The single sample at station 3 revealed moderately high faunal abundance (33,060 individuals/m^2),

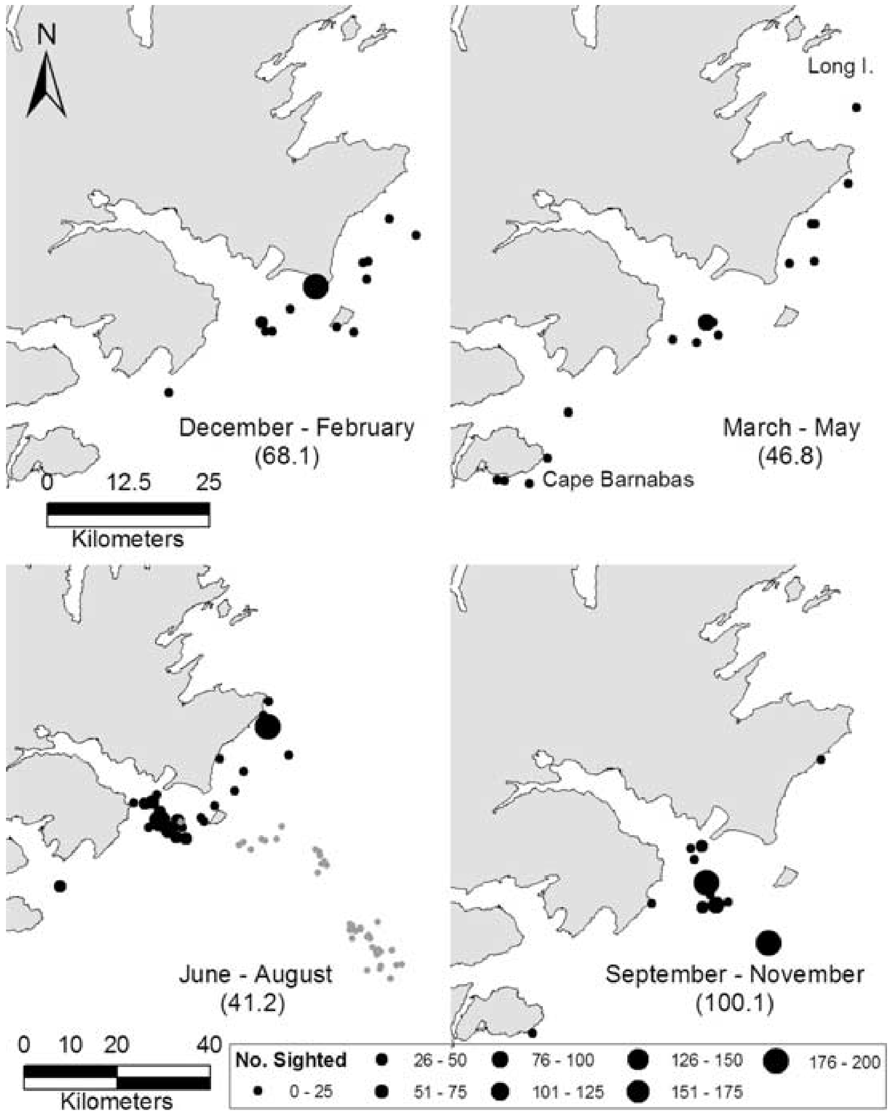

Figure 2. Cumulative gray whale distribution and provisional sighting rates by season: December–February (winter); March–May (spring); June–August (summer), and September–November (autumn). Note difference in spatial scale for the June–August panel, required to show data from the July 2000 survey.

consisting of polychaete worms (*Phyllodocidae* = 54.3%) and bivalves (*Tellinidae* = 33.6%), which resulted in the highest biomass measures (3,950 g/m^2; 125 g C/m^2) of all the stations. Evidence that gray whales were consuming cumaceans resulted from gross examination of the fecal samples, which contained voluminous quantities of (usually partially digested) Diastylidae. Notably, amphipods (*Ampelisca* spp.), a

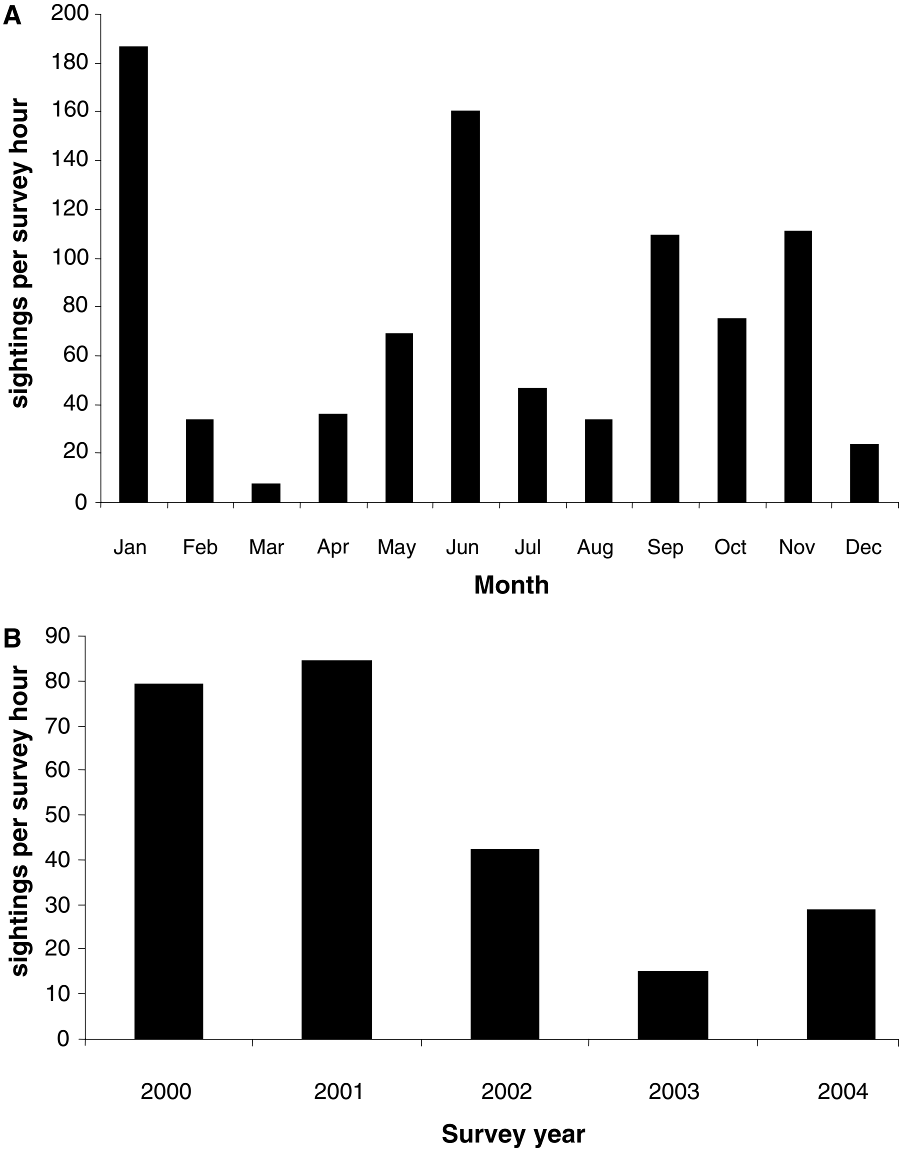

Figure 3. Provisional sighting rates for gray whales seen during pinniped-related surveys along southeastern Kodiak Island, by month (A) and year (B). Annual rates were not calculated for 1999 or 2005 because surveys were conducted only during part of those years.

common gray whale prey, were found only at station 2 and in low densities (0.7% of 57,210 individuals/m^2) and station 6 (15.6% of 1,105 individuals/m^2).

Although many of the gray whales seen near Ugak Bay since 1999 may be migrating through the area, some clearly stop to feed there, perhaps for much of the year. The

Table 1. Summary of benthic samples at nine stations near the entrance to Ugak Bay, Kodiak, Alaska. Abundance (individuals/m^2) and carbon biomass (g C/m^2) provided for each station and for the dominate families (top 3) at each station; bold indicates stations with cumacean abundance >93% (Fig. 1 inset: boxed stations).

Station number	Depth (m)	Abundance (individuals/m^2)	Biomass (g C/m^2)	Abundance: top 3 (individuals/m^2)	%	Biomass: top 3 (g C/m^2)	%
1	52	4,163	7.14	Diastylidae	51.8	Diastylidae	23.0
				Spionidae	20.3	Pharidae	12.6
				Rhyncocoela	2.2	Ophiuridae	9.3
2	62	57,210	45.28	Diastylidae	**94.4**	Diastylidae	84.5
				Lysianassidae	1.4	Pharidae	7.2
				Spionidae	0.7	Rhyncocoela	1.7
3	13	33,060	124.87	Phyllodocidae	54.3	Tellinidae	86.7
				Tellinidae	33.6	Glycymerididae	8.3
				Polygordidae	6.4	Opheliidae	2.7
4	84	55,030	49.21	Diastylidae	**96.2**	Diastylidae	81.1
				Thyasiridae	0.7	Ophiuridae	4.3
				Ophiuridae	0.5	Ophiuroidea	4.2
5	89	91,995	66.70	Diastylidae	**93.6**	Diastylidae	85.0
				Thyasiridae	1.7	*Macoma sp.*	8.0
				Lumbrinereidae	0.9	Lumbrinereidae	2.7
6	72	1,105	8.21	Ampelicidae	15.6	Pharidae	58.4
				Diastylidae	13.6	Lumbrinereidae	13.6
				Thyasiridae	12.9	Ophiuridae	6.5
7	55	1,450	3.25	Spionidae	47.2	Amphiurida	20.9
				Phyllodocidae	7.6	Rhyncocoela	15.5
				Tellinidae	5.5	Spionidae	10.8
8	101	49,478	30.83	Diastylidae	**98.4**	Diastylidae	97.9
				Macoma sp.	0.6	Gastropoda	0.8
				Lumbrinereidae	0.4	Lumbrinereidae	0.5
9	58	8,218	10.72	Spionidae	43.0	Pharidae	20.9
				Cirratulidae	13.4	Mactridae	19.6
				Magelonidae	8.7	Ampharetidae	16.5

seasonal variability in gray whale distribution and sighting rates offshore Kodiak may be related both to migration timing (Rugh *et al.* 2001) and to whale responses to prey availability and composition, as demonstrated elsewhere on their range (Darling *et al.* 1998, Dunham and Duffus 2001, Moore *et al.* 2003). The high counts of gray whales near Kodiak in 2000 and 2001 may have been related somehow to the 1999–2000 mortality event (Gulland *et al.* 2005), or to feeding opportunities resultant from ecosystem responses to the 1997–1998 El Nino in the North Pacific, although specific mechanisms for this remains unexplored. We note that Benson *et al.* (2002) report gray whales feeding on large surface swarms of euphausiids (*Thysanoessa spinifera*) in Monterey Bay, California, during May 1999, which they interpret as a short-term response to prey availability linked to the 1997–1998 El Nino and 1999 La Nina.

The cumacean densities sampled at the entrance of Ugak Bay are among the highest reported anywhere in the world. Cumaceans are usually considered atypical gray whale prey (Nerini 1984, Darling 1998, Dunham and Duffus 2002) and have a low dry weight energy content (14.33 J/mg) compared to amphipods (16.37 J/mg; Cauffope and Heymans 2005). In a prey sampling effort co-located with feeding gray whales at fourteen sites along the Alaskan coast from Wainright south to Dutch Harbor, cumaceans were the dominant species only at Icy Cape in the Chukchi Sea (Kim and Oliver 1989). Core samples from that site resulted in wet weight biomass values of roughly 169 g/m^2, 51% of which was attributed to cumaceans. In contrast, at our sampling site 5 in outer Ugak Bay, wet weight biomass was 1024 g/m^2, 75% of which was attributed to cumaceans. Because sampling methods differed between the two studies, these specific measurements must be compared with caution; however, the extreme densities of prey suggest that the Ugak Bay site offered gray whales an exceptional opportunity to feed on swarming cumaceans, at least during August 2002.

Available records suggest pockets of gray whales can be found, often feeding, from Kodiak to northern California. These records include (1) gray whales reported here; (2) the report of approximately ninety feeding whales near Yakutat Bay in May 2000 (Moore, unpublished data); (3) summertime occurrence of roughly 30–50 gray whales feeding along the outer coast of Southeast Alaska since the mid-1990s;[2] and (4) whales routinely photo-identified at various sites between Kodiak and northern California (Calambokidis *et al*. 2004). Although the gray whales offshore Kodiak may simply represent a reoccupation of former feeding areas, there appears to be now some consistency in their use of these waters. When combined with observations of localized aggregations reported in Calambokidis *et al*. (2004), a pattern similar to that described for white-bearded wildebeests (*Connochaetes taurinus mearnsi*) is suggested wherein roughly 3,000 animals out of a population of 14,000 behave as "residents" that forage and breed in localized areas that are unused by the main migratory population (Estes 2006).

In summary, we suggest that (1) as flexible foragers, gray whales are responsive to feeding opportunities along their entire range; (2) an expanding ENP population may be meeting with new and more variable forage challenges in the wake of alteration of marine ecosystems associated with global climate warming; and (3) research focus on this population may provide novel insight into large whale population dynamics, behavioral ecology, and the capacity of a mysticete species to exploit disparate forage opportunities and respond to environmental changes.

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[2] Personal communication from Jan Straley, University of Alaska Southeast, 1332 Seward Avenue, Sitka, Alaska 99835, U.S.A., 13 January 2006

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Recent Observations of the Gray Whale in British Columbia

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Hatler, D. F. and J. D. Darling. 1974. Recent observations of the gray whale in British Columbia. Canadian Field-Naturalist 88: 449–459.

Abstract. Observations of gray whales along the British Columbia coast confirm the occurrence of a peak in spring migration there during the first half of April, and provide further evidence that the animals follow a near-shoreline route while both north- and south-bound, especially along Vancouver Island. At Wickaninnish Bay on the central west coast of Vancouver Island, gray whales have been seen regularly, apparently feeding, during each of nine summers 1965–1973 except 1967, and similar sightings have been made each month between October and February in both 1971–1972 and 1972–1973. Among the gray whales recorded have been two females with young, one pair of which summered at Wickaninnish Bay in 1969, a pair engaged in mating or erotic play, a young animal apparently feeding in protected inlet waters, and a naturally marked individual that appeared at Wickaninnish Bay in 1970, 1972, and 1973.

Introduction and Methods

In their definitive work on the gray whale (*Eschrichtius robustus*), Rice and Wolman (1971) have drawn largely from data obtained along California shores, near the southern end of the eastern Pacific population's range. Information from farther north, particularly that relating to aspects of migration and feeding, has been provided largely by Pike (1962) and Pike and MacAskie (1969). During recent years we have had frequent opportunity to observe gray whales along the central west coast of Vancouver Island and have gathered additional information from knowledgeable residents of that area. Our data, given below, supplement the picture of migration given by the authors cited above, and introduce some previously undocumented aspects of the occurrence of the gray whale along this lower central portion of its annual range.

Most observations were made incidental to other work. While carrying out an inventory survey of mammals in Pacific Rim National Park (Hatler 1972), the senior author observed whales both from shore and from a small boat at irregular intervals in 1971 and 1972, and obtained additional information from local crab fishermen who regularly worked in the main whale-watching areas. The junior author observed whales throughout the summer of 1972 while conducting guided sea-mammal observation tours for a private concessionaire in Pacific Rim Park, and prepared a gray whale bibliography and status report for the park during the following winter and spring (Darling 1973). Observation forms were provided to several lightstations along the west coast of Vancouver Island in 1972, and personnel at some of these provided records of migrating whales during winter and spring 1972–1973, as weather and opportunity permitted. Observations, again at irregular intervals, continued through September 1973.

We are confident that most observations reported here involved gray whales and not other species. All were made within 1 mile from shore and most were within 1/2 mile. Pike (1962) has shown that such near-shore sightings rarely involve species other than gray whales, a conclusion which our observations support but which we did not accept complacently. We actively looked for other species, but rarely saw them. At Wickaninnish Bay especially, approaches to 100 m or less of observed whales was the rule, and under such conditions we nearly always saw the series of humps or "knuckles" along the posterior dorsum which is characteristic of the gray whale. The crab fishermen who provided data are keen observers who are thoroughly familiar with this and other common species, and among our respondent lightkeepers, at least two indicated their competence by noting "identification not certain" for some sightings they recorded on our observation forms.

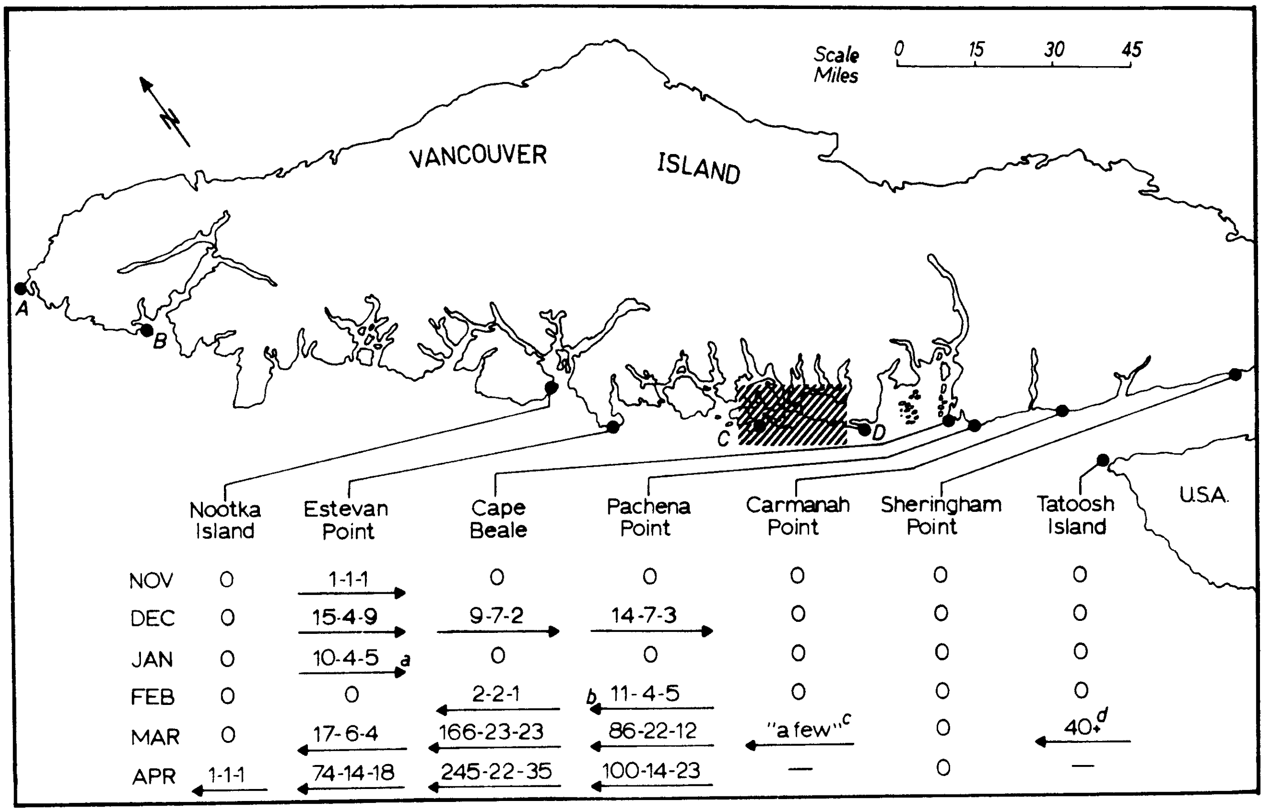
Results

Migration

Counts and direction of movement of passing gray whales, as recorded by lightkeepers along the west coast of Vancouver Island, are shown in

Figure 1. As Pike (1962) has suggested, the paucity of observations of southbound animals along the Vancouver Island coast in winter has probably been due largely to the inclement weather and subsequent poor visibility typical of that time of year. He had just three significant winter observations from this area and a few more from other British Columbia locations, but from these he inferred that gray whales pass British Columbia shores in December and January with a peak in late December. Pike and MacAskie (1969) provided additional records including sightings of small groups of gray whales passing Langara Island (northwest Queen Charlotte Islands) in October–December 1960, peaking in December, and a count of 22 moving south past Kains Island, northwest Vancouver Island (see Figure 1), in December 1962. Our lightstation records (Figure 1) also indicate a rather strong southward movement in December. Despite the fact that weather conditions made observations impossible on 10–15 days or more, whales were seen on 7 days of that month at both Cape Beale and Pachena Point. We emphasize that these counts are minimal as the light personnel were not spending long hours looking for whales, but were simply recording them when they saw them.

Information received from marine mammal biologists M. Bigg and I. MacAskie (personal communication) includes a lightkeeper's sighting of 12 to 15 gray whales moving south past Cape St. James (south Queen Charlotte Islands) be-



	Nootka Island	Estevan Point	Cape Beale	Pachena Point	Carmanah Point	Sheringham Point	Tatoosh Island
NOV	0	1-1-1 →	0	0	0	0	0
DEC	0	15-4-9 →	9-7-2 →	14-7-3 →	0	0	0
JAN	0	10-4-5[a] →	0	0	0	0	0
FEB	0	0	2-2-1 ←	[b] 11-4-5 ←	0	0	0
MAR	0	17-6-4 ←	166-23-23 ←	86-22-12 ←	"a few"[c] ←	0	40+[d] ←
APR	1-1-1 ←	74-14-18 ←	245-22-35 ←	100-14-23 ←	—	0	—

FIGURE 1. Observations, by Vancouver Island lightkeepers, of apparently migrating gray whales, November through April 1972–1973. Closed circles indicate locations of Department of Transport Lightstations, including four from which no data were obtained (A, Cape Scott; B, Kains Island; C, Lennard Island; D, Amphitrite Point), but which are mentioned in the text. The three numbers shown for any given month and location are, respectively, the total number of whales counted during the month, the number of days on which whales were counted, and the maximum number seen on any one day. The arrows beneath the sets of numbers indicate the direction observed whales were travelling (left=north; right=south). The cross-hatched area is that shown at larger scale in Figure 2.

Explantory footnotes, tabular data:

[a] One whale moving north, it and one southbound animal not positively identified as gray whales;

[b] Single gray whales seen moving south on 22 and 26 February;

[c] Those seen probably gray whales, but not positively identified;

[d] All seen during the period 1–3 March; no other reports received from this station.

tween 20 December 1972 and 3 January 1973, and an additional 10 (not positively identified) on 7–9 January. Bigg saw about a dozen southbound gray whales during a flight along the west coast of the Queen Charlotte Islands in December 1971, and in a flight on 9 January 1973, the junior author saw six gray whales moving slowly southeast in Wickaninnish Bay (see Figure 2). December observations at three of our respondent lightstations occurred on the following days (numbers seen each day shown in parentheses):

Estevan Point:
5th (1), 7th (4), 8th (9), 10th (1);

Cape Beale:
2nd (1), 4th (2), 6th (2), 7th (1), 10th (1), 13th (1), 14th (1), 31st (1 found dead);

Pachena Point:
3rd (2), 6th (3), 12th (1), 17th (4), 21st (2), 29th (2).

Thus, during winter 1972–1973, gray whales moved steadily by the British Columbia shores throughout a 5- to 6-week period including all of December and early January. This result is in general agreement with the winter movement pattern suggested by Pike and MacAskie (1969), although these authors' conclusion that there is a peak movement in late December now seems less certain. Weather conditions may have obscured either this peak during our observations or the strength of the early December movement during theirs. Future observers may find that southbound gray whales do not peak in local occurrence to the extent that they do while heading north in the spring.

Among the April lightstation records, 56 of 74 whales counted at Estevan Point, 98 of 100 at Pachena Point, and 210 of 245 at Cape Beale were seen by the 15th of the month. Thus, our records precisely corroborate those of Pike (1962), who wrote that northbound whales appear on the British Columbia coast in February and peak during the first two weeks of April. Pike and MacAskie (1969) have later indicated that there is relatively little movement by Vancouver Island shores in spring until late March.

Our observations from Estevan Point, Cape Beale, and Pachena Point (Figure 1) along with earlier records from Lennard Island, Amphitrite Point (Pike 1962), and Kains Island (Pike 1962; Pike and MacAskie 1969) indicate that numbers of whales do pass close to the Vancouver Island shore, along most of its length, during both north- and south-ward migrations. This is contrary to the views of Gilmore (1960, 1969) who postulated a more pelagic route across the Gulf of Alaska, which resulted in most southbound animals' bypassing Vancouver Island in the fall. He felt that the first landfall occurred at about the Columbia River. The additional records given above for the Queen Charlotte Islands suggest that Pike (1962) was correct in concluding that most whales pass from the north tip of Vancouver Island to the west side of the Queen Charlottes. But the paucity of records from the mainland coast along the east side of Hecate Strait at this latitude may be reflective more of an absence of interested observers rather than an absence of whales. H. D. Fisher (personal communication) saw three gray whales moving north in Higgins Passage at the mouth of Milbanke Sound, mainland coast (52° 20′ N, 128°30′ W), on 11 April 1973.

At the south end of Vancouver Island, the relative lack of information at Carmanah Point (as compared to that from Pachena Point just 18 miles north) and the complete absence of sightings at Sheringham Point (see Figure 1) may indicate that most whales leave (and arrive at) the Vancouver Island shoreline somewhere between Pachena and Carmanah and cross the Strait of Juan de Fuca to (or from) Cape Flattery on the Washington Coast. We are aware of a single record from east of Sheringham, that of Carl (1967) who reported that one animal apparently summered in inside waters near Victoria during 1967.

Occurrence in Summer

Rice and Wolman (1971) acknowledge that not all gray whales migrate to the Arctic in the summer, and list a number of scattered and irregular summer sightings at locations from southern California to the Queen Charlotte Islands. It is common local knowledge, but it has not been documented previously, that gray whales are seen regularly each summer in the immediate vicinity of Wickaninnish Bay, a shallow sand-bottom bay adjacent to Long Beach in what was formerly Wickaninnish Provincial Park and is now Pacific Rim National Park (see Figure 2). The first significant observations on this regularity of occurrence were noted by provincial naturalists in reports on their summers in the area. Table 1 summarizes their information and that which we have gathered subsequently, providing coverage over nine summers from 1965 through 1973.

These data show that occurrence throughout the summer (roughly June through September) has been common, although a recurring feature (1965, 1966, 1973) has been a temporary scarity or absence in late July and August. Since most observations have been limited to Wickaninnish Bay, it is possible that these "absences" have been purely local. Gray whales have been seen, at times other than during migration, in Florencia Bay just south of the above area and in Schooner Cove, Cox Bay, and Ahous Bay (Vargas Island) to the north (see Figure 2). During the July period of apparent scarcity in 1973, gray whales were seen in Florencia Bay on at least one day (T. R. Bailey, personal communication). Another possibility is that these temporary disappearances and the nearly complete absence in summer 1967 have reflected changing feeding conditons in this area. The question of whether gray whales actually feed there is discussed later in this paper.

During the years of our observations, 1971–1973, the extent of our opportunity to record gray whale observations has varied considerably. In 1971 neither of us was present in the Wickaninnish Bay area after the April migration period until 1 August. On that date the senior author and park naturalist D. Foskett, conducting an aerial census of sea lions (*Eumetopias jubata*), counted four different gray whales between Sea Lion Rocks and the north end of Wickaninnish Bay. On 10 August and 26 September small-boat censuses of the same area by the senior author and an assistant, J. Biggar, yielded counts of five and three gray whales respectively. During this late summer period, sightings were common. Crab fisherman D. Arnet (personal communication) reported seeing as many as 10 whales (extent of duplication unknown) during a day's fishing on 13 September, but saw only two on 15 September. Vancouver Natural History Society members on charter boat tours near Sea Lion Rocks saw three, two, and three whales, respectively, on 18 and 26 September and 2 October (R. W. Campbell, personal communication), and Biggar saw four gray whales in Schooner Cove on 28 September.

TABLE 1 — Summer occurrence of gray whales in the vicinity of Wickaninnish Bay, Vancouver Island, British Columbia, 1965–1973

Year	Source	Remarks
1965	Buffam (1965)	Gray whales seen "virtually every day of the summer" but less commonly during the first three weeks of August than before or after this period
1966	Buffam (1966)	Seen until 15 July, but then disappeared and only one sighted from then through August
	Pike and MacAskie (1969)	One stranded in Florencia Bay in mid-August
1967	Campbell (1967)	Scarce all summer (19 June to 6 September), with only two sightings made: single whales on 24 June and 11 August
1968	Campbell (1968)	"At least six whales frequented Wickaninnish Bay the entire summer" (4 June through 2 September)
1969	Campbell (personal communication)	Gray whales again present throughout the summer
1970	Belton (1970)	Gray whales seen commonly during summer
1971	This study	Whales present at least through August and September (details in text)
1972	This study	Up to six or seven whales seen almost daily between 29 June and 4 September (details in text)
1973	This study	Apparently present throughout the summer but with temporary period of scarcity during last two weeks of July (details in text)

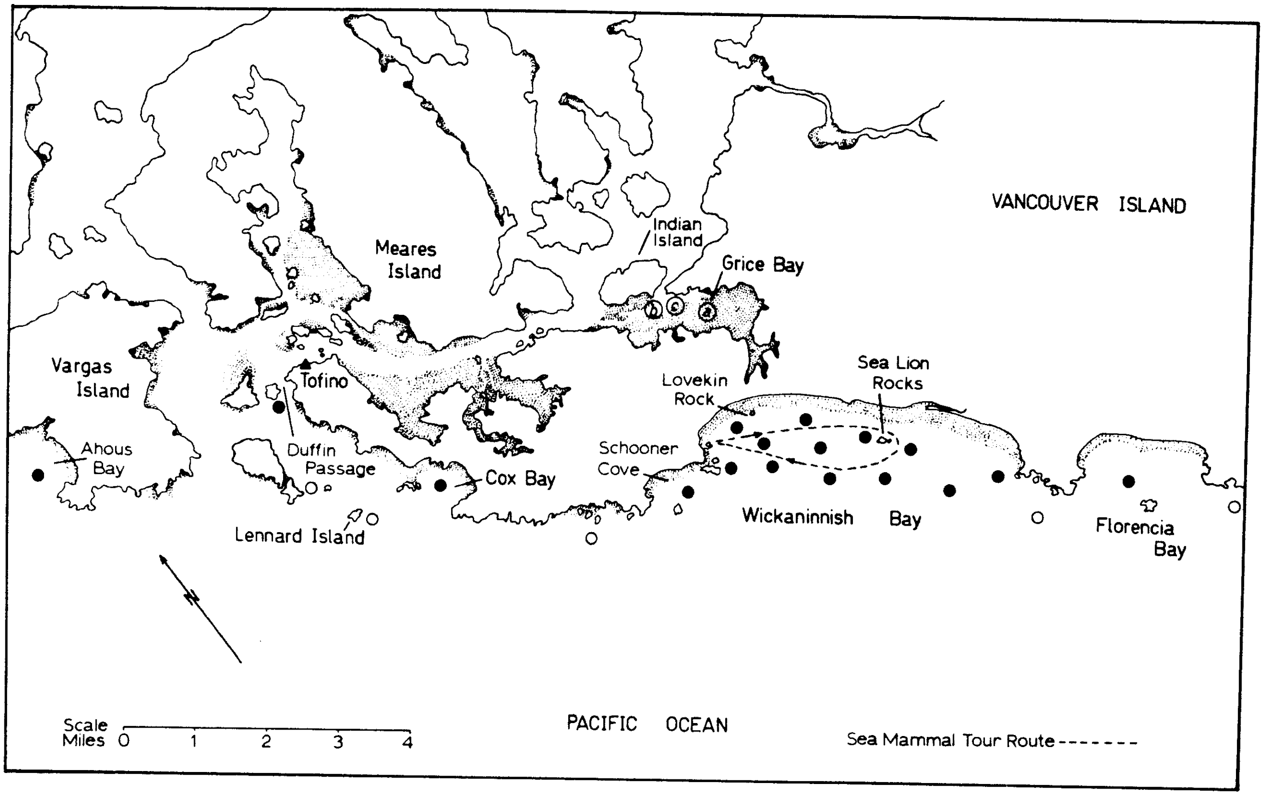


FIGURE 2. Observations of gray whales in the vicinity of Wickaninnish Bay, Vancouver Island, British Columbia, at times other than during migration. Closed circles represent approximate locations at which gray whales have been seen more than once, while open circles indicate single sightings. The three sightings in Grice Bay (labelled a, b, and c) were made on 27, 28, and 29 October 1971 respectively. Stippled areas indicate tidal mudflats (inside waters) and sand beaches (exposed waters). The entire area shown is indicated by a cross-hatched rectangle on Figure 1.

Our most intensive series of observations was recorded in summer 1972 when the junior author operated a commercial cruise boat for Pacific Rim Expeditions, Ltd. This firm's sea-mammal observation tours, run daily as weather permitted, covered an approximately 3-mile stretch of water between the north end of Wickaninnish Bay and Sea Lion Rocks (see Figure 2), and whales were seen only when they occurred on or near this route. From one to perhaps seven gray whales were seen each day of operation (29 June through 4 September) except on 14 and 24 August and 4 September. On these 3 days when no whales were seen, less than the full day of cruises was run owing to adverse weather conditions. The maximum count of six or seven (depending upon possible duplication) was obtained on 6 July; on 27 other days during which counts were possible numbers seen occurred in the following frequencies: one whale (5), two (2), three (8), four (5), five (6), six (1).

In 1973 our observations were again sporadic, but were sufficient to show that gray whales were present in the Wickaninnish Bay vicinity throughout the summer. Sightings of gray whales were a regular feature of nature walks conducted by park naturalists, and there were few days on which no whales were seen. The maximum count for any one time and place was seven, obtained by the junior author between north Wickaninnish Bay and Schooner Cove on 20 June. The apparent scarcity in late July, mentioned previously, was reported by the cruise-boat operators who were greatly disappointed at the fact, after having all but guaranteed visitors an opportunity to see whales. Sightings increased again in August, and the junior author counted four along the cruise route on 22 August and two just to the south on 4 September.

Among the summer observations, of particular interest have been sightings of apparent mother-young pairs. One cow and calf occupied

Wickaninnish Bay for most of the summer in 1969 (R. W. Campbell, personal communication). The senior author, on board a commercial cruise vessel near the north end of Wickaninnish Bay in July of that year, saw this pair but was unaware of the significance of the observation at the time, and more precise details were not recorded. There are apparently no published records of adults with young summering south of the Arctic feeding grounds, and even sightings during migration are exceedingly rare (Rice and Wolman 1971). We have one other probable record of a cow and calf gray whale: on an exploratory cruise with Pacific Rim Expeditions owner, J. Hudnall, on 29 June 1972, we were observing two feeding whales some 350 m northwest of Sea Lion Rocks (Figure 2) when a third suddenly blew just a few meters from the rocks and within 100 m of our boat. Attention was shifted to this third whale just as what appeared to be a very small whale surfaced and blew quickly, immediately beside it. Although it seemed evident that this was a mother-young pair, both disappeared seconds later and we were unable to find them again for confirmation. On 19 and 20 July a large and small gray whale pair, the two always side by side and blowing in unison, were seen at close range by the junior author and Hudnall. They were assumed to be a cow and calf, and may have been the pair glimpsed on 29 June.

Occurrence in Winter

Table 2 lists some of our gray whale observations between October and February in each of two winters (1971–1972 and 1972–1973). We have recorded whales at least once during each month of this period during both years, in partial confirmation of the remarks of longtime crab fisherman John Svoboda, Sr. (personal communication) who has told us that at least a few whales are always present. We stress that heavy surf, wind, fog, and rain are the rule at this time and on most days whales are not easily seen. We do not know where the whales weather out severe storms, but whales (presumably the same ones) may be seen in Wickaninnish Bay within a few days both before and after such storms, suggesting that they do not go far. During moderately rough weather, i.e., when observation is difficult but is still possible, whales may often be seen at the semi-protected north end of the bay, just north of Lovekin Rock (Figure 2).

Southbound migrants pass the Vancouver Island coast largely in December and perhaps early January, while some northbound animals appear

TABLE 2 — Observations of gray whales in the vicinity of Wickaninnish Bay, Vancouver Island, British Columbia, winters of 1971–1972 and 1972–1973

Date	Remarks[1] and Source[2]
27 Oct. 1971	At least one at north end of W. Bay[3] (dh)
5 Nov. 1971	At least three blowing near Lovekin Rock (dh)
15 Dec. 1971	One seen during sea-mammal census flight along Pacific Rim National Park shoreline, that in W. Bay (dh)
27 Dec. 1971	Independent reports from two crab fishermen that only one seen during day, that at south end of W. Bay (D. Arnet; J. Svoboda, Jr.)
13 Jan. 1972	One "feeding" among flock of sea ducks near Lovekin Rock (dh)
19 Jan. 1972	Two "feeding" 150–200 m out from Lovekin Rock (dh)
3 Feb. 1972	Four or five different animals seen in day's crab fishing at W. Bay (J. Svoboda, Jr.)
10 Mar. 1972	Two at Sea Lion Rocks and one north of W. Bay (D. Arnet)
24 Oct. 1972	Two in north half of W. Bay (dh)
1 Nov. 1972	One just south of Sea Lion Rocks (dh)
16 Nov. 1972	One "feeding" at north end of W. Bay (B. Campbell)
23 Nov. 1972	Two in north W. Bay; one behaving as though feeding (jd)
24 Nov. 1972	One apparently feeding in north W. Bay (jd)
2 Dec. 1972	Four in W. Bay near Sea Lion Rocks (J. Dyer)
7 Dec. 1972	One "breeched" twice in north W. Bay (jd)
11 Dec. 1972	Three near Sea Lion Rocks (J. Dyer)
13 Dec. 1972	Two at north W. Bay (jd)
14 Dec. 1972	Three apparently feeding near Sea Lion Rocks; observed at close range from a small boat for about one hour (jd)
28 Dec. 1972	One in north W. Bay (jd)
9 Jan. 1973	Two blowing at 3- to 4-minute intervals near Lovekin Rock; six moving slowly southeast just north of W. Bay (jd)
10 Jan. 1973	Several seen coming from the northwest into W. Bay (G. Trenholme)
6 Feb. 1973	Three near Sea Lion Rocks; diving pattern of two suggested feeding (jd)
7 Feb. 1973	One near Sea Lion Rocks (G. Trenholme)
23 Feb. 1973	One in south W. Bay blowing and diving in shallow water (B. Campbell)

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[1] All observations by authors made on occasional visits to the area, as weather permitted.

[2] Source = observers. The initials dh and jd designate the senior author and junior author respectively.

[3] W. Bay = Wickaninnish Bay.

as early as February although they rarely show up in numbers until mid-March. This schedule would suggest that the vanguard of the northbound might meet the laggards of those moving south in our area, and it is difficult to determine the significance of our winter observations. As the remarks in Table 2 show, and as the discussion immediately following will indicate, we have seen gray whales apparently feeding in Wickaninnish Bay during January and February of two consecutive years, a time during which most of the population is supposed to be fasting in the warm waters off the coast of lower California (Rice and Wolman 1971). Since "feeding" animals have also been observed in the months preceding this period, it is tempting to speculate that some animals actually spend the winter at Wickaninnish Bay and do not make the full migration south. It would be necessary to have recognizably marked whales present in order to confirm this.

Feeding

Pike (1962) reviewed information on feeding and concluded that the gray whale "feeds little outside its arctic habitat." Gilmore (1969) stated flatly that gray whales do not feed on the southward migration, and Rice and Wolman (1971) support his statement for California shores with their analyses of 180 stomachs, none of which contained food. The stomachs of all but two of the 136 northbound whales examined by these authors were also empty, as were the stomachs of 10 animals taken in April off northwestern Vancouver Island (Pike 1962), although there were some intestinal contents in the Vancouver Island specimens, and Pike noted that these animals had "probably done some feeding." Later, reporting an observation of whales apparently feeding in Wickaninnish Bay in April, Pike and MacAskie (1969) generalized that some northbound animals do stop to rest or feed in British Columbia waters. More recently, three gray whales observed at Rose Spit, Queen Charlotte Islands, on 11 April 1973 were causing "upwellings of sand and mud from the bottom," i.e., perhaps feeding (H. D. Fisher, personal communication). Whether or not gray whales feed while migrating, it seems evident that those animals known to have spent all or much of the summer well south of the Arctic (including those listed by Rice and Wolman (1971) and those reported in this paper) must have sustained themselves by feeding locally.

Though there have been no whales collected in Wickaninnish Bay, thus making it impossible for us to demonstrate that they actually have food in their stomachs, we nevertheless are almost certain that they are feeding there, possibly throughout the year. Most of our summer observations, and many from other times of year, involve animals in water ranging in depth from about 5 to 15 m, and engaged in the following activity. Characteristically, a long dive of 2 to 3 minutes is followed by a series of short blows, usually three, the first of which is accompanied by the release of a brownish stain into the water (presumably waste material from the baleen). Following these short emergences, the animal arches forward in another deep dive, and during this motion it exposes most of its dorsal surface, although the flukes rarely appear. Whales engaged in this activity often worked back and forth through the same small area for long periods of time and the junior author, while piloting the cruise boat in 1972, noted that these could be encountered in the same general area on successive trips throughout one day.

Among our October–February observations, a number involved animals engaged in the above activity, our description of which matches the "feeding behavior" described by Wilke and Fiscus (1961). These authors have observed "seabirds" settling into the brown muddy patches produced by surfacing whales, implying that organic matter is included in the material released; we have seen gulls do the same at Wickaninnish Bay, and have noticed that "feeding" whales are often accompanied by sea ducks. On 19 January 1972, the senior author watched two whales apparently feeding near Lovekin Rock for over 1 hour. During this time two bunches of scoters (*Melanitta perspicillata* and *M. deglandi*) had divided from one large raft and each was following a whale. The whales moved back and forth over an area of less than 150 m^2 during the period of observation, changing direction frequently, and each group of ducks (most members of which were diving regularly and apparently feeding) maintained orientation with its respective whale. It was evident that either the scoters and the whales were exploiting a common food source or that the scoters were opportunistically snatching organisms stirred up by the whales.

In considering the rather well-documented concept that migrating gray whales do not feed, we are left with three alternative explanations for our observations. (1) The whales of our observations are not actually feeding. As indicated, we believe that they are; they at least appear to be trying. (2) These whales are not migrating. Because we have not been working with individually marked whales, there is little evidence either for or against this alternative and the question must be deferred at this time. Comments on one recognizable whale will be presented later. (3) Some or all migrating whales feed in suitable habitats along the migratory route, but there are few such areas south of the Arctic and perhaps none of significance south of Vancouver Island. This alternative seems reasonable and would explain the absence of food in the digestive tracts of animals off the California coast, where many of the absolutes of gray whale biology have been established.

Occurrence in Protected Waters

Gray whales occasionally enter the more protected waters of Clayoquot Sound, 10 miles north of Wickaninnish Bay (Figure 2). On 30 April 1969 the senior author observed one in Duffin Passage near the mouth of Tofino Harbour. The late R. Folker (personal communication) had seen gray whales "rubbing themselves" on a gravel bar at that location several times in the past. The most extreme inland record we are aware of occurred in October 1971. A Tofino resident had reported seeing a whale blow in Grice Bay (8 miles or more inland from Tofino; see Figure 2) on about 20 October, but had acknowledged that he had seen it at some distance and that it could have been a killer whale (*Orcinus orca*). This would not have been an unusual sighting, and the report was not followed up.

On 27 October, the senior author visited the area to carry out other biological duties and found a gray whale in 3–4 m of water in this mud-bottom bay. The animal was approached in a small boat to within 30 m to confirm identification, and was then watched for several minutes. It was a small animal, no more than 9 m in length, and it was apparently feeding. This whale was still present on both 28 and 29 October, but was working the deeper waters (6–10 m) near Indian Island on those days (locations plotted in Figure 2). Duties elsewhere made further observation of this animal impossible, and we do not know when it left Grice Bay. The earlier report from the Tofino resident suggests that it may have been present there for 10 days or more.

Possible Mating

On 26 April 1971, the senior author was attracted to a disturbance in the water about 1/2 mile offshore at the north end of Wickaninnish Bay. Through a 20-power telescope set up on a nearby knoll, he obtained a clear view of two gray whales engaged in vigorous activity. At least one of the animals frequently rolled over on its back with its flippers protruding from the water. There was much rolling and sounding, the latter frequently occurring with the flukes coming high out of the water and slapping the water surface with a large splash. Once both animals sounded, both sets of flukes showing at once and disappearing together.

Most often only one animal showed at the surface except when they were moving. Then one followed the other, both close to the surface and blowing often. These straight-line movements were usually only 50–75 m, at which time the trailing animal (perhaps the female judging from the observations of others (e.g., Sauer 1963)) initiated activity by speeding up, sounding, and coming up beneath the other. Frequently this started a series of rolls. On several occasions the male's conspicuously pink, erect penis showed clearly as the animal rolled over on the surface. Once the other animal's head emerged from the water and nudged the penis. Heads were seen frequently, but always only one at a time. These two whales maintained nearly continuous activity from 15:05 to 16:35 Pacific Standard Time. Observation was continued until 17:20, by which time no further activity had occurred. There were then five whales in the area, all apparently feeding, and there was no obvious pair among these, thus it was not evident which had been the original two. It was not possible to determine whether copulation had actually occurred, but the erotic nature of the activity was evident.

Rice and Wolman (1971) have provided sufficient histological evidence that reproductively functional breeding occurs before the spring migration. But they cite other records of apparent mating activity in northern areas, including observations from northern California, Washington, and northern Alaska. It may be that erotic play, and perhaps copulation, is a common recreational pursuit in this species.

A Naturally Marked Whale

Hubbs (1959) has called attention to conspicuous whitish patches, constituted by groups of epizoites and/or scars, which develop on the skin of gray whales. During the 1972 daily summer cruises at Wickaninnish Bay, the junior author was subjectively certain that he recognized some individuals repeatedly on the basis of these markings, but such information is difficult to document. One whale, however, was easily recognizable and we have obtained photographic proof that this animal has appeared in Wickaninnish Bay on more than one occasion (or perhaps over a long period of time). This whale possessed a large, rounded and distinctly orange-colored scar on its left side just below the "knuckles" on the lower back.

Figure 3 shows two views of this whale. The first photograph (A) was obtained by the senior author when the animal was first seen in October 1970. At this time it was "feeding" in company with two others near Sea Lion Rocks in Wickaninnish Bay. Without knowing that this photograph had been taken, the junior author first noted seeing this animal on 20 August 1972, recognizing it as one he had seen several weeks previously. We compared notes the following winter, and determined to watch closely for this whale. It appeared again during the summer of 1973, and Darling obtained the photograph of Figure 3B on 12 July.

The whale with the orange scar was seen again on 12, 18, and 20 August by cruise boat operator A. Oliver (personal communication), who had accompanied Darling when the animal was photographed on 12 July; on 22 August Darling obtained a third photograph of this animal. It was last seen during that summer on 2 September, by Oliver.

Thus, it is evident that at least one gray whale has been faithful to the Wickaninnish Bay area, returning to it in at least three of four summers between 1970 and 1973 and conceivably even residing there the year round during that time. Observation effort has been sporadic enough, especially during the winter months, that it could easily have been missed most of the time. In addition, as mentioned earlier, gray whales have been seen "feeding" in other areas within 10 or 12 miles of Wickaninnish Bay; if the naturally marked whale had occupied any of these areas, we probably would not have seen it, owing to our concentration of activities at Wickaninnish.

Another whale with a large white patch on its upper right side just below the rudimentary dorsal fin was photographed in Wickaninnish Bay on 14 December 1972. A photograph taken near Sea Lion Rocks on 22 August 1973 appears to portray this same animal, but we cannot generate the certainty, in this case, that is possible with the orange-scarred individual. The photos in Figure 3 have been reproduced from color transparencies; duplicate transparencies of these, of the 22 August (third) photo of the orange-scarred whale, and of the two photos of the white-scarred whale have been placed on file (PDF Number 320) at the British Columbia Provincial Museum, Victoria, British Columbia and are available for loan. Interested persons should write to Assistant Curator of Birds and Mammals, R. W. Campbell, at that institution.

Discussion

The annual migration route of the gray whale covers a distance, one way, of over 4500 miles (Pike 1962). Along this route, studies have been concentrated chiefly within the southernmost 500 miles, with occasional observations providing at least moderate knowledge of the species' occurrence as far north as Vancouver Island (about 1500–1700 miles north of the breeding area). As results reported in this paper indicate, our knowledge even at this latitude is fragmentary. Little is actually known of the species over the remaining (northern) two-thirds of its annual range, and many of the assumptions about its occurrence there (chief among which seems to be that it does nothing over most of this distance except swim) may be unwarranted.

We have found that gray whales may be seen, apparently feeding, during all months of the year at Wickaninnish Bay, Vancouver Island, British Columbia. This fact is somewhat at variance with previously published work, which has established that *most* members of the eastern Pacific population annually migrate between arctic waters where virtually all annual feeding is done, and lower California breeding grounds. If Wickanin-

FIGURE 3. A recognizably marked whale seen repeatedly in the Wickaninnish Bay area. (A) Photograph obtained when animal first seen, in October 1970. (B) The same whale, photographed on 12 July 1973.

nish Bay is the only area south of the Arctic which is occupied in the manner we have described, then our observations are of little consequence. But if small "pockets" of habitat between southern Vancouver Island and Alaska are regularly occupied by whales in this way, then it will be important to learn the nature of this occurrence. For instance, if it were found that certain classes of whales, such as first-year animals or non-breeders of one or both sexes, often do not make the complete migration to the breeding grounds, then the very sophisticated data on population dynamics obtained by Rice and Wolman (1971) could be badly biased. Having said this, we hasten to point out that we have no evidence that this is so; our data are sufficient only to suggest that further evidence may be required to demonstrate that it is not.

Perhaps the eastern Pacific population, having recovered from severe overexploitation relatively recently (Rice and Wolman 1971), is only now in the process of recolonizing feeding areas used previously. Perhaps the paucity of sightings outside migration periods has been due largely to an absence of observers. We received an unconfirmed report of four gray whales feeding near Nootka Island, 65 miles north of Wickaninnish Bay, in August 1973, and Pike and MacAskie (1969) report that "several gray whales [were seen] in late August and early September" along the northern Queen Charlotte Islands. Both of these areas are more accessible than many others one might name between Wickaninnish Bay and arctic Alaska, yet neither is regularly frequented by potentially reporting observers; therefore regular occurrence, if it occurs, could easily go undetected.

Clearly our own data, obtained incidentally and sporadically, are deficient. We know only that gray whales occur regularly in Wickaninnish Bay. We do not know certainly that the same whales occur throughout the summer. If as we suspect, some do, how far do they range? We do not know the extent of local turn-over, if any, during migration nor the extent, if at all, to which migrating whales feed in the area. What food organisms are available in Wickaninnish Bay? The sex, age, and condition of most whales frequenting the bay has been largely unknown. Are whales seen in January and February in Wickaninnish Bay among those seen the previous (or following) summer, or are they others which do not complete the southward migration, or are they successive sets of migrants all of which eventually pass by? What is the migration route north of Vancouver Island? Is Wickaninnish Bay the only regularly frequented feeding (resting, staging) area south of the Arctic? An important function of this paper is to suggest that though the answers to all of these questions are presently unknown, perhaps none are unknowable.

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Addendum

In late spring, 1974, the naturally marked (orange-scarred) whale reappeared in Wickaninnish Bay and reportedly stayed there throughout the summer. It was again photographed twice by Darling, on 19 May and 30 July.

The Gray Whale

Eschrichtius robustus

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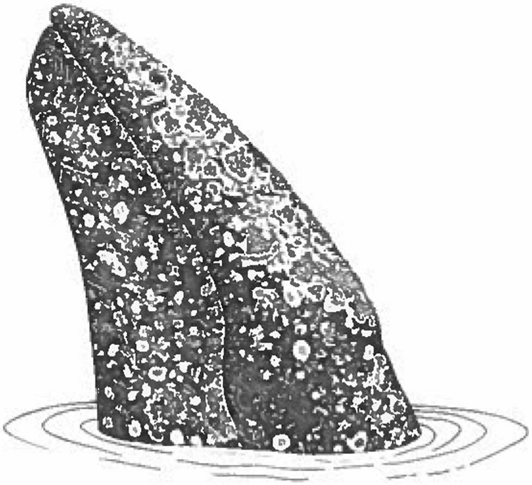

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Gray Whales off Vancouver Island, British Columbia

James D. Darling

Introduction

Each spring, gray whales (*Eschrichtius robustus*) migrate from calving lagoons in Baja, California, along the west coast of North America to feeding grounds in the Bering and Chukchi Seas (Scammon, 1869; Pike, 1962; Rice and Wolman, 1971). Although censuses conducted at Unimak Pass, Alaska (Hall *et al.*, 1977; Rugh and Braham, 1979; Chapter 10, this volume) indicated that the majority reached northern seas, sightings in summer off California, Oregon, Washington, and British Columbia suggested some whales terminate their migration far to the south (Gilmore, 1960; Pike, 1962; Pike and MacAskie, 1969; Rice and Wolman, 1971; Hatler and Darling, 1974; Darling, 1978; J. Sumich, cited in Chapter 13, this volume).

For waters off Vancouver Island, British Columbia (B.C.), three earlier studies demonstrated that (1) north- and southbound migrants pass along the west coast (Pike, 1962; Pike and MacAskie, 1969; Hatler and Darling, 1974; (2) gray whales regularly occur in summer along the outer coast (Hatler and Darling, 1974); and (3) at least one gray

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whale, recognized in photographs by its unique natural markings, remained off the island throughout one summer and returned for several years (Hatler and Darling, 1974).

Techniques for identifying individual whales from photographs were developed in the early 1970s for southern right whales, *Eubalaena australis* (Payne *et al.*, 1981); for killer whales, *Orcinus orca* (Bigg *et al.*, 1976; Bigg, 1982); for humpback whales, *Megaptera novaeangliae* (Katona *et al.*, 1979); and, as described here, for gray whales. Such techniques have supported long-term studies of abundance and behavior by allowing repeated observations of the same individuals without the need for tagging.

This chapter describes the abundance, stability, distribution, and general behavior of gray whales that spend the summer off Vancouver Island.[1] It is based on direct observations and photoidentifications over the 10 years since the first individuals were identified in 1970–1973 (Hatler and Darling, 1974).

Methods

STUDY AREA

Vancouver Island (Fig. 1) is located approximately halfway between the Mexican calving lagoons and the northernmost Chukchi Sea feeding grounds. Its west coast is characterized by sandy bays and beaches (e.g., Long Beach, Wickaninnish Bay, is 11.3 km in length) separated by rocky headlands or long stretches of rocky coast and cliffs. Along the central west coast, a system of protected waterways exists between coastal islands.

Small craft surveys (1972–1976) initially centered on a 40-km stretch of the west coast (circled in Fig. 1). After 1976, these surveys were gradually extended to cover most areas accessible to small craft between the entrance to the Straits of Juan de Fuca and Cape Scott (Fig. 1). With cooperation from personnel at 10 Vancouver Island lightstations (Fig. 2), much of the west coast of the island was monitored during the migrations. All observation was coastal, within 4 km of shore; no offshore surveys were attempted.

MIGRATIONS

The present study was primarily concerned with gray whales which summer along the Vancouver Island coast. Therefore, migrations past the island were observed mainly to determine the interval between the spring (northbound) and winter (southbound) migrants. Lightstation personnel recorded the following data on gray whales that they saw between November and May: date, number of whales seen, direction of movement, and appropriate comments. Observations were incidental to their other duties, but reports did include records of any whales noticed and the number of days of poor visibility. The reporting lightstations from south to north, as indicated by triangles in Fig. 2, were Sheringham Point, Carmanah Point, Pachena Point, Cape Beale, Amphitrite

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[1] This chapter summarizes an unpublished M.Sc. thesis by Darling (1978) which will be referred to throughout.

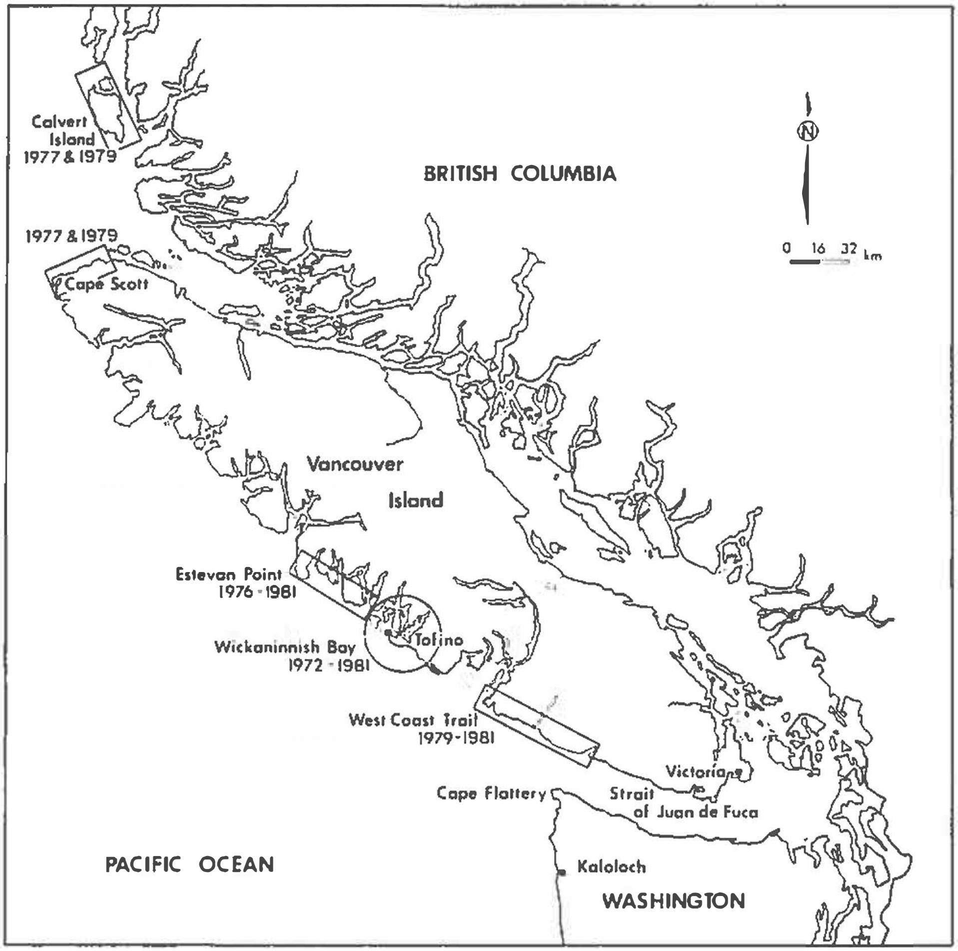

Fig. 1. *Vancouver Island, British Columbia, showing the central study area; areas surveyed frequently (circled) and areas reached less regularly (rectangles) in the years indicated.*

Point, Lennard Island, Estevan Point, Nootka, Kains Island, and Cape Scott. Lightstation records were used to monitor migrations in four seasons; 1972–1973 (reported in Hatler and Darling, 1974), 1973–1974, 1975–1976, and 1976–1977. In 1975 and 1976, the author also observed the spring migrations (February–June) from shore stations in the central study area and from small craft; the winter (November–January) migration was observed sporadically from shore; and incidental sightings reported by some residents of the area, particularly Pacific Rim National Park naturalists, were logged.

To establish timing of the migrations and indicate their peaks, all reporting lightstations were treated as one locus, that is, "the west coast of Vancouver Island." All sightings for each 2-week period, November 15 to May 1, from the four winters 1972–1973, 1973–1974, 1975–1976, and 1976–1977 were averaged. Intensive observations in the study area by the author, beginning in March of the years 1975 and 1976, allowed

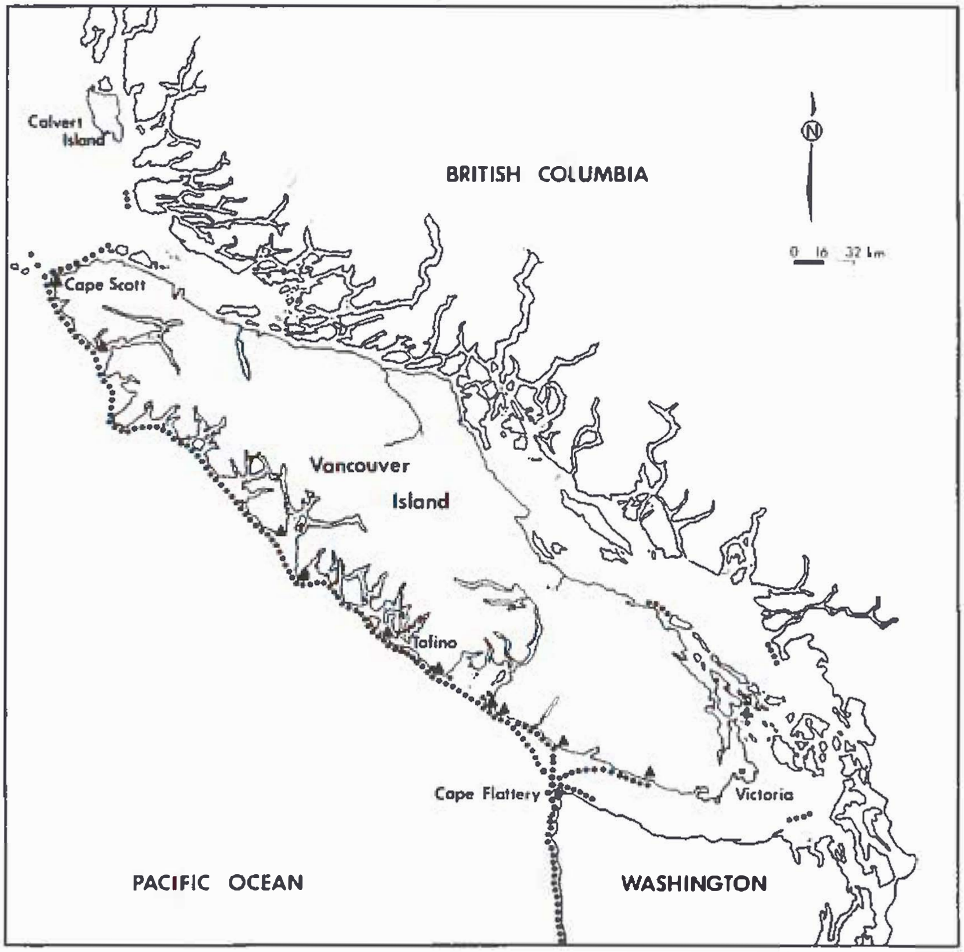

Fig. 2. *The spring (northward) migratory route of gray whales along the west coast of Vancouver Island, based on all data available, is shown by large dots. Triangles mark the position of the following lightstations, south to north: Sheringham Point, Carmanah Point, Pachena Point, Cape Beale, Amphitrite Point, Lennard Island, Estevan Point, Nootka, Kains Island, and Cape Scott.*

further delineation of the northward migratory period; there were no comparable observations of the southward migration.

INDIVIDUAL IDENTIFICATION

Photographs were taken of pigmentation patterns on visible portions of whales' backs[2] with a 35-mm camera with a 200- or 300-mm lens, Kodak Tri-X Pan Film pushed

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[2] Examinations of a cross-section of the skin of a dead whale indicated that these patterns were indeed pigmentation patterns and not superficial.

to 1600 ASA, and a shutter speed of 1000th/sec (cf. Bigg *et al.*, 1976; Bigg, 1982). Any scars or other prominent natural markings were also photographed.

Once photographed, the patterns were sketched on a data chart and corresponding film frames noted. These patterns were used for identification because for most animals they were the only part regularly seen. Most of the whales encountered were feeding in shallow water and rarely raised their flukes above the water surface. Therefore, identification by fluke patterns, as has been done in humpback whales (Katona *et al.*, 1979) was impractical.

The need to recognize individuals from side patterns complicated identification work because it required photographs of both sides to avoid duplication in counts. However, once photographs of both sides of an individual were on record, a picture of either side was sufficient. To avoid double counting in abundance analysis, when there were uncertainties about assignment of a photograph to an individual whale only photographs of the left side were used. Identification photographs were cataloged by year and records of repeat sightings established.

SUMMER POPULATION

During the summer, whales were located, observed, and photographed for individual identification from a small outboard-powered boat (5 m in length). Each whale's position, companions, and behavior were noted. Numerous reefs, islands, and other points in the study area allowed accurate positioning by landmark. Observations were made from within 100 m by the author and an assistant, usually during the 8 AM–1 PM period. Westerly winds beginning after noon are usual in the study area and make work after that time more difficult. Flights to locate whales were carried out weekly in 1976 and sporadically in other years. Behavioral observations were incidental to photo-identification and aerial survey work. Summer effort, summarized in Table I, varied from year to year.

Results

MIGRATIONS

Timetable

The first northbound whales passed Vancouver Island in February; numbers peaked the last 2 weeks of March then declined (Fig. 3 and Table II). Lightstation sightings were not reported after April 30. However, there were still some whales moving north in May and early June, as will be shown.

Southbound migrants pass Vancouver Island from November to late January with peak numbers during the last 2 weeks in December (Fig. 3 and Table II). From mid-January to mid-February, sightings were rare. The whales occasionally seen during this interval are discussed below.

Table I
Study Effort off the West Coast of Vancouver Island, B.C., 1972–1981

Year	Months of Observations	Methods				Number of Days Identification Photos Taken	Comments
		Boat	Aircraft	Shore	Lightstation		
1972	July–Dec.	Daily in July and Aug.	—	Sporadic	Nov. 1–Apr. 30, 1972–1973	<5	Observations incidental to operation of whale-watch boat; also Dec. 14 boat survey and identification photographs
1973	Jan.–Dec.	Occasional May–Sept.	—	Sporadic	Nov. 1–Apr. 30, 1973–1974	<10	Observations incidental to other work in the area
1974	May–Sept.	Occasional, May–Sept.	—	Sporadic	—	<10	Observations incidental to other work in the area
1975	Mar.–Dec.	Daily Mar.–May & Aug.–Oct. Frequent, June–Jul.	Occasional (opportunistic)	Regular Mar.–May	Nov. 1–Apr. 30, 1975–1976	53	In June and July, observations were incidental to other work in the area
1976	Mar.–Oct.	Daily	Weekly	Regular Mar.–May	Nov. 1–Apr. 30, 1976–1977	54	By boat as *weather allowed*
1977	June–Sept.	Daily	One survey flight of study region	Sporadic	—	39	Reached Cape Scott and Calvert Island Area (see Fig. 1.)
1978	July–Aug.	Occasional		Sporadic	—	9	Observations incidental to other work in the area
1979	June–Sept.	Daily	One survey flight of study region	Sporadic	—	18	Reached Cape Scott and Calvert Island Area (see Fig. 1.)
1980	June–Sept.	Occasional	—	Sporadic	—	9	Observations incidental to other work, plus one complete boat survey of south coast
1981	June–Sept.	Occasional	—	Sporadic	—	8	Observations incidental to other work, plus one complete boat survey of south coast

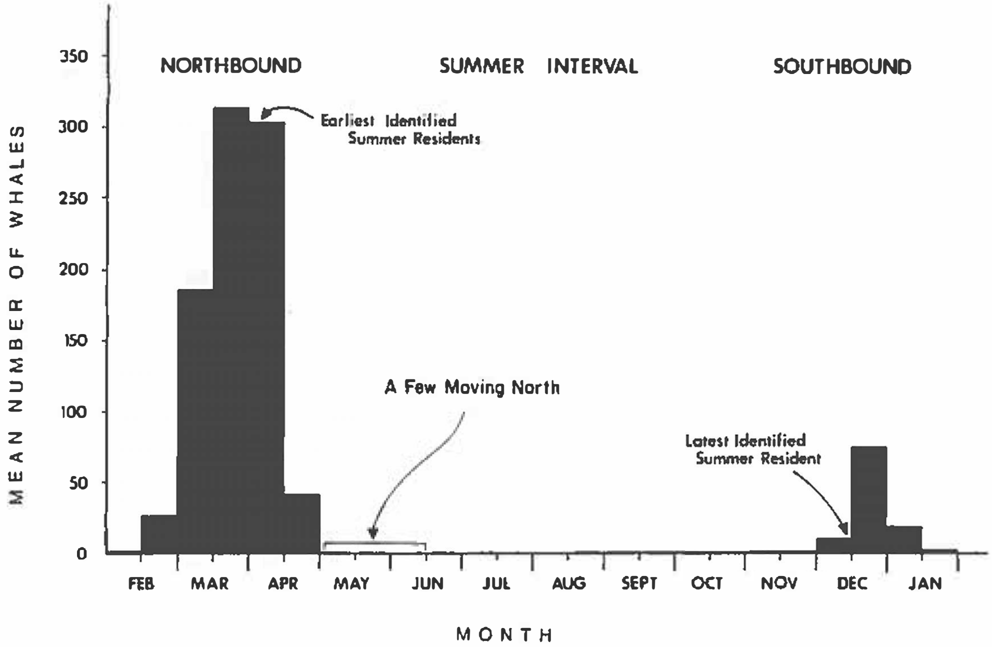

Fig. 3. *Timing of gray whale migrations past Vancouver Island based on lightstation sightings, 1972–1977 (data are unavailable for the period November 1974 through November 1975). See also Table I.*

Fewer whales were sighted during the southward migration than during the northward migration, probably reflecting poor winter weather rather than differences in numbers of whales passing. Two bits of evidence support this conclusion. A note received from the Kains Island lightkeeper in December, 1974 with his sighting forms for that month stated: "On about three days the visibility was clear enough to encourage us to glance out to sea and to see the odd whale . . . at least that is how it would appear from our fog alarm report." On those 3 days, they saw 26 whales. Also, in December, 1977, when weather was unseasonably good, significantly more whales were reported (Table II).

Intensive observations by the author allowed some further delineation of the spring migratory period (Darling, 1978). During this period whales were either (1) moving steadily north; (2) slowly and sporadically, but still obviously, moving north, or (3) lingering in the area. As was expected from lightstation reports, obvious northbound migrants were common through April, although they were fewer after mid-month. In May most whales observed were stationary and feeding; however, a few were still obviously migrating. A photographically identified cow and calf appeared in Wickaninnish Bay on June 2, 1976 and remained until June 5, 1976. They were observed to be feeding and were not traveling. They were gone on June 6 and had probably moved northwards as they were not seen again. This is the latest reasonably clear record of a migrant. Other whales identified in May and June were also not seen a second time, suggesting that they too had destinations farther north. Southbound migrants were sighted in Wickanin-

Table II
Lightstation Reports of Gray Whales Migrating Past the West Coast of Vancouver Island

	Number of whales sighted					
Dates	1972–1973	1973–1974	1975–1976	1976–1977	Total	Average
Nov. 1–15	0	—[a]	0	5	5	1
Nov. 16–30	1	3	0	1	5	1
Dec. 1–15	30	3	4	7	44	11
Dec. 16–31	8	22	36	233	299	75
Jan. 1–15	18	30	30	79	157	39
Jan. 16–31	0	2	—	4	6	2
Feb. 1–15	0	—	5	16	21	5
Feb. 16–28	13	1	22	70	106	27
Mar. 1–15	86	28	230	411	755	189
Mar. 16–31	183	162	271	631	1247	312
April 1–15	364	100	311	445	1220	305
April 16–31	55	35	11	66	167	42

[a] A dash (—) indicates no reports. Averages are rounded to the nearest whole number.

nish Bay in December and January, consistent with lightstation reports (Darling, 1978).

The winter interval between the last southbound and first northbound migrants was not clear cut. Lightstation reports indicate it occurs from approximately mid-January to mid-February, although in some years whales were sighted during that period.

Route

The migratory route observed during this investigation is shown in Figure 3. It conforms with the accounts of earlier researchers (Pike, 1962; Pike and MacAskie, 1969; Hatler and Darling, 1974). Northbound whales leave the Washington coast at Cape Flattery, head generally north until they reach Vancouver Island then change course to follow its west coast. All sightings were within 4 km of shore; most were within 1 km and many within 100 m. Occasional sightings of gray whales in the Straits of Juan de Fuca and Georgia Strait (Darling, field notes, 1975–1981) indicate that a few animals turn southeast at Cape Flattery.

INDIVIDUAL IDENTIFICATION

Approximately 5000 photographs were taken. Over 100 different gray whales have been identified off the west coast of Vancouver Island since 1970. Most markings were light, white or gray on a darker background. Extent, intensity, and location of identifying elements in the pattern varied dramatically (Figs. 4–6). They ranged from large portions of white, to varied combinations of white patches, slashes, dots, and speckles, to almost total black. Most individuals were immediately recognizable; all were distinguishable on close examination.

The longevity of observed patterns is suggested in Fig. 5, animal No. 741, pho-

Fig. 4. *Examples of pigmentation patterns used to identify individual gray whales.*

tographed over 5 years—in which there was no significant change in markings—and in Fig. 6, both sides of animal No. 756 over 2 years, 1975 and 1976—in which the smallest details of the patterns are constant (arrows). Some half-moon-shaped marks (circled) present on the left side of No. 756 in 1976 were not there the previous year. Similar superficial, nonpermanent marks noticed on some whales were not sufficiently large or common to interfere with identification. From a photograph of a near-term fetus with white skin patterns (see Rice and Wolman, 1971, p. 78), it appears whales are born with

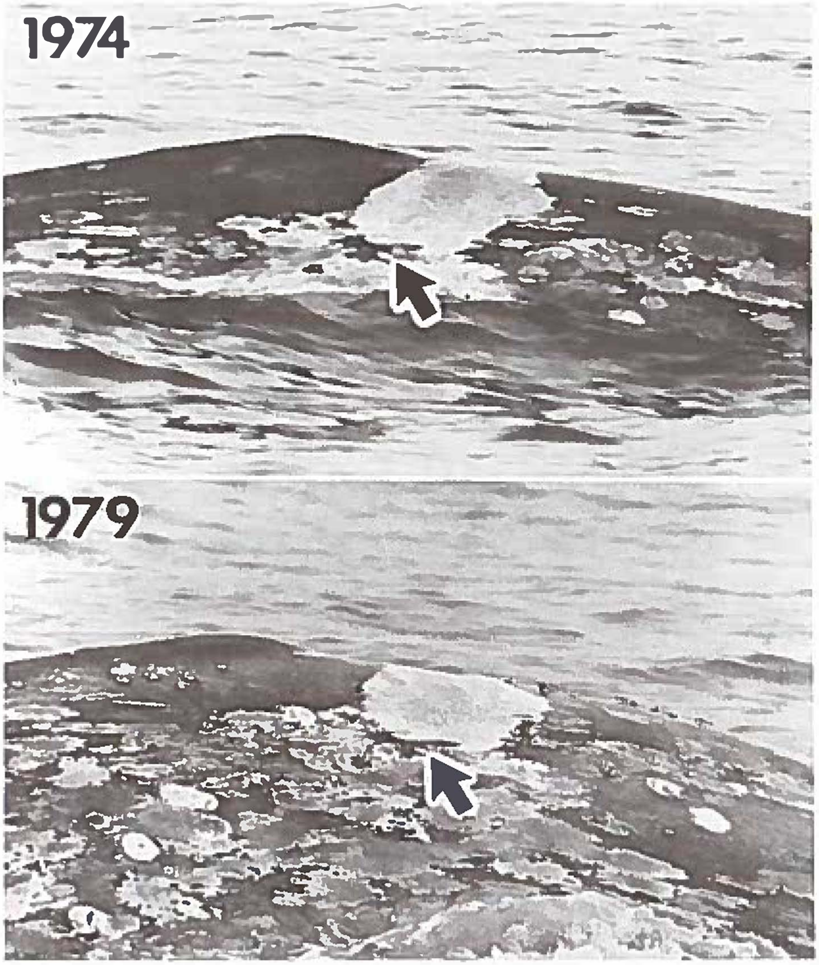

Fig. 5. *Photographs of whale No. 741 in 1974 and 1979. The photographs were taken at slightly different angles. Arrows indicate a common reference point.*

these patterns and maintain them throughout their lives although scratches or superficial growths may partially obscure them at times.

When a scar was the dominant marking, it was used as the basis for identification along with skin patterns. Such was the case with the scarred whale first described by Hatler and Darling (1974). The scar on this whale remained obvious from at least 1970 to 1975, the years it was recorded off Vancouver Island. No substantial change in the scar was noted.

Gray whales have patches of barnacles (*Cryptolepas rhachianceti*), especially on the head and the most anterior portion of the back, and cyamids (*Cyamus scammoni, C. ceti,*

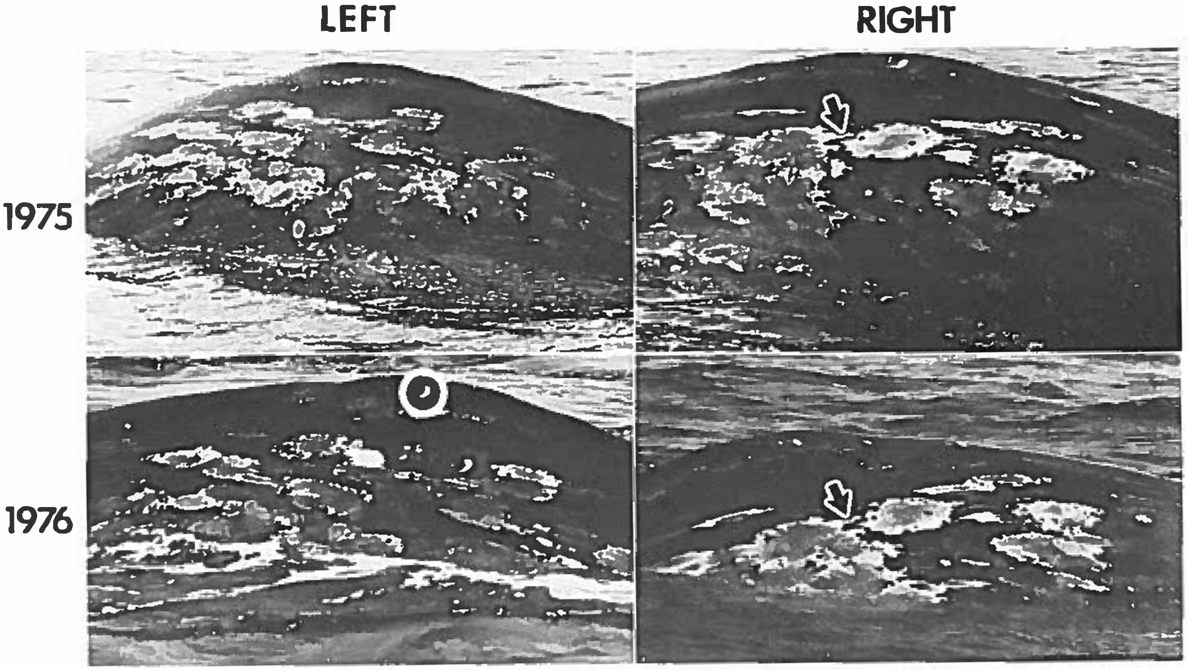

Fig. 6. *Pigmentation patterns of whale No. 756 in successive years. Note the half moon-shaped markings (circled) on the left side in 1976, which are not present in 1975. Arrows indicate a common reference point.*

and *C. kessleri*), particularly around the barnacles and on wounds (Rice and Wolman, 1971). Barnacles and cyamids were not used for individual recognition.

SUMMER POPULATION

Arrival and Departure of Summer Residents

As has been shown, the majority of northward migrants reach Vancouver Island between February and June. Summer residents, animals which remained in the area during the summer interval, were identified as early as April 8 (Whales #701, 721, and 752), April 11 (whale #7513), April 16 (whale #741, and April 17 (whale #754) in 1975, and April 12 (whale 754), and May 13 (whale #759 in 1976. Therefore, summer residents can be present in the area by the time of the local peak of the northward migration in late March and early April (Fig. 3).

Data indicating when summer residents leave for the winter are sketchy because day-to-day observation ended in September when many, if not all, identified whales were still present. The latest sighting of a positively identified summer resident was December 14, 1972 when whale #721 was seen feeding in Wickaninnish Bay. Other summer residents were identified as late as October 12, 1975 (whale #701) and October 23, 1976 (whales #759, 756, and 7511). Small craft searches were not made after these dates.

Apparently the duration of a whale's stay can be from peak to peak of the migrations or about 8–9 months (Fig. 3). The longest recorded stay of a single individual in 1 year was 7 months; whale #701 was first identified on April 8, 1974 and last identified on October 12, 1974.

Abundance

The largest number of resident whales identified in one summer was 34 in 1976 and 1977, the years of maximum effort (Tables I and III). Numbers identified in other years reflect effort level (Tables I and III). In both 1976 and 1977 previously unidentified whales were still being "discovered," albeit rarely, at the end of the season, indicating that not

Table III
Identification of Individual Whales, 1975–1981

Category	1975	1976	1977	1978	1979	1980	1981
A. Number of whales identified in the summer	27	34	34	13	25	10	20
B. Number of A seen in other years	20	25	22	8	14	7	10
C. Percentage of A seen in other years	74	65	65	61.5	56	70	50
D. Number of A seen only that year	7	9	11	5	11	3	10

all residents had been identified. It is not likely, however, that the maximum number of whales which summer in the area is much higher than 34. Aerial surveys carried out in the middle of summer did not indicate that large numbers of animals were "missed" in the identification effort. One of the best such surveys, considering weather and the amount of time spent searching for whales, was that on August 29 and 30, 1977, in which

Table IV
Individual Whales Identified off Vancouver Island in More than 1 Year

Whale ID number	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981
701	x		x	x	x	x						
711		x				x	x	x				
721			x	x	x	x	x	x	x			
741					x	x	x	x		x	x	x
742					x	x	x	x		x		
751						x	x	x		x		x
752						x	x	x		x	x	
753						x	x	x	x	x		
754						x	x	x		x		
755						x	x	x				
756						x	x	x				
757						x	x	x				
758						x	x	x				
759						x	x	x				
7510						x		x	x			
7511						x	x					
7512						x		x				
7513						x	x					
7514						x	x					
7515						x	x					
761							x	x	x			x
762							x	x		x		
763							x	x	x			
764							x	x	x			
765							x			x		
766							x		x			
767							x		x			
768							x	x				
771								x		x		
772								x		x		
791										x	x	x
792										x	x	x
793										x		x
794										x		x
802											x	x
803											x	x
804											x	x

the entire west coast of the island from Port Renfrew at the southern end of the West Coast Trail to Cape Scott was searched. Twenty-nine whales were counted, compared to 34 identified in that year. In 1979, in a survey from the Kaloloch on the Washington Coast to Calvert Island, north of Vancouver Island, we saw an estimated 30–40 whales; 22 individuals were identified that year. From the above, it seems unlikely that more than 50 whales range onto the Vancouver Island coast in any one summer, and a reasonable estimate might be 35–50.

In the six summers from 1975 to 1981, 93 individual whales were identified on this coast. This is the total of the 56 identified whales seen in only one summer [Table III, (D)] plus those 37 seen in more than 1 year (Table IV). It is thought that not all of these return to Vancouver Island each year.

Annual Returns

Since 1970, 37 whales have been seen in more than 1 year (Table IV). Whale #741 was seen for 8 years (1974–1981); whale #711, 7 years (1971–1977); whale #721, 7 years (1972–1978); and whales #701, #742, and #751, 5 years (1970–1975, 1974–1979, and 1975–1981, respectively) (Table IV). Among the animals identified each year there were those which had been identified in other years (average, 63%) and those which were seen only that year (average, 37%). In 15 cases (in Table IV), a whale was "missed" in one or more summers but seen in subsequent years.

Although some identified whales were resighted in the exact location in which they were identified the previous years (e.g., whale #701 in Wickaninnish Bay in 1970, 1973, 1974, and 1975), others were resighted in different years as much as 150 km from previous sighting location(s) (Table VA and Fig. 1).

Distribution and Movements

The combined locations where gray whales were found during the summers of 1975–1981 cover most of the Vancouver Island coast from Victoria to Cape Scott and

Table VA
Changes in Location of Photoidentified Whales from One Summer to the Next

Whale ID Number	First Location and Date	Second Location and Date	Direction	Distance (km)
762	Wickaninnish Bay Aug. 4, 1976	Estevan Point Aug. 11, 1977	NW	80
803	Wickaninnish Bay July 9, 1980	West Coast Trail Aug. 6, 1981	SE	77
804	West Coast Trail Aug. 23, 1979	Wickaninnish Bay July 9, 1980	NW	77
771	Estevan Point Aug. 17, 1977	West Coast Trail Aug. 5, 1979	SE	150

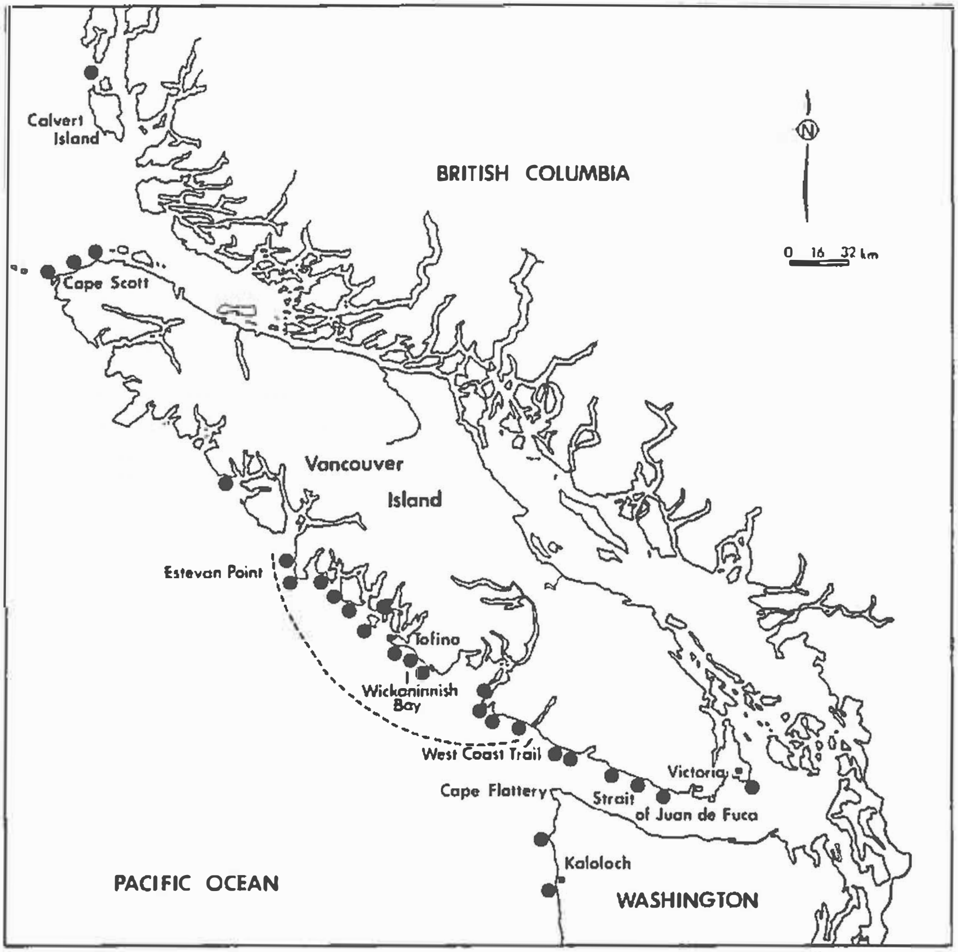

Fig. 7. *Locations of sightings of gray whales in summer (June–October), 1975 to 1981, indicated by small solid circles.*

farther north off Calvert Island along the mainland B. C. coast (Fig. 7). The relatively larger gaps between sightings towards the north may well reflect the spacing of observers. The whales were feeding in all locations. All sightings were within 1 km of the shore; most were within 100 m. Apparently suitable habitat on exposed coast includes shallow sandy bays, areas along rocky coastlines and cliffs, and areas off sandstone shelves. Whales were repeatedly but less commonly seen feeding in protected waterways near Tofino.

Whales traveled among sites at least 77 km apart within a summer [Table VB; Fig. 7 (semicircle)]. The maximum distance traveled is not known but the six whales identified off Cape Scott, 220 km north of Estevan Point on July 20, 1977 were not among whales identified off southern Vancouver Island. Apparently, movements are among feeding

Table VB
Travels of Individual Whales along the West Coast of Vancouver Island, within One Summer

Whale ID Number	First Location and Date	Second Location and Date	Direction	Distance (km)
794	Wickaninnish Bay July 14, 1979 (traveling SE)	West Coast Trail Aug. 23, 1979 (feeding)	SE	77
7913	West Coast Trail Aug. 23, 1979 (feeding)	Wickaninnish Bay Aug. 28, 1979 (traveling NW)	NW	77
761	Wickaninnish Bay June 2, 1977 (feeding)	Estevan Point Aug. 17, 1977 (feeding)	NW	80
791	Wickaninnish Bay July 9, 1980 (traveling NW)	West Coast Trail Sept. 10, 1980 (feeding)	SE	77

areas, although traveling whales may not stop at the next nearest area and may bypass feeding whales en route. Whales were seen traveling alone, in pairs, in trios, and in patterns from slow and wandering to quick and direct. On occasion traveling whales moved to a riptide sand bar area where they remained for at least as long as 30 min to several hours.

In some areas whales remained only momentarily, and some animals had as many as four destinations in 1 week, covering a distance of approximately 40 km (whales #741 and 752 in August, 1975). At the other extreme, whales #701 and #754 each remained in Wickaninnish Bay for 80+ days in 1975 and 1976, respectively (Darling, 1978).

Discussion

MIGRATION TIMETABLE

Migratory times and peaks determined during this study generally agree with the observations of Pike (1962), Pike and MacAskie (1969), and Hatler and Darling (1974). The northern migration past the island begins in February, peaks in late March and early April, and continues through May or early June. There may be some slight variance in the timing among years. Based on sightings off Vancouver and Queen Charlotte Islands, Pike (1962) and Pike and MacAskie (1969) suggested the southbound migration occurs from late September or early October until early January, with a peak in the last 2 weeks of December. The sightings in September and October seem early for Vancouver Island. Sightings reported by Hatler and Darling (1974) occurred from the end of November through mid-January. Observations reported here confirmed that this migration occurs from November to mid-January with a peak the last 2 weeks in December. These findings are consistent with predictions from observations in other areas along the migratory route (Leatherwood, 1974; Reilly *et al.*, 1980; Chapters 10, 13, and 16, this volume).

The interval between the last northbound and first southbound migrants extends from mid-June to November. Summer residents were present off Vancouver Island throughout this period, confirming the speculations of Pike (1962) and Pike and MacAskie (1969) and reports by Hatler and Darling (1974). Many of the same identified individuals were seen repeatedly during the summer, as was one whale observed in 1971 (Hatler and Darling, 1974). Summer residents were present by early April, the peak of the northern migration, and stayed 8–9 months until December and the peak of the southern migration. Whales making the full migration to the Bering and Chukchi Seas must budget 2 months more traveling time than those resident off Vancouver Island, arriving in northern areas 1 month later and leaving 1 month earlier (Pike, 1962). They are left with only 6–7 months to feed. Many migrants do, however, feed sporadically while enroute north (Darling, 1978; Wilke and Fiscus, 1961).

The winter interval between the last southbound and first northbound whales is short and not always clear cut. To date there is no direct evidence that Vancouver Island summer residents migrate and in some years unidentified whales have been sighted in the area throughout the winter (Hatler and Darling, 1974). These authors note that it is possible the whales sighted during this period were successive groups of migrating animals, southbound and northbound. The degree of turnover of identified animals each summer suggests that some, if not all, join the rest of the herd.

INDIVIDUAL IDENTIFICATION

Several researchers have used natural markings to identify individual gray whales over the short term; Sauer (1963), describing apparent sexual activity off St. Lawrence Island, Alaska, stated that individual whales could be recognized by skin patterns. Leatherwood (1974) used natural markings to identify three gray whales on successive days off the California coast. Photographic identification work described in Hatler and Darling (1974) and in this chapter show the technique can be used as a basis for long-term studies in which every animal can be permanently identifiable. Swartz and Jones (1978, 1981) and Bryant and Lafferty (1980) have identified gray whales in Mexican calving lagoons and are constructing identification catalogs. Comparison of identified whales from different parts of the gray whales range may elucidate associations of the Vancouver Island whales with the rest of the eastern Pacific herd.

THE SUMMER POPULATION

Gilmore (1960) suggested that the whales lingering all summer on the northwest coast did so because they found themselves too far behind to reach the Bering Sea on time to store enough fat so stayed on more southerly feeding grounds. This explanation can be ruled out based on the facts that individuals return to Vancouver Island year to year, and that they are present at the peak of the northern migration.

Hatler and Darling (1974) speculated that "pockets" of habitat suitable for regular occupancy by gray whales occur between southern Vancouver Island and Alaska. Such "pockets" apparently do exist throughout the species range, off California (Dohl *et al.*, 1981), Oregon (J. Sumich in Chapter 13, this volume), Washington (Darling, 1979), and British Columbia (this chapter).

The Vancouver Island "pocket" is occupied by 35–50 whales each summer. These animals may well be part of a larger "northwest coast" population. Approximately 75 whales summer off Oregon each year (B. R. Mate, 1979, personal communication), so it is likely there are at least 100 in the British Columbia–Washington–Oregon area. This is a small part of the approximately 17,000 animals estimated in the eastern Pacific herd (Reilly *et al.*, 1980, Chapters 9 and 13, this volume).

Votrogov and Bogoslovskaya (1980) and Bogoslavskaya *et al.*, (1981) found gray whales unevenly distributed in "divisions" along the Asian coast. Between these were empty areas through which whales passed rapidly. Presumably these were not good feeding areas. These reports identify two apparent types of whale assemblage, small groups of 20–50 containing a high proportion of young, found mostly in shallow coastal waters, and larger concentrations of as many as 400 adults, feeding in apparently rich areas farther offshore. From observations of whaling operations along that coast in 1936, Zenkovich (1937) reported areas that he suggested may be permanent feeding grounds for younger, apparently recently weaned animals. Almost all whales captured in these areas were less than 2 years old, from which Zenkovich (1937) concluded that young gray whales form separate schools at weaning. Bogoslovskaya *et al.* (1981) suggested that such separation does exist but may not always be so well defined.

The "divisions" described above may equate with the "pockets" along the North American coast. The Vancouver Island summer population does include young animals, apparently recently weaned (Darling 1978). From individual sighting records reported in this chapter, others proved to be at least 8 years old. A more complete investigation of the age structure of this population is necessary; one tempting hypothesis is that the Vancouver Island summer assemblage is similar in age structure to the inshore "divisions" of predominantly young animals off the Asian coast.

The present observations suggest that a gray whale has a preferred location, extending over at least 150 km of coastline, to which it returns for at least part of its life. There are at least two plausible explanations for the variable turnover patterns of identified whales observed in the present study. The first is that they may result from incomplete and varying identification effort among years and mixing within a larger "northwest coast" population. The second assumes that the Vancouver Island whales are a distinct group and that the observed patterns are significant. Some animals return annually for a series of years (2, to at least 8) then go elsewhere, probably on full migration; others spend only one summer in the area. To speculate, the former group might well be immature whales and the latter related to the younger animals or attracted to the area by chance. This explanation suggests a dynamic relationship with the rest of the herd and is tempting because it is compatible with the observations by Votrogov and Bogoslovskaya (1980) and Bogoslovskaya *et al.* (1981) of separate assemblages of younger animals; however, it is far from proven.

The predominant behavior of the Vancouver Island whales is feeding (Darling, 1977, 1978). Feeding behavior and food of gray whales is discussed for the entire range by Nerini (Chapter 18, this volume) and for Vancouver Island by Murison *et al.* (Chapter 19, this volume). Three nonfeeding behavior patterns of note were observed off Vancouver Island in the summer: traveling, apparent resting, and rubbing at a sand bar–riptide area (Darling, 1978). Traveling, discussed above, essentially involves movement among feeding and riptide areas. Whales apparently resting were observed lying low and motionless in the water with just the top of the back above the surface and with wavelets breaking over them; they blew at regular intervals.

At the seaward entrance of several passages to extensive inlet systems in the study area, a "riptide" occurs with each tide change over a sand bar. Whales in these areas engage in stereotyped behavior; rising head-first out of the water and "falling" over backwards, clapping the jaws, spitting water, and apparently rubbing on the sand bar (Darling, 1978). This is probably "grooming" or "recreational," perhaps similar to the rubbing behavior described for killer whales (*Orcinus orca*) off the east coast of Vancouver Island (Ford and Fisher, 1983).

Summary

This study examines the abundance, distribution, and behavior of gray whales, *Eschrichtius robustus*, which are summer residents along the west coast of Vancouver Island, British Columbia. The migratory timetable was determined by observations during four winters from 10 west coast lightstations. The study of the summer population was based on individual identification of animals from photographs of natural markings, and on repeat observations of "known" whales for 10 years, 1972–1981. Direct observations were made from small boats and aircraft.

The northern migration begins in mid-February, peaks in late March, and continues through early June. It is followed by a summer interval lasting until November when the first southbound migrants pass; the southern migration peaks in late December and continues to approximately mid-January. Each year, 35–50 whales are resident in this area off British Columbia during the summer interval. An average of 63% of these returned for more than one summer; 37% were seen in 1 year only. Some individuals returned for at least 8 years. Whales were found feeding in numerous locations along the coast from Victoria to Cape Scott. Individual whales were identified in locations up to 150 km apart in different years, and within one summer they traveled between feeding areas at least 77 km apart. Feeding is the predominant behavior, although whales were also observed traveling, apparently resting, and rubbing at a sand bar–riptide area.

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FINAL REPORT

GRAY WHALE PHOTOGRAPHIC IDENTIFICATION IN 1999: COLLABORATIVE RESEARCH BY CASCADIA RESEARCH, THE NATIONAL MARINE MAMMAL LABORATORY, AND HUMBOLDT STATE UNIVERSITY

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EXECUTIVE SUMMARY

This report summarizes activities and results of gray whale photographic identification research conducted by Cascadia Research in collaboration with the National Marine Mammal Laboratory and Humboldt State University in 1999. This represents a continuation of photographic identification surveys for gray whales that have been conducted annually in the Pacific Northwest since 1991. These surveys are part of an ongoing research effort to study the abundance, movements, residence times and return rates of gray whales that feed in these waters in spring, summer, and fall (so-called "seasonal residents"). A broader ongoing effort has also been conducted in collaboration with researchers from a number of other organizations.

Research effort by the three groups centered in different areas. Between 14 March and 30 October 1999, Cascadia personnel conducted a total of 45 boat and land surveys for gray whales (dedicated and opportunistic) in the waters off northern California, Oregon, and Washington. Biologists from the National Marine Mammal Laboratory (NMML) provided identification photographs from surveys they conducted between 16 April and 23 November 1999 off the Washington outer coast, the western Strait of Juan de Fuca, northern Puget Sound and along the west coast of Vancouver Island, British Columbia. Identification photographs provided by Humboldt State University were from their work conducted off northern California and surveys off whale-watching boats out of Depoe Bay, Oregon from 7 July to 11 October 1999. On 516 occasions good quality identification photographs were obtained of 216 different gray whales. Individuals were seen up to 8 times with a mean of 2.4 (SD= 2.1). Overall 84 (39%) of the whales identified in 1999 were known from previous years.

There were dramatic differences in resighting rates among whales identified in different regions and time periods. Results off Vancouver Island were generally consistent with past years with large numbers of whales identified and high resighting rates both within season and between years. Identifications from other areas were more varied. Very few gray whales were seen off the Washington coast in the summer, but a limited effort in May (immediately after the Makah whale hunt) yielded identifications of a large number of whales that included a small number of known seasonal residents but mostly animals not previously identified. In Washington inland waters, unusually high numbers of gray whales were seen including sightings in areas where whales have not been generally observed previously. Other than six regular returning animals in northern Puget Sound, however, none of these animals were known from previous years and only a few were seen outside this region. Results from Oregon and California were more mixed, with a inter-year resighting rates high off Oregon but low off California.

Mark-recapture estimates of abundance made using annual samples (excluding identifications from early season and inland waters) from 1998 and 1999 yielded an estimate of 269 gray whales, higher than estimates made previously. One reason for the higher estimate was due to the 1999 sample from California, where only 9 of the 39 whales identified had been seen in a previous year. Exclusion of California data from the 1999 sample dropped the estimates to 222; more similar to the estimates obtained previously.

INTRODUCTION

This report summarizes activities and results of gray whale photographic identification research conducted by Cascadia Research in collaboration with the National Marine Mammal Laboratory and Humboldt State University in 1999. This represents a continuation of photographic identification surveys for gray whales that has been conducted annually in the Pacific Northwest (Calambokidis *et al*. 1994, 1999, Calambokidis 1996, Calambokidis and Quan 1997, Calambokidis and Schlender 1998). These surveys are part of an ongoing research effort to study the abundance, movements, residence times and return rates of gray whales that feed in these waters in spring, summer, and fall (which we refer to as seasonal residents in this report). Summer feeding aggregations of gray whales have been observed in a number of areas along the coasts of California (Patten and Samaras 1977, Mallonee 1991, Avery and Hawkinson 1992), Oregon (Sumich 1984), Washington (Flaherty 1983, Calambokidis *et al*. 1992, 1994, Wietkamp *et al*. 1992) and British Columbia (Darling 1984, Murison *et al.* 1984, Plews *et al.* 1985). Gray whales in these regions feed on a variety of prey including herring eggs/larvae, crab larvae, amphipods, mysids, and ghost shrimp, with locations of feeding often shifting from year and by season in response to shifting prey types and distribution (Darling *et al*. 1998, Nerini 1984).

The issue of "seasonal resident" whales has gained significance due to the resumption of whaling for gray whales by the Makah Tribe of Washington State. Although the whaling Management Plan calls for targeting migratory whales, there remains concern over the possible management implications of the hunt on seasonal resident whales (Quan 2000). Limited genetic testing has not revealed a difference in mtDNA haplotypes between seasonal resident and migratory gray whales off Vancouver Island although samples sizes were small (Steeves 1998). Genetic differences may not be detected even when sub-populations are distinct enough to warrant management as separate units (Taylor 1997).

In addition to the research reported here, other researchers continue photographic identification studies from British Columbia to southwestern Alaska. Starting in 1998, there has been a collaborative effort among these groups to conduct an expanded photographic identification comparison. In addition to the research reported here by Cascadia Research, the National Marine Mammal Laboratory, and Humboldt State University, other organizations participating in this broader comparison include: West Coast Whale Research Foundation, University of Victoria, University of British Columbia, Vancouver Aquarium, Department of Fisheries and Oceans, Coastal Ecosystem Research Foundation, and the operator of the Juan de Fuca Express (a coastal ferry service). Results of the larger effort from California to Alaska for 1998 (Calambokidis *et al.* 2000) have been summarized in a draft manuscript and efforts to complete this larger comparison for 1999 are planned.

METHODS

Surveys were conducted by three organizations from northern California to British Columbia (Figure 1). Between 14 March and 30 October 1999, Cascadia personnel conducted a total of 45 boat and land surveys for gray whales (dedicated and opportunistic) in the waters off northern California, Oregon, and Washington (Table 1 and 2). These surveys were conducted in a number of regions and utilized several platforms including:

- small boat surveys in southern and northern Puget Sound, the Straight of Juan de Fuca, and Grays Harbor, primarily using Cascadia's RHIB and other platforms of opportunity (including whale watch boats out of Everett and Port Townsend) on 14 days between 2 April and 13 August 1999,
- small boat surveys of the Washington Coast using both Cascadia's RHIB and some opportunistic effort in association surveys conducted with the Olympic Coast National Marine Sanctuary on 4 days between 20 May and 20 October 1999,
- small boat surveys using Cascadia's RHIB off Oregon including a search from Tillamook Bay to south of Newport on 5 days from 6 September to 13 October 1999,
- small boat surveys using Cascadia's RHIB off northern California in association with humpback whale effort on 5 days from 14 September to 30 October 1999,
- placing observers on the whale watch boat, the *Victoria Express*, operating out of Westport, WA on 12 days between 14 March and 25 April 1999,
- effort from land photographing gray whales in Discovery Bay, southern Puget Sound and near Neah Bay on 5 days between 1 and 18 April 1999,
- opportunistic photographs were also provided to us by other naturalists and researchers who opportunistically photographed gray whales in Puget Sound including Dyanna Lambourn, Mark Sears, and Mike Felber.

Biologists from the National Marine Mammal Laboratory (NMML) provided identification photographs from surveys they conducted between 16 April and 23 November 1999 (Tables 2 and 3). The photographs from NMML represent surveys from the Washington outer coast, the western Juan de Fuca Strait, northern Puget Sound and along the west coast of Vancouver Island, British Columbia.

Identification photographs were provided by Humboldt State University from their work conducted off northern California and Oregon (Tables 2 and 4). Identifications off northern California were primarily made out of Trinidad and Crescent City from 12 July to 11 October 1999 aboard a 16 ft inflatable. Identifications off Oregon were made primarily aboard Tradewind Charter company whale watch boats operating out of Depoe Bay from 7 July to 6 October 1999.

Procedures during Cascadia vessel surveys were similar to those used previously (Calambokidis *et al.* 1994). Effort data were recorded every 30 min and when there was either a course change or a change in the environmental conditions. We recorded time, position (latitude and longitude from GPS) and environmental conditions (sea state, visibility, precipitation, cloud cover, and swell height). When a gray whale was found, the time, position, number of animals, and behaviors were recorded. Whales were approached to 30-50 m and followed through several dive sequences until suitable identification photographs could be obtained. At the end of a sighting the time, location, and roll and frame numbers of photographs taken during each observation were also noted.

For photographic identification of gray whales, both left and right sides of the dorsal region around the dorsal hump were photographed when possible. *Ilford* HP-5 negative film was used with *Nikon* 35mm cameras with 300mm f4.5 lenses. We also photographed the ventral surface of the flukes for identification when possible. The latter method was not as reliable as the sides of the whale because the gray whales did not always raise their flukes out of the water. Markings used to distinguish whales included pigmentation of the skin, mottling, and scarring, which varied among individuals. These markings have provided a reliable means of identifying gray whales (Darling 1984).

We also utilized the relative spacing between the knuckles along the ridge of the back behind the dorsal hump. The size and spacing of these bumps varies among whales and does not change over the years we have tracked whales. Measurements were made based on coordinates marked on a scanned image of the whale and compared to a database of values for all the whales in our catalog. A computer program (developed by Joe Evenson) provided a prioritized list of potential matches and then the match was verified or rejected based on the pigmentation and other markings described above.

Comparisons of whale photographs were made in a series of steps. First, all negatives of gray whales were examined and the best shot of the right and left sides of each whale (for each sighting) were selected and printed (7 x 2.5 inch). To determine the number of whales seen during the season, the prints were then compared to one another to identify whales seen multiple days. Finally a comparison was made to our catalog of whales seen in past years. Whale photographs that were deemed of suitable quality but did not match our existing catalog (compared by two independent matchers) were assigned a new identification number and added to the catalog.

RESULTS AND DISCUSSION

On 477 occasions, good quality identification photographs were obtained of 216 different gray whales by Cascadia Research, NMML, and Humboldt State University in 1999 (Table 2). Whales were seen up to 8 times with a mean of 2.4 (SD= 2.1). Overall, 84 (39%) of the whales identified in 1999 were known from previous years. Identifications, including sighting history, are summarized by organization (Tables 3 and 4).

Resighting rates were different among whales identified in different regions and time periods (Tables 5 and 6). Results from off Vancouver Island were generally consistent with past years with large number of identifications and high resighting rates both within season and between years. The number of newly identified whales and the resighting rates from other areas were more varied than off Vancouver Island. Very few gray whales were seen off the Washington coast in the summer. A limited effort in May immediately after the Makah whale hunt, yielded identifications of a large number of whales which included only a small number of known seasonal residents; most of the whales during this time period had not been previously identified. In Washington inland waters (including Puget Sound and Hood Canal) there were unusually high numbers of gray whales and newly identified individuals. Furthermore, whales were concentrated in a number of infrequently used areas. Aside from six regular returning animals in northern Puget sound, however, none of these were previously identified animals and few were seen outside this region again. Results from Oregon and California were more varied, with inter-year resighting rates high off Oregon but low off California. The different findings by broad region are described in more detail below.

From matching photographs of identified animals, we documented the overall movement patterns throughout the study season in 1999 (Figure 2). While these patterns are partly biased by the timing of effort in different locations, they do reveal movements of some known individuals. In general, a northward shift in areas of use by some gray whales was noted from May to August with identified gray whales moving from the Washington coast, southern Vancouver Island, and the Strait of Juan de Fuca northward to areas off central and northern Vancouver Island. From August to October, movements in the opposite direction predominated with whales identified off Vancouver Island being photographed in the Strait of Juan de Fuca and off the Washington coast in August and September, and then off Oregon in September and October. Despite these overall patterns, there were also movements opposite to those described above, indicating variability in the behavior of animals and not a unified migration or shift.

Identifications off Vancouver Island

Identifications of gray whales reported here were obtained from along the western and northern Vancouver Island regions during two region-wide surveys conducted by NMML in early August and September as well as more frequent coverage of southern Vancouver Island. This report does not include results from survey effort along Vancouver Island obtained by other research groups affiliated with West Coast Whale Research Foundation, University of Victoria, University of British Columbia, Coastal Ecosystems Research Foundation, and Juan de Fuca Express. Because photographic matching between the samples reported here and those from these other groups have not been completed, the results for this region are preliminary.

These relatively few surveys yielded a large number of identifications from broad coverage of most of the outside coastal waters of Vancouver island. In total, 18 individual gray whales were identified off southern Vancouver Island, 48 from western Vancouver Island (from Barkley Sound to Cape Scott), and 10 from northern Vancouver Island. In all three areas, a high proportion of the animals (65-100%) were individuals identified in previous years including a high proportion (60-94%) identified in 1998 (Table 6).

Early season identifications off the northern Washington coast

A large number of identifications of whales came from an early season sample taken on a single day off the Washington Coast. A total of 71 identifications of 45 different individuals were made on 20 May 1999, 5 nmi north of La Push on the Washington outer coast. An estimated 50 to 100 gray whales were in this general area, a larger concentration than we generally encounter. This was less than 10 nmi south and a week after the successful Makah take of a whale. In past years, identifications were generally not made in this area early in the season because it is in the migratory corridor and would likely include migratory animals. This sample in 1999, however, is of interest because of the similar timing and location to the area of the Makah hunt.

Although this large group of whales was in the migratory corridor, their behavior was more suggestive of feeding than of migrating. Of the 60 groups (singles or pairs) of gray whales made that day, all but two groups were judged to be milling rather than travelling in a consistent direction. Surface direction of animals was recorded on 54 occasions and varied widely. Similar proportions of animals had a southerly direction (SW, S, or SE) compared to a northernly direction (35% vs. 44%). Similarly, multiple identifications of 15 of the 45 individuals photographed during the day indicated little movement with again a roughly equal split between those that had shifted slightly to the north or south.

Only 6 of the 45 (or 13%) identifications made off northern Washington in May were individuals known from previous years, a lower percentage than was found for most other areas. These six whales had been first identified between 1994 and 1998. Five were seen in 1998; four had been seen off southern and central Vancouver Island, two off Oregon, and one off the Washington coast. Even though only one was seen in 1998 off northern Washington, two others had been seen there in previous years. One of the six gray whales that we had identified from past years (ID# 191) was a whale seen only in 1996 once again in the early season but this time off Grays Harbor. This whale was identified six times between 7 April and 12 May 1996 in an area off Grays Harbor called the "Whale Hole". Although this spot is in the migratory corridor, it is an area where feeding whales, some of which are seen later in the season, have been identified (Calambokidis and Quan 1997).

Similarly, only 4 of the 45 whale identified off the Washington coast in May 1998 were seen later in the season in the effort by Cascadia, NMML, and HSU. All four of these whales were also whales that had been documented in previous years. Three of these whales were seen later in the season in July and August off central Vancouver Island and one was seen beginning in July off Oregon.

These findings indicate that seasonal resident whales are present during the time and in the area of the Makah whale hunt but are a relatively small proportion of the animals. There did not appear to be any clear way to distinguish between those whales that remained in the Pacific Northwest and those that moved out of the area. These results should be treated cautiously, however, since 1999 appeared to have been an anomalous year in a number of respects including unusually large numbers of whales apparently feeding in atypical areas and high observed mortality.

Identifications in Washington inside waters

A higher than usual number of whales was seen in a number of areas of Puget Sound in spring 1999 (Table 5). These included sightings of multiple whales in Discovery Bay, around northern and southern Puget Sound, around the San Juan Islands, and in Hood Canal. A total of 95 identifications of 33 different whales were made in these combined regions with only six known from previous years (Table 6).

Some of these sightings in inland waters were in unusual areas. In Discovery Bay, six whales were identified in April 1999 near Adelma Beach, an area where gray whales have not generally been seen in past years. None of these whales had been identified previously but several were seen in other regions later in the season. Two (ID# 350 and 396) were seen in Admiralty Inlet later in April and May; one of these was seen off west Seattle in June. Another whale (ID# 351) seen in Discovery Bay was later identified at the very end of Hood Canal near Belfair on 29 April and then was seen by NMML off Bajo Reef, off western Vancouver Island on 8 August.

Although spring-time sightings have been common in past years off Whidbey Island in northern Puget Sound, there were differences in the locations and resighting rates of animals seen in 1999 compared to past years. Many of these whales were feeding in shallow waters of the Snohomish Delta in April and May. Although our effort did not continue through the summer, gray whales were reported in this region through the summer. Five of the 19 whales identified in this region were animals that had been seen in this same areas most years since 1991, one other individual was known from a sighting in a previous year elsewhere and the remaining 13 had not been seen previously. Unlike the whales that we have identified in the past in this region, which we rarely see in other areas, four of these whales were seen elsewhere in 1999, one in southern Puget Sound and around the San Juan Islands, another off west Seattle, a third in Hood Canal and off western Vancouver Island, and a fourth off Oregon.

Sightings around southern Puget Sound were reported through the spring and summer and identifications were obtained of six whales between 4 April and 8 July. Two of these whales were seen near Purdy in early April. One of these was seen only once and the other (ID 459) was seen multiple times later in April and in May in northern Puget Sound and then in June in the San Juan Islands. Two other whales gathered considerable attention when they swam under the 4th Avenue bridge on 8 July and spent most of the day gathering crowds of several hundred people in downtown Olympia. Neither of these two whales has been seen at any other time.

Similarly, of the two whales seen off west Seattle in early June, one was not seen at any other time and the other was a whale seen prior to this in the Discovery Bay area.

The frequent sightings and identifications of a few gray whales in the San Juan Island area in 1999 were also unusual because gray whales have previously been uncommon in these waters. The 40 identifications made from 4 April to 18 June were all of five whales seen up to 20 times each. None had been seen in a previous year and only one had been seen in a different area (the animal mentioned above identified in southern and northern Puget Sound in April and May).

Many of the areas where we identified gray whales in inside waters were near areas where we had strandings of gray whales in 1999. Ten gray whale strandings were recorded between 18 April and 6 July 1999 in Washington inside waters including six in northern Puget Sound, two in the San Juan Islands, and one each in southern Puget Sound and Hood Canal. In many cases, suitable identification photographs of stranded animals could not be obtained and did not allow us to make a positive match between live and stranded whales.

In past years, high rates of gray whale mortality have corresponded with years of high numbers of animals sighted in inside waters (for example 1990 and 1991, Calambokidis *et al.* 1994). As in past years, of the stranded gray whales from which we could get suitable photographs, none matched those of previously known seasonal resident whales. The high mortality in 1999 in Washington State was consistent with elevated mortality of gray whales documented from Mexico to Alaska. We suspect that gray whales that came into many areas of Puget Sound were primarily stragglers from the migration that were not in good health.

Identifications in Oregon and California

Identifications by Humboldt State University and Cascadia yielded 31 unique animals from 51 identifications off central Oregon and 36 individuals from 59 identifications off northern California in July through October (Table 5). Identifications in Oregon were made from July to October with most made in October. A high proportion of the gray whales identified off Oregon were known from previous years (19 / 31 or 61%). Most of these had been seen in other regions with only five whales identified in past years off Oregon.

Results from California were different than from Oregon. Most of the whales were identified off California in July and August. Only six of the 36 (17%) were known from previous years and only two of these from California. Similarly, there was relatively little interchange with other areas documented with this region in 1999. Only five of the whales identified in California were seen in other areas that year and all these were whales that moved between northern California and central Oregon.

Estimates of abundance

Mark-recapture estimates of abundance made using annual samples from 1998 and 1999 yielded higher estimates than using previous years (Table 7). The 1998 sample encompassed broad coverage of a number of areas from California to southeastern Alaska gathered by a number of collaborating organizations (Calambokidis *et al.* 2000). Data from 1999, while not quite as large or as complete geographically, still provided broad coverage from northern California to north of Vancouver Island. To insure identifications were of seasonal resident whales, only identifications taken from 1 June or later were used and identifications from inland waters of Washington were excluded (see Table 7).

The abundance estimate based on 1998 and 1999 samples was 269 (Table 7). This is higher than the estimates of 169 and 175 obtained using 1996 and 1997 annual samples, respectively, in conjunction with 1998 (Calambokidis *et al.* 2000). One reason for the higher estimate using the 1999 data is the sample from California, where there were 39 identifications but only 9 matched a previous year. Exclusion of California from the 1999 sample dropped the estimates to 222 (Table 7). It is unclear why the 1999 California sample was so different. It could be part of the high mortality and unusual distribution of gray whales seen in 1999 resulting in an anomalous occurrence of whales that were stragglers from the main migration.

These mark-recapture estimates should be viewed as tentative until more is learned about the range and movements of these whales to allow testing of some of the assumptions behind mark-recapture estimates. The 1999 sample used here, does not yet include identifications from some of the other collaborating researchers participating in the 1998 comparison.

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TABLES AND FIGURES

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Appendix Tables

Table 1. Summary of field effort by Cascadia Research personnel off California, Oregon and Washington in 1999.

			Time			Dist	Latitude		Gray whale		
Date	**Vessel**	**Region**	**Start**	**End**	**Duration**	**nmi**	**South**	**North**	**Sit #**	**An #**	**Pho #**
Washington outer coast											
20-May-99	N1	OC	8:20	18:05	9.8	70	47.849	48.390	61	86	66
4-Aug-99	OC2	OC	13:10	19:58	6.8	58	48.159	48.387	2	3	3
10-Oct-99	N2	OC	8:45	19:00	10.3	108	48.305	48.498	2	2	1
20-Oct-99	N2	OC	8:04	18:05	10.0	150	47.859	48.385			
Total	4		days		36.8	386			65	91	70
Washington inside waters											
2-Apr-99	PAT	NPS	10:27	17:00	6.6	25	48.102	48.267	2	2	2
4-Apr-99	N1	SPS	13:30	19:00	5.5	31	47.165	47.381	1	2	1
6-Apr-99	N1	NPS	11:35	19:45	8.2	48	47.980	48.142	12	19	16
9-Apr-99	GS	NPS	9:41	9:41	0.0	-	48.257	48.257	1	1	1
14-Apr-99	GS	NPS	9:30	9:30	0.0		48.257	48.257	1	1	
20-Apr-99	MIS	NPS	15:00	15:45	0.8		47.967	47.971	1	1	1
9-May-99	WB	NPS	10:12	19:38	9.4	34	47.943	48.103	6	9	7
20-May-99	GS	NPS	8:45	18:48	10.1	70	48.112	48.517	2	4	3
23-May-99	N1	NPS	11:25	17:50	6.4	39	47.987	48.159	5	8	4
28-Jun-99	OOS	OC	8:00	17:06	9.1	80	47.995	48.398	3	4	2
8-Jul-99	N1	SPS	12:10	16:00	3.8	2	47.043	47.062	1	2	2
21-Aug-99	N2	GH	13:11	16:00	2.8	11	46.905	46.968	2	2	2
27-Aug-99	RAV	NPS	5:02	14:34	9.5	121	48.156	48.368			
31-Aug-99	RAV	GH	9:50	9:50	0.0	-	46.907	46.907	1	1	
Total	14				72.2	462			38	56	41
Opportunistic effort from Grays Harbor whalewatching boats											
14-Mar-99	VE	GH	13:54	16:14	2.3	10	46.907	46.942			
20-Mar-99	VE	GH	14:02	16:36	2.6	9	46.907	46.943	2	2	-
27-Mar-99	VE	GH	14:02	16:28	2.4	6	46.907	46.933	1	1	-
28-Mar-99	VE	GH	13:59	16:20	2.4	5	46.907	46.924	1	1	-
3-Apr-99	VE	GH	11:01	16:14	5.2	17	46.907	46.932			
4-Apr-99	VE	GH	14:01	16:44	2.7	8	46.908	46.923	6	8	3
10-Apr-99	VE	GH	11:00	16:32	5.5	16	46.900	46.938	22	23	12
11-Apr-99	VE	GH	14:07	16:48	2.7	9	46.911	46.928	13	16	13
17-Apr-99	VE	GH	11:02	13:29	2.5	6	46.907	46.924	3	5	4
18-Apr-99	VE	GH	11:01	16:32	5.5	25	46.903	46.953	8	9	8
24-Apr-99	VE	GH	11:06	13:25	2.3	6	46.911	46.938	2	2	2
25-Apr-99	VE	GH	11:01	16:33	5.5	13	46.908	46.962	10	11	7
Total	12		days		41.7	131.1			68	78	49
Oregon											
6-Sep-99	RAV	Southern	12:52	19:44	6.9	46	44.184	44.608			
8-Sep-99	RAV	Southern	8:33	18:33	10.0	49	42.908	43.370			
13-Sep-99	N1	Central	11:37	19:54	8.3	82	44.488	45.598	9	12	10
12-Oct-99	N2	Central	8:17	19:15	11.0	96	44.411	44.837	12	20	16
13-Oct-99	N2	Central	8:03	18:10	10.1	90	44.399	44.651			
Total	5		days		46.2	363			21	32	26
California											
14-Sep-99	N1	CA	11:00	13:15	2.3	10	41.742	41.790			
20-Sep-99	N2	CA	9:00	19:58	11.0	82	37.862	38.323	1	1	1
23-Sep-99	N2	CA	16:48	19:41	2.9	37	41.737	41.872			
11-Oct-99	N2	CA	7:51	18:13	10.4	124	41.449	42.107	1	1	1
30-Oct-99	N1	CA	10:17	17:46	7.5	112	41.516	42.083	3	4	3
Total	5		days		34.0	365			5	6	5
Supplemental identifications made from land											
1-Apr-99	LND	SJF	13:30	17:40	4.2		48.358	48.358	3	7	1
10-Apr-99	LND	SJF	11:00	12:30	1.5		48.044	48.044	1	3	3
13-Apr-99	LND	SPS	18:00	19:15	1.3		47.118	47.118	1	1	1
14-Apr-99	LND	SJF	10:09	19:00	8.9		48.044	48.044	1	5	
18-Apr-99	LND	SJF	13:00	15:00	2.0		48.044	48.044	1	4	3
Total	5		days		17.8	-			7	20	8
Total all area	45		days		248.6	1,707			204	283	199

Table 2. Summary of effort and identifications of gray whales off California, Oregon, Washington, and British Columbia by organization for 1999.

Collection	**Identifications**	**Unique IDs**	**Start**	**End**
Cascadia Research	233	115	3/14/99	10/30/99
Humboldt State University	89	49	7/7/99	10/11/99
National Marine Mammal Laboratory	194	78	4/16/99	11/23/99
All	516	216	3/14/99	11/23/99

Unique IDs for all is adjusted for whales seen by multiple organizations

Table 3. Summary of regions, dates, and sighting histories of whales identified by NMML in 1999.

	Times seen by org.				Times seen in 1999 by region								Dates in 1999		1st yr	
ID	CRC	NMML	HSU	Total	OR	NWA	SJF	HC	NPS	SVI	WVI	NBC	First	Last	seen	Regions seen in 1998
15			2	2						2			8/4/99	8/14/99	1984	NWA,SVI
21	3		1	4					4				4/6/99	5/21/99	1990	NPS
22	3		1	4					4				4/6/99	5/21/99	1990	NPS
30			5	5							5		8/7/99	9/12/99	1983	SJF,SVI
32			2	2								2	8/11/99	8/11/99	1985	NBC
37			2	2							2		8/8/99	8/8/99	1988	NWA,SVI,WVI
41			2	2						1		1	6/30/99	8/10/99	1990	SJF,SVI,WVI
42			10	10			6			3	1		7/23/99	10/19/99	1984	SJF,SVI,WVI
43	3	2	3	8	5					3			7/23/99	10/12/99	1984	NWA,SVI
67	3		1	4	3	1							9/13/99	11/23/99	1992	
79			1	1		1							6/29/99	6/29/99	1993	NWA,SVI
80			3	3		2				1			7/23/99	10/13/99	1993	NWA,SVI,WVI
81			5	5		1					4		8/8/99	9/29/99	1993	NWA,SVI,WVI
83	1	1	2	4	2						2		8/12/99	10/12/99	1993	NWA,WVI
84	1	1	3	5	2						3		8/7/99	9/19/99	1990	OR,SVI
86			3	3							2	1	8/10/99	9/12/99	1975	NBC
87	1		4	5	1						4		8/7/99	10/12/99	1993	CVI,WVI
92			5	5						1	4		6/30/99	9/11/99	1993	NWA,SVI
94		1	1	2	1						1		8/13/99	10/5/99	1993	WVI
98			1	1								1	8/10/99	8/10/99	1992	
105			1	1								1	8/10/99	8/10/99	1994	OR,SVI,WVI
123			1	1						1			7/23/99	7/23/99	1984	SVI
135			5	5							5		8/8/99	9/12/99	1990	SVI,WVI
136			1	1							1		8/8/99	8/8/99	1990	WVI
138			2	2								2	8/11/99	8/11/99	1979	SVI,WVI
141			4	4		1					3		8/7/99	9/29/99	1976	SVI,WVI,NBC
143			5	5						1	4		6/30/99	9/12/99	1990	SVI,WVI,NBC
144			1	1							1		8/13/99	8/13/99	1990	SVI,WVI
152			2	2							2		8/13/99	9/12/99	1995	
153			1	1								1	8/10/99	8/10/99	1994	
166			2	2						2			8/4/99	8/4/99	1995	NWA,SVI
175			3	3							3		8/7/99	9/11/99	1995	NWA,SVI,WVI
177	1		8	9		3				6			5/20/99	10/18/99	1995	SVI,WVI
178	2		1	3		2					1		5/20/99	8/7/99	1995	WVI
185			6	6			4			1	1		6/30/99	10/19/99	1994	SVI,WVI
186	1		1	2	1						1		8/13/99	10/12/99	1994	OR,SVI,WVI
187			4	4						3	1		7/23/99	9/12/99	1996	NWA,SJF,SVI
192			3	3						3			6/30/99	8/4/99	1996	NWA,SVI,WVI
205			6	6		6							8/28/99	11/2/99	1996	
212			2	2						2			7/23/99	9/10/99	1996	SVI
219			2	2						2			7/23/99	8/14/99	1997	SVI
229			3	3							3		8/8/99	8/12/99	1998	SJF
231			3	3						3			6/30/99	8/14/99	1998	SVI
236	1		1	2	1							1	8/10/99	9/13/99	1996	SVI,WVI,NBC
238			2	2								2	8/11/99	8/11/99	1996	SVI,WVI
242			8	8			5			3			7/23/99	11/3/99	1998	NWA,SJF,SVI
244			3	3							3		8/8/99	8/13/99	1998	SVI,WVI
254			4	4							4		8/7/99	9/12/99	1998	SVI,WVI
273			2	2					2				4/16/99	5/21/99	1998	GH
281	1	1	3	5	2						3		8/8/99	10/12/99	1991	
296			2	2							2		8/13/99	9/12/99	1998	OR
300	1		2	3		1					2		5/20/99	9/11/99	1998	OR,WVI
309	1		1	2	1						1		8/13/99	9/13/99	1998	WVI
315			1	1								1	8/11/99	8/11/99	1996	WVI,NBC
317			1	1							1		8/13/99	8/13/99	1998	WVI
320			1	1							1		8/13/99	8/13/99	1994	WVI,NBC
328			3	3							3		8/13/99	9/12/99	1996	NBC
351	3		2	5				1	2		2		4/14/99	8/8/99		
355			1	1			1						7/28/99	7/28/99		
372		2	4	6	2					4			7/23/99	10/5/99		
382			3	3							3		8/8/99	9/12/99		
384			2	2							2		8/8/99	8/8/99		
385			2	2							2		8/12/99	8/12/99		
386			3	3							3		8/13/99	9/12/99		
392			4	4							4		8/7/99	8/13/99		
393			2	2							2		8/8/99	8/12/99		
424			1	1							1		8/13/99	8/13/99		
425			1	1					1				5/21/99	5/21/99		
427			1	1							1		8/12/99	8/12/99		
433			1	1							1		8/8/99	8/8/99		
434			1	1							1		8/13/99	8/13/99		
451			1	1							1		8/8/99	8/8/99		
467			1	1					1				5/21/99	5/21/99		
477			1	1							1		8/8/99	8/8/99		
480			1	1							1		9/12/99	9/12/99		
483			1	1							1		8/13/99	8/13/99		
485			2	2							2		8/8/99	8/8/99		
490			1	1							1		8/13/99	8/13/99		

Table 4. Summary of regions, dates, and sighting histories of whales identified by HSU in 1999.

	Times seen by org.				Times seen in 1999 by region						Dates in 1999		1st yr	
ID	CRC	NMML	HSU	Total	CA	OR	NWA	SVI	WVI	NBC	First	Last	seen	Regions seen in 1998
43	3	2	3	8		5		3			7/23/99	10/12/99	1984	NWA,SVI
83	1	1	2	4		2			2		8/12/99	10/12/99	1993	NWA,WVI
84	1	1	3	5		2			3		8/7/99	9/19/99	1990	OR,SVI
85	1	1		2		2					8/10/99	9/13/99	1984	NWA,SVI,WVI
93		2		2	1	1					7/30/99	10/11/99	1984	NWA,SVI
94		1	1	2		1			1		8/13/99	10/5/99	1993	WVI
206		2		2	2						7/12/99	7/12/99	1996	CA
237		1		1		1					10/5/99	10/5/99	1997	SVI,WVI,NBC
274		1		1	1						8/24/99	8/24/99	1991	CA
276		1		1	1						7/18/99	7/18/99	1991	CA
281	1	1	3	5		2			3		8/8/99	10/12/99	1991	
291		2		2	2						7/12/99	10/11/99	1998	CA
301	1	2		3	1	2					7/12/99	10/12/99	1998	OR
302	5	3		8		4	4				5/20/99	9/13/99	1998	OR
303	1	1		2		2					9/13/99	9/19/99	1998	OR
310		1		1	1						8/24/99	8/24/99	1998	CBC
361		2		2	2						7/12/99	8/17/99		
362		1		1	1						8/24/99	8/24/99		
363	1	2		3	3						8/20/99	10/30/99		
372		2	4	6		2		4			7/23/99	10/5/99		
373		2		2		2					7/7/99	7/8/99		
374		2		2	1	1					8/10/99	8/24/99		
375		2		2	2						7/12/99	7/12/99		
376		1		1		1					9/19/99	9/19/99		
377		6		6	6						7/12/99	7/18/99		
378		2		2	2						7/12/99	7/17/99		
379		4		4	4						7/12/99	7/18/99		
380		3		3	3						7/17/99	7/18/99		
407		1		1	1						7/12/99	7/12/99		
408		1		1		1					10/6/99	10/6/99		
412		2		2	2						7/12/99	8/24/99		
419		1		1		1					9/19/99	9/19/99		
428		1		1	1						7/12/99	7/12/99		
429		4		4	3	1					8/20/99	10/6/99		
432		1		1	1						7/12/99	7/12/99		
439		2		2	2						7/18/99	7/18/99		
440		2		2	2						7/12/99	7/12/99		
444		3		3	3						7/12/99	7/18/99		
448		5		5	5						7/12/99	7/18/99		
449		2		2	2						7/12/99	7/18/99		
450		1		1	1						8/24/99	8/24/99		
460		1		1		1					9/19/99	9/19/99		
468		2		2	2						8/24/99	8/24/99		
470		1		1	1						8/24/99	8/24/99		
471		1		1	1						7/17/99	7/17/99		
474		1		1	1						7/12/99	7/12/99		
476		2		2	2						7/12/99	7/18/99		
478		1		1	1						7/12/99	7/12/99		
489		2		2	1	1					8/20/99	10/6/99		

Table 5. Summary of identifications of gray whales by Cascadia, NMML, and HSU by region and month in 1999. Resightings of individuals are counted.

	Month									
Region	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**Total**
N. Vancouver Island						13				13
W Vancouver Is. (central)						78	25			103
S Vancouver Is.				6	11	24	1			42
N Washington coast			71	1		2	6	3	2	85
Str. Juan de Fuca (US)					1	2	2	10	1	16
San Juan Islands		1	20	19						40
Hood Canal		2								2
N Puget Sound		31	16							47
S Puget Sound		2		2	2					6
Grays Harbor area	2	37			1					40
Oregon					5	3	18	25		51
N Califonria					46	16	2	7		71
All regions	2	73	107	28	66	138	54	45	3	516

Table 6. Summary of resighting rates by region of gray whales seen in 1999 by Cascadia, NMML, and HSU.

Region	**Unique IDs 1999**	**Seen more than one day in 1999**		**Seen in another region in 1999**		**Seen in a previous year**		**Seen in 1998**		**Seen in 1998 in same area**	
		#	**%**	**#**	**%**	**#**	**%**	**#**	**%**	**#**	**%**
N. Vancouver Island	10	3	30%	3	30%	10	100%	8	80%	4	40%
W. Vancouver Is. (central)	48	31	65%	18	38%	31	65%	29	60%	21	44%
S Vancouver Is.	18	16	89%	11	61%	17	94%	17	94%	17	94%
N. Washington coast (summer-fall	7	6	86%	5	71%	7	100%	5	71%	3	43%
N. Washington coast (May)	45	4	9%	4	9%	6	13%	5	11%	1	2%
Str. Juan de Fuca (US)	4	3	75%	3	75%	3	75%	3	75%	2	50%
San Juan Islands	5	5	100%	1	20%	0	0%	0	0%	0	0%
Hood Canal	2	1	50%	1	50%	0	0%	0	0%	0	0%
N. Puget Sound	24	9	38%	4	17%	6	25%	4	17%	3	13%
S. Puget Sound	6	2	33%	2	33%	0	0%	0	0%	0	0%
Grays Harbor area	17	6	35%	0	0%	6	35%	3	18%	3	18%
Oregon	31	22	71%	18	58%	19	61%	16	52%	5	16%
N Califonria	39	17	44%	5	13%	9	23%	9	23%	4	10%
All regions	216	85	39%	35	16%	84	39%	71	33%		

Table 7. Petersen capture-recapture estimates for seasonal resident gray whales. Both samples include only IDs after 1 June and exclude IDs from Puget Sound area and Grays Harbor.

Sample 1		**Sample 2**					
Year	**n**	**Year**	**n**	**Match**	**Est.**	**CV**	**Comments**
Estimates using 1999 data							
1999	127	1998	134	63	**269**	0.06	
1999	93	1998	134	56	**222**	0.06	Excluding 1999 California sample
Estimates based on previous years (from Calambokidis et al. In prep.)							
1997	29	1998	134	22	**175**	0.09	
1996	28	1998	134	22	**169**	0.09	

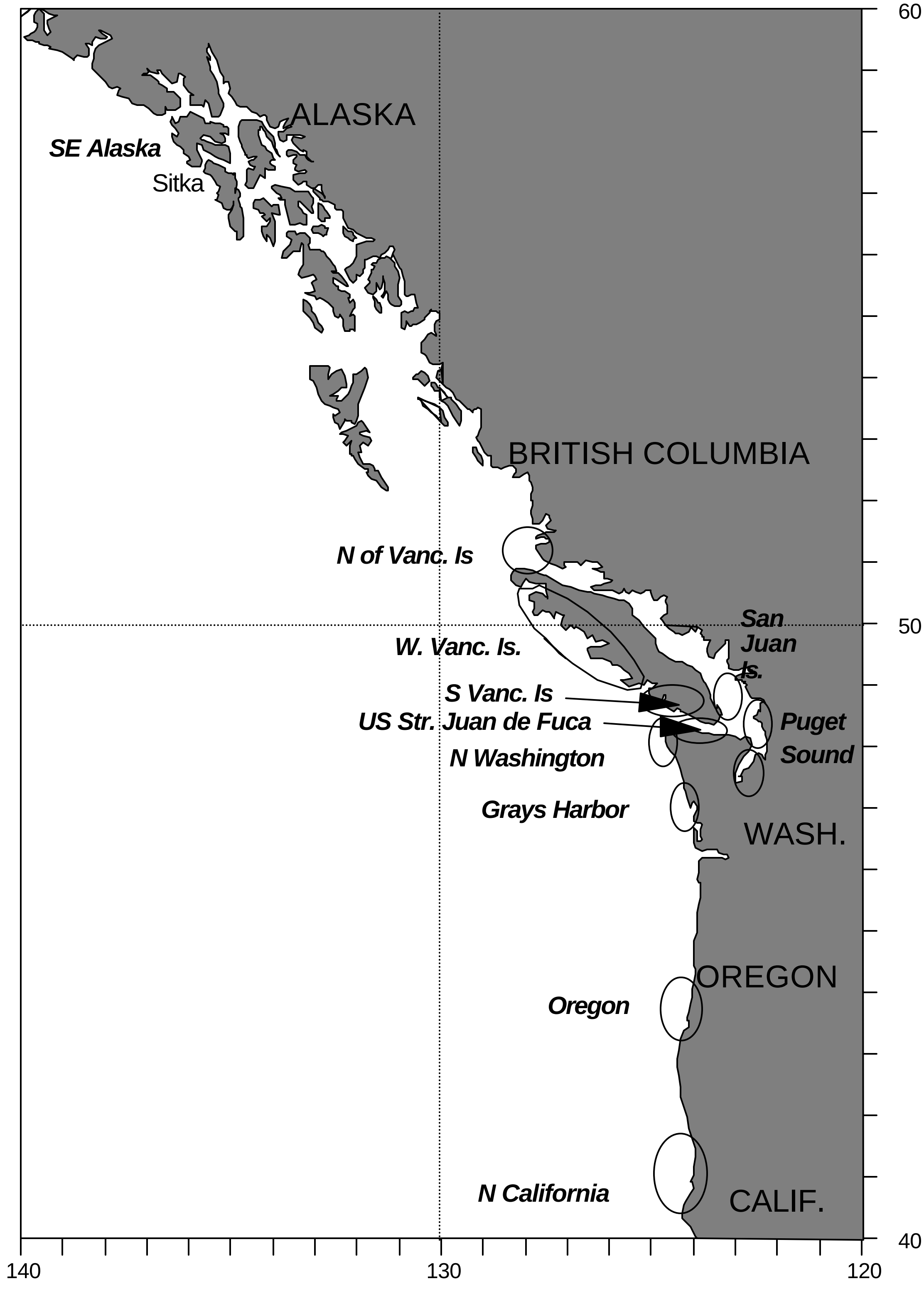

Figure 1. Study area showing regions and areas of effort in 1999.

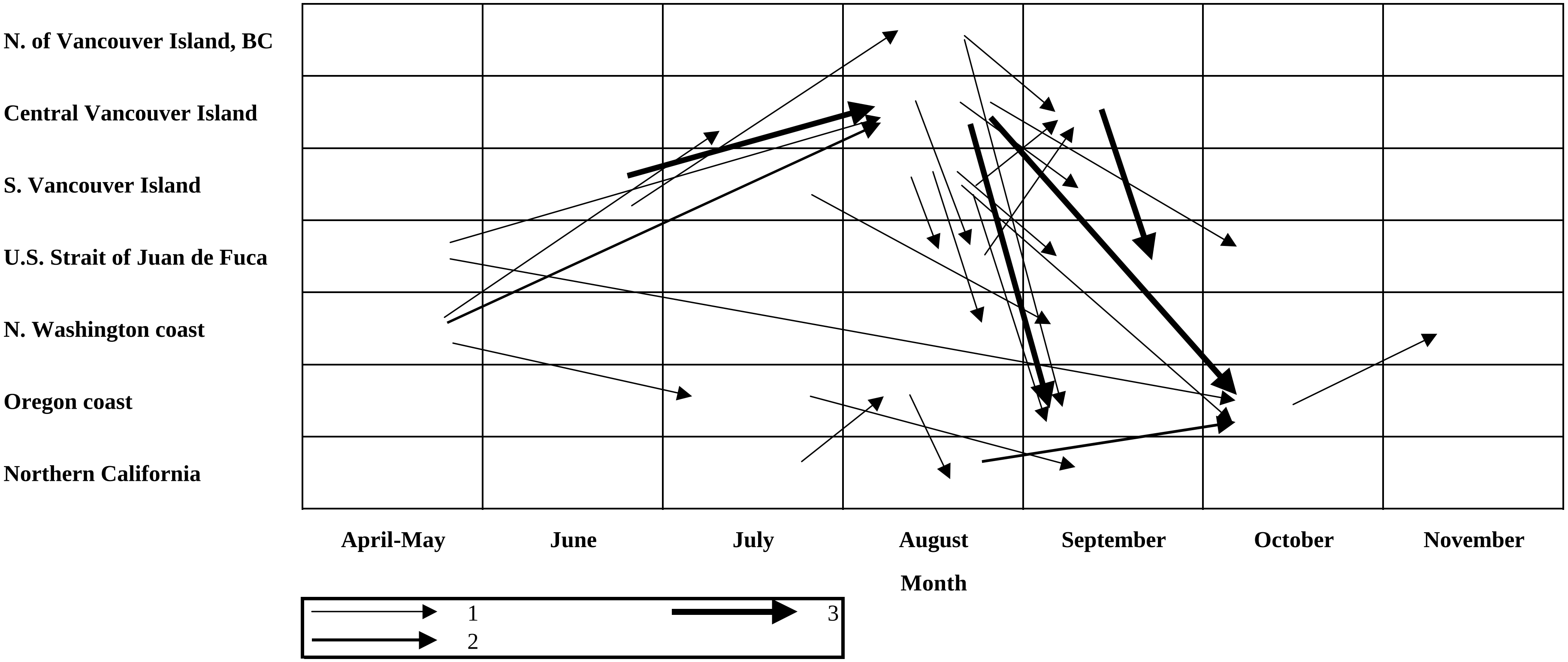

Figure 2. Movements of gray whales among locations in 1999 based only on CRC, NMML, and HSU data. Size of arrow indicates number of transits.

Appendix Table 1. List of identifications by ID and date for Cascadia, NMML, and HSU in 1999.

ID	QL	QR	QF	Col	Pho	Roll	Frames	Date	Time	Sight#	No	Region	Location	Lat	Long	Comments
15	B	B		NMML	MG	12	01-14	8/4/99	18:44		1	SVI	WEST OF PACHENA PT	48 44.020	125 07.380	
15	B	B		NMML	MG	29	01-12	8/14/99	14:41		1	SVI	TSUSIAT PT.	48 40.77	124 54.66	Added late
21	B	B		CRC	JAC	4	5A-22A	4/6/99	12:37	N1-1	2	NPS		48 05.1	122 25.2	BIG, BRN. FCS COLL.
21		B	B	CRC	JAC	5	7A-10A	4/6/99	14:50	N1-4	2	NPS		48 06.4	122 28.5	22 LEAD; 21 TRAIL
21	A	C		CRC	JAC	4	31A-END	4/6/99	14:15	N1-3	2	NPS		48 06.9	122 28.1	SAME AS #1
21	B	A	C	NMML	MG	3	10-37	5/21/99			2	NPS	ELGER BAY	48 07.157	122 28.072	
22	A		B	CRC	JAC	4	31A-END	4/6/99	14:15	N1-3	2	NPS		48 06.9	122 28.1	SAME AS #1
22	A	B		CRC	JAC	4	5A-22A	4/6/99	12:37	N1-1	2	NPS		48 05.1	122 25.2	BIG, BRN. FCS COLL.
22		B		CRC	JAC	5	7A-10A	4/6/99	14:50	N1-4	2	NPS		48 06.4	122 28.5	22 LEAD; 21 TRAIL
22	B	B	B	NMML	MG	3	10-37	5/21/99			2	NPS	ELGER BAY	48 07.157	122 28.072	
30	A	B	C	NMML	MG	16	10-19	8/7/99	16:49		1	WVI	SOUTH OF ESCALANTE PT.	49 29.530	126 35.367	
30	B			NMML	MG	26	05A-21A	8/13/99			2	WVI	SO. OF ESCALANTE ROCKS	49 30.160	126 34.962	
30		B		NMML	PJG	9	29	9/11/99			1	WVI	SPLIT CAPE			
30	A	A		NMML	PJG	9,10	30-36,01A-04A	9/11/99			4	WVI	INSHORE OFF SPLIT CAPE			
30	A			NMML	PJG	10	19A-34A	9/12/99			4	WVI	OFF ESCALANTE (ROCKS)			
32		A		NMML	PJG	6	17-26	8/11/99			3	NBC	SOUTH CAPE CAUTION			
32	A	A		NMML	MG	23,24	14A-37A,01-22	8/11/99			3	NBC	WEST OF WILKIE POINT	51 07.837	127 42.962	
37		B	B	NMML	MG	16,17,18,19	20-37,01A-36A,01-36,01-0	8/8/99				WVI	OFF BAJO PT.	49 36.437	126 52.073	
37		B		NMML	PJG	5	01-24	8/8/99				WVI	BAJO REEF			
41	A	A		NMML	MG	4	14A-24A	6/30/99			1	SVI	NITINAT MOUTH	48 39.989	124 51.228	
41	A	B		NMML	MG	22	01-37	8/10/99			4	NBC	SE OF CHRISTENSEN POINT			
42	B	A		NMML	PJG	2	01-36	7/23/99			9	SVI	2 MI. W OF NITINAT			
42	B			NMML	PJG	3	33-35	8/4/99			2	SVI	KLANAWA RIVER			43 IS DIAMOND, 42 IS BUDDY
42	B	A		NMML	MG	9,10,11	23-37,01-37,01-12	8/4/99	16:44		2	SVI		48 42.188	124 59.705	
42	B	B		NMML	PJG	8	06-19	8/26/99			2	SJF	E. BULLMAN BEACH			Added late
42	A			NMML	PJG	11	01-07	9/12/99			3	WVI	N. OF SPLIT CAPE			
42	B	B		NMML	MG	30	04-20	9/29/99	10:46		2	SJF	OFF SNOW CREEK			BUDDY; Added late
42		B		NMML	PJG	13	08-23	10/4/99			3	SJF	THIRD BEACH			
42		A		NMML	MG	31	01-04	10/13/99	10:50		1	SJF	OFF SAIL RIVER MOUTH			BUDDY; Added late
42		B		NMML	MG	31	18-34	10/14/99	9:58		2	SJF	OFF SAIL RIVER			Added late
42	B			NMML	PJG	14	11-15	10/19/99			3	SJF	SAIL ROCK & RASMUSSEN			Added late
43	A	B		NMML	PJG	2	01-36	7/23/99			9	SVI	2 MI. W OF NITINAT			
43		A		NMML	PJG	3	33-35	8/4/99			2	SVI	KLANAWA RIVER			43 IS DIAMOND, 42 IS BUDDY
43	A	A		NMML	MG	9,10,11	23-37,01-37,01-12	8/4/99	16:44		2	SVI		48 42.188	124 59.705	
43	B	B		CRC	JAC	34	29-35	9/13/99	17:50	N1-8	1	OR		44 45.3	124 04.4	RLNG IN KELP, MED-L
43	A	B		HSU	CT	12	14,16	9/19/99				OR	Depoe Bay			
43	C			HSU	CT	15	14	10/5/99				OR	Depoe Bay			
43	B	C		CRC	TEC	57	16-17	10/12/99	12:00	N2-10	1	OR		44 46.9	124 04.6	
43	B	A		CRC	TEC	57	18	10/12/99	12:15	N2-12	1	OR		44 44.8	124 04.6	
44	B	A	C	CRC	JAC	6	14-END	4/6/99	18:15	N1-10	1	NPS		48 04.4	122 18.7	BIG,DUB-KNUK?
49	A	A	A	CRC	JAC	5,6	28A-END,1-5	4/6/99	16:50	N1-7	3	NPS		48 03.4	122 22.9	PATCH BIGGEST,LT MED
53	B	A		CRC	JAC	4	23A-30A	4/6/99	13:05	N1-2	1	NPS		48 04.0	122 26.0	WHT SPT L BHND HUMP
62	C	A		CRC	HS	I7	19-20	4/11/99	16:27	VE-18	1	GH		46 55.4	124 02.5	
62		C		CRC	HS	I8	01-08	4/17/99	11:18	VE-1	1	GH		46 55.0	124 06.4	HEADING INTO HARBOR
62	A			CRC	HS	I8	20-24	4/17/99	12:30	VE-5	2	GH		46 55.3	124 04.9	SAME AS S#3
62	B			CRC	HS	I8,I9	34-36,01-10	4/18/99	11:15	VE-1	2	GH		46 54.8	124 06.8	
64	B	B		CRC	HS	1	14-27	3/20/99	15:13	VE-4	2	GH		46 55.7	124 05.3	INSIDE HARBOR
64	C			CRC	SEL	I3	10-21	4/10/99	12:05	VE-6	1	GH		46 55.6	124 05.9	SMALL WHITE PATCH
64	B	B		CRC	SEL	I4	04-19	4/10/99	12:38	VE-7	1	GH		46 55.6	124 04.6	PROB SAME AS S#6
64	C			CRC	HS	I5,I6	31-36A,4-11	4/11/99	14:20	VE-1	1	GH		46 55.3	124 06.5	ENTRNG HRBR AGNST CR
66	B			CRC	HS	I9	17-27	4/18/99	12:20	VE-4	3	GH		46 55.6	124 02.2	ONE HAD TORN UP DRSL
67	B	B		CRC	JAC	34	13-24	9/13/99	17:20	N1-5	2	OR		44 45.7	124 04.2	FD ON SD IN KLP,LRG
67	C	C		CRC	TEC	57	12-15	10/12/99	11:45	N2-9	5	OR		44 49.3	124 04.1	
67	B	B		CRC	TEC	56,57	30-END,1-10	10/12/99	10:08	N2-6	3	OR		44 48.9	124 04.4	IN THICK KELP FOREST
67		A		NMML	PJG	16	01-03	11/23/99	12:44		1	NWA	GUANO ROCK TO CANNONBALL			Added late
74	C	C		CRC	LLF	I1,I2	02-36,01-03	4/3/99	11:48	VE-3	2	GH		46 55.3	124 02.0	ALL W/IN HARBOR
74	C			CRC	HS	I2	04-08	4/3/99	14:22	VE-4	1	GH		46 54.5	124 06.3	PROB. SAME AS S#3
74		B		CRC	HS	I4,I5	30-36,05	4/10/99	14:35	VE-13	1	GH		46 55.5	124 05.6	SCAR ON R SIDE
74	A	A		CRC	SEL	I10	13-24	4/18/99	15:41	VE-14	1	GH		46 56.6	124 05.9	
74	B			CRC	SEL	I10	25-30	4/18/99	16:21	VE-15	1	GH		46 56.3	124 04.6	SAW MUD PLUME
79	A	B		NMML	MG	4	01A-13A	6/29/99			1	NWA	SKAGWAY/MUSHROOM ROC	48 22.071	124 43.655	
80	B			NMML	PJG	2	01-36	7/23/99			9	SVI	2 MI. W OF NITINAT			
80	B	A		NMML	PJG	13	02-06	9/14/99			1	NWA	BODELTEH/GUANO RK.			
80	B	B		NMML	MG	31	05-17	10/13/99	12:24		1	NWA	BTWN GREEN BANK AND WAATCH PT.			BIOPSIED NB-45 Added late
81	A	A		NMML	MG	16,17,18,19	20-37,01A-36A,01-36,01-0	8/8/99				WVI	OFF BAJO PT.	49 36.437	126 52.073	
81	C			NMML	PJG	5	01-24	8/8/99				WVI	BAJO REEF			
81	B			NMML	PJG	9,10	30-36,01A-04A	9/11/99			4	WVI	INSHORE OFF SPLIT CAPE			
81	B			NMML	PJG	10	06A-18A	9/12/99			3	WVI	OFF BAJO REEF			
81	A	B	A	NMML	MG	30	21-END	9/29/99	14:30		2	NWA	OFF GUANO ROCK	48 11.96	124 44.22	Added late
83		A		NMML	PJG	6	34-36	8/12/99			1	WVI	1 MILE NORTH OF BAJO POINT			
83		A	B	NMML	MG	24,25,26	23-36,01-37,01A-04A	8/12/99			8	WVI	BAJO POINT	49 37.757	126 51.225	
83	A	A		HSU	CT	11;12	34;04	9/19/99				OR	DB			
83	A	A		CRC	TEC	58A	8-10	10/12/99	13:57	N2-18	1	OR		44 32.7	124 06.0	
84		B		NMML	MG	13	01-19	8/7/99	14:29		3	WVI	PEREZ ROCKS	49 23.955	126 35.501	
84	A	A	C	NMML	MG	15	14-37	8/7/99	15:43		2	WVI	W. OF ESTEVAN PT.			
84		B		NMML	MG	28	01-37	8/13/99			8	WVI	APPROX. 8 OFF MATLAHAW PT.			
84	A	A		CRC	JAC	34	1-12	9/13/99	16:30	N1-4	2	OR		44 46.2	124 04.6	FDNG SD IN KLP,MED.
84	A			HSU	CT	12	05,10	9/19/99				OR	Depoe Bay			Yo-Yo
85	B			HSU	DG?	3?	17,20,22	8/10/99				OR	OR?			
85	A	B		CRC	JAC	34,35	27-28,1	9/13/99	17:50	N1-7	1	OR		44 45.3	124 04.4	RLNG IN KELP,MED-L
86	A	A		NMML	MG	21	07-36	8/10/99			2	NBC	OFF NAHWITTI	50 48.514	128 16.223	
86	B	B		NMML	PJG	9	01-24	9/11/99			4	WVI	BARCHESTER BAY TO NW OF PEREZ RKS			
86	B	B		NMML	PJG	11	01-07	9/12/99			3	WVI	N. OF SPLIT CAPE			
87		C		NMML	PJG	4	19-25	8/7/99				WVI	PEREZ ROCKS, V. IS.			
87	A	B		NMML	MG	13	20-37	8/7/99	14:52		2	WVI	OUTSIDE			
87	B	B		NMML	MG	15	14-37	8/7/99	15:43		2	WVI	W. OF ESTEVAN PT.			
87	B	B	B	NMML	MG	14,15	15A-37,01-13	8/7/99	15:11		3	WVI	OUTSIDE PEREZ ROCKS			
87	A	B		CRC	TEC	56	15-24	10/12/99	8:37	N2-2	2	OR		44 38.1	124 05.5	
92	A	B		NMML	MG	4,5	25A-36A,01-09	6/30/99			2	SVI		48 40.319	124 52.539	

Appendix Table 1. List of identifications by ID and date for Cascadia, NMML, and HSU in 1999.

ID	QL	QR	QF	Col	Pho	Roll	Frames	Date	Time	Sight#	No	Region	Location	Lat	Long	Comments
92		B		NMML	MG	16	07-09	8/7/99	16:45		1	WVI		49 26.319	126 35.340	
92	A			NMML	MG	27	22-36	8/13/99			3	WVI		49 23.922	126 36.018	
92		B		NMML	MG	27	07-21	8/13/99			3	WVI		49 23.922	126 36.018	
92	A	B		NMML	PJG	9	01-24	9/11/99			4	WVI	BARCHESTER BAY TO NW OF PEREZ RKS			
93		C		HSU	JH	1	23,26	7/30/99				OR	Depoe Bay			BC055
93	A	B		HSU	RJ	3	15,13	10/11/99				CA	Crescent City			BC055
94	B		C	NMML	MG	28	01-37	8/13/99			8	WVI	APPROX. 8 OFF MATLAHAW PT.			
94	C			HSU	CT	15	18	10/5/99				OR	DB			
98		B		NMML	MG	22	01-37	8/10/99			4	NBC	SE OF CHRISTENSEN POINT			
105	A	B	C	NMML	MG	21	07-36	8/10/99			2	NBC	OFF NAHWITTI	50 48.514	128 16.223	
106	B	C		CRC	JAC	33	15-END	9/13/99	15:51	N1-3	2	OR		44 49.7	124 04.1	ROLLING,PLYNG W/KELP
107	A			CRC	JAC	11	35-END	5/20/99	12:30	N1-22	2	OC		47 58.5	124 42.6	FORMER RESIDENT?
123	B			NMML	PJG	2	01-36	7/23/99			9	SVI	2 MI. W OF NITINAT			
127	B	B		CRC	JAC	33	15-END	9/13/99	15:51	N1-3	2	OR		44 49.7	124 04.1	ROLLING,PLYNG W/KELP
127	A	B		CRC	TEC	56,57	30-END,1-10	10/12/99	10:08	N2-6	3	OR		44 48.9	124 04.4	IN THICK KELP FOREST
127		A		CRC	TEC	57	12-15	10/12/99	11:45	N2-9	5	OR		44 49.3	124 04.1	
135		A	B	NMML	MG	16,17,18,19	20-37,01A-36A,01-36,01-0	8/8/99				WVI	OFF BAJO PT.	49 36.437	126 52.073	
135		B		NMML	PJG	5	01-24	8/8/99				WVI	BAJO REEF			
135		A		NMML	MG	24,25,26	23-36,01-37,01A-04A	8/12/99			8	WVI	BAJO POINT	49 37.757	126 51.225	
135	B	A		NMML	PJG	9	25-28	9/11/99			1	WVI	OFF SPLIT CAPE			
135	A	B		NMML	PJG	10	19A-34A	9/12/99			4	WVI	OFF ESCALANTE (ROCKS)			
136	A	A	B	NMML	MG	19	04-37	8/8/99	13:13		3	WVI	NEAR BAJO PT.			
138	A	B	B	NMML	MG	23,24	14A-37A,01-22	8/11/99			3	NBC	WEST OF WILKIE POINT	51 07.837	127 42.962	
138		B		NMML	PJG	6	17-26	8/11/99			3	NBC	SOUTH CAPE CAUTION			
140	B	B		CRC	TEC	62	1A-28A	10/30/99	16:22	N1-6	2	CA		41 47.7	124 16.0	MATING BEH.,FR 7&8=6
141	B	A		NMML	MG	14	01A-14A	8/7/99	15:05		1	WVI				
141		A		NMML	MG	28	01-37	8/13/99			8	WVI	APPROX. 8 OFF MATLAHAW PT.			
141		B		NMML	PJG	11	01-07	9/12/99			3	WVI	N. OF SPLIT CAPE			
141	A	B		NMML	MG	30	21-END	9/29/99	14:30		2	NWA	OFF GUANO ROCK	48 11.96	124 44.22	Added late
143	A	B		NMML	MG	5	39-37	6/30/99			1	SVI		48 42.138	125 00.635	
143	B	B		NMML	PJG	5	01-24	8/8/99				WVI	BAJO REEF			
143	B	A	B	NMML	MG	20	24-37	8/8/99	13:52		3	WVI				
143	B	B	C	NMML	MG	24,25,26	23-36,01-37,01A-04A	8/12/99			8	WVI	BAJO POINT	49 37.757	126 51.225	
143	A	A		NMML	PJG	10	06A-18A	9/12/99			3	WVI	OFF BAJO REEF			
144	B	B		NMML	MG	26,27	32A-37A,01-06	8/13/99			2	WVI	NORTH PEREZ ROCK	49 25.938	126 35.549	
152	B	C		NMML	MG	28	01-37	8/13/99			8	WVI	APPROX. 8 OFF MATLAHAW PT.			
152	B	A		NMML	PJG	11	08-27	9/12/99			8	WVI	S. OF SPLIT CAPE			
153	A	B		NMML	MG	22	01-37	8/10/99			4	NBC	SE OF CHRISTENSEN POINT			
166	B	B		NMML	MG	11	13-21	8/4/99	18:05		1	SVI	IN 18' WATER	48 42.658	125 02.042	
166	C		B	NMML	MG	7,8	22-37,01-37	8/4/99	15:09		4	SVI		48 41.321	124 56.391	
175	B	B		NMML	MG	12	28-37	8/7/99	10:51		1	WVI	BETW RAPHAEL PT. & SIWASH			
175		B	C	NMML	PJG	7	01-17	8/13/99			2	WVI	SIWASH PT.			
175	B			NMML	PJG	9,10	30-36,01A-04A	9/11/99			4	WVI	INSHORE OFF SPLIT CAPE			
177	C	C	C	CRC	JAC	14	19-22	5/20/99	14:57	N1-57	3	OC		48 04.0	124 43.5	HEADING E & N
177	C	B		NMML	PJG	3	01-13	7/23/99			2	SVI		48 42.490	125 00.69	
177		A		NMML	PJG	3	29-31	8/4/99			1	SVI	3 MI. W OF TSUSIAT FALLS			
177		A		NMML	MG	9	01-22	8/4/99	16:19		2	SVI		48 41.931	124 57.920	
177		B		NMML	MG	7,8	22-37,01-37	8/4/99	15:09		4	SVI		48 41.321	124 56.391	
177	B	B	C	NMML	MG	9,10,11	23-37,01-37,01-12	8/4/99	16:44		2	SVI		48 42.188	124 59.705	
177	B	B		NMML	PJG	7	23-36	8/14/99			4	SVI	1/4 MI. W. OF PACHENA PT.	48 42.227	124 59.656	
177		A		NMML	MG	29,30	32-END,01-02	9/28/99	14:26		2	NWA	GUANO ROCK	48 10.77	124 44.96	Added late
177	B	B		NMML	PJG	14	02-10	10/18/99			2	NWA	1 MI. N WHITE ROCK			Added late
178	B	A	C	CRC	JAC	10	1-9	5/20/99	9:55	N1-4	1	OC		47 56.5	124 40.7	BIG, HEADING NW
178		B		CRC	JAC	10	14-15	5/20/99	10:32	N1-6A	1	OC		47 58.1	124 42.4	6-8WHLS IN AREA, MED
178	B	A	B	NMML	MG	14,15	15A-37,01-13	8/7/99	15:11		3	WVI	OUTSIDE PEREZ ROCKS			
185	B	B		NMML	MG	6	01-37	6/30/99			2	SVI		48 42.924	125 03.348	
185	B	A		NMML	MG	12	15-27	8/7/99	10:30		1	WVI	SIWASH COVER			
185	C	A		NMML	PJG	8	06-19	8/26/99			2	SJF	E. BULLMAN BEACH			Added late
185	A	A		NMML	PJG	13	08-23	10/4/99			3	SJF	THIRD BEACH			
185	B			NMML	MG	31	18-34	10/14/99	9:58		2	SJF	OFF SAIL RIVER			Added late
185		C		NMML	PJG	14	11-15	10/19/99			3	SJF	SAIL ROCK & RASMUSSEN			Added late
186	A			NMML	MG	26	05A-21A	8/13/99			2	WVI	SO. OF ESCALANTE ROCKS	49 30.160	126 34.962	
186		B		CRC	TEC	57	12-15	10/12/99	11:45	N2-9	5	OR		44 49.3	124 04.1	
187	B	B		NMML	PJG	2	01-36	7/23/99			9	SVI	2 MI. W OF NITINAT			
187	B			NMML	MG	9	01-22	8/4/99	16:19		2	SVI		48 41.931	124 57.920	
187	B	B		NMML	MG	7,8	22-37,01-37	8/4/99	15:09		4	SVI		48 41.321	124 56.391	
187	C	A		NMML	PJG	10	35A-36A	9/12/99			1	WVI	2 MI. NW OF SPLIT CAPE			
191	B		C	CRC	JAC	13	34-35	5/20/99	14:10	N1-48	2	OC		48 00.0	124 43.6	
192	B	A	C	NMML	MG	6	01-37	6/30/99			2	SVI		48 42.924	125 03.348	
192	A	A		NMML	PJG	3	01-13	7/23/99			2	SVI		48 42.490	125 00.69	
192	B	B		NMML	MG	11	22-36	8/4/99	18:15		1	SVI	EAST OF PACHENA POINT	48 42.852	125 03.041	
205	C	C		NMML	PJG	8	20-21	8/28/99			1	NWA	WAATCH POINT			Added late
205	B	A		NMML	MG	29	23-38	8/29/99	10:45		1	NWA	GREEN BANK/WAATCH PT.	48 20.44	124 42.43	Added late
205	C			NMML	MG	29	29-31	9/28/99	12:22		1	NWA	GUANO ROCK	48 10.75	124 45.06	Added late
205		A		NMML	MG	29,30	32-END,01-02	9/28/99	14:26		2	NWA	GUANO ROCK	48 10.77	124 44.96	Added late
205	B	B		NMML	PJG	14	02-10	10/18/99			2	NWA	1 MI. N WHITE ROCK			Added late
205	B	B		NMML	PJG	14	16-19	11/2/99			1	NWA	NORTH WHITE RK			Added late
206		A		HSU	CT	6;7	33;04A	7/12/99				CA	TH			
206	B			HSU	CT	4;5;7	5A,32A;20;31A,33A	7/12/99				CA	TH			
212	A	B		NMML	PJG	3	14-18	7/23/99			1	SVI	1 mi W of Pachena			
212		C		NMML	PJG	8	22-23	9/10/99			1	SVI	PACHENA PT.			Added late
219	B	B		NMML	PJG	1	31-36	7/23/99			1	SVI	1 MILE WEST OF NITINAT			
219	B	B		NMML	PJG	7	23-36	8/14/99			4	SVI	1/4 MI. W. OF PACHENA PT.	48 42.227	124 59.656	
226	A	B		CRC	TEC	55	12-15	10/11/99	9:14	N2-1	1	CA		41 36.0	124 07.6	
229		A		NMML	MG	20	24-37	8/8/99	13:52		3	WVI				
229		B		NMML	PJG	5	01-24	8/8/99				WVI	BAJO REEF			
229	B		B	NMML	MG	24,25,26	23-36,01-37,01A-04A	8/12/99			8	WVI	BAJO POINT	49 37.757	126 51.225	
231	A	A		NMML	MG	5	10-28	6/30/99			1	SVI	SMALL, 1/4 MI. EAST OF WA	48 41.088	124 55.414	
231	C	A		NMML	MG	7	09-21	8/4/99	13:08		1	SVI	EAST OF BONILLA PT.	48 35.050	124 42.017	

Appendix Table 1. List of identifications by ID and date for Cascadia, NMML, and HSU in 1999.

ID	QL	QR	QF	Col	Pho	Roll	Frames	Date	Time	Sight#	No	Region	Location	Lat	Long	Comments
231	B	A		NMML	MG	29	13-22	8/14/99			1	SVI	W. OF BONILLA PT.	48 37.93	124 41.37	Added late
236	B	A		NMML	MG	22	01-37	8/10/99			4	NBC	SE OF CHRISTENSEN POINT			
236	B	B		CRC	JAC	34	13-24	9/13/99	17:20	N1-5	2	OR		44 45.7	124 04.2	FD ON SD IN KLP,LRG
237	B			HSU	CT	15	20	10/5/99				OR	DB			
238	A	A	B	NMML	MG	23,24	14A-37A,01-22	8/11/99			3	NBC	WEST OF WILKIE POINT	51 07.837	127 42.962	
238	B	B		NMML	PJG	6	17-26	8/11/99			3	NBC	SOUTH CAPE CAUTION			
242	B			NMML	PJG	2	01-36	7/23/99			9	SVI	2 MI. W OF NITINAT			
242	B	B		NMML	MG	9,10,11	23-37,01-37,01-12	8/4/99	16:44		2	SVI		48 42.188	124 59.705	
242	B	B		NMML	PJG	7	23-36	8/14/99			4	SVI	1/4 MI. W. OF PACHENA PT.	48 42.227	124 59.656	
242	C	B		NMML	MG	30	04-20	9/29/99	10:46		2	SJF	OFF SNOW CREEK			Added late
242	A	B		NMML	PJG	13	08-23	10/4/99			3	SJF	THIRD BEACH			
242	B	B		NMML	MG	31	18-34	10/14/99	9:58		2	SJF	OFF SAIL RIVER			Added late
242	B			NMML	PJG	14	11-15	10/19/99			3	SJF	SAIL ROCK & RASMUSSEN			Added late
242	B	C		NMML	PJG	15	17-19	11/3/99			1	SJF	JENSEN CREEK			Added late
244	A	A		NMML	MG	16,17,18,19	20-37,01A-36A,01-36,01-0	8/8/99				WVI	OFF BAJO PT.	49 36.437	126 52.073	
244	A	B		NMML	PJG	5	01-24	8/8/99				WVI	BAJO REEF			
244	B	B		NMML	MG	26	28A-31A	8/13/99			1	WVI	BARCRSTE BAY	49 26.550	126 34.700	
254	B			NMML	MG	13	20-37	8/7/99	14:52		2	WVI	OUTSIDE			
254	B	C		NMML	PJG	4	19-25	8/7/99				WVI	PEREZ ROCKS, V. IS.			
254	A	A	B	NMML	MG	27	22-36	8/13/99			3	WVI		49 23.922	126 36.018	
254	A			NMML	PJG	11	08-27	9/12/99			8	WVI	S. OF SPLIT CAPE			
269		B		CRC	HS	I2	10-23	4/4/99	14:30	VE-2	1	GH		46 55.0	124 03.2	
269		B		CRC	HS	I5	18-19	4/10/99	15:51	VE-23	1	GH		46 55.9	124 05.2	
269		B		CRC	HS	I5	20-29	4/10/99	15:57	VE-24	1	GH		46 55.9	124 05.6	APR STY IN SML AREA
269	C	B		CRC	LF	I11	12-36	4/24/99	11:42	VE-2	1	GH		46 56.0	124 04.6	SML WHL 30FT,HR OFTN
270	C			CRC	LF	I12	08A-26A	4/24/99	12:45	VE-3	2	GH		46 56.0	124 05.8	COW W/LST YEAR CALF?
273	C	B		NMML	MG	1	01A-10A	4/16/99			1	NPS	EVERETT, OUTSIDE JETTY	48 00.129	122 15.176	
273			C	NMML	MG	2	01-28	5/21/99			2	NPS	EVERETT, NW OF JETTY	48 00.855	122 15.980	
274	B	A		HSU	DG	6	25a,28a	8/24/99				CA	Crescent City			Added late, missing negs
276		C		HSU	RJ	2a	03	7/18/99				CA	Trinidad Head			Added late, missing negs
281	B	A	C	NMML	MG	16,17,18,19	20-37,01A-36A,01-36,01-0	8/8/99				WVI	OFF BAJO PT.	49 36.437	126 52.073	
281		A		NMML	PJG	5	01-24	8/8/99				WVI	BAJO REEF			
281		B		NMML	MG	24,25,26	23-36,01-37,01A-04A	8/12/99			8	WVI	BAJO POINT	49 37.757	126 51.225	
281		A		HSU	CT	15	11	10/5/99				OR	DB			
281	B			CRC	TEC	56,57	30-END,1-10	10/12/99	10:08	N2-6	3	OR		44 48.9	124 04.4	IN THICK KELP FOREST
291	C			HSU	CT	5	19	7/12/99				CA	TH			
291	B	B		HSU	RJ	3	10,17	10/11/99				CA	Crescent City			
296		B		NMML	MG	28	01-37	8/13/99			8	WVI	APPROX. 8 OFF MATLAHAW PT.			
296	A	A		NMML	PJG	11	08-27	9/12/99			8	WVI	S. OF SPLIT CAPE			
297		B		CRC	TEC	57	24-28	10/12/99	12:52	N2-15	1	OR		44 40.8	124 04.8	
297		A		CRC	TEC	57,58	29-END,1-7	10/12/99	13:37	N2-17	2	OR		44 32.7	124 05.8	FR33<>32,FR36=35
300	A		C	CRC	JAC	11	35-END	5/20/99	12:30	N1-22	2	OC		47 58.5	124 42.6	FORMER RESIDENT?
300	A	A		NMML	MG	13	01-19	8/7/99	14:29		3	WVI	PEREZ ROCKS	49 23.955	126 35.501	
300	A	B	B	NMML	PJG	9	01-24	9/11/99			4	WVI	BARCHESTER BAY TO NW OF PEREZ RKS			
301	B	B		HSU	CT	4;6;7;8	35A;27,28;26A;5A,6A	7/12/99				CA	TH			
301	C			HSU	CT	12	20	9/19/99				OR	Depoe Bay			Whaley
301	B	C		CRC	TEC	57	19-22	10/12/99	12:38	N2-13	1	OR		44 44.6	124 04.0	
302	B		B	CRC	JAC	11	27-34	5/20/99	12:20	N1-21	3	OC		47 58.6	124 42.8	ALL MEDIUMISH
302	A		B	CRC	JAC	12	20-22	5/20/99	12:50	N1-30	1	OC		47 59.1	124 43.0	
302	A		B	CRC	JAC	12	23-24	5/20/99	12:58	N1-31	1	OC		47 59.3	124 43.1	
302	A	C		CRC	JAC	13	7-9	5/20/99	13:19	N1-39	1	OC		47 59.3	124 43.8	COULD BE 2 ANIMALS
302	B	B	C	HSU	CT	1	2,4,6,8,9,10,11,17,18,21	7/7/99				OR	DB			
302	C	C		HSU	CT	2	17,27,28	7/8/99				OR	DB			
302	C	A		HSU	DG	3	4,6,9,25	8/10/99				OR	OR			
302	B	B		CRC	JAC	34	25-26	9/13/99	17:31	N1-6	1	OR		44 45.7	124 04.7	
303	B			CRC	JAC	35	2-4	9/13/99	18:02	N1-9	1	OR		44 44.5	124 04.3	MED
303	B			HSU	CT	12	21	9/19/99				OR	DB			
309	B	C		NMML	MG	27	07-21	8/13/99			3	WVI		49 23.922	126 36.018	
309	B	B		CRC	JAC	34	1-12	9/13/99	16:30	N1-4	2	OR		44 46.2	124 04.6	FDNG SD IN KLP,MED.
310	A			HSU	DG	6	18a	8/24/99				CA	Crescent City			Added late, missing negs
315	A	A	C	NMML	MG	23	01A-13A	8/11/99			1	NBC	OFF WILKIE POINT	51 08.000	127 42.146	
317		B		NMML	MG	28	01-37	8/13/99			8	WVI	APPROX. 8 OFF MATLAHAW PT.			
320	A	A		NMML	PJG	7	01-17	8/13/99			2	WVI	SIWASH PT.			
328	B	B	B	NMML	MG	26	22A-27A	8/13/99			1	WVI		49 28.073	126 35.373	
328		B		NMML	PJG	9	01-24	9/11/99			4	WVI	BARCHESTER BAY TO NW OF PEREZ RKS			
328	C	B		NMML	PJG	11	08-27	9/12/99			8	WVI	S. OF SPLIT CAPE			
350	B	B		CRC	HH	6	15-END	4/10/99	11:00	LND-1	3	NPS	Disco Bay	48 02.6	122 49.5	ALSO 2 ROLLS COLOR
350	B	B		CRC	SEL	1-4	1-END (ALL)	4/14/99	12:34	LND-1	5	NPS	Disco Bay	48 02.6	122 49.5	
350		C		CRC	HS	CRC1	21-36	4/20/99	15:15	LND-1	1	NPS		47 58.0	122 40.2	
350	B			CRC	HH	COLOR	22-30	5/9/99	11:07	WB-1	2	NPS		47 56.7	122 39.9	
351	C	C		CRC	SEL	1-4	1-END (ALL)	4/14/99	12:34	LND-1	5	NPS	Disco Bay	48 02.6	122 49.5	
351	B			CRC	MF			4/16/99		LND-1	6	NPS	Disco Bay	48 03.0	122 50.0	
351	B	B		CRC	JAC	8	1-END	4/29/99	14:15	BSP-1	2	HC		47 23.5	122 55.4	
351	A			NMML	MG	20	07-13	8/8/99	13:39		1	WVI	STILL AT BAJO PT.			
351	C			NMML	PJG	5	01-24	8/8/99				WVI	BAJO REEF			
352	B	C		CRC	LF	I6	28-36	4/11/99	15:50	VE-10	2	GH		46 55.6	124 00.9	SAME SIZE,CLS TOGTHR
352	B	C	B	CRC	HS	I7	03-08	4/11/99	16:00	VE-11	1	GH		46 55.6	124 00.9	WHITE PATCH
352	B			CRC	HS	I7	09-10	4/11/99	16:07	VE-12	1	GH		46 55.6	124 01.0	WATR DPTH 15-17 FT
352	C			CRC	HS	I7	11-12,14	4/11/99	16:12	VE-13	1	GH		46 55.6	124 00.8	
353	B	B	B	CRC	HH	7,CLR	1-6,31-36	5/9/99	12:00	WB-2	2	NPS		47 56.6	122 40.2	
353	B			CRC	HH	7	7	5/9/99	12:18	WB-3	1	NPS		47 56.6	122 40.3	PROB DUPE
353	B	B		CRC	HH	COLOR	22-30	5/9/99	11:07	WB-1	2	NPS		47 56.7	122 39.9	
354	B	B		CRC	JAC	15	1A-6A	5/23/99	11:53	N1-1	3	NPS		48 00.9	122 15.9	MED-LARGE,SIDE FDNG
355	B	C		NMML	PJG	3	19-28	7/28/99			1	SJF	KOITLAH JETTY			
356	B	B		CRC	HH	6	2-5	4/2/99	12:52	PAT-6	1	NPS		48 13.9	122 46.5	
356	B	B	C	CRC	TEC	56	25-29	10/12/99	9:31	N2-5	1	OR		44 45.7	124 04.7	SMALL
357	B	C		CRC	JAC	FUJI	1-22	7/8/99	12:28	N1-1	2	SPS	Olympia	47 02.6	122 54.6	BCK&FRTH UNDR BRDG
358	C	B		CRC	JAC	FUJI	1-22	7/8/99	12:28	N1-1	2	SPS	Olympia	47 02.6	122 54.6	BCK&FRTH UNDR BRDG
359	B	C		CRC	JAC	3,4	14-ND,1A-3A	4/4/99	14:30	N1-1	2	SPS	Purdy	47 22.8	122 37.7	FR.33 SMALLER,OTH MD

Appendix Table 1. List of identifications by ID and date for Cascadia, NMML, and HSU in 1999.

ID	QL	QR	QF	Col	Pho	Roll	Frames	Date	Time	Sight#	No	Region	Location	Lat	Long	Comments
359	C			CRC	HS	CRC1	21-36	4/20/99	15:15	LND-1	1	NPS		47 58.0	122 40.2	
359		C		CRC	HH	COLOR	22-30	5/9/99	11:07	WB-1	2	NPS		47 56.7	122 39.9	
359	B	B	C	CRC	HH	8,9	30-ND,1A-4A	5/22/99	15:15	WB-2	1	NPS		47 59.9	122 40.6	
359		C		CRC	HH	11	13-22	6/5/99	13:00	GS-1	2	SJI		48 27.4	122 48.3	
360	B	B		CRC	HH	8	10-29	5/20/99	10:19	GS-3	3	SJI		48 28.6	122 50.4	
360	B	B		CRC	HH	8	10-29	5/20/99	10:19	GS-3	3	SJI		48 28.6	122 50.4	
360	B			CRC	HH	9	06A-27A	5/24/99	11:00	GS-2	3	SJI		48 27.8	122 48.4	
360		B		CRC	HH	9	28A-35A	5/27/99	10:19	GS-1	3	SJI		48 28.2	122 48.3	
360		C		CRC	HH	10	19A-31A	6/2/99	16:30	GS-2	2	SJI		48 28.2	122 48.3	
360		A		CRC	HH	11	23-END	6/6/99	10:30	GS-1	2	SJI		48 28.3	122 48.3	
360		B		CRC	HH	12	11A-12A	6/14/99	10:30	GS-1	2	SJI		48 27.6	122 48.3	
360		B		CRC	HH	12	14A-19A	6/17/99	10:30	GS-2	2	SJI		48 27.6	122 48.3	
361	A	B	A	HSU	CT	6;8	32;7A,8A,10A,13A,28A,30	7/12/99				CA	TH			
361	A			HSU	RJ	1	34,36	8/17/99				CA	TH			
362	A	B		HSU	DG	5	5,10	8/24/99				CA	CC			
363	B			HSU	DG	2	03,20	8/20/99				CA	TH			
363		B		HSU	DG	2	17	8/20/99				CA	TH			
363	A		B	CRC	TEC	62	1A-28A	10/30/99	16:22	N1-6	2	CA		41 47.7	124 16.0	MATING BEH.,FR 7&8=6
364	B	A	B	CRC	TEC	57,58	29-END,1-7	10/12/99	13:37	N2-17	2	OR		44 32.7	124 05.8	FR33<>32,FR36=35
365	A	B	C	CRC	TEC	62	1A-28A	10/30/99	16:22	N1-6	2	CA		41 47.7	124 16.0	MATING BEH.,FR 7&8=6
366	A	A	C	CRC	TEC	56	15-24	10/12/99	8:37	N2-2	2	OR		44 38.1	124 05.5	
367	C			CRC	SEL	I3	03-09	4/10/99	11:54	VE-5	1	GH		46 55.6	124 05.9	
367	B			CRC	HS	I5	16-17	4/10/99	15:47	VE-22	1	GH		46 56.0	124 05.8	
367	A	C		CRC	HS	I8	09-18	4/17/99	11:48	VE-3	2	GH		46 55.4	124 04.3	ONE WHALE LRG,ONE SM
367		B		CRC	SEL	I10	31-34	4/18/99	16:21	VE-16	1	GH		46 56.3	124 04.6	
367		B		CRC	SEL	I10	35-36	4/18/99	16:21	VE-17	1	GH		46 56.3	124 04.6	
367	C			CRC	HS	I13	23-27	4/25/99	15:18	VE-8	1	GH		46 57.7	124 05.4	
368	C	B		CRC	HS	I9	29-30,32-33	4/18/99	13:12	VE-6	1	GH		46 56.9	124 05.9	WHITE PATCH
368		C		CRC	DL			7/16/99	12:00	-1	1	GH		46 55.0	124 07.0	
369	C	B		CRC	HS	I12	28A-END	4/25/99	12:09	VE-4	1	GH		46 55.7	124 03.3	SPYHPD 5-6X
370	A		B	CRC	JAC	12	29-33	5/20/99	13:03	N1-34	3	OC		47 59.3	124 43.2	
371	B		B	CRC	JAC	12	11-12	5/20/99	12:45	N1-27	1	OC		47 59.0	124 43.1	HEADING N
371	B	A		CRC	JAC	13	3-5	5/20/99	13:15	N1-37	1	OC		47 59.2	124 43.3	
372	B	A		NMML	PJG	2	01-36	7/23/99			9	SVI	2 MI. W OF NITINAT			
372	B	B	C	NMML	MG	7,8	22-37,01-37	8/4/99	15:09		4	SVI		48 41.321	124 56.391	
372	C	B		NMML	MG	9	01-22	8/4/99	16:19		2	SVI		48 41.931	124 57.920	
372	A	B		NMML	PJG	7	23-36	8/14/99			4	SVI	1/4 MI. W. OF PACHENA PT.	48 42.227	124 59.656	
372	B	B		HSU	CT	15	17 (CRC adds 16)	10/5/99				OR	Depoe Bay			BC013
372		C		HSU	CT	15	15	10/5/99				OR	DB			
373	A	B		HSU	CT	1,2	34,36,4	7/7/99				OR	DB			
373		B		HSU	CT	2	22	7/8/99				OR	DB			
374	B		C	HSU	DG	3	06,04,35,26 (CRC not 04,0	8/10/99				OR	Depoe Bay			*Chg date/initials
374	B	B		HSU	DG	5	34,33, 27, 12(CRC adds)	8/24/99				CA	Crescent City			*Chg date/initials
375		B		HSU	CT	7;8	13A;15A	7/12/99				CA	TH			
375	B			HSU	CT	7	22A	7/12/99				CA	TH			
376		C		HSU	CT	12	12	9/19/99				OR	DB			
377		B		HSU	CT	6	14	7/12/99				CA	TH			
377	A	A		HSU	CT	4;6;8	16A,34A;18,21;12A	7/12/99				CA	TH			
377		A		HSU	RJ	1	22,23	7/17/99				CA	TH			
377	B	B		HSU	RJ	1	4,12,14,19,32,35	7/17/99				CA	TH			
377	B			HSU	DG	1	6	7/18/99				CA	TH			
377		C		HSU	RJ	2b	28	7/18/99				CA	Trinidad Head			Added late, missing negs
378	A	A	B	HSU	CT	4;5;6;7	10A;4;8,12,13,17,25,34;1A	7/12/99				CA	TH			
378	B	B		HSU	RJ	1	7,27	7/17/99				CA	TH			
379	A			HSU	CT	8	22A	7/12/99				CA	TH			
379		A		HSU	CT	4;7	24A;28A	7/12/99				CA	TH			
379	B			HSU	RJ	1	11,15	7/17/99				CA	TH			
379		B		HSU	RJ	2b	11	7/18/99				CA	Trinidad Head			Added late, missing negs
380	B	B		HSU	RJ	1	03,05,08,09	7/17/99				CA	TH			
380		A		HSU	DG	1	1	7/18/99				CA	TH			
380		A		HSU	RJ	2b	09	7/18/99				CA	Trinidad Head			Added late, missing negs
381		B		CRC	JAC	10	29-31	5/20/99	11:03	N1-10	2	OC		47 58.2	124 42.3	381 SMALLER, HDNG S
381	B	B		CRC	JAC	10	35-END	5/20/99	11:15	N1-12	1	OC		47 58.1	124 42.3	MED, CLS TO BT,HD SW
381	B	A		CRC	JAC	11	2-8	5/20/99	11:20	N1-14	3	OC		47 57.5	124 41.8	HEADING E & N
382	A	A		NMML	MG	16,17,18,19	20-37,01A-36A,01-36,01-0	8/8/99				WVI	OFF BAJO PT.	49 36.437	126 52.073	
382	A			NMML	PJG	5	01-24	8/8/99				WVI	BAJO REEF			
382	B	B		NMML	PJG	10	19A-34A	9/12/99			4	WVI	OFF ESCALANTE (ROCKS)			
383	B	B	B	CRC	JAC	5	11A-27A	4/6/99	15:58	N1-6	2	NPS		48 04.1	122 23.6	LIKELY SAME AS #5
383		A		CRC	JAC	5,6	28A-END,1-5	4/6/99	16:50	N1-7	3	NPS		48 03.4	122 22.9	PATCH BIGGEST,LT MED
384		A		NMML	MG	20	24-37	8/8/99	13:52		3	WVI				
384	B	A		NMML	PJG	5	01-24	8/8/99				WVI	BAJO REEF			
385	A	A		NMML	PJG	6	34-36	8/12/99			1	WVI	1 MILE NORTH OF BAJO POINT			
385	A	A		NMML	MG	24,25,26	23-36,01-37,01A-04A	8/12/99			8	WVI	BAJO POINT	49 37.757	126 51.225	
386	A	A	B	NMML	MG	26,27	32A-37A,01-06	8/13/99			2	WVI	NORTH PEREZ ROCK	49 25.938	126 35.549	
386		A		NMML	PJG	9,10	30-36,01A-04A	9/11/99			4	WVI	INSHORE OFF SPLIT CAPE			
386	A	A		NMML	PJG	10	06A-18A	9/12/99			3	WVI	OFF BAJO REEF			
387	A	B	B	CRC	JAC	12	14-19	5/20/99	12:48	N1-29	2	OC		47 59.2	124 43.1	
388		A		CRC	JAC	10	20-26	5/20/99	10:57	N1-8	3	OC		47 58.2	124 42.3	MED, HEADING W
388	B			CRC	JAC	10	27-28	5/20/99	11:00	N1-9	2	OC		47 58.3	124 42.3	MED, HEADING N & S
389		A	B	CRC	JAC	12	25-27	5/20/99	13:01	N1-32	2	OC		47 59.3	124 43.2	HEADING NE
389	B	B	B	CRC	JAC	12	34-END	5/20/99	13:08	N1-35	1	OC		47 59.4	124 43.2	
390	B			CRC	JAC	10	34	5/20/99	11:20	N1-13	1	OC		47 57.9	124 42.0	LRG WHT PATCH, HD SW
390	B	B		CRC	JAC	11	9-12	5/20/99	11:50	N1-15	2	OC		47 57.6	124 41.6	LRG WHT PTCH NR DRSL
390		B		CRC	JAC	11	13-14	5/20/99	11:53	N1-16	1	OC		47 57.5	124 41.7	HEADING S
390		C	A	CRC	JAC	11	2-8	5/20/99	11:20	N1-14	3	OC		47 57.5	124 41.8	HEADING E & N
391	A	B	B	CRC	JAC	12	3-6	5/20/99	12:38	N1-24	1	OC		47 58.8	124 43.0	SML-MED, LKD FMLIAR
392	B	A	B	NMML	MG	14,15	15A-37,01-13	8/7/99	15:11		3	WVI	OUTSIDE			
392	A		B	NMML	MG	16	01-06	8/7/99			1	WVI		49 24.996	126 36.420	
392		C		NMML	PJG	4	19-25	8/7/99				WVI	PEREZ ROCKS, V. IS.			

Appendix Table 1. List of identifications by ID and date for Cascadia, NMML, and HSU in 1999.

ID	QL	QR	QF	Col	Pho	Roll	Frames	Date	Time	Sight#	No	Region	Location	Lat	Long	Comments
392	A	A	B	NMML	MG	27	07-21	8/13/99			3	WVI		49 23.922	126 36.018	
393		B	C	NMML	MG	20	14-23	8/8/99	13:48		1	WVI		49 38.353	126 53.222	
393	A			NMML	MG	24,25,26	23-36,01-37,01A-04A	8/12/99			8	WVI	BAJO POINT	49 37.757	126 51.225	
394	B		C	CRC	JAC	6	6-12	4/6/99	17:50	N1-8	1	NPS		48 03.3	122 17.9	SMALL, LT. COLOR
394	B	B		CRC	JAC	7	3-11	4/6/99	19:05	N1-11	1	NPS		48 01.5	122 16.1	SMALL
395	B	B		CRC	HH	6	15-END	4/10/99	11:00	LND-1	3	NPS	Disco Bay	48 02.6	122 49.5	ALSO 2 ROLLS COLOR
396	C			CRC	SEL	1-4	1-END (ALL)	4/14/99	12:34	LND-1	5	NPS	Disco Bay	48 02.6	122 49.5	
396	B			CRC	MF			4/16/99		LND-1	6	NPS	Disco Bay	48 03.0	122 50.0	
396	C	C		CRC	HH			4/18/99	13:00	LND-1	4	NPS	Disco Bay	48 02.6	122 49.5	NO FILM INFO
396		B		CRC	HS	CRC1	21-36	4/20/99	15:15	LND-1	1	NPS		47 58.0	122 40.2	
396	B	B		CRC	MS	SL		6/7/99	11:30	MS-99J	1	SPS	W Seattle	47 32	122 24	
397	B	C		CRC	MS	SL		6/2/99	19:00	MS-99J	1	SPS	W Seattle	47 31	122 24	
398	B	B		CRC	JAC	5	11A-27A	4/6/99	15:58	N1-6	2	NPS		48 04.1	122 23.6	LIKELY SAME AS #5
398	C	A		CRC	JAC	5,6	28A-END,1-5	4/6/99	16:50	N1-7	3	NPS		48 03.4	122 22.9	PATCH BIGGEST,LT MED
399	C	B		CRC	HH	SL	15-20	4/30/99	10:30	GS-1	1	SJI		48 28.1	122 48.3	
399	C	B		CRC	HH	7	19A-23A	5/14/99	10:30	GS-1	2	SJI		48 27.4	122 48.0	
399	B	A		CRC	HH	7,8	24-END,1-4	5/16/99	10:30	GS-1	2	SJI		48 27.6	122 48.5	MUD ON EVERY SRFCNG
399	C	B		CRC	HH	8	05-09	5/17/99	10:30	GS-1	2	SJI		48 27.4	122 48.5	
399		B		CRC	HH	8	10-29	5/20/99	10:19	GS-3	3	SJI		48 28.6	122 50.4	
399		B		CRC	HH	8	10-29	5/20/99	10:19	GS-3	3	SJI		48 28.6	122 50.4	
399	B			CRC	HH	9	06A-27A	5/24/99	11:00	GS-2	3	SJI		48 27.8	122 48.4	
399	C			CRC	HH	9	28A-35A	5/27/99	10:19	GS-1	3	SJI		48 28.2	122 48.3	
399		B		CRC	HH	10	01A-03A	5/28/99	10:30	GS-1	3	SJI		48 28	122 48	
399		A		CRC	HH	10	14A-18A	5/30/99	10:00	GS-1	2	SJI		48 28	122 48	
399	B	B		CRC	HH	10	19A-31A	6/2/99	16:30	GS-2	2	SJI		48 28.2	122 48.3	
399	B	A	C	CRC	HH	10,11	32A-ND,1-12	6/3/99	10:30	GS-1	2	SJI		48 27.4	122 48.3	
399	C	B	C	CRC	HH	11	13-22	6/5/99	13:00	GS-1	2	SJI		48 27.4	122 48.3	
399	C	A		CRC	HH	11	23-END	6/6/99	10:30	GS-1	2	SJI		48 28.3	122 48.3	
399		B		CRC	HH	12	01A-02A	6/7/99	10:15	GS-1	1	SJI		48 28.3	122 48.3	
399	C	B		CRC	HH	12	03A-07A	6/10/99	10:00	GS-2	1	SJI		48 27.1	122 48.3	
399	C			CRC	HH	12	08A-10A	6/12/99	10:00	GS-1	2	SJI		48 27.5	122 48.2	
399	B			CRC	HH	12	11A-12A	6/14/99	10:30	GS-1	2	SJI		48 27.6	122 48.3	
399	B			CRC	HH	12	14A-19A	6/17/99	10:30	GS-2	2	SJI		48 27.6	122 48.3	
399		A		CRC	HH	12	21A-24A	6/18/99		GS-1	2	SJI		48 27.6	122 48.4	
400	B		A	CRC	JAC	14	23-25	5/20/99	15:03	N1-58	1	OC		48 04.0	124 43.6	HEADING NW
400		A		CRC	JAC	14	28-29	5/20/99	15:23	N1-61	1	OC		48 04.2	124 43.6	MEDIUM, HEADING N
401	B		B	CRC	JAC	14	1-2	5/20/99	14:13	N1-49	1	OC		48 01.0	124 43.4	HEADING E
401	A			CRC	JAC	10	20-26	5/20/99	10:57	N1-8	3	OC		47 58.2	124 42.3	MED, HEADING W
401	A			CRC	JAC	11	2-8	5/20/99	11:20	N1-14	3	OC		47 57.5	124 41.8	HEADING E & N
402	B			CRC	JAC	14	15-17	5/20/99	14:37	N1-55	2	OC		48 01.9	124 43.5	HEADING N
403	A		B	CRC	JAC	14	5-7	5/20/99	14:22	N1-51	1	OC		48 01.1	124 43.6	MED SIZE, HEAD NE
404	B			CRC	JAC	13	6	5/20/99	13:17	N1-38	2	OC		47 59.3	124 43.6	
405	A		B	CRC	JAC	11	21-23	5/20/99	12:12	N1-19	1	OC		47 58.2	124 42.4	BIG, HEADING NW
405			B	CRC	JAC	12	29-33	5/20/99	13:03	N1-34	3	OC		47 59.3	124 43.2	
406	B			CRC	SEL	I9,10	34-36,01-12	4/18/99	14:54	VE-10	1	GH+		46 54.1	124 12.8	OUTSIDE HARBOR
407	A			HSU	CT	8	19A	7/12/99				CA	TH			
408	B			HSU	CT	13	4,18	10/6/99				OR	Depoe Bay			
409	A	B		CRC	JAC	8	1-END	4/29/99	14:15	BSP-1	2	HC		47 23.5	122 55.4	
410	C			CRC	TEC	51	20-21	9/20/99	11:04	N1-6	1	CA		38 13.0	123 20.1	
410	B			CRC	JAC	40	23-26	9/20/99	11:23	N2-5	1	CA		38 12.1	123 19.6	W/N1 V.SM,CLF OR YRL
411	B			CRC	TEC	62	29A-30A	10/30/99	17:09	N1-7	1	CA		41 47.6	124 16.0	
412	A			HSU	CT	5;7	15;7,18A	7/12/99				CA	TH			
412	B			HSU	DG	5	6,7	8/24/99				CA	CC			
413	B			CRC	JAC	10	19	5/20/99	10:53	N1-7	1	OC		47 58.2	124 42.3	MED, HEADING SW
413	A		C	CRC	JAC	10	32-33	5/20/99	11:10	N1-11	2	OC		47 58.0	124 42.2	HEADING S
413		B		CRC	JAC	10	27-28	5/20/99	11:00	N1-9	2	OC		47 58.3	124 42.3	MED, HEADING N & S
413		B	B	CRC	JAC	10	29-31	5/20/99	11:03	N1-10	2	OC		47 58.2	124 42.3	381 SMALLER, HDNG S
413		B		CRC	JAC	11	9-12	5/20/99	11:50	N1-15	2	OC		47 57.6	124 41.6	LRG WHT PTCH NR DRSL
413	B			CRC	JAC	11	2-8	5/20/99	11:20	N1-14	3	OC		47 57.5	124 41.8	HEADING E & N
414	A		C	CRC	JAC	13	12-19	5/20/99	13:33	N1-42	3	OC		47 59.9	124 43.9	GO IN DIFF DIR.
415	A			CRC	JAC	13	30-33	5/20/99	14:03	N1-47	3	OC		48 00.7	124 43.6	HEADING N & E
416	B			CRC	JAC	13	12-19	5/20/99	13:33	N1-42	3	OC		47 59.9	124 43.9	GO IN DIFF DIR.
417	B		A	CRC	JAC	13	1-2	5/20/99	13:10	N1-36	1	OC		47 59.4	124 43.2	SMALL
418	B			CRC	JAC	14	27	5/20/99	15:19	N1-60	1	OC		48 04.1	124 43.5	HEADING W
419	B			HSU	CT	11	2	9/19/99				OR	DB			
420	B			CRC	HS	I13	14-18	4/25/99	14:21	VE-5	1	GH		46 55.4	124 06.9	
421	B			CRC	HS	1	05-08	3/14/99	14:13	VE-1	1	GH		46 55.1	124 06.3	SMALL,BTWN HRB & OCN
423	B			CRC	JAC	14	1-2	5/20/99	14:17	N1-50	1	OC		48 01.3	124 43.5	HEADING E
423	A			CRC	JAC	14	8-9	5/20/99	14:24	N1-52	1	OC		48 01.2	124 43.6	MED, HEADING SW
424	B		C	NMML	MG	28	01-37	8/13/99			8	WVI	APPROX. 8 OFF MATLAHAW PT.			
425	B	B		NMML	MG	2,3	29-37,01-09	5/21/99			1	NPS	NORTH OF SANDY PT.	48 02.519	122 24.082	
426	A		C	CRC	JAC	11	24-26	5/20/99	12:16	N1-20	1	OC		47 58.2	124 42.5	LOOKED SML, HEAD SW
427	B		C	NMML	MG	24,25,26	23-36,01-37,01A-04A	8/12/99			8	WVI	BAJO POINT	49 37.757	126 51.225	
428	A		B	HSU	CT	5;6;7	18,33,34,35;6;30A	7/12/99				CA	TH			
429	B			HSU	DG	2	9	8/20/99				CA	TH			*Chg date/initials
429	B			HSU	DG	2	21	8/20/99				CA	TH			
429	B			HSU	DG	6	31a	8/24/99				CA	Crescent City			Added late, missing negs
429	B			HSU	CT	13	09,03,01	10/6/99				OR	Depoe Bay			*Chg date/initials
430	B	B		CRC	HH	6	15-END	4/10/99	11:00	LND-1	3	NPS	Disco Bay	48 02.6	122 49.5	ALSO 2 ROLLS COLOR
430	C	C		CRC	SEL	1-4	1-END (ALL)	4/14/99	12:34	LND-1	5	NPS	Disco Bay	48 02.6	122 49.5	
431	B			CRC	JAC	3,4	14-ND,1A-3A	4/4/99	14:30	N1-1	2	SPS	Purdy	47 22.8	122 37.7	FR.33 SMALLER,OTH MD
432	B			HSU	CT	4;7	13A;35A	7/12/99				CA	TH			
433	B		B	NMML	MG	20	01-06	8/8/99	13:33		1	WVI	STILL AT BAJO PT.			
434	B		C	NMML	MG	28	01-37	8/13/99			8	WVI	APPROX. 8 OFF MATLAHAW PT.			
435	B			CRC	JAC	13	12-19	5/20/99	13:33	N1-42	3	OC		47 59.9	124 43.9	GO IN DIFF DIR.
436	B	B	B	CRC	JAC	14	30-34	5/20/99	15:30	N1-62	1	OC		48 04.6	124 43.8	SMALL, HEADING NE
437	B			CRC	HH	6	15-END	4/10/99	11:00	LND-1	3	NPS	Disco Bay	48 02.6	122 49.5	ALSO 2 ROLLS COLOR
438	C			CRC	HH	9	06A-27A	5/24/99	11:00	GS-2	3	SJI		48 27.8	122 48.4	
438	A			CRC	HH	9	28A-35A	5/27/99	10:19	GS-1	3	SJI		48 28.2	122 48.3	

Appendix Table 1. List of identifications by ID and date for Cascadia, NMML, and HSU in 1999.

ID	QL	QR	QF	Col	Pho	Roll	Frames	Date	Time	Sight#	No	Region	Location	Lat	Long	Comments
438	C			CRC	HH	10,11	32A-ND,1-12	6/3/99	10:30	GS-1	2	SJI		48 27.4	122 48.3	
438	C			CRC	HH	11	23-END	6/6/99	10:30	GS-1	2	SJI		48 28.3	122 48.3	
438	C			CRC	HH	12	14A-19A	6/17/99	10:30	GS-2	2	SJI		48 27.6	122 48.3	
438	A			CRC	HH	12	21A-24A	6/18/99		GS-1	2	SJI		48 27.6	122 48.4	
439	A		A	HSU	DG	1	9	7/18/99				CA	TH			
439	B			HSU	RJ	2b	30	7/18/99				CA	Trinidad Head			Added late, missing negs
440	B			HSU	CT	6;7	03,19,23;06A,24A	7/12/99				CA	TH			
440	A			HSU	CT	7	15A	7/12/99				CA	TH			
441	B			CRC	SEL	I9,10	34-36,01-12	4/18/99	14:54	VE-10	1	GH+		46 54.1	124 12.8	OUTSIDE HARBOR
444		B		HSU	CT	8	2A	7/12/99				CA	TH			
444		B		HSU	RJ	1	16	7/17/99				CA	TH			
444		B		HSU	RJ	2b	17	7/18/99				CA	Trinidad Head			Added late, missing negs
445		B	B	CRC	JAC	11	15-17	5/20/99	11:59	N1-17	1	OC		47 57.4	124 41.5	POSS W/PTCH, HD N
446		A	B	CRC	JAC	12	1-2	5/20/99	12:30	N1-23	1	OC		47 58.5	124 42.6	MEDIUM, HEADING E
446		A	A	CRC	JAC	11	27-34	5/20/99	12:20	N1-21	3	OC		47 58.6	124 42.8	ALL MEDIUMISH
447		B		CRC	JAC	13	10	5/20/99	13:26	N1-40	1	OC		47 59.6	124 44.0	
448		B		HSU	CT	4;6	36A;01	7/12/99				CA	TH			
448	B			HSU	CT	8	20A,24A	7/12/99				CA	TH			
448		B		HSU	RJ	1	17	7/17/99				CA	TH			
448	B			HSU	RJ	1	24,29,30	7/17/99				CA	TH			
448		A		HSU	DG	1	3	7/18/99				CA	TH			
449		B		HSU	CT	4;8	19A;26A	7/12/99				CA	TH			
449		C		HSU	RJ	2b	20	7/18/99				CA	Trinidad Head			Added late, missing negs
450		B		HSU	DG	5	14,22	8/24/99				CA	CC			
451		B		NMML	MG	16,17,18,19	20-37,01A-36A,01-36,01-0	8/8/99				WVI	OFF BAJO PT.	49 36.437	126 52.073	
452		B		CRC	JAC	12	13	5/20/99	12:46	N1-28	1	OC		47 59.1	124 43.1	MED SIZE, HEADING NW
453		A		CRC	JAC	11	18-20	5/20/99	12:03	N1-18	1	OC		47 57.6	124 41.5	HEADING NW
454		B	B	CRC	JAC	10	10-13	5/20/99	10:28	N1-5	1	OC		47 58.0	124 42.2	MEDIUM
454		B	C	CRC	JAC	10	16-18	5/20/99	10:44	N1-6B	1	OC		47 57.9	124 42.1	HEADING SOUTH
455		B	B	CRC	JAC	13	20-22	5/20/99	13:43	N1-43	1	OC		47 59.9	124 43.8	HEADING S
456		A	C	CRC	JAC	14	12-14	5/20/99	14:30	N1-54	1	OC		48 01.2	124 43.6	
456		B		CRC	JAC	10	20-26	5/20/99	10:57	N1-8	3	OC		47 58.2	124 42.3	MED, HEADING W
457		B		CRC	HS	I4	22-29	4/10/99	14:18	VE-11	1	GH		46 55.3	124 06.0	SHWD FLK FDNG
459		B	B	CRC	JAC	14	10-11	5/20/99	14:27	N1-53	1	OC		48 01.1	124 43.6	SMALL, HEADING SE
460		B		HSU	CT	11	04,06	9/19/99				OR	DB			
461		B		CRC	JAC	14	18	5/20/99	14:44	N1-56	1	OC		48 01.2	124 43.5	HEADING E
462		B		CRC	HS	I9	11-16	4/18/99	11:51	VE-3	1	GH		46 55.4	124 05.9	
463		C		CRC	HS	I6	13	4/11/99	14:50	VE-2	1	GH		46 55.3	124 05.9	
463		A		CRC	HS	I6	14-19	4/11/99	15:12	VE-3	1	GH		46 55.3	124 03.9	POSS SAME AS S#2
466		B	C	CRC	JAC	11	27-34	5/20/99	12:20	N1-21	3	OC		47 58.6	124 42.8	ALL MEDIUMISH
467		B		NMML	MG	2	01-28	5/21/99			2	NPS	EVERETT, NW OF JETTY	48 00.855	122 15.980	
468		B		HSU	DG	5	16	8/24/99				CA	CC			
468	B			HSU	DG	6	01a	8/24/99				CA	Crescent City			Added late, missing negs
470		B		HSU	DG	5	11	8/24/99				CA	CC			
471		B		HSU	RJ	1	13	7/17/99				CA	TH			
472		A		CRC	JAC	14	15-17	5/20/99	14:37	N1-55	2	OC		48 01.9	124 43.5	HEADING N
473		B		CRC	JAC	14	26	5/20/99	15:11	N1-59	1	OC		48 03.8	124 43.8	SMALL, HEADING SE
474		B		HSU	CT	5	12,27	7/12/99				CA	TH			
476		B		HSU	CT	5	31	7/12/99				CA	TH			
476		A		HSU	RJ	2b	34	7/18/99				CA	Trinidad Head			Added late, missing negs
477		B		NMML	MG	19	04-37	8/8/99	13:13		3	WVI	NEAR BAJO PT.			
478		B		HSU	CT	8	14A,17A	7/12/99				CA	TH			
479		B		CRC	JAC	13	11	5/20/99	13:30	N1-41	1	OC		47 59.9	124 43.9	
479		B		CRC	JAC	13	26-28	5/20/99	13:52	N1-45	2	OC		48 00.1	124 43.8	HEADING NE & S
480		A		NMML	PJG	10	19A-34A	9/12/99			4	WVI	OFF ESCALANTE (ROCKS)			
481		B		CRC	JAC	15	9A	5/23/99	13:50	N1-3	1	NPS		48 09.5	122 23.1	MED
482		C		CRC	JAC	15	7A-8A	5/23/99	13:03	N1-2	2	NPS		48 01.5	122 15.8	MED-LARGE,SIDE FDNG
482		A		CRC	JAC	15	15A-16A	5/23/99	17:17	N1-5	1	NPS		48 00.4	122 16.0	
483		B		NMML	MG	28	01-37	8/13/99			8	WVI	APPROX. 8 OFF MATLAHAW PT.			
484		B	B	CRC	JAC	12	8-9	5/20/99	12:41	N1-25	1	OC		47 58.9	124 43.1	MED SIZE, HD NE
485		B		NMML	MG	19	04-37	8/8/99	13:13		3	WVI	NEAR BAJO PT.			
485		B		NMML	PJG	5	01-24	8/8/99				WVI	BAJO REEF			
487		A		CRC	HH	7,8	24-END,1-4	5/16/99	10:30	GS-1	2	SJI		48 27.6	122 48.5	MUD ON EVERY SRFCNG
487		C		CRC	HH	8	05-09	5/17/99	10:30	GS-1	2	SJI		48 27.4	122 48.5	
487		B		CRC	HH	8	10-29	5/20/99	10:19	GS-3	3	SJI		48 28.6	122 50.4	
487		B		CRC	HH	8	10-29	5/20/99	10:19	GS-3	3	SJI		48 28.6	122 50.4	
487		C		CRC	HH	9	06A-27A	5/24/99	11:00	GS-2	3	SJI		48 27.8	122 48.4	
488		B		CRC	HH	10	04A-13A	5/29/99	9:27	SH-1	3	NPS		48 00.9	122 17.9	
489		B		HSU	DG	2	14	8/20/99				CA	TH			*Chg date/initials
489		B		HSU	CT	13	8	10/6/99				OR	Depoe Bay			
490	B			NMML	MG	28	01-37	8/13/99			8	WVI	APPROX. 8 OFF MATLAHAW PT.			

SC/A17/GW/05

Updated analysis of abundance and population structure of seasonal gray whales in the Pacific Northwest, 1996-2015

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INTERNATIONAL
WHALING COMMISSION

Updated analysis of abundance and population structure of seasonal gray whales in the Pacific Northwest, 1996-2015

John Calambokidis, Jeffrey Laake, and Alie Pérez

Abstract

We update the results of a 20-year (1996-2015) collaborative study examining the abundance and the population structure of these animals conducted over a number of regions from Northern California to British Columbia using photographic identification. Some 21235 identifications representing 1638 unique gray whales were obtained during 1996-2015 from Southern California to Kodiak, Alaska. Gray whales seen from 1 June - 30 Nov (after the northward and before southward migrations) were more likely to be seen repeatedly and in multiple regions and years;therefore only whales seen during those data were included in the abundance estimates. Gray whales using the Pacific Northwest in summer and fall include two groups: 1) whales that return frequently and account for the majority of the sightings and 2) transients seen in only one year, generally for shorter periods and in more limited areas. A time series of abundance estimates of the non-transient whales for 1996-2015 was constructed for the region from N. California (NCA) to N. Vancouver Island (NBC). The most recent estimate for 2015 was 243 whales (se=18.9). The estimated abundance increased in the late 1990s and early 2000s during the period when the eastern North Pacific gray whale population was experiencing a high mortality event and this created an apparent influx of whales into the area. The earlier estimates for 1996-1997 are biased low because the survey coverage area was much smaller but those data were included to improve estimates later in the time series. The abundance estimates since the early 2000s has been relatively stable but it has increased in 2013-2015.

1 Introduction

Beginning in 1996, a collaborative effort among a number of research groups was initiated to conduct a range-wide photographic identification study of gray whales in the Pacific Northwest (Calambokidis et al. 2000, 2002b). An initial publication of findings from 1998 demonstrated there was considerable movement of individual whales among sub-areas from northern California to southeastern Alaska (which we broadly refer to as the Pacific Northwest) and also provided initial estimates of the abundance of whales within that geographical area (Calambokidis et al. 2002a). The ability to look at movements and employ more sophisticated capture-recapture models, however, was restricted by the lack of multiple years of data with broad geographic coverage. A subsequent report by Calambokidis et al. (2004) characterized the group of whales feeding in these survey areas during the summer-fall period as a “Pacific Coast Feeding Aggregation” (PCFA). They proposed that a smaller area within the PCFA survey areas – from Oregon to Southern Vancouver Island (OR-SVI) – was the most appropriate area for abundance estimation for managing a Makah gray whale hunt (Calambokidis et al. 2004). Subsequently the IWC has adopted the term PCFG for Pacific Coast Feeding group so we will use PCFG in place of PCFA.

This report updates information through 2015 from a collaborative effort to collect photographic identifications of gray whales from California to Alaska has continued since 1996 and these data now cover 20 years (1996-2015) and span fifteen survey regions along the coast from Southern California to Kodiak, Alaska (Figure 1). We provide estimates of abundance for the summer-fall seasons (1 June to 30 November) during 1996–2015 for survey regions between Northern California and Northern British Columbia (NCA-NBC), the region chosen by the IWC to represent the PCFG. For the National Marine Fisheries Service development of an Environmental Impact Statement, we also provide estimates for the smaller regions between Oregon and Southern Vancouver Island (OR-SVI) and Makah Usual and Accustomed area (MUA) which includes the outer coastal area of the Olympic Peninsula (NWA) and the Strait of Juan de Fuca (SJF), even though this area is quite small relative to the observed movements of whales within the PCFG.

2 Methods

Gray whales were photographed during small boat surveys conducted from California to Alaska by collaborating researchers (Table 1) between 1996 and 2015. Gray whale identifications were divided into the following regions (Figure 1): 1) SCA: Southern California, 2) CCA: Central California, 3) NCA: Northern California, 4) SOR: Southern Oregon, 5) OR: central Oregon, 6) GH+: Gray’s Harbor and the surrounding coastal waters, 7) NWA: Northern Washington coast, 8) SJF: Strait of Juan de Fuca, 9) NPS: Northern Puget Sound, 10) PS: which includes southern Puget Sound, Hood Canal (HC), Boundary Bay (BB) and San Juan Islands (SJ), 11) SVI: Southern Vancouver Island, 12) WVI: West Vancouver Island, 13) NBC: Northern Vancouver Island and coastal areas of British Columbia, 14) SEAK: Southeast Alaska, and 15) KAK: Kodiak, Alaska. With some exceptions, research groups work primarily in one or two regions. Details of identifications obtained by the different research groups are are summarized in Tables 1-2.

2.1 Photographic Identification Procedures

Procedures during surveys by different research groups varied somewhat but were similar to one another in identification procedures. When a gray whale was sighted, the time, position, number of animals, and behaviors were recorded. Whales were generally approached to within 40-100 m and followed through several dive sequences until suitable identification photographs and associated field notes could be obtained.

For photographic identification of gray whales, both left and right sides of the dorsal region around the dorsal hump were photographed when possible. Most identification photographs were obtained with were obtained with 35mm cameras prior to 2004 and primarily with digital SLR after 2004 with both camera types paired with a telephoto lens (generally 200-300 mm). Researchers also photographed the ventral surface of the flukes for further identification when possible. The latter method was not as reliable since gray whales did not always raise their flukes out of the water. Markings used to distinguish whales included pigmentation of the skin, mottling, and scarring, which varied among individuals. These markings have provided a reliable means of identifying gray whales (Darling 1984). We also identified gray whales using the relative spacing between the knuckles along the ridge of the back behind the dorsal hump. The size and spacing of these bumps varies among whales and has not changed throughout the years these whales have been tracked, except with injury. Figure 2 shows typical photographs and features used in making gray whale identifications.

Comparisons of whale photographs were made in a series of steps. All photographs of gray whales were examined and the best photograph of the right and left sides of each whale (for each sighting) were selected. Identification photographs were initially compared within year to identify resightings and compared to the CRC catalog of whales seen in past years. Whale photographs that were deemed of suitable quality but did not match our existing catalog (compared by two independent persons) were considered “unique” identifications and assigned a new identification number and added to the catalog.

2.2 Data Analysis

The abundance of gray whales was estimated with open population models for three nested spatial scales consisting of contiguous survey regions (Figure 1; Table 3) 1) NCA-NBC: the coastal survey regions from Northern California (NCA) through Northern Vancouver Island/British Columbia (NBC) which matches the IWC definition of the PCFG, 2) OR-SVI: survey regions from southern Oregon through Southern Vancouver Island (SVI) identified in the Makah waiver request, and 3) MUA - survey regions NWA and SJF. Inland waters in WA (other than SJF) and in BC are excluded from the abundance estimates because these are used primarily by transient whales in the northward spring migration.

Gray whales photographed and identified anytime during the period between 1 June and 30 November (hereafter referred to as the “sampling period”) within the defined region were considered to be “captured” or “recaptured”. For each unique gray whale photographed, a capture history was constructed using 20 years of data from 1996-2015. For example, the capture history 00010010010000000000 could represent a gray whale photographed in 1999, 2002 and 2005 in the PCFG. The same gray whale may have had a capture history 00010010000000000000 for a smaller spatial scale such as OR-SVI or may not have been seen at all (00000000000000000000) and would not be used at the smaller spatial scale.

Multiple “detections” of a single whale within the sampling period were not treated differently than a single detection. A “1” in the capture history meant that it was detected on at least one day during the sampling period. However, multiple detections in the same year were used to construct an observed minimum tenure (MT) for each whale. MT was defined as the number of days between the earliest and latest date the whale was photographed with a minimum of one day for any whale seen.

We fitted open population models to the 20 yearly time series of capture history data for each spatial scale to estimate abundance and survival. Open models allow gains due to births/immigration and losses due to deaths/emigration. Using the RMark interface (Laake and Rexstad 2008) to program MARK (White and Burnham 1999), we fitted a range of models to the data using the POPAN model structure. The POPAN model structure (Schwarz and Arnason 1996) provides a robust parametrization of the Jolly-Seber (JS) model structure in terms of a super population size (N), probability of entry parameters (immigration), capture probability (p), and survival/permanent emigration (φ).

It is essential to consider the population structure and its dynamics to build adequate models. In particular, we know from previous analysis of a subset of these data (Calambokidis et al. 2004) that some whales were seen in only one year between 1 June and 30 November and were never seen again. Transient behavior is a well-known problem in capture-recapture models and it is often addressed using a robust design which involves coordinated multiple capture occasions within each year and typically assumes closure within the sampling period (June-November). Region-wide coordinated surveys may be possible but would be difficult with variation in weather conditions. Also, the closure assumption within the year would be suspect due to variable timing of whales arrivals and departures into the PCFG, so it would require nested open models. We know from prior analysis that whales newly seen in year (y) were less likely to return (i.e., seen at some year >y) than previously seen whales but also newly seen whales that stayed longer during their first year (i.e., longer MT) in the PCFG were more likely to return. Likewise, previously seen whales were more likely to be seen in the following year (y+1), if they had a longer MT in year y. Calambokidis et al. (2004) postulated that these observations were consistent with whale behavior that was determined by foraging success.

Transient behavior in which an animal is seen only once can be modeled by including a different "first year" survival (Pradel et al. 1997) for the newly seen animals. Survival in the time interval after being first seen is dominated by permanent emigration rather than true mortality. Survival in subsequent time intervals represents true survival under the assumption that animals do not permanently emigrate except in their first year. Pradel et al. (1997) were working with release-recapture data (Cormack-Jolly-Seber) where modeling this transient effect on survival is straightforward. For a Jolly-Seber type analysis where the first capture event is also modeled, the inclusion of a transient effect is less easily accommodated.

We divided the whales into cohorts based on the year in which they were first seen ("newly seen"). In the model, their first year survival could differ from subsequent annual survival as in Pradel et al. (1997). "Newly seen" is not a particularly useful concept for the first year of the study (1996), because all whales were being seen for the first time. The survey effort and coverage in 1996 and 1997 were not nearly as expansive as 1998 and later. We considered models that had three different first year survivals (1996&97, 1998, and >1998) and we also considered a model that allowed for a different first year survival for each year (cohort) to allow for different transient proportion in each year. The first year survival was also allowed to vary as a function of MT with a model in which the relationship was constant across years and varied for (1996&97, 1998, and >1998). We also considered models that allowed a different first-year survival for whales identified as calves under the presumption that their true survival might be lower but that their probability of returning to the PCFG might be higher. Discussion at the 2012 intersessional AWMP meeting led to consideration of an additional covariate which split whales into 2 groups for estimation of post-first-year survival. Whales seen initially as calves and any whale newly seen in 1998 or was in the CRC catalog because it had been seen prior to 1998 were put in one group and the remaining whales newly seen in 1999 or later were put in another group. The expectation was that the first group would have higher post-first-year survival because many of the newly seen whales that entered after the stranding event in 1999/2000 might eventually emigrate. When this covariate was included it made such a large improvement that any model without it would have no support. Therefore, it was included in all 10 models for survival (Table 4).

In Calambokidis et al. (2010) we estimated a cohort-specific super-population size for each cohort using the median MT covariate value for unseen whales but during the April 2011 AWMP meeting it became apparent that this may lead to bias in estimating abundance. Therefore, we used the method outlined in the 2011 AWMP report which is similar to the method used by Calambokidis et al. (2004) in that we assume that all whales in the PCFG for the first year are seen so the super-population size for each cohort is the number seen and thus there are no unknown covariate values. We fixed capture probability (p) and probability of entry (pent) to 1 for each cohort in their entry year. We are not interested in the number of transient whales so we used an estimator of abundance for non-transient whales (2011 AWMP report) which is a modification of the Jolly-Seber estimator which for any year can be expressed as:

$$\hat{N} = n/\hat{p} = (u + m)/\hat{p}$$

where $n = u + m$, n is the number seen in a year being composed of new animals (u=unmarked) and previously seen animals (m=marked), and $\hat{p}$ is the capture probability estimate. For the PCFG we are assuming that any new whale is sighted ($p = 1$) and we are only interested in estimating the abundance of whales that will remain part of the PCFG which is the portion of the new whales that do not permanently emigrate from the PCFG. We can modify the estimator for year j as follows:

$$\hat{N}_j = u_j\hat{\phi}_j + m_j/\hat{p}_j$$

where ϕ_j is the first year survival rate of "new" whales. When ϕ and p contain whale specific covariates like minimum tenure (MT) the estimator becomes:

$$\hat{N}_j = \textstyle\sum_{i=1}^{u_j} \hat{\phi}_{ij} + \sum_{i=1}^{m_j} 1/\hat{p}_{ij}.$$

To obtain an abundance estimate for 2015, we assumed that the parameter for first year survival intercept in that year was the same as in 2014. A variance-covariance matrix for the abundance estimates was constructed using the variance estimator in Borchers et al. (1998) for a Horvitz-Thompson type estimator with an adaptation for the first component of the abundance estimator for prediction of number of new whales that do not permanently emigrate. For the estimated capture probabilities (p) not fixed to 1, we fitted 3 models that varied by time (year) and/or varied by MT in the previous year (Table 4).

We used Test 2 and Test 3 results from the Cormack-Jolly-Seber structure (Lebreton et al. 1992) as a general goodness of fit for the global model and as a measure of possible over-dispersion creating the lack of fit. We fitted each combination of models for S (survival) and p (capture probability) and used AICc (Burnham and Anderson 2002) to select the most parsimonious model of the 30 fitted models. Model averaging was used for all models to compute estimates and unconditional standard errors and confidence intervals.

3 Results

The database contains 25580 records for whales photographed between 1996 to 2015 from California to Kodiak, Alaska; however 4345 are replicate identifications of whales on the same day. We define a sighting as one or more photographs of a whale on a day. The number of sightings varied annually from 131 and 1959 with a total of 21235 sightings of 1638 unique gray whales (Table 1). The average number of sightings/whale was 13 (range: 1-339). Identifications were made throughout the year but with most effort from June to September. Number of sightings were most numerous in NCA, SVI, WVI, and NBC and (Table 2). The number of uniquely identified whales was greatest in NCA, NWA, SVI and WVI (Table 2).

3.1 Seasonal Sighting Patterns

Whales have been photographed in every month of the year (Table 5) but with very few during December-February when most of the whales are in or migrating to Mexico and survey effort is reduced. Previous analysis of these data have always used 1 June - 30 November as the sampling period to describe the whales in the PCFG because whales seen prior to 1 June and after 30 November are more likely to be whales that are migrating through the region. The southbound migration starts in December and the separation between May and June is clearly supported by the data. For example, of the 1638 unique whales sighted from California to Kodiak, Alaska, 666 whales were only seen between 1 Dec - 31 May and 87.2% of those were only sighted once (one day). Of the 972 whales sighted between 1 June -30 November at some time, 38.8% were only sighted once (one day). If sightings in Alaska are excluded, then only 31.7% of the 833 were seen only once (one day).

The break between May and June is apparent in various measures such as proportion of whales sighted more than once, sighted in more than one region, and sighted in more than one year (Figure 3). However, the break is more apparent if we separate out SJF, NPS and SVI from the other survey regions (Figure 4). The difference across months is not as strong for inland waters of Washington and British Columbia (NPS, SJF) because these are whales that have diverted from the migration and are either more likely to remain after 1 June or demonstrate high year-to-year fidelity during spring such as with NPS. Also, even though Southern Vancouver Island (SVI) is in the main migration corridor and not an inland water, the pattern across months is also weaker because the sampling has been focused on the spring herring spawn in Barkley Sound (effectively an inland waterway) and has purposefully undersampled passing migrant whales (Brian Gisborne, pers. comm.).

The break between May and June is much more apparent for NWA and the other areas in the migration corridor which is consistent with the northbound migration of gray whales proceeding past Washington through May. Resighting rates of whales seen after 1 June remained high through November.

A large photo-ID sample of gray whales in the MUA was conducted in 2015 by Makah Tribal biologists. At the time of this report the full comparison of these whales to historical images had not been completed but in the future will provide a better indication of proportion of PCFG whales present prior to 1 June.

Capture (sighting) histories of whales seen at least once in the PCFG from 1 June - 30 November are provided in Appendix Table 1 which show sightings of whales in 1 Mar -31 May only, 1 June - 30 Nov only and in both time periods within a year.

3.2 Regional Sighting Patterns

There is considerable variation in the annual regional distribution of numbers of whales photographed during the sampling period (Table 6) which is in part due to variation in effort. Although not a true measure of effort, the number of days whales were seen (Table 7) does reflect the amount of effort as well as abundance of whales. In particular, in comparison to other regions, the large number of sightings in SVI partly reflects large numbers of sampling days by Brian Gisborne who has routinely sampled SVI from summer through fall on almost a daily basis. On the other hand, the decline in sightings in SVI during 2007 was not due to reduced effort but to the distribution of whales with many of the whales having moved to waters off Oregon and Washington (Calambokidis et al. 2009b). Similarly, there were 40 survey days in SJF in 2010 but only 4 whales were seen on 4 different days (Table 6, Table 7) so this drop relative to other years was not due to lack of effort.

Whales were sighted across various survey regions and the interchange of whales (Table 8) between survey regions during 1 June - 30 November depends on proximity of the regions (Calambokidis et al. 2004). During 1 June-30 November for 1996 to 2015, 793 unique whales were seen in the PCFG range and 68.6% (544 of the 793 whales seen in the PCFG range) were seen within the smaller OR-SVI region and approximately 36.3% (288 of the 793 whales seen in the PCFG range) were seen within the smaller MUA area; however, there is variation in interchange between areas in the PCFG and the MUA. Of the whales sighted in regions from NCA to NBC, from 39.8% to 59.6% of the whales were seen at some point within MUA (Figure 5). If we exclude transients (whales seen in only one year), the interchange rates with MUA are much higher but the pattern is similar (Figure 6) with a range of 47.7% to 77.5%. Appendix Table 2 provides capture histories using data from 1 June - 30 Nov of whales seen in the MUA at least once. For each year, the table shows whether the whale was sighted in PCFG but not in the MUA during that year, only seen in MUA that year, and seen in both MUA and another PCFG area in that year.

Whales seen in the PCFG exhibited a wide range of movement across and within years. The 143 whales seen in 9 or more years provide a useful example. None of those whales was seen exclusively in a single region, and 67.1% were seen in at least 4 of the 9 survey regions from 1996 to 2015. However, whales did regularly visit the same regions across years with 94.4% were seen in at least one of the regions during six or more of the years they were seen and 65.7% were seen in a region two-thirds or more of the years they were seen. SVI was the region with the maximum number of years seen for 65 of the 143 whales, which in part reflects the larger amount of survey effort in SVI (Calambokidis et al. 2004a, Calambokidis et al. 2013). Thus, some whales regularly visit particular regions more often than others, but they are seen across the other regions as well.

Some of the whales not seen in the PCFG in a year were seen in Kodiak and Southeast Alaska (Table 9). Of the 25 whales identified in Southeast Alaska and the 153 whales identified in Kodiak, Alaska, 14 (56%) and 24 (15.7%), respectively have been seen farther south in the PCFG.

If we look at latitudes of sightings of individual whales across the 20 years using whales that have been sighted on at least 6 different days (Figure 7), we see that sightings of some whales are highly clustered; whereas, sightings of other whales are highly dispersed across several regions. We defined each whales primary range by the 75% inner quantile which is the middle of the range that includes 75% of the locations. The length of the 75% inner quantile in nautical miles exceeded 60 nautical miles (or 1 degree of latitude) for 49.0% of the whales (Figure 8) and it was more than 180 nautical miles for more than 29.6% of the whales. Thus, it makes little sense to compute an estimate of abundance for any region that spans less than a degree of latitude.

3.3 Annual Sighting Patterns

The average number of whales identified in any one year was 156, 104, and 37 for the PCFG, OR-SVI, and MUA, respectively (Table 10). However, those numbers do not represent the total numbers of whales that use each of these areas because not all whales using a region in a year are seen, not all whales return to the same region each year, and not all of the whales return to the PCFG region each year. The annual average number of newly seen whales (excluding 1996-1998 when the photo-id effort expanded to cover all survey regions) was 37.2, 25.8, and 13.6 for PCFG, OR-SVI, and MUA, respectively. The annual average number of newly seen whales that were "recruited" (seen in a subsequent year), excluding 1996-1998 and 2015, was 14.9, 12.6, and 6.4 for PCFG, OR-SVI, MUA respectively. Thus, there were a substantial number of new whales seen each year and 40.6, 49.6, and 47 percent of those were seen again in a subsequent year in the 3 regions respectively. The number of newly seen whales and the number newly seen and recruited (i.e., seen in at least one more year after the initial year it was seen) (Table 11) are displayed as discovery curves in Figures 9 and 10.

Of the whales that were seen during June-November 1996-2015 in the PCFG (NCA to NBC) about half were only seen in one year and the whales that were seen in more years were sighted more often each year and therefore represented a large proportion of the sightings (Figure 11). Of the 750 identified whales first seen before 2015 between 1 June and 30 November in the PCFG range (NCA-NBC), 52% were seen in only one year and only represent about 5% of the sightings (Figure 11). Many of the newly seen whales did not return in subsequent years. Some whales were seen in every year with 9.3% that were seen in every year after their initial identification, including 5 whales first seen in 1996 that were seen in all of 20 subsequent years. The remaining 39% were seen more than once but not in every year.

Likewise, examination of MT in the first sighting year demonstrates that whales who stay longer in their first year were more likely to be seen in a following year (Figure 12). Whales “first” seen in the first few years of the study (1996-1998) includes some whales that were truly new to the PCFG in those years but many were only “new” because it was the first year of the study or as the surveyed regions expanded over time. This is evident (Figure 12) in the much higher proportions for 1996-1998 than for the other years. These relationships will be important in the capture-recapture models for abundance estimation because whales that do not return after their first year (a large percentage in this analysis) would appeared to have not survived because they have permanently emigrated (with a small fraction that died).

3.4 Open Population Capture-Recapture Models

If the yearly cohorts were pooled, Test2+Test3 statistics indicated a significant lack of fit for the PCFG and subsets (Table 12) primarily resulting from Test 3. This was expected due to the different “survival” rates of previously seen whales (true survival) and newly seen whales of which many never returned (i.e., permanently emigrated) (Table 13) . By separating the cohorts, survival for each cohort was time-varying and thus each cohort has a separate first year survival. The goodness of fit test (Test 2) demonstrated a lack of fit for NCA-NBC and OR-SVI (Table 12). For those regions, we estimated an over-dispersion values of $\widehat{c}$=2.29 and $\widehat{c}$=1.23 respectively to adjust AICc and estimated standard errors.

For all areas, the best fitted model (Table 14) was model 2 for p with capture probability varying across years and higher when MT was greater in the previous year. Likewise, for φ the best model was model 4 for all areas. Model 9 was the second best model. Both models 4 and 9 included a separate first year survival which depends on MT. Model 9 included a different calf first-year “survival” which gave a higher survival for calves than non-calves the first year seen (redundant for calves) because they are more likely to return. In models 9 and 4, there are 3 intercepts for first year survival (1996&97, 1998, >1998) and in model 9 the slopes for MT differ as well. These results were consistent with Calambokidis et al. (2004) who demonstrated strong support for the effect of MT on first year survival (Figure 13) and capture probability (Figure 15) in the following year. These results differ some from Calambokidis et al. (2010) who used an annual median-centered MT. Use of MT with median centering was necessary to construct open model abundance estimates in the manner described in Calambokidis et al. (2010). However, that was not necessary for JS1 and the use of MT without median-centering resulted in lower AICc values.

There was large year to year variation in capture probability. The values for NCA-NBC ranged from 0.42 to 0.98 depending on the year and value of MT (Figure 15). The lowest values were from 2007 which reflects the temporary emigration of whales from MUA and SVI to waters offshore of Oregon in that year. In contrast, for MUA capture probabilities were much lower ranging from 0.08 to 0.76 depending on the year and value of MT (Figure 16). The lower overall capture probability and weaker relationship between capture probability and MT reflect the transitory behavior of whales in such a small area. The lower estimates of of capture probability in 1999-2004 for MUA was due to decreased effort by NMML which spread their survey effort across MUA to WVI during 1999-2002, lost a vessel in 2002 and had no funding in 2004 (Figure 16).

First year survival estimates were dominated by permanent emigration. For NCA-NBC, the estimates varied from 0.30 to 0.81 for non-calf whales with MT=1 in their first year and from 0.69 to 0.95 for MT>80 in their first year (Figure 13). Calf survival is by definition a first year survival rate and potentially includes permanent emigration from the PCFG. Depending on the value of MT, calf survival estimates ranged from about 0.35 to over 0.90 (Figure 14). The average calf survival estimate was 0.63 (se = 0.090). There was some support for a different first year calf survival with model 9 being the second best model (ϕ in Table 14) because calves are less likely to permanently emigrate. Unfortunately there is no way to separate permanent emigration from mortality with the existing data.

Survival subsequent to the first year was assumed to be constant but was less for non-calf whales that were newly seen in 1999 or later. Post-first-year suvival for calves and whales present in 1998 or earlier presumably represents true survival assuming there was little permanent emigration after the first year. Those estimates were 0.967 (se=0.0062) and 0.967 (se=0.0066) for OR-SVI and NCA-NBC respectively. The post-first-year survival estimates for whales that entered in 1999 or later and not identified as a calf were 0.912 (se=0.0125) and 0.917 (se=0.0142) for OR-SVI and NCA-NBC respectively.

3.5 Abundance and Recruitment

For NCA-NBC, OR-SVI and MUA annual estimates of abundance were constructed with model averaged values for JS1 (Table 15-16). Estimates for NCA-NBC in Figure 17 are only shown for 1998-2015 with the open models $p = 1$ for 1996 so it will certainly be an underestimate and the survey coverage in 1996 and 1997 was not as extensive as the later years.

The value of N_{min} for 2015 is 228 for NCA-NBC (Table 15). To gain a sense for how these values might be relevant to estimating a possible level of removal (e.g., due to harvest) we computed the MMPA's Potential Biological Removal (PBR) (typically reserved for stock-level assessments). Using the PBR formula, with an Rmax of 6.2% and a recovery factor of 0.5 (Caretta et al. 2013), the PBR for NCA-NBC (PCFG) would be 3.5.

New whales that are not identified as calves have appeared annually and many of these new (non-calf) whales have subsequently returned and been re-sighted (Table 13). In NCA-NBC from 1999-2014, an average of 32.1 (range: 8.0, 68.0) new whales not identified as a calf were seen each year. Of these new non-calf whales, on average 11.8 (range: 1.0, 28.0) whales returned and were seen in subsequent years. It is unknown what proportion of the non-calves used the PCFG as a calf but were not seen in that year. Currently recruitment appears to be offset by losses (either mortality or permanent emigration) as the abundance estimates have been fairly stable since 2002 and recently increasing.

4 Discussion

The population structure of gray whales using the Pacific Northwest in summer and fall is complicated and involves two elements. One group of whales return frequently and account for the majority of the sightings in the Pacific Northwest during summer and fall. This group is certainly not homogeneous and even within this group, there is some degree of preference for certain subareas. Despite widespread movement and interchange among areas, some of these gray whales are more likely to be seen returning to the same areas they were seen before. The second group of whales are transients that are seen in only one year, tend to be seen for shorter periods that year, and in more limited areas.

The existence of these two groups in the study area and their dynamics complicate estimating abundance. While the JS1 estimator may not be optimal, it provides a practical way of handling transients in this open population. Excluding 1996-1997, the JS1 sequence of abundance estimates provides the most reliable assessment of trend for the non-transient abundance and the best estimate of current abundance in 2015.

Despite extensive interchange among subregions in our study area, whales do not move randomly among areas. Abundance estimates were lower when using more limited geographic ranges but these more limited areas do not reflect closed populations. While the use of geographically stratified models can be useful in cases where populations have geographic strata they use (see for example Hilborn 1990), this would be difficult in our case because of the frequent sightings of animals in multiple regions within the same season and these models typically only allow an animal to be sighted in one strata per period. This could be dealt with by assigning animals to only a single region per season but this would be forcing the data into a somewhat inaccurate construct.

Several studies have considered the question of gray whale population structure. There is widespread agreement that at least two populations of gray whales in the North Pacific exist, a western North Pacific population (also called the Korean population) and an eastern North Pacific (ENP) population (sometimes called the California population) (Swartz et al. 2006; Angliss and Outlaw 2008; Rugh et al. 1999). The population structure of the gray whales feeding in the Pacific Northwest has remained in question and only a few studies have examined this. Steeves et al. (2001) did not find mtDNA differences in a preliminary comparison of gray whales from the summer off Vancouver Island and those from the larger ENP population. Ramakrishnan et al. (2001) did not find evidence that the Pacific Northwest whales represented a maternal genetic isolate, although even very low levels of recruitment from the larger overall population would prevent genetic drift. More recently, Frasier et al. (2011) generated mtDNA sequences from a larger sample of gray whales from Vancouver Island than tested by Steeves et al. (2001). They found significant differences in the haplotype frequencies between that sample and mtDNA sequence data reported for ENP gray whales, most of which were animals that stranded along the migratory route. The Frasier et al. (2011) samples were from a relatively small area; however, Lang et al. (2011) evaluated biopsy samples from California to southern Vancouver Island in the PCFG and ENP samples from whales sampled north of the Aleutians and also found significant mtDNA halpotype frequency differences. These two studies provide the strongest evidence to date that the Pacific Northwest whales might be sufficiently isolated to allow maternally inherited mtDNA to differ from the overall ENP population.

Population structure in other large whales has been the subject of recent inquiry and has revealed diverse results for different species. Clapham et al. (2008) examined 11 subpopulations of whales subjected to whaling that were extirpated possibly due to the loss of the cultural memory of that habitat and concluded subpopulations often exist on a smaller spatial scale than had been recognized. Studies of other baleen whales, particularly humpback whales, have shown evidence of maternally directed site fidelity to specific feeding grounds based on photographic identification studies (Calambokidis et al. 1996, 2001, 2008). This high degree of fidelity to specific feeding areas is often discernible genetically. In the North Pacific strong mtDNA differences were found among feeding areas even when there was evidence of low level of interchange from photo-ID (Baker et al. 2008). Similar findings were documented for humpback whales in the North Atlantic which feed in different areas but interbreed primarily on a single breeding ground (Palsboll et al. 1995) like ENP gray whales. In the North Pacific the differences for humpback whales were often dramatic. For example, humpback whales that feed off California have almost no overlap in mtDNA haplotypes with humpback whales feeding in Southeast Alaska (Baker et al. 1990, 1998, 2008). One difference between humpback and gray whales is the coastal migration route of gray whales which means gray whales going to arctic waters to feed would migrate right through the feeding areas to the south. Other species of large whales have not shown as strong site fidelity to specific feeding grounds. Blue whales have undergone an apparent shift in their feeding distribution in the North Pacific apparently due to shifting oceanographic conditions (Calambokidis et al. 2009a). Fin whales in the North Pacific have long migrations and while there do not appear to be multiple distinct feeding areas as was the case for humpback whales, there were some distinct and isolated apparently nonmigratory populations (Mizroch et al. 2009; Berube et al. 2004).

Even though the population structure of gray whales off the Pacific Northwest remains unresolved, there is a consistent group of animals that use this area and we provide several estimates of their abundance. Different abundance methods and geographic scopes yield varied results but all suggest the annual abundance of animals using the Pacific Northwest for feeding through the summer is at most a couple hundred animals depending on the estimating method and how broadly the region is defined geographically.

The rapid increase in the abundance estimates at the start of this study is in part due to the smaller area of coverage during 1996 and 1997. We included those years to improve the estimate in 1998-1999 and the estimate for 1998 did increase by 7% from previous analysis. The increase from 1998-2000 occurred during a period the overall eastern North Pacific gray whale population was experiencing a high mortality event that included unusually high numbers of gray whales showing up in areas they were not common. The high rate of increase in the late 1990s and early 2000s should be verified with additional data such as compiling photographic identifications for this area from multiple sources to attempt to verify if the abundance of animals prior to the start of our study was as low as suggested by these trends. Even though the rate of increase may be too high, we believe the abundance did increase and now appears to be relatively stable since 2002.

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Table 1: Contributions of numbers of sightings (one or more photographs of a whale per day) by reseach group for 1996-2015 and resulting number of uniquely identified whales. Totals for whales are unique whales across all research groups.

	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	Whales
Brian Gisborne	0	4	342	305	634	505	363	786	288	393	406	101	484	297	556	540	521	695	638	472	505
Canada Fisheries/Oceans	0	0	0	0	0	0	0	0	0	0	0	0	0	1	14	8	0	0	0	0	22
Carrie Newell	0	0	0	0	0	0	0	0	0	0	12	72	0	18	2	0	138	190	127	0	129
CERF	13	260	101	124	203	346	271	125	761	11	33	11	38	4	7	40	26	50	7	0	137
CRC	54	36	127	179	91	60	89	85	135	31	61	92	69	58	50	56	83	61	22	41	457
Dawn Goley-HSU	0	0	21	74	56	60	63	0	0	0	0	0	42	19	50	227	228	73	78	28	333
Jan Straley-UASE	0	0	0	0	0	0	0	7	0	0	1	1	0	0	0	0	0	0	0	0	7
Jeff Jacobsen-HSU	0	0	0	0	0	0	0	0	0	0	0	1	0	5	127	327	124	229	141	88	332
Jim Darling	18	0	48	0	0	34	13	0	0	0	0	0	0	0	0	23	0	0	0	0	80
MAKAH	0	0	0	0	0	0	0	0	30	45	129	62	247	102	45	66	145	196	150	202	284
MAKAH-NMML	0	0	0	0	0	0	0	0	0	0	0	0	0	71	24	45	116	53	43	9	137
NMML	34	110	125	159	121	115	71	64	13	99	46	37	65	25	6	11	19	13	25	28	377
North Slope Borough	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Opportunistic	12	3	8	14	1	1	0	0	0	1	28	46	66	82	70	196	43	183	70	38	314
OSU	0	0	0	0	0	0	0	0	0	0	0	0	0	212	68	0	91	45	0	34	119
SWFSC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	131	118
UAF	0	0	0	0	0	0	0	0	0	0	0	0	24	0	0	0	0	0	0	0	23
UVIC	0	0	308	125	128	0	113	0	0	0	0	1	0	0	0	0	0	0	58	100	177
Volker Deecke	0	0	39	40	26	2	0	0	0	0	11	0	0	0	0	0	0	0	0	0	73
Wendy Szaniszlo	0	0	0	0	0	0	0	0	0	87	50	58	117	4	23	90	136	171	52	32	150
Photo Totals	131	413	1119	1020	1260	1123	983	1067	1227	667	777	482	1152	898	1042	1629	1670	1959	1411	1203	
Whale Totals	70	77	158	247	179	196	251	178	196	202	182	159	225	242	234	284	330	384	295	266	1638

Table 2: Regional distribution of numbers of sightings (one or more photographs of a whale per day) and resulting number of uniquely identified whales by reseach group for 1996-2015. Totals for whales are unique whales across all research groups. NPS is northern Puget Sound and PS includes southern Puget Sound, San Juan Islands, Hood Canal and Boundary Bay.

	CA	NCA	SOR	OR	GH+	NWA	SJF	PS	NPS	SVI	WVI	NBC	SEAK	KAK
Brian Gisborne	0	0	0	0	0	0	0	1	0	8073	254	2	0	0
Canada Fisheries/Oceans	0	0	0	0	0	0	0	0	0	18	5	0	0	0
Carrie Newell	0	0	0	559	0	0	0	0	0	0	0	0	0	0
CERF	0	0	0	0	0	0	0	0	0	0	48	2383	0	0
CRC	23	98	117	100	254	112	40	68	521	38	0	95	14	0
Dawn Goley-HSU	0	919	64	36	0	0	0	0	0	0	0	0	0	0
Jan Straley-UASE	0	0	0	0	0	0	0	0	0	0	0	0	9	0
Jeff Jacobsen-HSU	13	992	31	6	0	0	0	0	0	0	0	0	0	0
Jim Darling	0	0	0	0	0	0	0	0	0	9	127	0	0	0
MAKAH	0	0	0	19	0	618	782	0	0	0	0	0	0	0
MAKAH-NMML	0	0	0	0	0	258	102	0	0	0	1	0	0	0
NMML	0	13	65	0	0	314	307	0	18	182	150	10	0	127
North Slope Borough	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Opportunistic	106	2	5	67	0	1	22	35	106	213	255	13	7	25
OSU	0	331	3	111	5	0	0	0	0	0	0	0	0	0
SWFSC	0	0	12	0	0	0	0	0	0	41	9	33	0	36
UAF	0	0	0	0	0	0	0	0	0	0	0	0	0	24
UVIC	0	0	0	0	0	0	0	0	0	1	832	0	0	0
Volker Deecke	0	0	0	0	0	0	0	1	0	71	0	42	4	0
Wendy Szaniszlo	0	0	0	0	0	0	0	0	0	467	353	0	0	0
Photo Totals	142	2355	297	898	259	1303	1253	105	645	9113	2034	2578	34	212
Whale Totals	121	526	122	188	146	357	210	44	51	489	338	138	25	155

Table 3: Survey regions and region subsets used for abundance estimation. Numbers refer to locations on the map in Figure 1.

Survey Region	Region Description	NCA-NBC	OR-SVI	MUA
(1) SCA = Southern California				
(2) CCA = Central California				
(3) NCA = Northern California	Eureka to Oregon border; mostly from Patricks Pt. and Pt. St George	x		
(4) SOR = Southern Oregon		x	x	
(5) OR = Oregon Coast	Primarily central coast near Depoe Bay and Newport, OR	x	x	
(6) GH+ = Gray's Harbor	Waters inside Grays Harbor and coastal waters along the S Washington coast	x	x	
(7) NWA = Northern Washington	Northern outer coast waters with most effort from Cape Alava (Sea Lion Rock) to Cape Flattery	x	x	x
(8) SJF = Strait of Juan de Fuca	US waters east of Cape Flattery extending to Admiralty Inlet (entrance to Puget Sound) with most effort ending at Sekiu Point	x	x	x
(9) NPS = Northern Puget Sound	Inside waters and embayments from Edmonds to the Canadian border			
(10) PS = Puget Sound	Central and southern Puget Sound (S of Edmonds), including Hood Canal, Boundary Bay, and the San Juan Islands			
(11) SVI = Southern Vancouver Island	Canadian waters of the Strait of Juan de Fuca along Vancouver Island from Victoria to Barkley Sound, along West Coast Trail	x	x	
(12) WVI = West Vancouver Island		x		
(13) NBC = Northern British Columbia	British Columbia waters north of Vancouver Island, with principal effort around Cape Caution	x		
(14) SEAK = Southeast Alaska	Waters of southeastern Alaska with the only effort in the vicinity of Sitka			
(15) KAK = Kodiak, Alaska				

Table 4: Model specifications for survival (φ) and capture probability (p) parameters in POPAN models for gray whale photo-identification data. For survival models, β_0 is the baseline intercept for non-transient survival. Fy is 1 if it is year the whale was first seen and 0 otherwise. A subscript for Fy means that it applies only for that cohort except that Fy_{99}applies to cohorts 1999 and beyond and Fy_c represents each of the cohorts from 1996 to 2015. C is 1 if identified as a calf in its first year and 0 otherwise. R is 1 for calves or any whale seen in 1998 or was already in the catalog prior to 1998 and 0 otherwise. β_r is an adjustment to post-first-year survival. MT is minimum tenure value of a whale and β_M is the estimated slope parameter for φ or p. $\beta_{M,96-97}$ applies to 1996-97, $\beta_{M,98}$ to 1998 and $\beta_{M,99}$ applies to 1999-2014. $\beta_{Fy,96-97}$, $\beta_{Fy,98}$ and $\beta_{Fy,99}$ are the first-year survival intercept adjustments for 1996-97, 1998 and cohorts 1999-2014 respectively and $\beta_{Fy,c}$ represents 19 cohort-specific first year survival parameters for 1996-2014. β_{CF} is an adjustment for calf first year survival and β_{CM} is an adjustment for calves to the slope of MT for survival. For the capture probability models, β_t has 18 levels for t=1998,...2015 and β_0 represents the 1997 value. For 1996 p=1.

Model	Parameter Logit Formula	Number of parameters
φ		
1	$\beta_0 + \beta_{Fy}Fy + \beta_r R(1 - Fy)$	3
2	$\beta_0 + \beta_{Fy}Fy + \beta_M MT\,Fy + \beta_r R(1 - Fy)$	4
3	$\beta_0 + \beta_{Fy,96-97}Fy_{96-97} + \beta_{Fy,98}Fy_{98} + \beta_{Fy,99}Fy_{99} + \beta R(1 - Fy)$	5
4	$\beta_0 + \beta_{Fy,96-97}Fy_{96-97} + \beta_{Fy,98}Fy_{98} + \beta_{Fy,99}Fy_{99} + \beta_M MT\,Fy + \beta_r R(1 - Fy)$	6
5	$\beta_0 + (\beta_{Fy,96-97} + \beta_{M,96-97}MT)Fy_{96-97} + (\beta_{Fy,98} + \beta_{M,98}MT)Fy_{98} + (\beta_{Fy,99} + \beta_{M,99}MT)Fy_{99} + \beta_r R(1 - Fy)$	8
6	$\beta_0 + \beta_{Fy,c}Fy_c + \beta_M MT\,Fy + \beta_r R(1 - Fy)$	22
7	$\beta_0 + \beta_{Fy,c}Fy_c + \beta_M MT\,Fy + \beta_{CF}C\,F_y + \beta_r R(1 - Fy)$	23
8	$\beta_0 + \beta_{Fy,c}Fy_c + \beta_M MT\,Fy + \beta_{CF}C\,F_y + \beta_{CM}C\,MT + \beta_r R(1 - Fy)$	24
9	$\beta_0 + (\beta_{Fy,96-97} + \beta_{M,96-97}MT)Fy_{96-97} + (\beta_{Fy,98} + \beta_{M,98}MT)Fy_{98} + (\beta_{Fy,99} + \beta_{M,99}MT)Fy_{99} + \beta_{CF}C\,F_y + \beta_r R(1 - Fy)$	9
10	$\beta_0 + (\beta_{Fy,96-97} + \beta_{M,96-97}MT)Fy_{96-97} + (\beta_{Fy,98} + \beta_{M,98}MT)Fy_{98} + (\beta_{Fy,99} + \beta_{M,99}MT)Fy_{99} + \beta_{CF}C\,F_y + \beta_{CM}C\,MT + \beta_r R(1 - Fy)$	10
p		
1	$\beta_0 + \beta_t$	19
2	$\beta_0 + \beta_t + \beta_M MT$	20
3	$\beta_0 + \beta_M MT$	2

Table 5: Regional distribution of numbers of whales seen by month for 1996-2015.

	1	2	3	4	5	6	7	8	9	10	11	12
CA	7	16	18	17	14	3	6	7	13	1	1	28
NCA	154	50	8	67	68	127	139	57	49	100	114	139
SOR	0	3	0	2	5	7	36	45	69	43	0	0
OR	0	1	4	4	30	28	53	83	93	64	2	0
GH+	6	2	30	60	29	17	3	0	27	1	0	0
NWA	7	5	26	61	110	79	78	102	103	73	13	1
SJF	0	0	3	15	32	47	60	62	83	105	79	21
PS-HC-BB-SJ	0	1	6	21	8	10	5	2	1	1	4	1
NPS	1	3	17	28	32	11	1	0	0	0	0	0
SVI	5	8	77	101	129	224	263	216	186	94	37	6
WVI	0	1	14	35	31	116	194	186	113	27	0	0
NBC	1	0	0	0	3	26	84	113	83	28	0	1
SEAK	0	0	0	0	0	17	4	1	3	0	5	0
KAK	0	0	0	0	2	19	34	57	60	0	0	0

Table 6: Regional distribution of numbers of whales seen during June-November for 1996-2015.

	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015
CA	0	0	0	1	0	5	0	0	4	0	3	0	0	3	7	1	7	0	0	2
NCA	0	0	16	38	27	32	37	15	3	0	0	1	47	62	62	82	95	81	53	8
SOR	0	0	0	0	0	2	46	24	16	1	0	23	15	2	15	10	11	5	26	30
OR	0	0	17	31	8	15	0	0	16	4	9	39	6	38	20	7	42	40	35	21
GH+	1	0	0	1	1	1	0	0	1	0	0	38	0	2	0	0	0	0	0	0
NWA	13	15	22	7	9	31	7	19	3	19	44	13	35	30	22	36	62	47	32	31
SJF	9	22	18	4	5	2	1	9	24	17	21	14	54	37	4	11	11	36	45	23
PS-HC-BB-SJ	0	0	3	8	4	0	0	0	0	1	0	0	0	4	0	0	1	0	0	1
NPS	0	0	0	0	10	0	0	0	0	0	0	0	0	1	2	0	0	0	0	0
SVI	13	17	60	45	55	101	66	90	86	89	67	37	78	75	62	62	73	99	84	98
WVI	8	0	57	66	53	29	85	9	0	52	40	13	23	23	9	53	28	114	50	46
NBC	13	33	23	25	23	40	43	51	88	12	21	5	21	3	4	2	15	31	7	28
SEAK	0	0	5	6	0	1	0	6	0	1	2	3	0	5	0	0	0	0	0	0
KAK	0	0	0	0	0	0	42	4	0	48	0	0	23	0	17	0	2	0	0	35

Table 7: Number of days in which whales were seen for each region and year from 1996-2015 from 1 June - 30 November.

	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015
CA	0	0	0	1	0	2	0	0	2	0	1	0	0	2	4	1	2	0	0	2
NCA	0	0	8	8	20	13	20	2	2	0	0	2	9	19	21	32	28	20	14	4
SOR	0	0	0	0	0	1	4	1	2	1	0	3	1	1	7	6	3	4	6	5
OR	0	0	6	9	5	7	0	0	1	1	7	38	1	22	8	11	70	54	18	13
GH+	1	0	0	1	1	1	0	0	1	0	0	3	0	1	0	0	0	0	0	0
NWA	9	12	22	10	7	11	3	9	1	12	13	7	8	7	14	23	20	16	17	16
SJF	9	42	16	9	9	4	2	15	7	13	18	26	36	30	4	11	17	25	31	33
PS-HC-BB-SJ	0	0	3	11	4	0	0	0	0	2	0	0	0	4	0	0	1	0	0	1
NPS	0	0	0	0	1	0	0	0	0	0	0	0	0	2	3	0	0	0	0	0
SVI	9	10	91	87	82	55	68	66	48	73	59	39	82	71	80	106	75	64	77	28
WVI	10	0	54	46	28	7	10	3	0	6	14	27	31	5	1	22	7	46	25	28
NBC	7	53	39	50	53	43	34	29	53	11	16	9	13	2	8	1	3	6	1	5
SEAK	0	0	2	3	0	1	0	3	0	1	2	2	0	2	0	0	0	0	0	0
KAK	0	0	0	0	0	0	4	2	0	7	0	0	5	0	2	0	1	0	0	10

Table 8: Interchange of whales across regions for all years (1996-2015) for June-November. The diagonal is the number of unique whales seen in that region over the 20 year time span. Many of those whales were only seen once. Here PS includes NPS and CA represents SCA and CCA.

	CA	NCA	SOR	OR	GH+	NWA	SJF	PS	SVI	WVI	NBC	SEAK	KAK
CA	28												
NCA	10	301											
SOR	6	73	112										
OR	8	103	69	166									
GH+	1	19	11	21	43								
NWA	9	83	54	87	27	203							
SJF	6	49	27	48	17	97	182						
PS	0	0	0	0	0	1	1	32					
SVI	10	101	56	96	30	148	118	2	343				
WVI	7	87	45	81	30	120	99	2	200	295			
NBC	3	23	13	33	15	42	38	2	84	82	133		
SEAK	0	3	1	3	2	6	7	0	9	10	12	25	
KAK	1	10	1	6	0	3	2	1	13	12	8	1	153

Table 9: Sighting histories of whales seen in the PCFG during 1 June - 30 November in at least one year and also in Southeast Alaska (SEAK) or Kodiak (KAK) in one year. 1: whale sighted in PCFG but not SEAK or KAK that year, 2: only seen in SEAK or KAK that year, and 3: seen in both PCFG and in SEAK and KAK in that year.

	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015
68	1	2	2																
187	1	1	1	1	1	1	1	1				1		1					2
126	1	1			1			1	2			1				1			
130	1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1	1		1
140	1	1	3	1	1	1	1	1		1		1	1	1	1	1	1	1	1
141	1	1	1		1	1	1	1	1	1	3	1	1			1	1		1
152	1		1			2			2					2					
229	1	1	1	1	1	1	1	1	1	2									
323	1	1				1	1	1	2	1		2							
325	1	1			1	1	1	1	3	1							1	1	
328	1	1	1	1	1	1	1	1	1	1		1	3		1	1	1	1	1
899	1							1	2										
227		1	2	1	1	1	1	1	1	1	1		1		1	1	1	1	1
232		1		1	1	2	1								1			1	1
261		2				1		1							1		1	1	
316		1					2		2										
628			2	1	1	1	1	1				1					1		1
538				1	1	1		1	2										
555				1		1	1			1		2	1	1	1	1	1		
566				1		2		1	2					1					
601				1	1		1	1	1	1						2			
612				1	1	1	3	1	1	2						1	1	1	1
581					1		1	1	2	1	1					2	1	1	1
604					1		1		2					2	1				
639					1	2					1		1						
684						1	2				1								
687						1			1	1	1	1	3	1					
691						1	3	1	2			1							
723						2													1
760						1	1	1	3							1			2
800							3	1	1										
815								1				2						1	
900								1					2			1			1
834									2				1				1	1	
893									2							1		1	
918									2							1			
993											1			1	1				3
1778																		1	2

Table 10: Number of unique whales seen by year for MUA, OR-SVI, and PCFG (NCA-NBC) during 1996-2015.

Region	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	Average
MUA	19	27	37	11	14	32	8	22	26	33	58	20	75	57	26	41	67	66	63	45	37
OR-SVI	30	36	86	71	70	128	103	110	118	107	96	114	123	118	93	91	127	145	151	161	104
PCFG	45	69	132	151	140	173	203	157	179	135	126	120	174	152	144	164	208	232	200	211	156

Table 11: Discovery of new unique whales over years 1996-2015 for PCFG,OR-SVI and MUA. Recruited only means that the whale was seen in at least one more year after the initial year it was seen. The number 'recruited' will usually be greater than the abundance estimate because some whales die and others may permanently emigrate and do not return.

Region	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015
PCFG	45	90	161	229	283	345	398	418	448	466	474	494	544	566	581	600	653	711	750	793
ORSVI	30	50	105	128	155	211	249	275	306	323	333	355	377	394	402	411	439	476	512	544
MUA	19	34	57	58	69	88	89	100	114	123	146	148	177	190	194	205	227	249	273	288
PCFG-recruited	40	76	123	135	163	189	219	234	247	257	258	267	285	292	304	309	328	350	362	
ORSVI-recruited	26	39	76	85	100	122	149	169	185	195	198	205	216	222	229	234	248	266	278	
MUA-recruited	17	28	36	36	44	51	52	58	68	74	91	93	109	111	113	119	126	133	138	

Table 12: RELEASE goodness of fit results for each region using pooled and separate cohorts. When cohorts are separated as groups, Test 3 is always 0 because there are no sub-cohorts.

Region	Cohort	Test	χ^2	df	P
MUA	Pooled				
		Test 2	75.1301	35	1e-04
		Test 3	73.6519	34	1e-04
		Total	148.782	69	0
	Separate				
		Test 2	17.4696	79	1
OR-SVI	Pooled				
		Test 2	207.9702	47	0
		Test 3	358.0037	35	0
		Total	565.974	82	0
	Separate				
		Test 2	172.5884	140	0.0319
NCA-NBC	Pooled				
		Test 2	381.7309	47	0
		Test 3	738.8561	35	0
		Total	1120.587	82	0
	Separate				
		Test 2	302.1301	132	0

Table 13: Number of whales seen each year, number that were new that year in that region, and number that were new and were seen in a subsequent year for whales seen between June-November 1996-2015 in each region. The year a whale was seen as new can vary across regions and if it differs will be later in the smaller region.

Region		1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015
MUA	Seen	19	27	37	11	14	32	8	22	26	33	58	20	75	57	26	41	67	66	63	45
	Non-calf: New	19	15	22	1	11	18	1	10	12	9	23	2	28	13	4	9	20	17	21	12
	Non-calf: New/Resighted	17	11	7	0	8	7	1	5	8	6	17	2	15	2	2	4	6	4	5	0
	Calf: New	0	0	1	0	0	1	0	1	2	0	0	0	1	0	0	2	2	5	3	3
	Calf: New/Resighted	0	0	1	0	0	0	0	1	2	0	0	0	1	0	0	2	1	3	0	0
OR-SVI	Seen	30	36	86	71	70	128	103	110	118	107	96	114	123	118	93	91	127	145	151	161
	Non-calf: New	30	20	54	23	27	51	31	23	26	14	10	20	20	16	7	4	21	26	25	26
	Non-calf: New/Resighted	26	13	36	9	15	19	22	17	13	9	3	6	10	6	6	2	8	9	7	0
	Calf: New	0	0	1	0	0	5	7	3	5	3	0	2	2	1	1	5	7	11	11	6
	Calf: New/Resighted	0	0	1	0	0	3	5	3	3	1	0	1	1	0	1	3	6	9	5	0
NCA-NBC	Seen	45	69	132	151	140	173	203	157	179	135	126	120	174	152	144	164	208	232	200	211
	Non-calf: New	45	45	68	68	54	57	44	17	25	15	8	17	48	21	12	13	44	47	24	32
	Non-calf: New/Resighted	40	36	45	12	28	23	23	12	10	9	1	8	17	7	9	1	12	12	5	0
	Calf: New	0	0	3	0	0	5	9	3	5	3	0	3	2	1	3	6	9	11	15	11
	Calf: New/Resighted	0	0	2	0	0	3	7	3	3	1	0	1	1	0	3	4	7	10	7	0

Table 14: Delta AICc and QAICc (for OR-NBC and NCA-NBC models) for 30 models fitted to each set of data.

		φ Model									
Region	p model	1	2	3	4	5	6	7	8	9	10
MUA	1	20.1	11.2	11.8	1.4	4.5	7.9	5.0	7.1	4.2	5.6
	2	17.2	9.5	9.2	0.0	3.2	7.4	4.3	6.4	2.6	4.0
	3	98.1	91.2	88.1	80.6	82.9	86.8	84.4	86.2	82.5	83.5
OR-SVI	1	223.1	181.7	214.9	170.4	173.4	176.2	174.5	173.4	172.8	173.3
	2	42.1	10.0	35.7	0.0	3.1	6.5	4.8	4.8	2.0	2.9
	3	42.9	11.4	36.9	1.7	4.9	9.3	7.9	8.4	3.4	4.3
NCA-NBC	1	185.3	149.8	159.4	120.1	123.6	129.3	127.3	129.3	121.3	123.4
	2	58.9	28.8	33.9	0.0	3.6	10.0	8.6	9.9	0.6	3.5
	3	62.8	33.4	39.5	5.4	8.7	16.6	13.0	NA	6.2	7.7

Table 15: JS1 abundance estimates $(\widehat{N})$, standard errors and minimum population estimate $N_{min} = \widehat{N}e^{-0.842\sqrt{log(1+(se(\widehat{N})/\widehat{N})^2}}$ using data from 1996-2015 in OR-SVI and NCA-NBC regions.

Region	Year	$\widehat{N}$	$se(\widehat{N})$	N_{min}
OR-SVI	1996	24	2.2	22
	1997	42	6.2	38
	1998	81	9.1	74
	1999	84	10.3	76
	2000	91	13.3	81
	2001	132	14.3	121
	2002	134	16.1	121
	2003	158	14.2	146
	2004	163	16.6	150
	2005	169	17.2	155
	2006	155	17.1	141
	2007	162	14.6	150
	2008	170	17.4	156
	2009	161	13.6	150
	2010	150	17.7	135
	2011	146	16.0	133
	2012	163	13.6	152
	2013	177	13.2	167
	2014	189	16.5	175
	2015	196	19.3	180
NCA-NBC	1996	38	2.8	36
	1997	80	10.5	72
	1998	126	11.0	117
	1999	145	14.6	133
	2000	146	14.4	135
	2001	178	13.5	167
	2002	197	14.1	185
	2003	207	17.5	193
	2004	216	16.6	202
	2005	215	26.7	194
	2006	197	21.4	180
	2007	192	26.0	171
	2008	210	18.6	195
	2009	208	21.2	191
	2010	200	19.1	184
	2011	205	15.9	192
	2012	217	11.3	208
	2013	235	14.0	224
	2014	238	19.0	222
	2015	243	18.9	228

Table 16: JS1 abundance estimates $(\widehat{N})$, standard errors and minimum population estimate $N_{min} = \widehat{N}e^{-0.842\sqrt{log(1+(se(\widehat{N})/\widehat{N})^2}}$ using data from 1996-2015 in MUA region.

Year	$\widehat{N}$	$se(\widehat{N})$	N_{min}
1996	18	1.5	16
1997	32	4.6	28
1998	40	9.3	33
1999	38	14.8	28
2000	41	26.4	25
2001	53	14.1	43
2002	48	23.7	33
2003	53	17.6	41
2004	58	17.7	45
2005	62	12.5	52
2006	70	8.8	63
2007	71	20.1	56
2008	84	7.6	78
2009	86	11.8	77
2010	80	20.3	65
2011	79	14.6	68
2012	88	10.8	80
2013	91	11.8	82
2014	100	15.2	88
2015	105	21.5	88

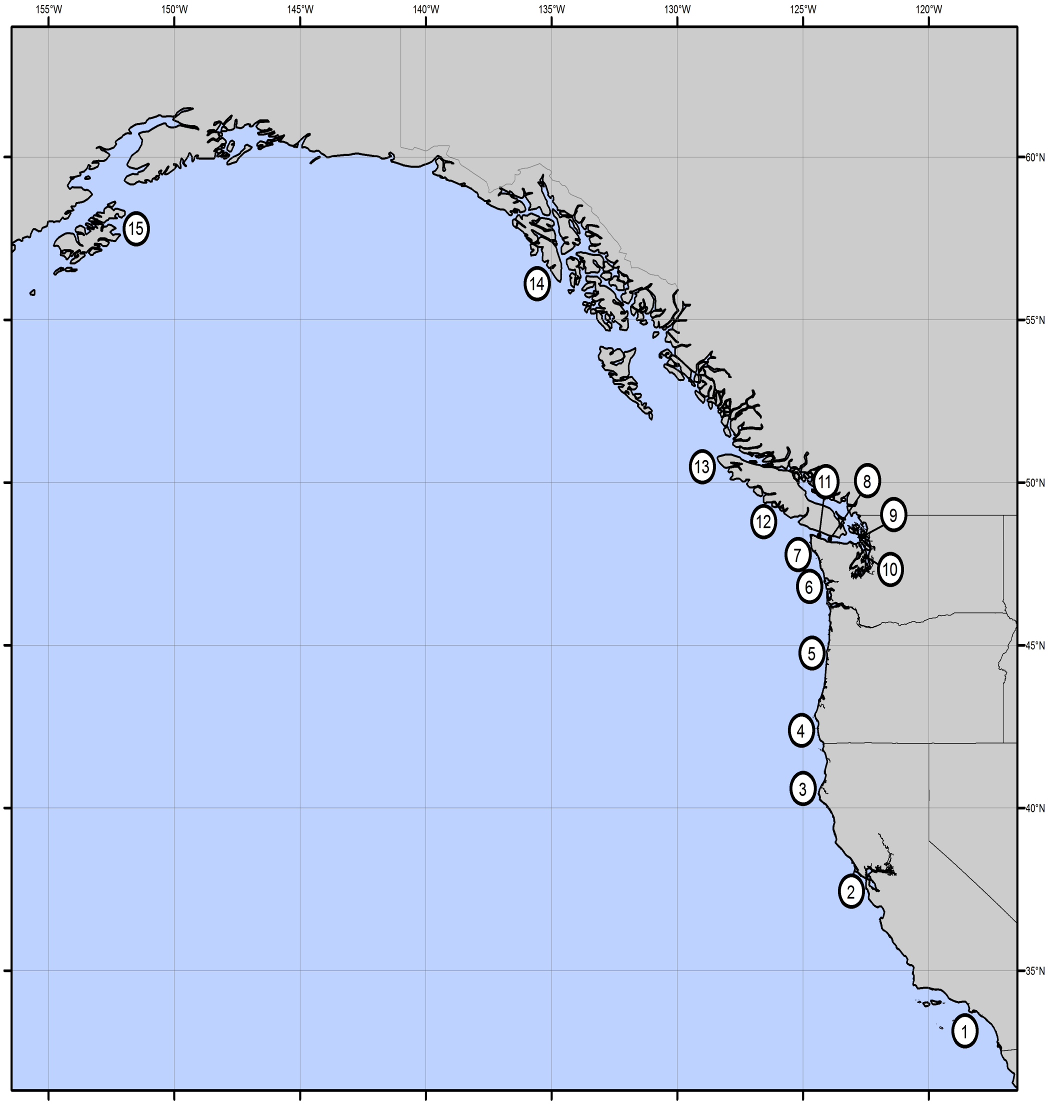

Figure 1: Locations for photo-identifications of gray whales. Numbers refer to values in Table 3.

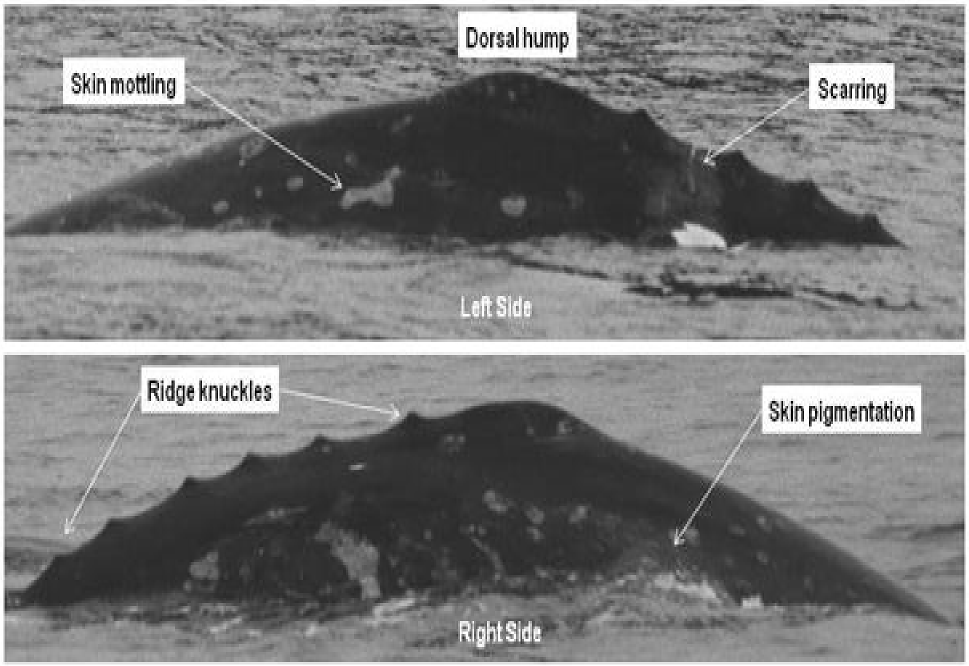

Figure 2: Characteristics used for gray whale photo-identification.

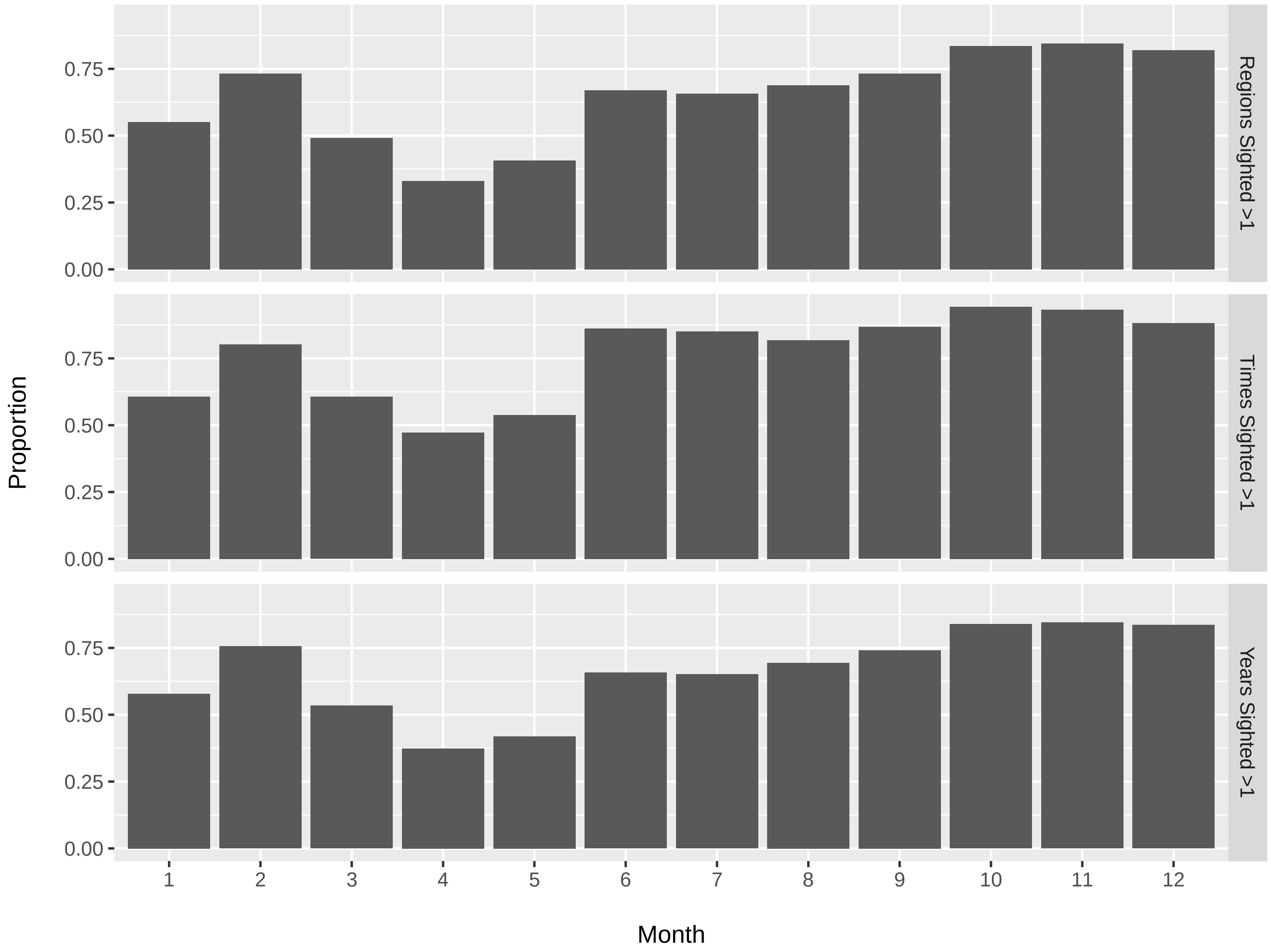

Figure 3: Monthly measures of proportion of whales that were seen in more than one region, seen on more than one day and seen in more than one year. The values include sightings from 1996-2015 in all regions from California to Alaska. Lower values imply whales were simply migrating through the area in a short time frame and were thus less likely to be seen at other times and in other regions. Values are not shown for months with fewer than 20 sightings. Whales seen more often are overrepresented because they are used in each month they were seen. For example a whale seen in June, July and August will be in each summary. Thus, these values may be larger than values computed without splitting by month (e.g., overall proportion of whales seen in more than one year).

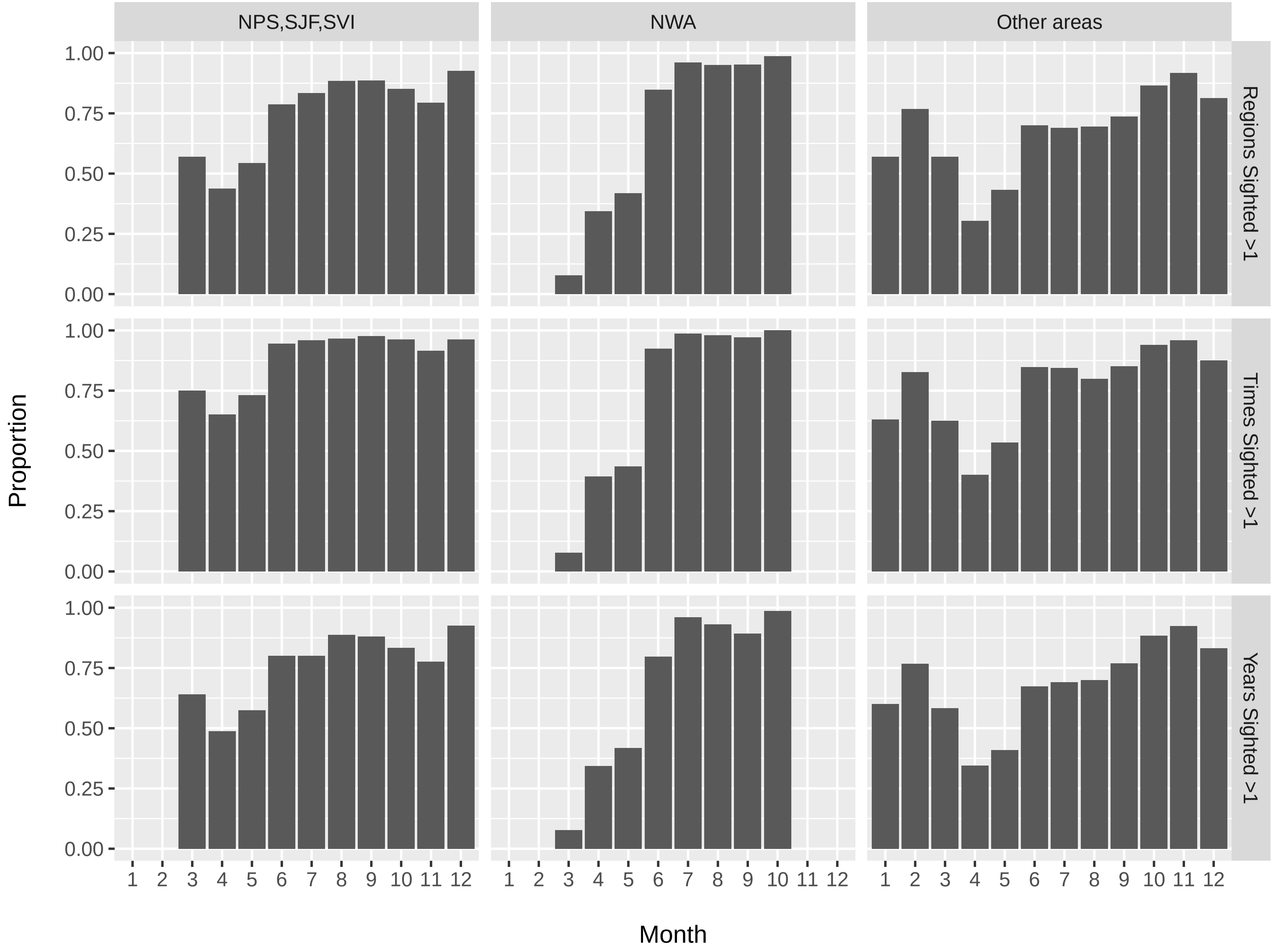

Figure 4: Region and monthly measures of proportion of whales that were seen in more than one region, seen on more than one day and seen in more than one year. The values include sightings from 1996-2015 in all regions from California to Alaska. Lower values imply whales were simply migrating through the area in a short time frame and were thus less likely to be seen at other times and in other regions. Values are not shown for months with fewer than 20 sightings. Whales seen more often are over-represented because they are used in each month they were seen. For example a whale seen in June, July and August will be in each summary. Thus, these values may be larger than values computed without splitting by month (e.g., overall proportion of whales seen in more than one year).

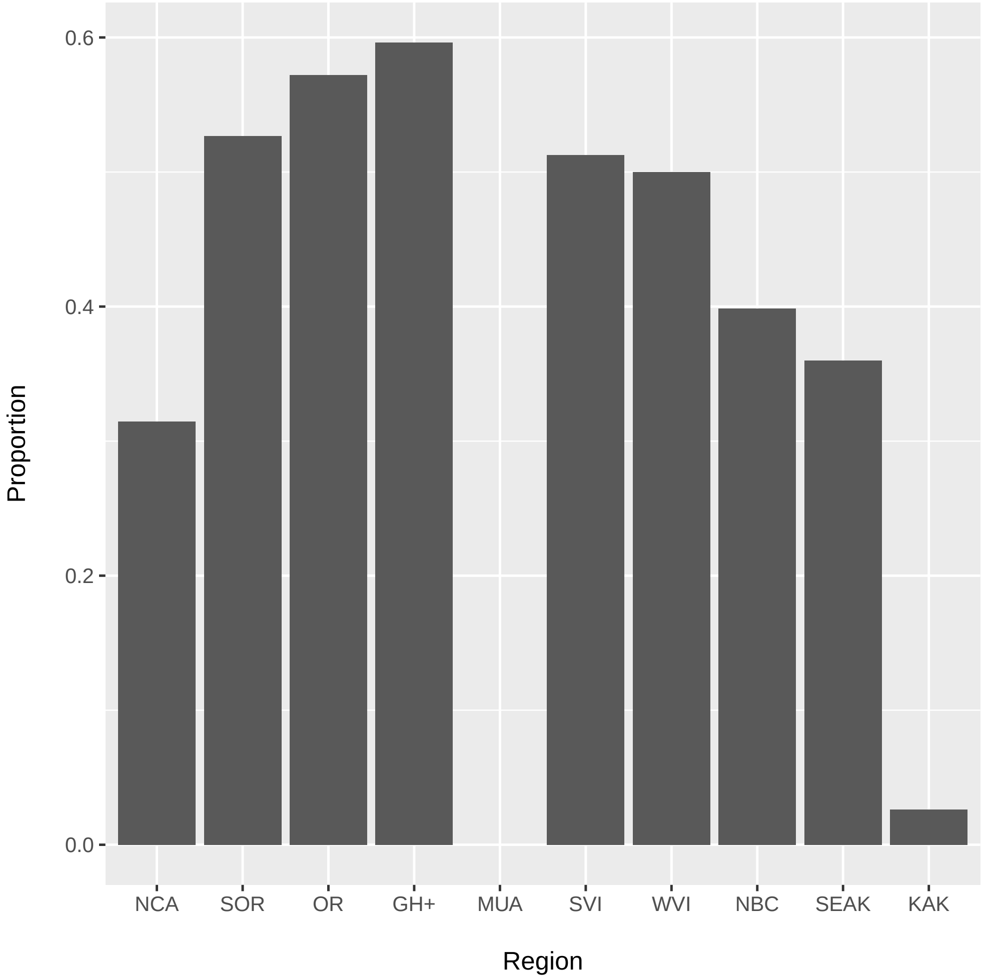

Figure 5: Proportion of whales in sub-regions from NCA to KAK that have been seen in the MUA using sightings after 1 June from 1996-2015.

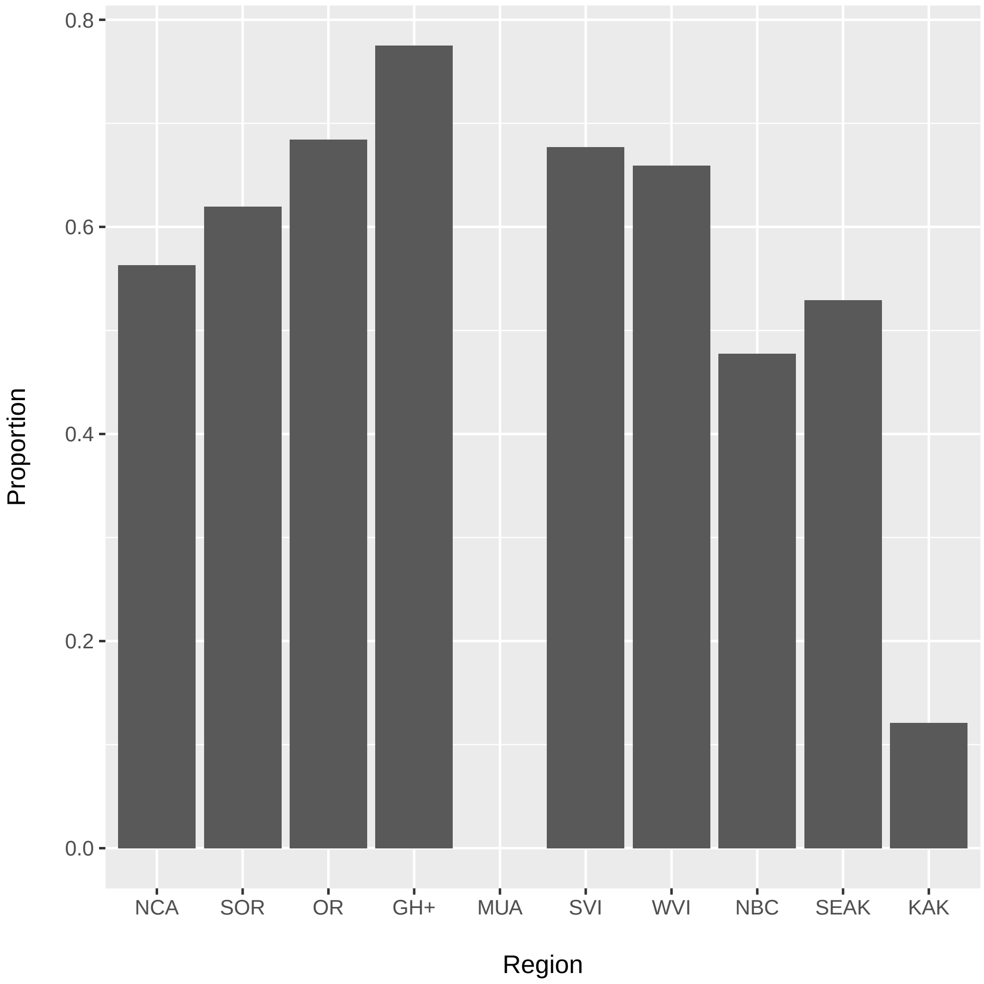

Figure 6: Proportion of whales seen in at least 2 years in sub-regions from NCA to KAK that have been seen in the MUA using sightings after 1 June from 1996-2015.

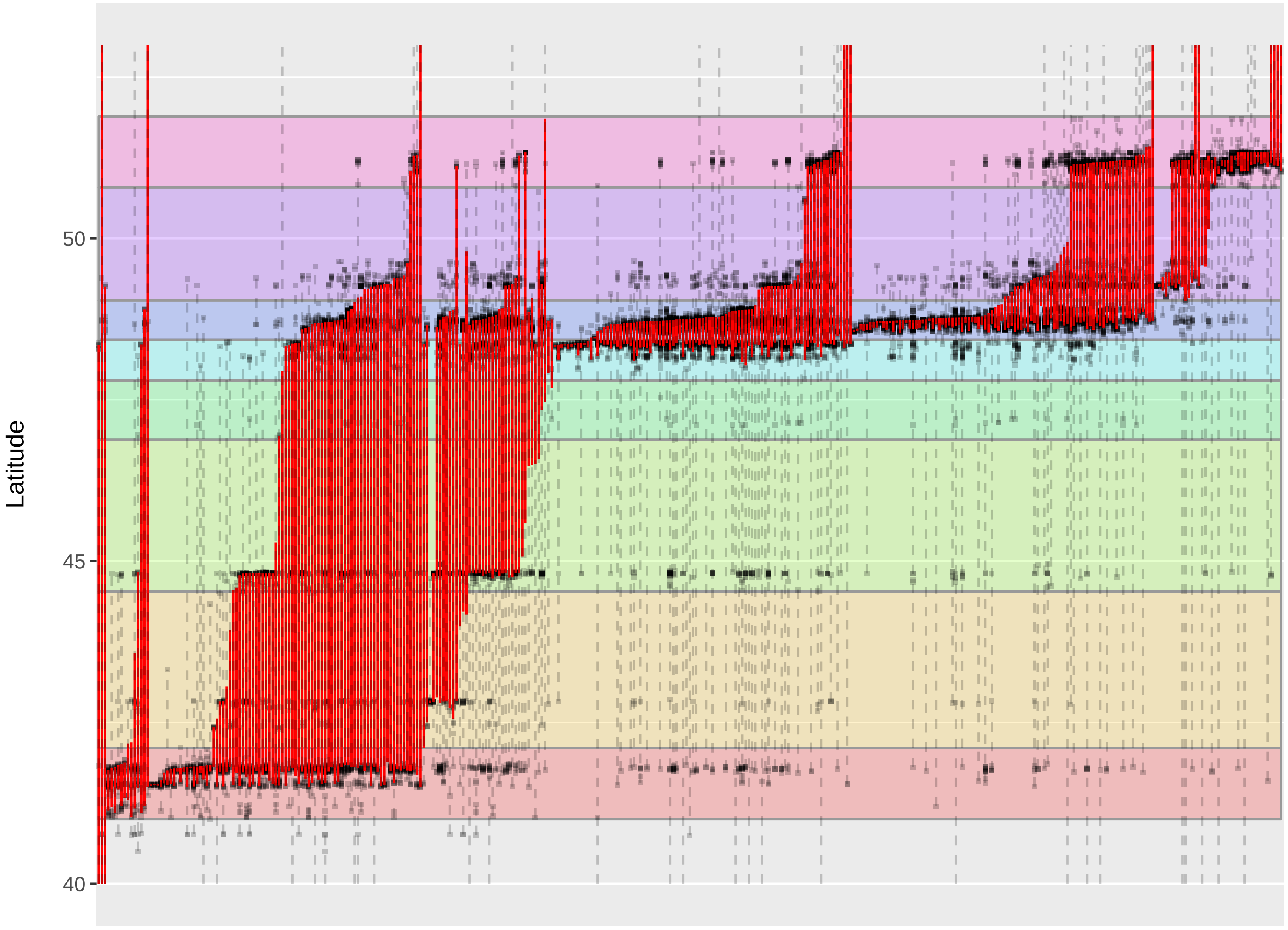

Figure 7: Distribution of latitudes of sightings (points) for whales with 6 or more sightings after 1 June from 1996-2015, the 75% inner quantile (solid thick line), and full range (light dashed line). Each position on the x axis represents an individual whale. Whales have been arranged on the plot by sorting first on the lower bound of the inner quantile (to a half-degree) and then the upper bound of the quantile. This has the effect of sorting from south to north and clusters whales with smaller quantile ranges followed by whales with larger ranges.

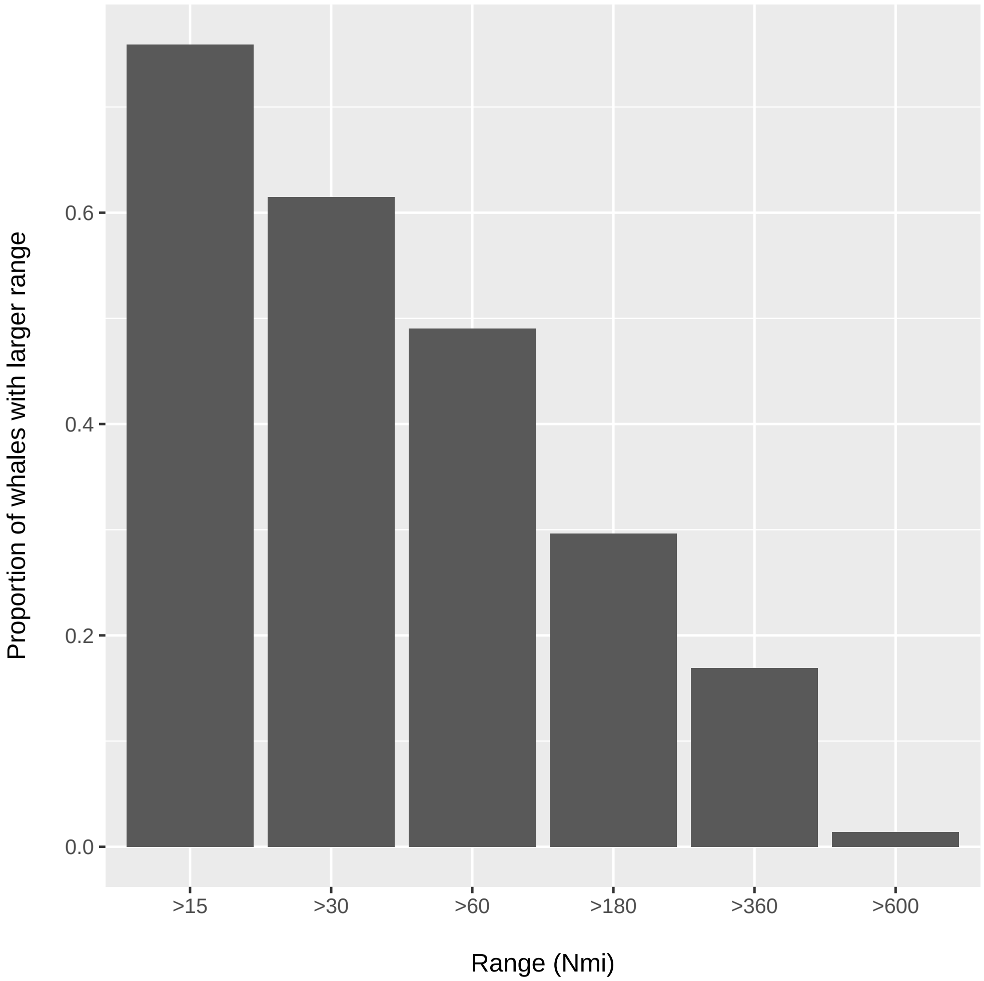

Figure 8: Distribution of ranges of 75% inner quantiles of latitudes expressed in nautical miles for whales sighted on 6 or more days during 1996-2015.

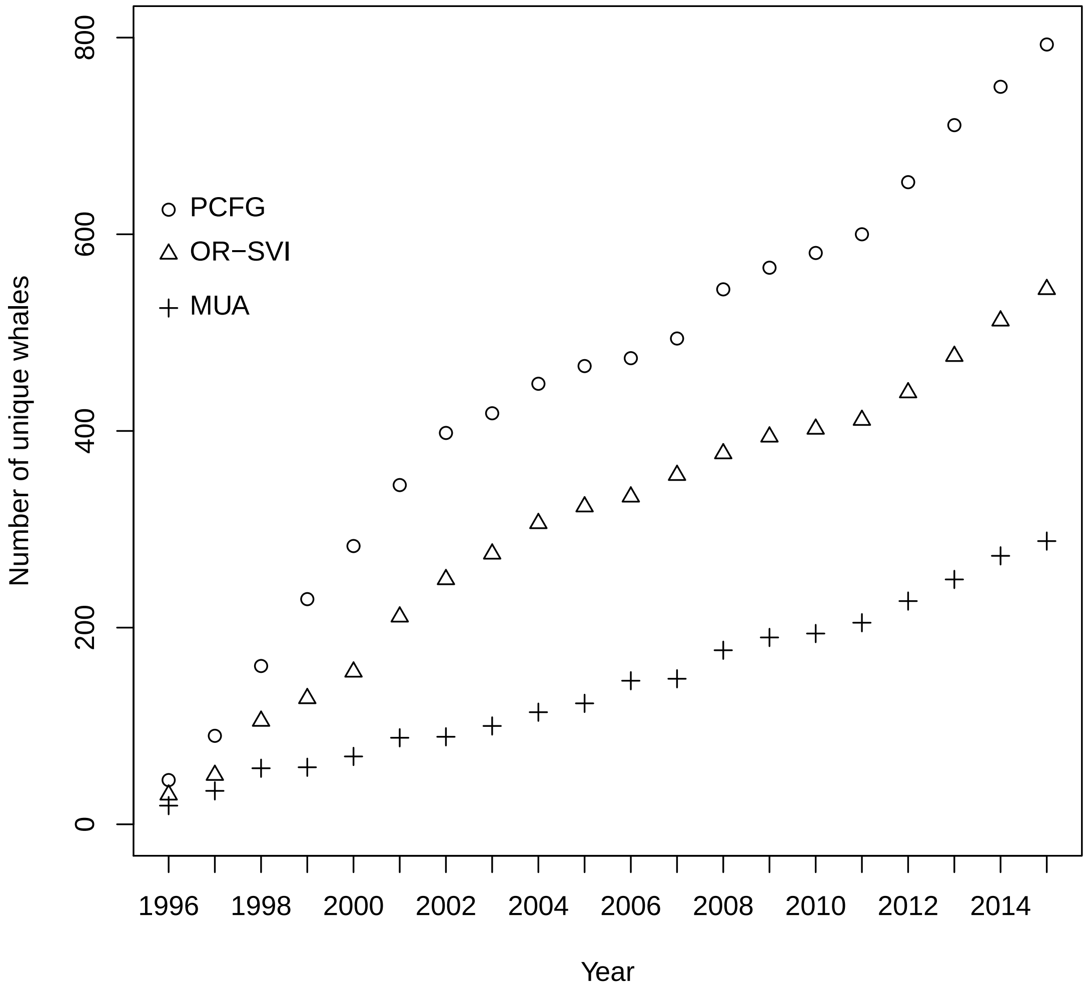

Figure 9: Discovery curves for unique whales seen in PCFG, OR-SVI and MUA for 1996-2015.

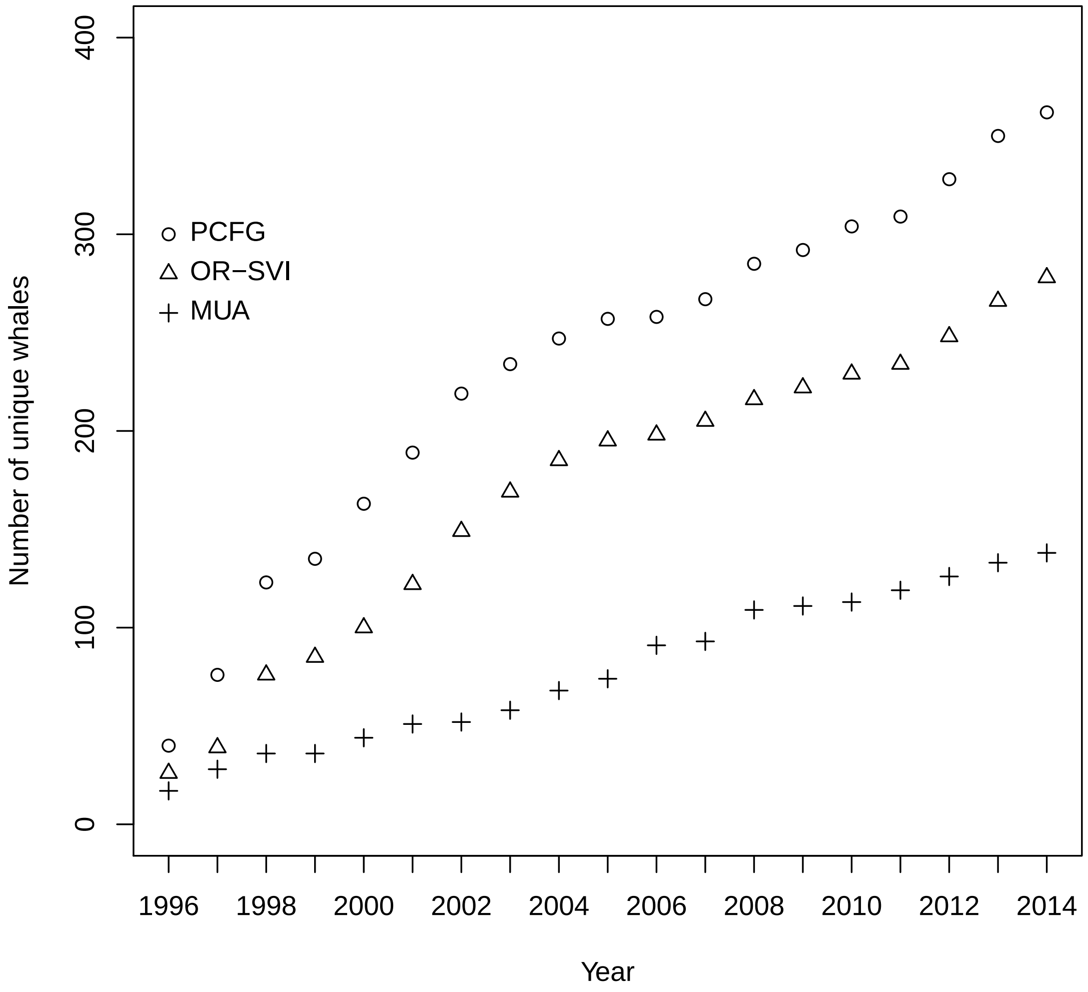

Figure 10: Discovery curves for unique recruited whales seen in PCFG, OR-SVI and MUA for 1996-2015.

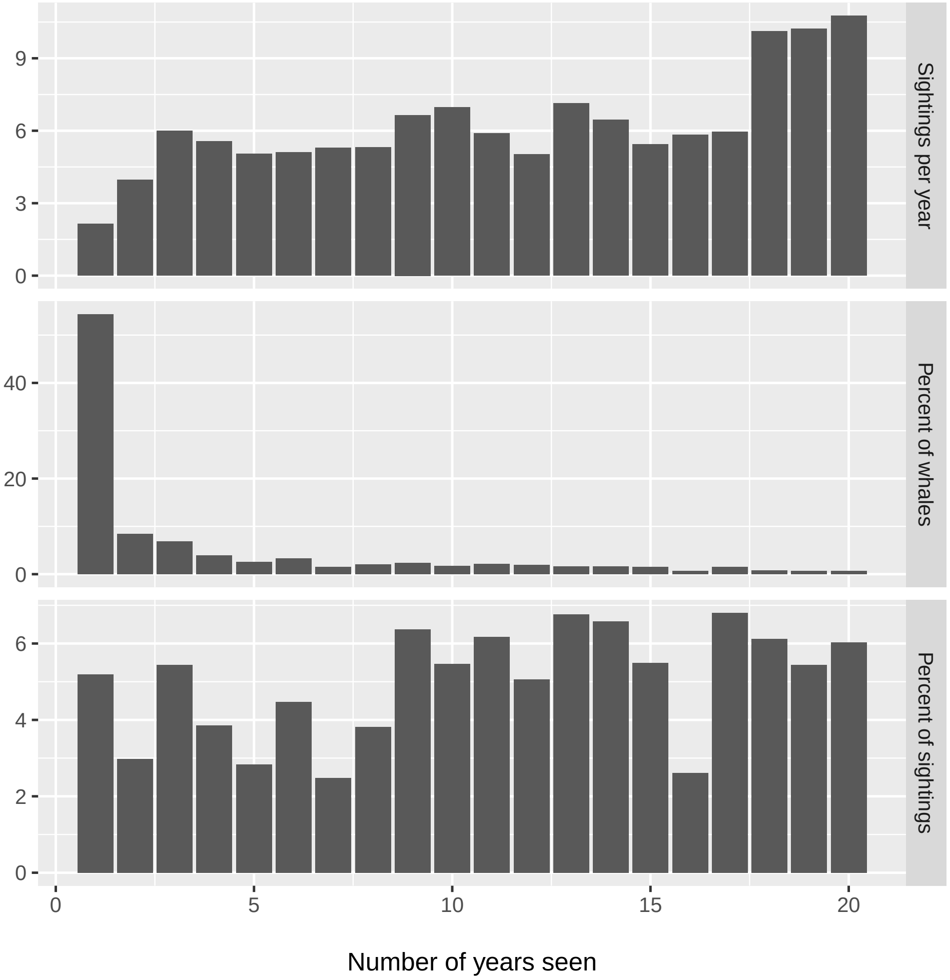

Figure 11: Average number of sightings per year and distribution of whales and numbers of sightings based on numbers of years a whale was seen in NCA-NBC between June-November during 1996-2015.

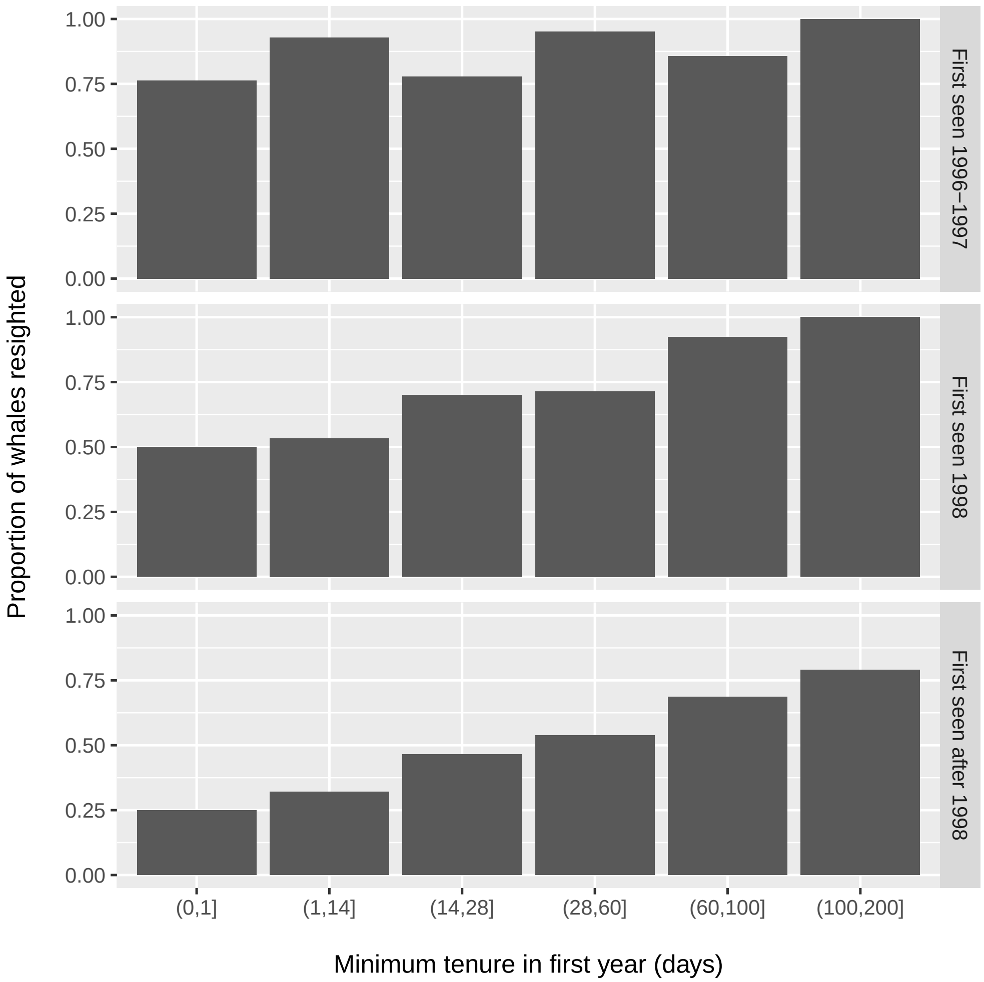

Figure 12: Influence of minimum tenure (MT) in the first year the whale was photographed on the probability it will be re-sighted in one or more following years for whales seen in NCA-NBC for June-November 1996-2015. The bar graphs are divided based on first year in 1996-1997, 1998 and after 1998. Re-sightings for 2015 are used but initial sightings for 2015 are excluded because there are no data beyond to evaluate re-sighting probability.

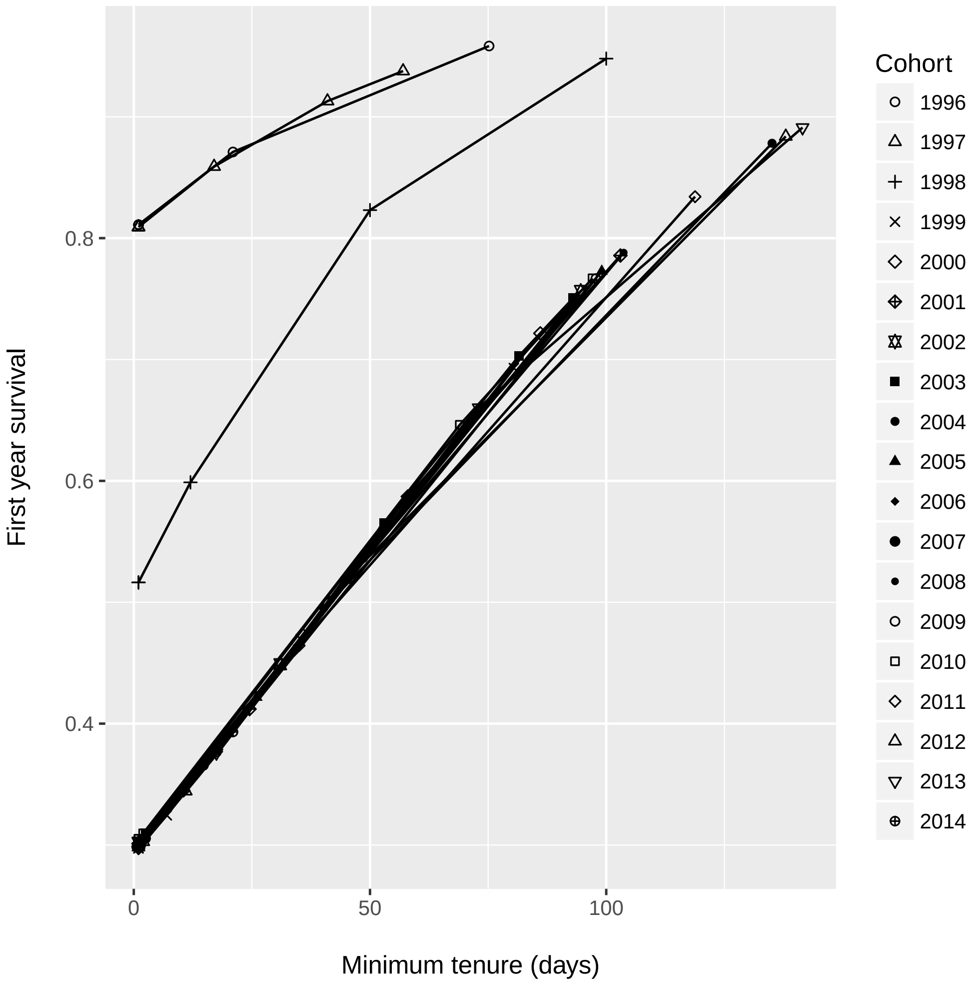

Figure 13: For NCA-NBC analysis of 1996-2015 data, model-averaged estimates of first year survival of non-calves for each cohort at 5%, 25%, 50%, 75%, and 95% quantiles of minimum tenure values for that cohort.

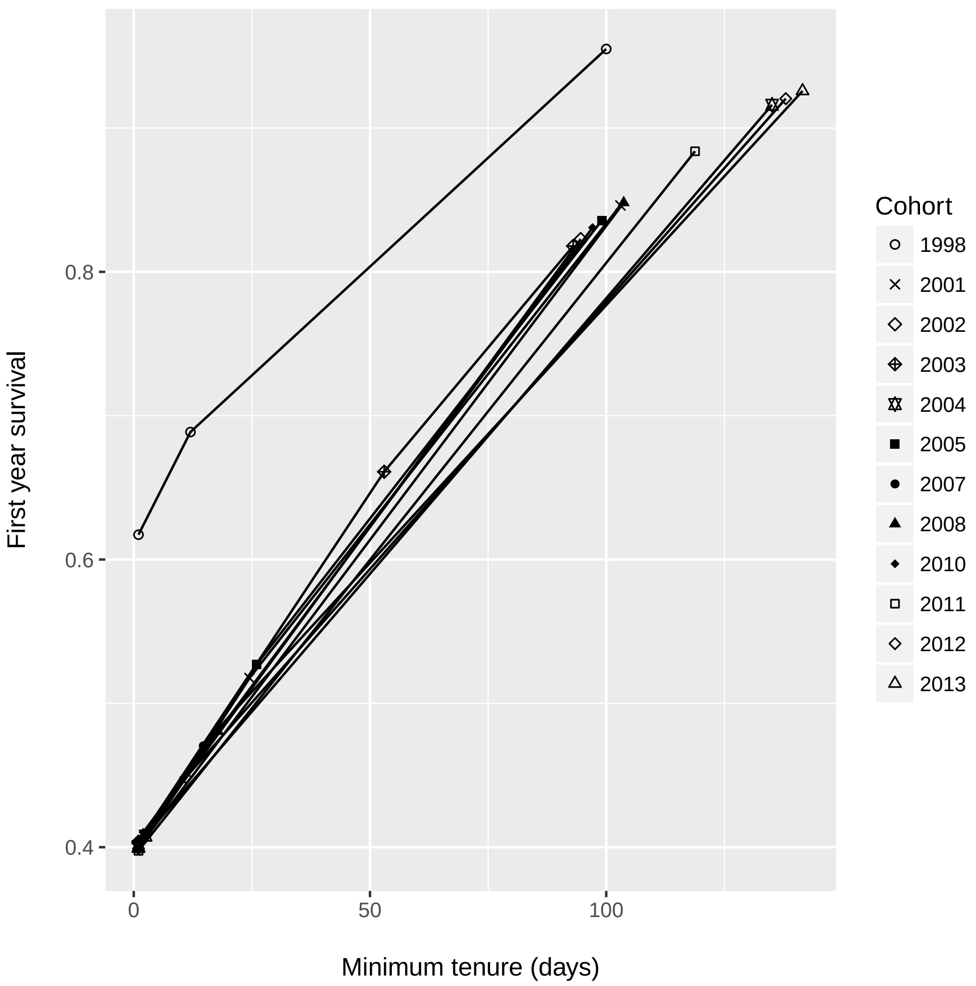

Figure 14: For NCA-NBC analysis of 1996-2015 data, model-averaged estimates of first year survival of calves for each cohort at 5%, 25%, 50%, 75%, and 95% quantiles of minimum tenure values for that cohort.

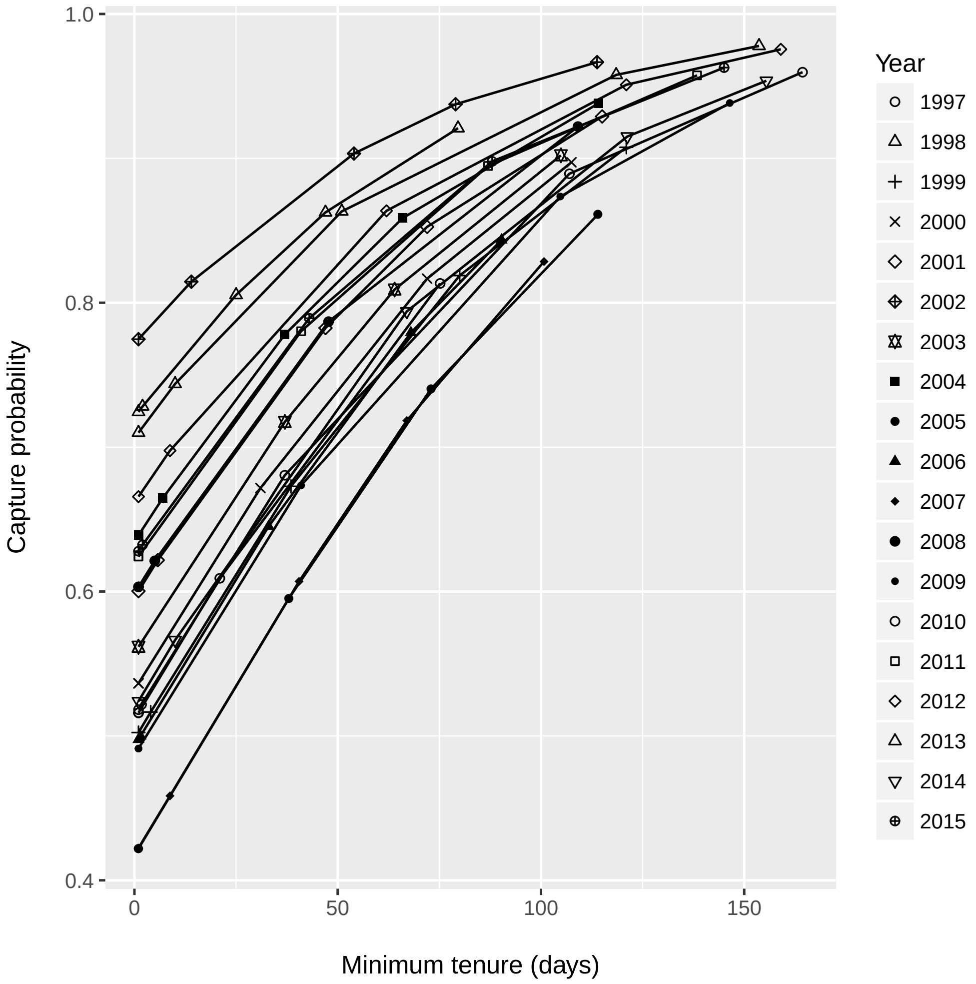

Figure 15: For NCA-NBC analysis of 1996-2015 data, model-averaged estimates of capture probability for each year at 5%, 25%, 50%, 75%, and 95% quantiles of minimum tenure values for whales in the previous year.

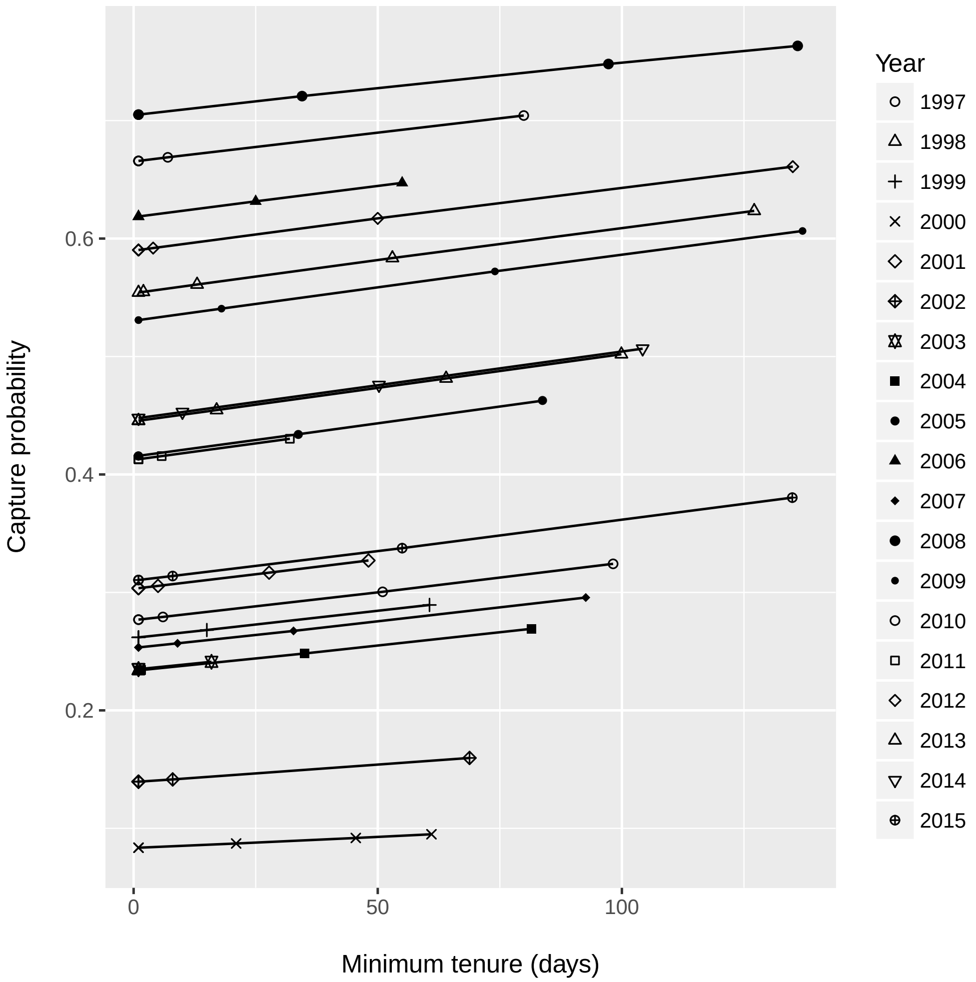

Figure 16: For MUA analysis of 1996-2015 data, model-averaged estimates of capture probability for each year at 5%, 25%, 50%, 75%, and 95% quantiles of minimum tenure values for whales in the previous year.

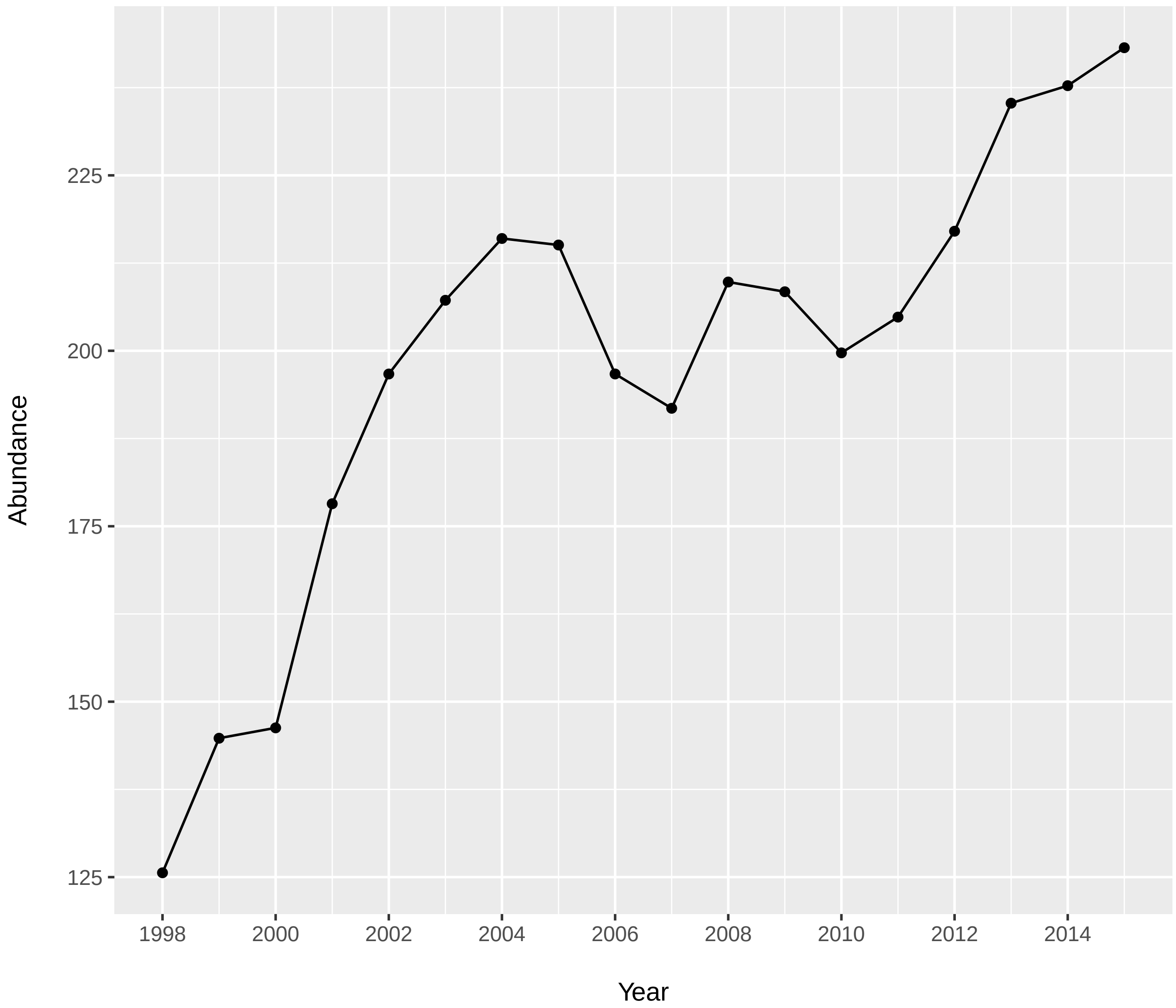

Figure 17: Annual abundance estimates for 1998-2015 in NCA-NBC using the open (Jolly-Seber; POPAN parametrization) population model approach JS1.

Appendix

Table 1 provides capture histories of whales seen in the PCFG at least once from 1 June - 30 November and displays by year, when they were seen only in spring (March-May), only from 1 June - 30 Nov and when they were seen in both time periods. Table 2 provides capture histories using data from 1 June - 30 Nov of whales seen in the MUA at least once. It shows when whales were seen only outside of the MUA but in the PCFG, only in the MUA and both inside the MUA and in the PCFG outside of the MUA

Table 1: Sighting histories of whales seen in the PCFG in at least one year. In year columns, a 1 means the whale was only sighted in the spring (March-May), 2 means it was only seen in June-Nov, and 3 means it was seen in both March-May and June-Nov. The region value is the nunber of years the whale was seen in that region.

1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	#years	NCA	SOR	OR	GH+	NWA	SJF	SVI	WVI	NBC	#areas
							2	2	2	2			2	2	2		2	2	2		2	2	2	2		2	2	2	2	2	20					1		4	15	9	4
							2	2	2	2	3			2																	9				1				9		2
																															1						1				1
																															1						1				1
				2	2						2	2	2	2	2	2	2		2	2	2										13					2	1	10	5	1	5
					2			2	2	2	2		2	2	2	2	2	2	2	2	2	2	2	2							18	1			1		6	15	7	4	6
					2		2	2	2	2	2	2	2	2	2	2	2	2	2												15		1	1		5	1	11	3	1	7
								2					2	2																	4			1		2		3	2		4
								2			2	2	2	2	2	2	2	2	2		2		2	2		2	2	2	2	2	19	3		5		5		12	7	4	6
			2				2		2	2	2		2	2	2	2	2	2	2	2	2	2	2	3	2	3	2	3	3	2	24	1			1	5	3	19	11	2	7
2										2			2	2			2	2	2			1						2			9							2		7	2
	3																														1						1				1
	3																														1					1	1				2
	2																														1						1				1
	2								2					2		3	2		2		1	2	2	2	2	2	2	2	2		15	7	5	4	3	1	1				6
	2											2	2	2	2	2	2	2		2		2		2	3	3	2	2	2	2	17	8	2	5		1	1	4	1		7
		2																													1							1			1
			2				2				2		2	2	2	2	2	2	2	2	2		2		2	3	2	3	2		18					1	2	9	10	3	5
				2			3	3		2	1		1		3	2	2		2												10		1	1	6	2			1	1	6
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				1														2													2				1			1			2
					2																										1							1			1
					2																										1							1			1
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					2																										1							1			1
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						2							2	2																	3	3									1
						2							2		2	2	2														5	5									1
						2							2	2																	3	3									1
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Cont.

Table 1: Sighting histories of whales seen in the PCFG in at least one year. In year columns, a 1 means the whale was only sighted in the spring (March-May), 2 means it was only seen in June-Nov, and 3 means it was seen in both March-May and June-Nov. The region value is the nunber of years the whale was seen in that region.

1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	#years	NCA	SOR	OR	GH+	NWA	SJF	SVI	WVI	NBC	#areas
								2					2	3	3	3	2	2	2	2	2	2	3	2	2	2	2	2	3	2	19	6	5	6		8		16	6		6
								2																							1					1					1
								2			2	2	2		2	2	2	2		2		2	2			2			2	2	14		2	1		3	2	7	2	9	7
								2			2	2	3	2	2	2	2	2	2	2	2	2	3	3	2	3	3	2	3	3	21				1	12	7	19	4		5
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									2	2	1																				3				1	1	1				3
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									2			2			2			2	2		2										6							1		6	2
										2																					1						1				1
										3	1																				2				2						1
										3	1																				2				2						1
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										2			2	2	2	2	2	3	2	3	2	3	3	3	1	3	3	3	2	3	19					1		14	10	7	4
										2		2		2												1					4							1	1	2	3
										2		2		2	2	2	2														6									6	1
										3																					1				1						1
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										2																					1						1				1
										2	2	2	2																		4					3	2	1	1		4
										2	2	2	3	2	3	2	2	3	2	2	2	2									13	1		1		5	5	9	7		6
										2		2	2	3																	4					3	2	2	1		4
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										2		2																			2						2				1
										2																					1						1				1
										2																					1						1				1
										2																					1						1				1
										2	2	2	3	2		3	2		2									1			9					1	2	5	3		4
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										2		2		2			2	2	2						1	2					8	1				1				6	3
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										2																					1							1			1
											2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	20	5		2	1			18	5	2	6
											1	2	2	3	3	2	2	2		2	3	3	2	2	1	2	3	3	2	3	19							16	12	3	3

Cont.

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1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	#years	NCA	SOR	OR	GH+	NWA	SJF	SVI	WVI	NBC	#areas
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											2	2	2	2	3	3	2	2	2				2		2						11					3	3	10	2		4
											2		1																		2				2						1
											1			1			2	2	2	2	2										7				1	1	1	5	1	1	6
											2	2	3	3	3	3	3	3	2	2	2	2	2	3	3	3	3	2	2	3	20		1	4	1	7	5	18	4		7
											1				2		2	2		3	2	2	3	3	2	2	2	3	2	2	15	6	1	5	1	7		10	2		7
											1		2																		2	1			1						2
											1	1	2	2	2	2	2	2		2	2	2	2	2	2	3	2	2	2	3	19	8	2	8	2	8		7	2		7
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											1		2	2	2	2	2	2				2		2	2	2	2	3	2	2	15	9	6	6	2						4
											1												2								2				1		1				2
											2	2	2																		3					2	1	2			3
											2																				1					1					1
											1		2				2	2	2			2		2							7	2	3	3	1	1	1				6
											1		2		2	2	2	2	2	2	3	2		2	1	3	2	2	2	3	17	1						17	4	6	4
											2	2	2	2	2	2	2	3	2												9			1				2	2	9	4
											2		2	2	2	2	2			2		3		2	2	2	3	3	2	2	15	2	1	2		2		11	9		6
											2	2	2	2	2	2	2	2	2							2	2	2			12							1	1	12	3
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											2	2	2																		3							1	1	3	3
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											2																				1									1	1
											2																				1									1	1
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												2	2	2	2	2	2	2	3	2											9					2	3	4	1	7	5
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												2																			1						1				1
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												2	2																		2							1		1	2
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													2																		1						1				1
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													2																		1						1				1
													2																		1						1				1
													2																		1						1				1

Cont.

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1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	#years	NCA	SOR	OR	GH+	NWA	SJF	SVI	WVI	NBC	#areas
													2																		1						1				1
													2																		1						1				1
													2																		1					1					1
													2		2									2		3	3	3			6	5			1	2			1		4
													2			2	2	2		2				2	3	3	2	2	2	2	12	10	1	1							3
													2																		1	1									1
													2				2	2			2	2		2	2	2	2	2	2	2	12	5	1		1	2	1	4	3	1	8
													2																		1	1									1
													2	2	2	2	2	2	2	2	2		2	2	2	2	3	2			15	11	2	4		1	1	3	1		7
													2																		1	1									1
													2			2	2	2	2			2				2	3	2	2	2	11	5	6	4		1					4
													2																		1	1									1
													2			2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	16	10	8	2		1		6	1		6
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													2																		1			1							1
													2	3	3			2			2	2	2	2							8	2		2		1		5	2		5
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													2	3	2		2	2	2	2	2	2	3	3	3	2	2	2	3		16	1		9	1	7	1	10	4	3	8
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													2																		1					1					1
													2	2	2	2	2	2	2		2		2								9							2	6	4	3
													2											1							2								2		1
													2	2			3	2	2	2	2	2	2	2		3	2	2	2	2	15	2		2				5	8	4	5
													2	2																	2	1							1		2
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														2																	1	1		1							2
														2																	1	1									1
														2																	1			1							1
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														2																	1	1									1

Cont.

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														2																	1			1							1
														2	2	2	2					2	2	2	3	3					9	8		3							2
														2																	1	1									1
														2																	1			1							1
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														2																	1			1							1
														1	2		2						2	2	3	2	2	3		3	10	8	1	2		1	1				5
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Cont.

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															2	2	2		2												4			1						3	2
															2		2														2					1			1		2
															2		2		2					2	3	2	2	2	2		9	6	3	3		1		2	1		6
															2		2		2	2											4	2						2			2
															2																1	1									1
															2		2	2			2			2	2	2	2	3			9	8	3	2				1			4
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															3																1	1									1
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Cont.

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1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	#years	NCA	SOR	OR	GH+	NWA	SJF	SVI	WVI	NBC	#areas
																2															1					1					1
																2		2								2					3	1				1		1			3
																2	2	2	2		1										5					4	2	2	1		4
																2															1							1	1		2
																2	2														2	1				2					2
																2															1					1					1
																2															1						1				1
																2						2		2	2	2	2	2	2		8	6	1	4				1	1		5
																2	3	3													3							3	1		2
																2															1							1			1
																2	2						2	2	2	2	2	2			8	7						1			2
																2															1	1						1			2
																2															1							1			1
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																2	2														2			1					1		2
																2															1			1							1
																2		2	2												3	1	2	1							3
																2						2		2							3	2		1							2
																2															1	1									1
																2	2	2													3	2				1		1			3
																2	2														2	1	1								2
																2	2	2		2			2	2	2	2	2	3	2	2	12	8		1	1	1		3	3		6
																2															1	1									1
																2															1									1	1
																2	2	2	2				2				2	2		2	8							3		7	2
																2	2	2	2	2		2	2	2	2	2	2	2	3		13				1	1		9	5	3	5
																	2		2							2		2	2		5	3				1			1	2	4
																	2														1	1									1
																	2														1		1								1
																	2	2													2		1					1			2
																	2	2													2		2								1
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																	2														1		1								1
																	2														1	1									1
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																	3	2	2	2	3	3	2	3	3	3	2	3	2	2	14	1			1	6	7	13	5		6
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																	2														1							1	1		2
																	2			2	2	2	2	2	2						7				1		1	4	3		4
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																	2	2	2				2								4							3	1		2
																	2														1							1			1
																	2	2	2	3	3		2	2	2	2	3	2			11	4		2		6	8	11	1		6
																	3			1						3					3						1	3			2
																	2	2	2	3	3	2	2	2	3	2	2	3	2	2	14	5	1	5	2	5		10	2		7
																	2	2	2	2											4	1						2	1		3
																	2														1	1									1

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																	2		2		3	2		1				2			6	2		2	1	3		2			5
																	2														1	1									1
																	2		2			2		2		2		2			6	5	1								2
																	2														1	1									1
																	2														1	1									1
																	2														1	1									1
																	2														1	1									1
																	2														1	1									1
																	2	2													2	1						1			2
																	2														1	1									1
																	2														1	1									1
																	2	2		2	2	2	2	3	2	2	2	2	2		12	3			1	1		4	8		5
																	2														1								1		1
																	2				2	2	2	2	3	2	3	2	2	2	11	4	2	2	1	6	2	3	6		8
																	2			1											2						1		1		2
																	2										2		1		3							2	1		2
																	2	2		2	2	1	2	3	3	3	3	2	1	2	13						1	10	8	2	4
																	2	2	2	2	2	2	2	3	2	2	3	3	3	3	14	1		2	1	7	5	12	7		7
																	2	2	2	2							3				5					1				5	2
																	2	2	2			2		2	3	2	3	3	3	2	11	6	3	5	1	2					5
																		2	2	2	2	2	2								6		1	2				2	2	1	5
																		3	2	3	2						2	2			6			1		1	1	6	1		5
																		2													1		1								1
																		2	2		2										3					1	2	1			3
																		3	2	3											3					1	3	2			3
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																		3		2	3	1	2	3	3	3	3	2			10					6	1	10	4		4
																		2	2	2				2	2	2	3	2	2	2	10	5				4	3	8	2		5
																		2	2												2							2			1
																		2													1							1			1
																		2													1							1			1
																		2	2												2							2			1
																		2	2	2	2	2	3	2						2	8			1		1	1	7	2		5
																		2	2	2											3			1			1	1		1	4
																		2													1									1	1
																		2	2			2									3			2						2	2
																		2	2	2	3	2	2	2	2	3	2	3	2	3	13			5		4	1	8	3		5
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																			2												1							1			1
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																			2	2	2	2	2	2	2	2	3	2	3	3	12	2		4		7	4	11	4		6
																			2												1							1			1
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																			2	2	3	1									4					1		4			2
																			2	3	2	2	2	2	2	3	2	2	2		11	1	1			4	7	6	4		6
																			2		1										2							2			1
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																			2												1		1								1
																			2												1			1							1
																			2	2											2							1		1	2
																			2	2	2	3	3	2	3	3	3	2		3	11					5	7	9	5		4
																			2		2		2								3						2		1		2
																			2	2											2						2	1			2

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																			2	2											2								1	1	2
																			2												1						1				1
																			2												1						1				1
																			2								2			2	3									3	1
																			2												1									1	1
																			2												1									1	1
																			2												1									1	1
																			2												1						1				1
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																				2											1								1		1
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																				2	2	3									3							1	3		2
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																				3											1						1	1			2
																				2											1							1			1
																				2											1						1		1		2
																				2	2	1	2		2	2	1	1			8					4	1	3	4		4
																				2	2		3					3		2	5		1	1		5		2			4
																				2	2	3	3	2	1						6						2	4	1		3
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																					2										1						1				1
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Cont.

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																							2			2	2				3					2	2	2	1		4
																							2								1									1	1
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																							2	2	1	3	3	2	2		7	3				2	6	3		1	5
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																							2	3	2	2	3	2	2		7	1					6	5	2		4
																							2								1						1				1
																							2	2	2						3						3				1
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																							2								1						1				1
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																								2							1	1									1
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Cont.

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																								1			3				2					1		1	1		3
																								2							1					1					1
																								2							1						1				1
																								2							1						1				1
																								2	2	2	3	2	2	2	7			3		3	1	4	2		5
																								2							1	1									1
																								2							1	1									1
																									2	2	2	2	2	2	6	2	1	4							3
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																									2	2	2	3	2	2	6	4	1			2	2	2			5
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																									2		2				2					2					1
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																									2	2	2	2			4	2	1	2				1			4
																									2	2	2	3	3	2	6	5	1	2							3
																									3	3	3	2	3	3	6							6	3		2
																									2	2	3	2	3	3	6					1	1	6	3		4
																									2		3	2	3	2	5	2	2	1		1		2	1		6
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																									2	2	2	3	3	2	6		3	1		3	1	2	3		6
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																										3	2	2	3	2	5						1	5	1		3
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																											2				1	1									1

Cont.

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1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	#years	NCA	SOR	OR	GH+	NWA	SJF	SVI	WVI	NBC	#areas
																											2				1	1									1
																											2	2	3	3	4	1		2			2	2	3		5
																											2				1	1									1
																											2	2	3	3	4	1						2	3		3
																											2				1	1									1
																											2				1	1									1
																											2				1	1									1
																											2				1	1									1
																											2				1	1									1
																											2	2	2	2	4	2	2	1							3
																											2				1	1									1
																											2				1					1					1
																											2				1			1		1					2
																											1	2			2	1							1		2
																											2				1	1									1
																											2	2	2	2	4		4								1
																											2	2			2			1		1					2
																											2	2	2	2	4					1	3	4			3
																											2		3	2	3	1		2				1			3
																											2	2	2	2	4	2					2	4	1		4
																											2				1									1	1
																											2	2	2	3	4	1					3	4	1		4
																											3	3	2		3							2	1		2
																											2	2	2	2	4						1	3	1		3
																											2				1					1					1
																											2	3	2	2	4	1					4	3	2		4
																											2				1					1					1
																											2				1					1					1
																											3				1					1					1
																											2				1					1					1
																											2				1					1					1
																											2	2	2	3	4	2	1			1		2	2		5
																												2			1		1								1
																												2	2	3	3	1		2		1	1				4
																												2	3	2	3							3			1
																												2			1	1									1
																												2			1	1									1
																												2	2		2	2							1		2
																												2			1					1			1		2
																												3	3	2	3	2	1								2
																												2			1						1				1
																												2			1					1	1		1		3
																												2			1						1				1
																												2	1		2					1	1		1		3
																												2			1						1				1
																												2			1					1	1		1		3
																												2	3	2	3					2		3			2
																												2			1			1		1					2
																												2			1	1					1	1	1		4
																												2	2	3	3	1					2	1	1		4
																												2			1	1									1
																												2			1	1									1
																												2		2	2					2		1			2
																												2			1								1		1
																												2			1								1		1
																												2			1								1		1
																												2	3	3	3						1	2	1		3
																												2			1								1		1
																												2			1								1		1
																												2	3	2	3					2	1	3			3

Cont.

Table 1: Sighting histories of whales seen in the PCFG in at least one year. In year columns, a 1 means the whale was only sighted in the spring (March-May), 2 means it was only seen in June-Nov, and 3 means it was seen in both March-May and June-Nov. The region value is the nunber of years the whale was seen in that region.

1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	#years	NCA	SOR	OR	GH+	NWA	SJF	SVI	WVI	NBC	#areas
																												2	3	3	3					1		3	1		3
																												2	2		2						1	2			2
																												2	2	2	3			1				3			2
																												2	3	2	3		2				2	1			3
																												2	3	2	3							3	1		2
																												2	3	3	3						2	3			2
																												2			1							1	1		2
																												2			1	1		1							2
																												2			1								1		1
																												2	3	3	3	1						3			2
																												2			1								1		1
																												3	2	3	3	1						3	1		3
																												2	2		2							2			1
																												2			1								1		1
																												3			1	1							1		2
																												2			1								1		1
																												2	3		2					1		1	1		3
																												2			1								1		1
																												2			1								1		1
																												2		2	2					1		1	1	1	4
																												3			1	1									1
																												3			1	1									1
																												2			1	1									1
																												2			1								1		1
																												2			1			1							1
																												2	2	2	3			1		1	2	1			4
																												2	2		2	1		1							2
																												2			1			1							1
																												1	2	2	3		2	1							2
																												2			1									1	1
																													2	2	2					1	1	1			3
																													2		1					1					1
																													2		1					1					1
																													2	2	2						1	1		1	3
																													2	2	2	1		2			1				3
																													3		1	1	1								2
																													2		1	1									1
																													2	3	2	2							1		2
																													2	2	2	1	1								2
																													2	2	2	2	1								2
																													2		1	1									1
																													2		1	1		1							2
																													2		1	1									1
																													2		1	1									1
																													2		1	1		1							2
																													2		1	1									1
																													2		1	1									1
																													2		1			1							1
																													2		1			1							1
																													2		1			1							1
																													2		1			1							1
																													2		1			1							1
																													2		1			1							1
																													2		1								1		1
																													2		1								1		1
																													2	2	2							2			1
																													2	2	2		1				1	1			3
																													2	3	2							2	1		2
																													2		1					1	1	1			3
																													2		1					1		1			2

Cont.

Table 1: Sighting histories of whales seen in the PCFG in at least one year. In year columns, a 1 means the whale was only sighted in the spring (March-May), 2 means it was only seen in June-Nov, and 3 means it was seen in both March-May and June-Nov. The region value is the nunber of years the whale was seen in that region.

1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	#years	NCA	SOR	OR	GH+	NWA	SJF	SVI	WVI	NBC	#areas
																													2		1	1						1	1		3
																													2	2	2							1		1	2
																													2		1								1		1
																													3	2	2					1			1		2
																													2		1						1				1
																													2		1						1				1
																													2		1						1				1
																													2		1			1			1				2
																														2	1							1			1
																														2	1		1				1				2
																														2	1									1	1
																														2	1					1					1
																														2	1					1					1
																														3	1							1	1		2
																														2	1						1				1
																														2	1						1				1
																														2	1						1				1
																														2	1		1								1
																														2	1		1								1
																														2	1		1								1
																														2	1		1								1
																														2	1	1	1								2
																														2	1		1								1
																														2	1							1			1
																														2	1								1		1
																														2	1								1		1
																														2	1								1		1
																														2	1								1		1
																														2	1								1		1
																														2	1								1		1
																														2	1							1	1		2
																														2	1							1			1
																														2	1								1		1
																														2	1								1		1
																														2	1							1			1
																														2	1					1		1			2
																														2	1							1			1
																														2	1							1			1
																														2	1							1			1
																														3	1							1			1
																														2	1							1			1
																														2	1								1		1
																														2	1					1		1			2
																														2	1									1	1
																														2	1									1	1
																														2	1									1	1
																														2	1		1			1					2
																														3	1		1				1				2
																														2	1		1	1							2
																														2	1						1				1

Table 2: Sighting histories of whales seen in the MUA during 1 June - 30 November in at least one year. 1: whale sighted in PCFG but not in the MUA during that year, 2: only seen in MUA that year, and 3: seen in both MUA and another PCFG area.

1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015
1	3	3	1	1	1	1		1	1	1									
1		3	1	1	1	1	1	1	1	1	1	1		1	1	1	1		1
1		3	1	1	1	1	1	1	1	1		2		3	1	1	1	1	
3		3	1	1	1	1	1	1	1	2		1	2	1	1	1	3	1	1
1		3	3	1	1	1	1	1	1	1	1	3	3						
1	3	3	1	1	1	1	3	1											
2	2		3			1		3	2	2					2	3	1	3	
2	2																		
1		3	3	1	1	1	1	3	3										
3		3	3	1	1	1	1	1	3										
3	2	3	1	3	3	1	1	1				1							
2		1	1	1	1	1	1	1	1	3	1	3	1	1	1	3	1	1	1
2																			
1	1	3		1	1	1	1		1		1	1			1			1	3
1	3	3	1	1	1	1	3	3	3	3	3	3	3	1	1	3	3	3	1
1	1	3	1	1	1	3	1	3		1		1	1		1	3	1	1	1
1		3	1	1	1	1	1	1	1	3	1	3	1	1	1	3	1	3	1
1		1	1	1	1	1	1		1	1		3	1	1	1	1	1	1	1
3		1	1	1	1			1	1	3									
2	2	3	1	1	3	1	1	1	1	1		3	1	1				1	3
2	3	2																	
2	2	3	1	1	1	1	1	1	3	3	3								
2	2	1	1	1	1		1	1	3	1	3	2	2		3		3	2	1
3	2	1	3	1	1	1	1	1	3	3	1	3	3	1	3	3	1	3	1
3	1	1	1	1	1	1	1	3	1	1	1	1	1	1	1	1	1	1	1
2	3	3	1	1	1	1	1	1				1		1					
2	3	3	1	1	1	1	1	1	1	3	1	3	3	1	3	1	3	3	1
2	2		2	2	2	1	3					3	3	1				1	
1	2	3																	
2																			
2	2	1	1		1	1		1											
1		1	1	1	1	1			1		1		1	1	3	3	1	1	1
	2	3	3	1	3	1	1	1	1	3	1		1				1		
	1	1	1	1	1	1	1	1	1	3	3	3	3	1	3	3	3	3	1
	3	3		1	3	2	3	1	1	1	1	3	1	3	1	3	1	1	1
	2	1	1	1	3	1	1		1		1		1	1	1	1	1	1	1
	1	1		1	3	1	1	1	1	1	1	3	3	1	1	1	3		1
	1	3	1	1	1	1	1	1		1		1	1	1	1	1	3	1	1
	3	1	3		1	1	1	1	3	1	3	1	1			1	1		1
	2	1	3																
	2																		
	2	1	1	1	1	1	2	3	3										
	2																		
	2																		
	2	1	1	1	1	1	1	3	1	3	1	3	3	1	1	3	3	1	1
	2																		
	1	1	1	1	1	1	1	1	3	3	3	3	3	1	1	3	1	1	1
	1	1	1	1	1	1		1	1	3	1	3				1	1		
	1	1		1	1		1	1	1	1		1				1	3		1
	1	1	1	1	1	1	1	1	1	1		3	1		1	1	1	1	1
	1			1	1	1	1	1		2	1	3	3	1	1			1	1
		1			3	1	3	1	3										
		3	1																
		1	1	1	1	1	1	1	3	1	1	3	3	3	3	3	3	1	1
		1	1	1	1	1	1	1	1	1	1	3	3	1	1	1	3	3	3
		1	1	1	1	1	1	1	1	3	3								
		1	1	1	1	1	1	1	1	1	1	3	1	1	1	1	1	1	1
		1	1	3	1	1	1		3	1	1	1	3	3	3	3	3	1	3
		1				1	2	1			1		1						
		1	1	1	3	1			1	3				1					3
		2																	
		1	1			1	1	1	1	3	1	1	1	1	1	3	1	2	
		1		1	1		1								1			1	2
		2																	
		3	3	3	3	1		1	1	3	2	3	1				1		3
		2																	
		2																	
		2																	
		2																	
		2																	
		2																	
		2																	
		2																	
		2																	
		1				1	1			1	1		1	1	3	1	3	1	1
		1	1	1	1	1	3	1	1	2		1	1	1	1	1	1		
		1			1	1	1	1	1	2	1	1	1	1	1	1	1	1	1
		1	1	2	2	3	3	1		3	3	2			1	1	3	1	2
		1	1		1	1	2		1	1		1	1		1	1		1	1
		1	1	1	1	1	1	2	3										
		1	1	1		1	1	1	1	3	1	3	1	3	3	3	3	1	
		1	1		1	1	1	1		2	1		1	1	1	1	1	1	1
		2																	
		1	1	1	1	1	1	1		1	1	1	1	1	3	3	1	1	1
		1	1	1	1	1	1	1	1	1	1	3	3		1	3	1	1	1
		1		3	3	1	1	1		3		3	1	1	1	1	1		

Cont.

Table 2: Sighting histories of whales seen in the MUA during 1 June - 30 November in at least one year. 1: whale sighted in PCFG but not in the MUA during that year, 2: only seen in MUA that year, and 3: seen in both MUA and another PCFG area.

1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015
		1				1	1	1		1		3	2	2		1	1		1
		2																	
			1		1	1		1			1	1	3	1	1	1	1	1	
			2																
			1	1		1			1		1		3	1	1	1	1	1	1
			1		1	1								1	1	1	3	1	1
			1	3		1	1	1	1	3	1		3	3	1	3	3	2	3
			1		1	1	3	1			1								
				1	3	1		1											
				1		1	1		1	3	3	1	3	3	1	3	3	1	3
				3	3	3	3	1		3		3	3	3	3	3		1	3
				1		1						1	1	1	3	1	1		1
				1	3														
				3															
				2	2	3	1	1		1	1	3	1	3	1	3	3	3	3
				3	3	1													
				2															
				1	1	1		1	1	1	1	3	1	3		1	1	1	1
				3	2	1	1	1	2	3		3	1	1	3	3	3	3	
				1			1				1	1	1	1	3	1	1		
				2		1													
				1		1		1					1	3	1	1	1	1	
				1	1	1	1	1	1	3	1	1	1	1	3	3	1		
				1	1	1	1	1	1							3	3	2	2
					3	1		1						1					
					2	1	1	1	3	2	1	3	1	1	1	3	1		1
					3	1	3												
					3														
					1	1	1		1	1	1	3	3	1	1	1	1		1
					3														
					3														
					3	1													
					2														
					2														
					2		1								1				
					3	3	2	2											
					2	3													
					2														
					2														
					1	1	3												
					1	1	1		1			1	1	1	1	3	1	1	1
					1	1	1	1	1		1	1	2	1	1	1	1	1	
						1	3	1	1	1									
						1		1							1		1	3	
						1		1				1	1	1	1	3		1	
						1		1			1					2		1	2
						1	1	2	1	3	1	3	3	1	3	1	3	3	3
						1			1	2	1	1	1	1					
						1	1	1	1	3	1	3		1	3	1	3		3
						3	3	3	3	2		3	3	3	3	3	1		
						1	1	1	1	3	1	3	1	1	3	1	3	1	1
						1		1		3	3						1		
						1	1		1	1	1	1	3	1	1	1	1	1	
						1				3	1	3	3	1	3	3	3	3	1
						1	1		1	1		3	1	1	1	1	1		1
						1	3	3	1	3	1	3	3	3	3	3	3	3	1
						1	1	1			1		1	1	1	1	3	1	1
							1	1	1	1						1	3		
							2	1		2									
							3	3	2										
							1	1	1	3	1	3	1	1	1	3	3	3	3
							1	3	2	2	1	3		1	3	1	1	3	3
							3		2										
							1		1	3		3	3	3	1	3	3		
							1	1	1				1	3	3	3	3	3	1
							1	1	1	1	1	3	1						1
							1	1	3										
							2	3	1	2	1	1	1	3	1	3	1	1	1
								2											
								3	3	3	1	3	3	1	3	3	1	3	3
								1	1	3									
								3	2	3	2	3	3	1	1	1	3	1	
								3	2	2	3	2	2	3	3	3	3	1	3
								3	3			3	3	3	3	3	1	3	1
								1	1	3	2	3	3	3	3	3	3	3	1
								2	3	3	3	3	1	3	1	3	3		1
								2		2		1							
								2	3										
								2											
								2											
								2											
									1			1	3	1	3	3	3	1	3
									2										
									1		2	2	2	1	3	1	1	3	1
									2			1	1	1	1	1	1	3	1
									3										
									2	3		2		2	1				

Cont.

Table 2: Sighting histories of whales seen in the MUA during 1 June - 30 November in at least one year. 1: whale sighted in PCFG but not in the MUA during that year, 2: only seen in MUA that year, and 3: seen in both MUA and another PCFG area.

1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015
									3	2		1					3		3
									1	1	2	1	2						
									3	3	2	3	3	1	3		3	1	1
									1	3									
									1	3	3	3	3	1	1	3	1	1	1
										3	2	3	3		1				
										2									
											1	1				2			
											1		2						
											1	2	3						
											1	1	3						
											1			1	2				1
												2							
												1	1	1	3	1	1	1	
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Cont.

Table 2: Sighting histories of whales seen in the MUA during 1 June - 30 November in at least one year. 1: whale sighted in PCFG but not in the MUA during that year, 2: only seen in MUA that year, and 3: seen in both MUA and another PCFG area.

1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015
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Report of the Scientific Committee

The meeting was held at Centre de Congrès, Les Dunes d'Or, Agadir, Morocco from 30 May-11 June 2010 and was chaired by Debra Palka. A list of participants is given as Annex A.

1. INTRODUCTORY ITEMS

1.1 Chair's welcome and opening remarks

Palka welcomed the participants to the meeting. She thanked the Government of Morocco for hosting the meeting and for providing excellent facilities along with fabulous weather. She also expressed thanks for the beautiful artwork exhibited throughout the meeting venue.

With sadness, the Committee noted that Sidney Brown had passed away since the 2009 meeting. Sidney was a long-standing member of the Committee from the early 1960s to the mid 1980s. He was particularly involved in the Discovery Whale Marking Scheme, for which he was responsible for maintaining records of marks fired and recovered, ordering supplies and ensuring their availability for relevant whaling and scientific operations, and writing up the results. His advice on all things cetacean was much sought and greatly respected. His modest English manner belied a shrewd intellect and wide range of interests in maritime history and exploration. A minute of silence was observed in his memory.

1.2 Appointment of rapporteurs

Donovan was appointed rapporteur with assistance from various members of the Committee as appropriate. The Committee gave particular thanks to Butterworth for rapporteuring Item 20. Chairs of sub-committees and Working Groups appointed rapporteurs for their individual meetings.

1.3 Meeting procedures and time schedule

Grandy summarised the meeting arrangements and information for participants. The Committee agreed to follow the work schedule prepared by the Chair.

1.4 Establishment of sub-committees and Working Groups

Two pre-meetings preceded the start of the Scientific Committee. The Working Group on the *pre-Implementation assessment* of Western North Pacific Common Minke Whales (NPM) and the correspondence Working Group on Abundance Analysis Methods for Southern Hemisphere Minke Whales met from 28-29 May, during which agenda items covered were incorporated into their main agendas and reports (Annexes D1 and G respectively).

A number of sub-committees and Working Groups were established. Their reports were either made annexes (see below) or subsumed into this report.

Annex D – Sub-Committee on the Revised Management Procedure (RMP);
Annex D1 – Working Group on the *pre-Implementation assessment* of Western North Pacific common minke whales (NPM);
Annex E – Standing Working Group on an Aboriginal Whaling Management Procedure (AWMP);
Annex F – Sub-Committee on Bowhead, Right and Gray Whales (BRG);
Annex G – Sub-Committee on In-Depth Assessments (IA);
Annex H – Sub-Committee on Other Southern Hemisphere Whale Stocks (SH);
Annex I – Working Group on Stock Definition (SD);
Annex J – Working Group on Estimation of Bycatch and other Human-Induced Mortality (BC);
Annex K – Standing Working Group on Environmental Concerns (E);
Annex K1 – Working Group to Address Multi-species and Ecosystem Modelling Approaches (EM);
Annex L – Standing Sub-Committee on Small Cetaceans (SM);
Annex M – Sub-Committee on Whalewatching (WW); and
Annex N – Working Group on DNA (DNA).

1.5 Computing arrangements

Allison outlined the computing and printing facilities available for delegate use. Requests for Secretariat computing are addressed according to the priority assigned by the Convenors.

2. ADOPTION OF AGENDA

The adopted Agenda is given as Annex B1. Statements on the Agenda are given as Annex U. The Agenda took into account the priority items agreed last year and approved by the Commission (IWC, 2010c). Annex B2 links the Committee's Agenda with that of the Commission.

3. REVIEW OF AVAILABLE DATA, DOCUMENTS AND REPORTS

3.1 Documents submitted

Donovan noted that the pre-registration procedure, coupled with the availability of electronic papers, had again been successful. With such a large number of documents, pre-specifying papers had reduced the amount of photocopying and unnecessary paper dramatically. He was pleased to note that this year, the percentage of people opting to receive their primary papers entirely electronically (27%) was almost triple that of last year (10%) and he hoped that this percentage would continue to grow in future years. The list of documents is given as Annex C.

3.2 National Progress Reports on research

National Progress Reports presented at the 2002-10 meetings are accessible on the IWC website. Reports from previous years will also become available in this format in the future.

The Committee reaffirmed its view of the importance of national Progress Reports and **recommends** that the Commission continues to urge member nations to submit them following the approved guidelines (IWC, 1993). Non-member nations wishing to submit progress reports are welcome to do so. The Secretariat is looking into the possibility of online submission of the data included in national Progress Reports; a simplified progress report template has also been developed (see Annex P).

A summary of the information included in the reports presented this year is given as Annex O; the report template,

Table 1

List of data and programs received by the IWC Secretariat since the 2009 meeting.

Date	From	IWC ref.	Details
Catch data from the previous season:			
03/05/10	Norway: N. Øien	E84 Cat09	Individual minke catch records from the Norwegian 2009 commercial catch. Access restricted (specified 14-11-00).
31/05/10	Iceland: G. Víkingsson	E87 Cat09	Individual catch records from the Icelandic commercial catch 2009.
31/05/10	Japan: H. Okada	E88 Cat09	Individual catch records from the Japanese 2009 North Pacific special permit catch (JARPN II) and 2009/10 Antarctic special permit catch (JARPA II).
31/05/10	Russia: R.G. Borodin	E89 Cat09	Individual catch records from the aboriginal harvest in the Russian Federation in 2009.
03/06/10	St.Vincent: L. Edwards	E90 Cat10	Individual catch records from St. Vincent and The Grenadines for the 2010 humpback harvest.
Sightings data/programs:			
22/02/10	K. Sekiguchi	E86 CD92a-n	2009/10 SOWER cruise photographs and data including sightings, effort, waypoint, ice edge, weather.
00/04/10	L. Burt	CD93	DESS Version 3.63 2010.
30/05/10	Japan: K. Matsuoka	CD94	ICR blue whale photo-id pictures from JARPA 1987/88-2004/05 submitted under IWC data access Procedure B.

is available on the IWC website (*http://www.iwcoffice.org/sci_com/scprogress/htm*). The importance of using the agreed template was **emphasised** by the Committee.

3.3 Data collection, storage and manipulation

3.3.1 Catch data and other statistical material

Table 1 lists data received by the Secretariat since the 2009 meeting.

3.3.2 Progress of data coding projects and computing tasks

Allison reported that work has continued on the entry of catch data into both the IWC individual and summary catch databases, including data received from the 2008 season. Work has focused on updating data for eastern North Pacific gray whales (see Item 9.2) and data from the North Atlantic in the period 1897-1930. Version 5.0 of the catch databases will be available shortly. Entry of data into the bycatch database developed by Simon Northridge has continued with data from the 2004 and 2008 seasons being added. Data from the 2008/09 SOWER sightings cruise have been validated and incorporated into the DESS database and work on encoding and validation of data from the 2009/10 cruise has begun. Burt and Hughes began an audit of the Western North Pacific Bryde's whale survey data intersessionally and this work was completed during the course of the meeting.

Programming work during the past year is discussed later under the relevant agenda items.

4. COOPERATION WITH OTHER ORGANISATIONS

4.1 Convention on the Conservation of Migratory Species (CMS)

4.1.1 Scientific Council

There were no meetings of the Scientific Council during the intersessional period. Perrin will represent the IWC at its next meeting.

4.1.2 Conference of Parties (COP)

There were no meetings of the Conference of Parties during the intersessional period. The Secretariat will represent the IWC at the next COP.

4.1.3 Agreement on Small Cetaceans of the Baltic and North Seas (ASCOBANS)

The report of the IWC observer at the 6th Meeting of the Parties to ASCOBANS held in Bonn, Germany from 16-18 September 2009 is given as IWC/62/4D. The main topics of relevance to the IWC are summarised as follows:

(1) a new version of the Recovery Plan for Baltic Harbour Porpoises was adopted;
(2) a new Conservation Plan for the Harbour Porpoise in the North Sea was adopted; and
(3) the meeting agreed on guidelines to address the adverse affects of underwater noise on marine mammals during offshore construction activities for renewable energy production.

The 17th meeting of the Advisory Committee to ASCOBANS had been scheduled to take place from 21-23 April 2010 in Cornwall. This was postponed due to flight restrictions caused by volcanic eruptions in Iceland. It has been rescheduled for 4-6 October 2010 in Bonn, Germany.

The Committee thanked Scheidat for her report and **agrees** that she should represent the Committee as an observer at the next ASCOBANS Advisory Committee meeting and Meeting of Parties. Further information can be found at *http://www.ascobans.org*.

4.1.4 Agreement on the Conservation of Cetaceans of the Black Sea, Mediterranean Sea and Contiguous Atlantic Area (ACCOBAMS)

The ACCOBAMS Scientific Committee met in Casablanca from the 11-13 January 2010, primarily to prepare information for the forthcoming Meeting of Parties that will be held from 9-12 November 2010 in Monaco. It was attended by members of the Scientific Committee, representatives from the Sub-Regional Coordination Units, representatives from International Organisations and observers including partners of ACCOBAMS. The report of the IWC observer is given as IWC/62/4M.

Nine recommendations and a Declaration expressing the Committee's concern about the slow and/or limited level of implementation of the Agreement to effectively address the conservation problems affecting cetaceans in the Agreement area were adopted by the Committee during the meeting:

Recommendation	Topic
6.1	ACCOBAMS Survey Initiative
6.2	Programme of work on population structure
6.3	Conservation of Mediterranean common dolphins
6.4	Ship strikes
6.5	Marine Protected Areas
6.6	Anthropogenic noise
6.7	Monitoring, assessment and reducing cetacean bycatch in the Black Sea
6.8	Climate change
6.9	Minimum funding for the Scientific Committee

The next meeting of the Scientific Committee is planned for early 2011. The full report of the Scientific Committee can be found on the ACCOBAMS website *http://www.accobams.org.* The Committee thanked Donovan for his report and **agrees** that he should represent the IWC at the forthcoming Meeting of the Parties and Scientific Committee meetings.

4.1.5 Memorandum of Understanding (MoU) on the Conservation of the Manatee and Small Cetaceans of Western Africa and Macaronesia

There was no report related to the MoU on the Conservation of the Manatee and Small Cetaceans of Western Africa and Macaronesia. Perrin will represent the Committee at future activities.

4.1.6 Memorandum of Understanding (MoU) for the Conservation of Cetaceans and Their Habitats in the Pacific Islands Region (MoU for Pacific Islands Cetaceans)

The report of the IWC observer at the 2nd meeting of the MoU for Pacific Islands Cetaceans held 28-29 July 2009 in Auckland, New Zealand is given as IWC/62/4E. The meeting was attended by most of the signatories (Australia, Cook Islands, Fiji, French Polynesia, New Caledonia, New Zealand, Niue, Papua New Guinea, Samoa and the Solomon Islands). Federated States of Micronesia was unable to attend, and Tonga attended as an observer. The UK, on behalf of the Pitcairn Islands, signed the MoU at the meeting, bringing the total number of signatories to twelve.

The meeting, *inter alia*, reviewed progress in cetacean conservation in the region, endorsed a proposal to develop an Oceania Humpback Whale Recovery Plan and adopted an Action Plan for the MoU. An offer by the Whale and Dolphin Conservation Society (WDCS) to convene a Pacific Cetaceans MoU Technical Advisory Group was gratefully accepted. The meeting also noted with appreciation the continued support by WDCS for the development of the CMS Pacific MoU website: *http://www.pacificcetaceans.org.* The Committee thanked Donohue for his report and **agrees** that he should represent the Committee at the next meeting of the MoU for Pacific Islands. Further information can be found at *http://www.cms.int/species/pacific_cet/pacific_cet_bkrd.htm.*

4.2 International Council for the Exploration of the Sea (ICES)

The report of the IWC observer documenting the 2009 activities of ICES is given as IWC/62/4B. The ICES Working Group on Marine Mammal Ecology (WGMME) met in February 2009. Issues considered included management procedures for estimating bycatch limits for small cetaceans, assessing population and stock structure in small cetaceans, improvements in the procedure for reporting on favourable Conservation Status (FSC) under the EU habitats Directive, and developing a framework for monitoring and surveillance of European marine mammal populations.

A review of the ASCOBANS/HELCOM Working Group (WG) on common dolphin population structure in the Northeast Atlantic was conducted. The WGMME concurred with the recommendation that only one common dolphin population inhabits the Northeast Atlantic, although the distributional range of the population is unknown. A separate Iberian harbour porpoise population has recently been identified using genetic analysis and the WGMME strongly recommended that this population be given a high priority for conservation. The WGMME also strongly recommended immediate action by the Spanish and Portuguese governments in monitoring and conserving the Iberian harbour porpoise population.

New data from the SCANS II and CODA projects were reviewed and the WGMME concurred with the recommendation to use the *Catch Limit Algorithm* approach for estimating bycatch limits for small cetaceans.

The WG noted that the continuation and establishment of national observer bycatch programmes is extremely important in order to obtain current estimates of incidental capture for all marine mammal species. The WG also noted the need for the continuation of surveys such as SCANS II and CODA at least every 5-10 years in order to estimate absolute abundance.

Initial development of a European framework for surveillance and monitoring of marine mammals was undertaken. While it is clear that monitoring of abundance, bycatch and health status may reasonably form the core of surveillance for cetaceans, the importance of other types of information (e.g. life history data) and monitoring of specific threats (e.g. offshore construction) should also be recognised when designing a surveillance strategy. Further, monitoring programme design should take account of new findings on the target stock's structure.

The 2009 ICES Annual Science Conference (ASC) was held in Berlin, Germany, 21-25 September 2009. Some sessions were designed with marine mammals included as an integral part. A number of sessions were of relevance to the Committee, including those describing:

(1) advances in marine ecosystem research;
(2) comparative study of climate impact on coastal and continental shelf ecosystems in the ICES area;
(3) habitat science to support stock assessment;
(4) avoidance of bycatch and discards; and
(5) ecological foodweb and network analysis.

The Committee thanked Haug for the report and **agrees** that he should represent the Committee as an observer at the next ICES meeting.

4.3 Inter-American Tropical Tuna Commission (IATTC)

No observer for the IWC attended the 2009 meeting of IATTC.

4.4 International Commission for the Conservation of Atlantic Tunas (ICCAT)

The report of the IWC observer to the 21st meeting of ICCAT is given as IWC/62/4J. The critical status of some stocks was highlighted, including the bluefin tuna, and measures adopted to allow the rebuilding of stocks as well as measures to improve the management frameworks and status for swordfish and albacore. The Committee thanked Corrêa for attaneding the meeting on its behalf.

4.5 Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR)

The report of the IWC observer at the 28th Meeting of the CCAMLR Scientific Committee (CCAMLR-SC), held in Hobart, Australia from 23-27 October 2009 is given as IWC/61/4A. The main items considered at the CCAMLR meeting of relevance to the IWC included: (1) fishery status and trends of Antarctic fish stocks, krill, squid and stone crabs; (2) incidental mortality of seabirds and marine mammals in fisheries in the CCAMLR Convention Area; (3) harvested species (krill, fish, and stone crabs and their assessment); (4) ecosystem monitoring and management; (5) management under conditions of uncertainty about stock size and sustainable yield; (6) scientific research exemption; (7) CCAMLR Scheme of International Scientific Observation; (8) new and exploratory fisheries; (9) joint CCAMLR-IWC workshop with respect to ecosystem modelling in the Southern Ocean; and (10) the CCAMLR performance review.

Marine Protected Areas were discussed in detail. The area of the southern South Orkney shelf and the Seasonal Pack-ice Zone and part of the Fast Ice Zone south of the Shelf was the first MPA designated by CCAMLR. The following milestones were previously agreed: (1) by 2010, collate relevant data for as many of the 11 priority regions as possible; (2) by 2010, submit proposals on a representative system of MPAs to the CCAMLR Commission; (3) by early 2011, convene a workshop to review progress, share experience and determine a work programme for the identification of MPAs; and (4) by 2011, submit proposals for areas for protection to the CCAMLR-SC.

Two reports of cetacean-fisheries interactions in the Southern Ocean were received by CCAMLR in 2009: (1) a killer whale hooked on a line was dead when brought to the surface; and (2) a sperm whale hauled up dead after being caught in discarded fishing gear on the seabed.

The Committee thanked Kock for attending on its behalf and **agrees** that he should represent the Committee as an observer at the next CCAMLR-SC meeting.

4.6 Southern Ocean GLOBEC (SO-GLOBEC)

The synthesis and analysis process under SO-GLOBEC has continued and has produced a number of papers relating cetacean distribution to prey and other environmental variables. There is no active work with respect to SO-GLOBEC at this time.

4.7 North Atlantic Marine Mammal Commission (NAMMCO)

Scientific Committee

The report of the IWC observer at the 16th meeting of the NAMMCO Scientific Committee held in Reykjavik, Iceland 19-22 April 2009 is given as IWC/62/4L.

The Working Group on Marine Mammals-Fisheries (MMFI WG) considered: (1) new developments in the quantitative description of marine mammal diet by species; (2) new developments in the estimation of energy consumption; and (3) recent developments in multi-species modelling. In light of the report of the WG, the NAMMCO SC agreed that multi-species modelling is a valid approach for understanding ecological relations between species. However, it was noted that ecosystem models have significant data requirements, many of which are currently unavailable. In order to improve the understanding of such modelling, an exercise is planned in which four different modelling approaches are used to describe the same ecosystem.

A successful survey of narwhals was conducted in East Greenland during August 2008. The abundance estimates developed from this are the first for the Scoresby Sound fjord system south to Ammassalik. The abundance estimate for narwhals in Melville Bay, developed from the 2007 survey is the first estimate from this locality. The NAMMCO SC recommended catches be set so that there is at least a 70% probability that management objectives be met for West and East Greenland narwhals, i.e. maximum total removals of 310 and 85 narwhals in West and East Greenland respectively.

At the last NAMMCO SC meeting it was recognised that the preliminary data on abundance of narwhals and white whales show higher estimates and encouraged Greenland to submit fully corrected estimates. These were submitted to and endorsed by the NAMMCO/JCNB Joint Working Group in February 2009.

The Committee thanked Walløe for attending on its behalf and **agrees** that he should represent the Committee as an observer at the next NAMMCO SC meeting.

Council

The report of the IWC observer at the 17th Annual Meeting of NAMMCO held in Tromso, Norway in September 2009 is given as IWC/61/4F. The whaling and sealing nations in the North Atlantic confirmed their commitment to ensuring the sustainable utilisation of marine mammals through science-bases management decisions, stressing the vital importance marine mammals have as renewable resources for economies and cultures across the region.

Key conclusions from the meeting relevant to IWC included:

(1) welcoming Greenland's multi-annual catch quotas for white whales and narwhal stocks;
(2) a recommendation from the NAMMCO SC that a quota of 10 humpback whales in West Greenland, including struck and lost animals, would be sustainable;
(3) initiation of an ecosystem modelling programme; and
(4) agreement to convene an expert working group to undertake a review and evaluate the whale killing data submitted to NAMMCO by Japan and to look at data and information on recent and ongoing research on improvements and technical innovations in hunting methods and gears used for the hunting of large whales in NAMMCO countries.

The Committee thanked Goodman for attending on its behalf and **agrees** that he should represent the Committee as an observer at the next NAMMCO Council meeting. Further information on NAMMCO can be found at *http://www.nammco.no.*

4.8 International Union for the Conservation of Nature (IUCN)

Cooke and Larsen, the IWC observers, reported on the considerable cooperation with IUCN that had occurred during the past year and this is given as IWC/62/4K.

Western gray whales (see also Item 10.4)

The IUCN Western Gray Whale Advisory Panel has continued its work (*http://www.iucn.org/wgwap*). The Panel had earlier advised that a seismic survey commissioned by Sakhalin Energy and scheduled for 2009 in the Astokh area be postponed, in view of the anomalous (and possibly disturbance-related) distribution of gray whales off Sakhalin in 2008. Given the apparent return to normal gray whale distribution in the area in 2009, the Panel agreed that carrying out of the survey in 2010 was acceptable, particularly in the light of the jointly developed, improved monitoring and mitigation measures and completion of the survey early in the season before large numbers of whales arrive in the Piltun feeding area.

The Panel was extremely concerned to learn that a further seismic survey is planned for July-September 2010 by the company Rosneft Shelf - Far East, to cover the Lebedenskoie field which underlies the northern part of the prime near-shore feeding ground of western gray whales The IUCN Director General has written to Prime Minister Putin urging the Russian government to order the postponement of the survey at least until 2011 to enable satisfactory mitigation measures to be put in place to minimise the disturbance to whales[1]. A draft Western Gray Whale Conservation Plan has been developed with the help of the IUCN Marine Programme as part of its Range-Wide Conservation Initiative for western Gray Whales (SC/62/BRG24).

Red List updates
Following the comprehensive updating of the Red List entries for cetaceans in 2008, the Cetacean Specialist Group has completed separate assessments of the two species of *Sotalia*, the freshwater tucuxi and the coastal marine and estuarine Guiana dolphin. Draft assessments of a number of Mediterranean subpopulations (fin whale, sperm whale, long-finned pilot whale, Risso's dolphin, striped dolphin, common bottlenose dolphin and Cuvier's beaked whale) are in review.

Asian freshwater cetaceans (see also Item 14.3)
The Cetacean Specialist Group has undertaken several initiatives in Asia over the past year. These have included, most notably a workshop in Samarinda, East Kalimantan, Indonesia in October 2009 on freshwater protected areas for dolphins; a special meeting in Phnom Penh, Cambodia in November 2009 on the conservation of Irrawaddy dolphins in the Mekong River; and a meeting in Patna, India in February 2010 to assist in the development of a national action plan for the conservation of Ganges river dolphins (*Susus*).

The Committee thanked Cooke and Larsen for their report and **agrees** that they should continue to act as observers to IUCN for the IWC. Further information on IUCN can be found at *http://www.iucn.org.*

4.9 Food and Agriculture Organisation (FAO) related meetings – Committee on Fisheries (COFI)
There was no meeting of COFI in 2010. Further information on FAO can be found at *http://www.fao.org*.

4.10 Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES)
The report of the IWC observer at the 15th meeting of the CITES Conference of the Parties held 13-25 March 2010 in, Doha, Qatar is given as IWC/62/4H. There were no proposals for changing the listing of whale stocks from Appendix I to Appendix II (downlisting). There were also no proposals for changing the listing of a dolphin or whale species from Appendix II to Appendix I (uplisting).

The CITES Secretariat reviewed all of the Decisions that were in effect after the 14th meeting of the Conference of the Parties, including a recommendation to delete Decision 14.81 relating to great whales. Decision 14.81 states that 'No periodic review of any great whale, including the fin whale, should occur while the moratorium by the International Whaling Commission is in place'. The CITES Secretariat recommendation also noted that if the substance of this Decision should remain in effect, it should be considered in the context of the draft resolution on the periodic review of the Appendices.

A number of Parties opposed its deletion on the basis that the draft resolution on the periodic review had not been accepted. After a vote, the recommendation to delete the Decision was rejected.

The Committee thanked the US Government for attending on its behalf and **agrees** that it should represent the Committee as an observer at the next CITES meeting. Information on CITES can be found at *http://www.cites.org.*

4.11 North Pacific Marine Science Organisation (PICES)
The report of the IWC observer at the 18th annual meeting of PICES held 23 October-1 November 2009 in Jeju, Republic of Korea is given as IWC/62/4G. The Marine Birds and Mammals Advisory Group (AP-MBM), cosponsored by ICES held a theme session on 'integrating marine mammal populations and rates of prey consumption in models and forecasts of climate change-ecosystem change in the North Pacific and North Atlantic Oceans'. A diverse range of topics were covered, including population trends, diet, estimates of prey consumption and models of trophic impact. AP-MBM reviewed aspects of the new PICES science programme (FUTURE), specifically: (1) understanding climate change and anthropogenic impacts on marine ecosystems; (2) forecasting future ecosystem change; and (3) better communication with society. The AP reiterated its primary mission to provide advice to the PICES community about the role of marine birds and mammals in marine ecosystems. Based on its role in FUTURE the AP-MBM defined its focal points as: (1) spatial ecology of predators in marine ecosystems; (2) models of prey consumption of top predators; (3) marine birds and mammals as indicators of ecosystem change; (4) marine mammals as autonomous oceanographic sampling devices; and (5) providing advice to the PICES community.

The Committee thanked Kato for attending on its behalf and **agrees** that he should represent the Committee as an observer at the next PICES meeting. Further information on PICES can be found at *http://www.pices.int*.

4.12 Eastern Caribbean Cetacean Commission (ECCO)
No information on the activities of ECCO was provided.

4.13 Protocol on Specially Protected Areas and Wildlife (SPAW) of the Cartagena Convention for the Wider Caribbean
There were no meetings of SPAW during the intersessional period. Carlson will represent the IWC at its next meeting. Further information on SPAW can be found at *http://www.cep.unep.org/cartagena-convention*.

4.14 Indian Ocean Commission (IOC)
No information on the activities of IOC was provided. Further information on the IOC can be found at *http://www.coi-ioc.org*.

4.15 Permanent Commission for the South Pacific (CPPS)
No information on the activities of CPPS was provided. Further information on CPPS can be found at *http://www.cpps-int.org*.

4.16 International Maritime Organisation (IMO)
The report of the IWC observer at the General Assembly of the IMO held 23 November-4 December 2009 is given as IWC/62/4I. The proposed Agreement of Cooperation between IMO and IWC was approved, which means that the IWC now has definitive IMO observer status. While the impetus for closer co-operation between IMO and IWC was in relation to ship strikes on cetaceans, there are a number of other issues of potential mutual relevance including habitat degradation and noise from shipping. Discussions on

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[1] See *http://www.iucn.org/wgwap/wgwap/public_statements/* for the text of this and other letters.

collisions with whales and underwater noise from shipping took place within the Marine Environment Protection Committee (MEPC) at its 59th session held in July 2009 and 60th session held in March 2010.

The MEPC has had 'noise from commercial shipping and its adverse impact on marine life' on its work programme since 2008. A correspondence group was established to identify and address ways to minimise the introduction of incidental noise into the marine environment from commercial shipping to reduce the potential adverse impact on marine life and in particular develop voluntary technical guidelines for ship-quieting technologies as well as potential navigation and operational practices. The IWC Secretariat is a member of this group.

The Committee thanked the IWC Secretariat for its report and **agrees** that it should represent the Committee at the next IMO meeting. Further information on IMO can be found at *http://www.imo.org.*

4.17 Other

An update was received on conservation in the Southeast Pacific under the framework of the Lima Convention and is given as IWC/62/4C. In January 2010 the 16th Meeting to the Parties to the Lima Convention was held in Guayaquil, Ecuador. The five member countries (Chile, Colombia, Ecuador, Panama and Chile) reviewed the activities regarding implementation of a Plan of Action for the Conservation of Marine Mammals in the Southeast Pacific (PAMM). The PAMM was formed to help countries to improve their policies on marine mammals' conservation and to develop activities that require regional cooperation.

In 2009 five pilot projects to mitigate the impacts of fishing activities were conducted: (1) implementation of actions for the conservation of the Chilean dolphin in the zone of Constitucion; (2) study to mitigate impact of the incidental entanglement of coastal cetaceans in the Columbia Pacific; (3) preliminary assessment of the interaction of cetaceans with artisanal fisheries in the Machalilla National Park, Ecuador; (4) reduction of the impact of gillnets on cetaceans in coastal waters within the Gulf of Chiriqui; and (5) study to test the use of pingers to reduce the incidental bycatch of small cetaceans in Peru.

As a result of these projects, a document entitled 'Efforts to mitigate the impact of fishing activities on cetaceans in the Southeast Pacific countries' will be published.

The first phase of a biodiversity and MCPA information system (SIBIMAP-PSE) was finalised. This is an online tool for searching and downloading information crucial for management and conservation of cetaceans, sea turtles and MCPA in the Southeast Pacific. The module on cetaceans is now complete.

A workshop on legal aspects of whalewatching was planned for March 2010, but was postponed until late 2010 due to an earthquake in Chile.

The Committee thanked Felix for his report and **agrees** that he should represent the Committee at future activities related to cetacean conservation in the Southeast Pacific under the framework of the Lima Convention.

5. REVISED MANAGEMENT PROCEDURE (RMP) – GENERAL ISSUES

5.1 Review MSY rates

5.1.1 Report of the intersessional workshop

The Committee has been discussing maximum sustainable yield rates (MSYR) for some time in the context of a general reconsideration of the plausible range to be used in population models used for testing the *Catch Limit Algorithm* (*CLA*) of the RMP (and see Item 5.1.2 below). At present, this range is 1% to 7% when expressed in terms of the mature component of the population. As part of the review process, information on observed population growth rates at low population sizes is being considered because Cooke (2007) noted that in circumstances where variability and/or temporal autocorrelation in the effects of environmental variability on population growth rates is high, simple use of such observed population growth rates could lead to incorrect inferences being drawn concerning the lower end of the range of plausible values for MSYR.

A Third Workshop was held intersessionally to examine whether the observed levels of variation in baleen whale reproduction and annual survival rate parameters were sufficiently large that biases of the nature identified from population models incorporating environmentally-induced variability might be of concern (SC/62/Rep2; Annex D, item 2.1.1).

At the Workshop, an analytical approach was developed and followed to estimate the coefficient of variation (CV) and temporal autocorrelation for the selected time series of calving proportion indices and calving interval data. This information, modified appropriately, provides input for a method developed to relate variability in calving proportion to variability in the annual growth rate of a population using a population dynamics model (see SC/62/Rep2). The model can take into account environmentally-induced variability in population abundance arising from variation in annual survival rate.

The Workshop identified two further steps needed before results from this model can be used to draw inferences about the plausible ranges for the CV and temporal autocorrelation parameters describing the effects of environmental variability on population dynamics in the model of Cooke (2007). The Committee incorporated these into its work plan under this item (see Annex D, item 2.1.2).

The Workshop received a revised approach for a meta-analysis of population growth rates previously discussed (IWC, 2010b) and suggested some additional work to be completed before the 2010 Annual Meeting. Item 5.1.2 and Annex D, item 2.1.1 describe progress made on three other issues listed in the work plan for completion of the MSYR review at last year's meeting.

5.1.2 Issues arising

The Committee received SC/62/RMP3 in response to the Workshop recommendations to: (1) apply the age-structured model of SC/62/Rep2, Annex D to all of the datasets assembled during the Workshop to estimate the resultant CV and temporal auto-correlation in growth rate; and (2) to conduct further tests of the Bayesian meta-analysis approach. More details are given in Annex D, item 2.1.2.

The Committee **agrees** that this Bayesian approach was an acceptable basis to compute a posterior distribution for r_0, once the inputs needed to apply it become available. It also **agrees** that account will need to be taken that the estimates of lower posterior percentiles from this method are positively biased, before making recommendations regarding appropriate values for MSYR for use in trials.

SC/62/RMP2 and SC/62/RMP4 responded to recommendations to use the environmental variability model of Cooke (2007) to provide CVs and temporal autocorrelation estimates for the growth of the population from one year to the next for the standard set of scenarios and to use this model to determine the predicted relationship between the length of series and the estimated level of variability in the population rate of increase. More details are given in Annex D, item 2.1.2. The Committee **agrees** that it now has a basis to link variability in demographic processes with the inputs of the Cooke (2007) model.

Efforts to fit models that account for both process and observation error to the data on calving rates and calving intervals had encountered numerical problems intersessionally The Committee **endorses** a work plan to address this (Annex D, Appendix 2) and looks forward to seeing the results of this work next year.

The Committee discussed how to relate variation in net recruitment rate, which depends on variation in both survival and reproduction, to variation in reproductive rates alone. Details are given in Annex D, item 2.1.2. The Committee considered the question of correlations between survival and reproductive rates to be potentially important for the question of estimating typical levels of variation in net recruitment rate for baleen whales, but **agrees** that more analysis is required before any general inference can be drawn. It **requests** in particular:

(1) a literature review with regard to the question of the circumstances under which correlations between survival and reproductive rates would be negative or positive;
(2) more extensive modelling to cover the full range of parameter values deemed to be plausible for baleen whales in order to determine whether general inferences can be drawn, or at least to identify the circumstances where substantial correlations of a specific sign would be expected;
(3) direct estimation of variability in survival rates to the extent that this is possible.

The Committee **agrees** that if results from this work are available at its next meeting, then they should be taken into account in its deliberations with respect to the level of variability in baleen whale demography. However, that lack of results will not preclude the Committee from completing its review of MSY rates next year.

The Committee considered the extent to which genetic data could place bounds on fluctuations in population size for some examples of trajectories arising for the environmental variation model of Cooke (2007). It recognised the potential of genetic methods to inform its deliberations on the plausible range of MSYR values, but **agrees** that these methods could not be used during the current review. However, it **recommends** that the number of haplotypes in whale populations, along with other population and demographic measures should be assembled since this might inform the current review. The Committee **encourages** completion of a compilation already initiated by Brownell.

The Committee also **agrees** that although the use of time-series of abundance estimates for species other than whales to make inferences regarding the extent of variation and the temporal auto-correlation of the rate of growth remained a good idea, the lack of such time-series at present means that this source of information cannot be pursued during the current review.

In conclusion, although considerable progress was made during the current meeting, the Committee was once again not in position to complete the review. It established a work plan (see Annex D, item 2.5) to address the final issues that need to be examined to complete the review at next year's meeting.

It **agrees** that the review will be completed at next year's meeting on the basis of the data and analyses available. It **accepts** that it is not appropriate to keep extending the time available for the review, particularly given its importance to Item 5.2 below.

5.2 Finalise the approach for evaluating proposed amendments to the *CLA*

The Committee noted that it could not complete discussions on amendments to the *CLA* until the range for MSYR values in the RMP was completed. Regarding the Norwegian proposal for amending the *CLA*, it was noted that all of the relevant trials/results had been presented in Aldrin and Huseby (2007), but that evaluation of this proposal could not occur until the review of MSY rates was complete.

5.3 Version of *CLA* to be used in trials

SC/62/RMP10 examined the sensitivity of catch limits to the level of accuracy when computing posterior distributions using the *CLA*. Four versions of programs used to implement the *CLA* were discussed. More details are given in Annex D, item 2.1.2.

The Committee **endorses** the recommendations in SC/62/RMP10 that: (a) only the Norwegian version of the *CLA* should be used when conducting future trials; (b) the Second Intersessional Workshop in an *Implementation* or *Implementation Review* will need to be carefully scheduled to ensure that all trials can be run before it takes place; (c) if special circumstances arise when it becomes necessary to run additional trials during a meeting (e.g. during the Second Intersessional Workshop), the 'intermediate' version of the Cooke implementation that is more accurate than the 'trials' version (but less accurate than the 'accurate' or Norwegian version) be used for this purpose and the results confirmed using the Norwegian 'CatchLimit' program after the meeting; and (d) a full set of revised results from the trials for North Atlantic fin whales, Western North Pacific Bryde's whales; and North Atlantic minke whales should be run using the Norwegian 'CatchLimit' program and the results placed on the IWC website.

5.4 Updates to RMP specification and annotations

In the context of applying the RMP pursuant to Item 20, the Committee identified some issues where updating and clarification of the specifications of the RMP and the accompanying annotations and guidelines was warranted (see Annex D, item 2.4).

(1) The provision for the adjustment for sources of human-caused mortality other than commercial catches, as recommended by the Scientific Committee in 2000 (IWC, 2001f, p.91), should be included in the RMP with the qualification specified by the Commission (IWC, 2001b) that the provision be limited to mortality due to bycatches, ship strikes, non-IWC whaling, scientific permit catches, and indigenous subsistence whaling. A new annotation should be added to provide the Committee with operational guidelines to implement this provision.
(2) The maximum period of validity of catch limit calculations should be extended from five to six years to be consistent with the six-year cycle of surveying specified in section 3.2.2 of the RMP, as currently implemented for minke whales in the North Atlantic.
(3) The rule for rounding of catch limits to a whole number of whales should be clarified.

(4) The guidelines for conducting surveys under the RMP and those for *Implementing* the RMP (IWC, 2005b; 2005c) should be modified to clarify that changes to the guidelines are not retroactive. That is, results from surveys conducted in accordance with earlier version of the guidelines would not become inadmissible for use in the RMP when the guidelines are changed.

Proposed amendments to the RMP and its annotations to address these issues are given in Annex D, Appendix 5, along with some background information. The Committee **recommends** adoption of these amendments to the RMP specification and annotations. The Committee further **requests** the Secretariat to prepare a proposal to next year's meeting to update the guidelines for conducting surveys and for *Implementations* to accommodate point (4) in Annex D, item 2.4.

Several amendments to the RMP specifications and annotations had been adopted since the most recent published version (IWC, 1999e). These are listed in Annex D, Appendix 5. The Committee **agrees** that the consolidated revised version be published in full in the next supplement to *J. Cetacean Res. Manage.*

6. RMP – *IMPLEMENTATIONS* AND *IMPLEMENTATION REVIEWS*

6.1 Western North Pacific Bryde's whales

6.1.1 Complete Implementation

6.1.1.1 RESEARCH PROPOSAL FOR THE 'VARIANT WITH RESEARCH'

The Committee had agreed in 2007 (IWC, 2008b) that three of the four RMP variants (1, 3 and 4) considered during the *Implementation* for western North Pacific Bryde's whales performed acceptably from a conservation perspective and recommended that those variants could be implemented without a research programme. It also agreed that variant 2 was only 'acceptable with research' because conservation performance was 'unacceptable' on three 'medium' plausibility trials incorporating stock structure hypothesis 4 i.e. two stocks of Bryde's whales in the western North Pacific, one of which consists of two sub-stocks (stock structure hypothesis 4).

In 2008, the Committee reviewed a research proposal (Pastene *et al.*, 2008) that aimed to determine whether or not sub-stocks occur in sub-area 1. Based on this review, the Committee had recommended that the *Implementation Simulation Trials* for the western North Pacific Bryde's whales be used to determine whether differences in age-compositions between sub-areas 1W and 1E could be used to resolve whether there are sub-stocks in these sub-areas and that results from previous (and any new) power analyses that assess the use of genetic methods to evaluate stock structure hypothesis 4 be included in the revised proposal.

This year, the Committee received a revised research plan (Annex D, Appendix 6) and welcomed work done to address several of its earlier recommendations. The results of the *Implementation Simulation Trials* showed that recent age structure data would not be able to distinguish between scenarios in which there is or is not age-structuring in sub-areas 1W and 1E.

The Committee **recommends** that the proposal be revised further and, in particular, that the power analyses focus more clearly on the specific hypotheses for the Western North Pacific Bryde's whales. The Committee was informed that a revised proposal will be presented next year that will focus to a greater extent on the use of genetic data.

6.1.2 Recommendations and work plan

The Committee **agrees** that its work plan for the 2011 Annual Meeting would be to review the revised research proposal for the 'variant with research'.

6.2 North Atlantic fin whales

6.2.1 Complete Implementation

Last year, the Committee had agreed that if the RMP is implemented for this species in this Region, variants 1, 3, 4, 5 and 6 (see Table 4 of IWC, 2010d) can be implemented without an associated research programme but that variant 2 (sub-areas WI+EG are a Small Area) was only acceptable with research.

This year, comparison of results from different versions of the *CLA* (see Item 5.2) revealed that variant 3 (sub-areas WI+WG+EI/F are a *Small Area*) does not have 'acceptable' performance for some of the trials and can no longer be considered to be acceptable without research but is rather only 'acceptable with research'.

Last year, the Committee had confirmed that use of variant 2 for ten years followed by variant 1 (sub-area WI is a *Small Area*) led to performance which was 'acceptable' for all trials and consequently that the requirements for stage 1 of the process for implementing a 'variant with research' had been met. The second stage of the process was for Iceland to demonstrate to the satisfaction of the Committee that a research programme has a good chance (within a 10-year period) of being able to confirm or deny that stock structure hypothesis IV is implausible.

The Committee received a research proposal (SC/62/RMP1) that followed the *pro forma* agreed by the Committee in 2007. Details are given in Annex D, item 3.2.2.

The Committee welcomed the proposal, noting that it was not final and that Iceland was inviting suggestions for how it can be improved. In discussion, it noted that the aim of the proposal should be to assess the probability of hypothesis IV relative to the probabilities for the other stock structure hypotheses. It noted that the *Implementation Simulation Trials* could be used to assess the effect sizes on which the power analyses are based.

In particular, the Committee **recommends** that the lowest rate at which the C sub-stocks mix in sub-areas EC, WG, EG, WI, EI+F, and N and the performance of variant 2 is 'acceptable' for all trials should be calculated and used when conducting power analyses. It further **recommends** that quantitative analyses along the lines of Appendix 3 of SC/62/RMP1 be conducted for each of the stock structure hypotheses.

6.2.2 Recommendations and work plan

The Committee **agrees** that its work plan for the 2011 Annual Meeting would be to review a revised research proposal for the 'variant with research' and to review any abundance estimates for use in the *CLA*.

6.3 North Pacific common minke whales

6.3.1 Initiate pre-Implementation assessment

In 2009, the Commission had agreed that the Scientific Committee should follow the option in its report (IWC, 2010e) that specified completing a full *Implementation Review* as soon as possible, ideally by the 2012 meeting. This timeline will be possible only if the *pre-Implementation assessment* can be completed this year. The Committee was undertaking a *pre-implementation assessment*, rather than immediately commencing an *Implementation Review*, because the 2003 *Implementation* had been conducted before the existing guidelines for *Implementations* had been developed and had focused primarily on 'O' stock.

Committee guidelines for *Implementations* (IWC, 2005b) state that the main focus of a *pre-Implementation assessment* is:

> 'the establishment of plausible stock hypotheses consistent with the data that are inclusive enough that it is deemed unlikely that the collection of new data during the *Implementation* process will suggest a major novel hypothesis (e.g. a different number of stocks) not already specified in the basic *Implementation Simulation Trial* structure.'

Additional foci are examination of available abundance estimates and information on the geographical and temporal nature of 'likely' whaling operations and future levels of anthropogenic removals other than due to commercial whaling.

The importance of creating a document that lists the various datasets and other information available for the *pre-implementation assessment* was recognised (this is normally provided by national scientists in the case of a new request for a *pre-Implementation assessment)*. This will be a living document, at least until the deadline is established for the consideration of no new data for the *Implementation Review* (this occurs at the First Intersessional Workshop although new *analyses* may be presented at the First Annual Meeting). A table containing this information is given in Annex D1, Appendix 2.

6.3.1.1 STOCK STRUCTURE

The goals for the *pre-Implementation assessment* with respect to stock structure were to agree to a set of inclusive plausible hypotheses consistent with the data, and to ensure that the types of information needed for the *Implementation Review* were available. Assessing the relative plausibility of alternative hypotheses regarding stock structure will be considered at the First Annual Meeting of the *Implementation Review*.

The Committee briefly discussed minimum standards for plausibility. It **agrees**, as it has in the past, that the most reasonable approach is to use best professional judgment and common sense, after considering all relevant information.

The Committee first reviewed past discussions on stock structure for western North Pacific minke whales. Details are given in Annex D1, item 5.1.

The Committee then received a number of papers providing new information relevant to stock structure. Details of these and the considerable discussions that ensued are given in Annex D1, item 5.3. The following summary focuses on issues where the Committee made specific statements.

SC/62/NMP22 provided results of a biopsy skin-sampling survey in July-August 2009 in the Okhotsk Sea. Unfortunately, none of the five biopsy samples taken could be removed from Russian waters because of CITES-related restrictions. This is discussed further under Annex D1, item 7.6. In spite of this, the Committee was pleased that that this research had been conducted within the Russian EEZ, and that it had been possible to collect biopsy samples from minke whales on the feeding grounds. The Committee **encourages** future collaborations and **strongly urges** all concerned to find ways to solve these CITES-related issues.

SC/62/NPM10 estimated the mixing proportion of 'O' and 'J' stocks in the Sea of Okhotsk using cookie-cutter shark scars from 22 animals. Based on previous research in sub-area 11 in 1996 and 1999, the maximum likelihood estimate for the proportion of 'J' stock in sub-area 12 was 0. The Committee welcomed this valuable new information, but **agrees** that the method used to estimate mixing proportions needed some refinement.

SC/62/NPM13 reviewed non-genetic biological information relevant to the stock structure of minke whales in the Yellow Sea, Sea of Japan (East Sea), and western Pacific Ocean. The review was structured to examine four key comparisons between: (1) the Yellow Sea and the Korean coast of the Sea of Japan; (2) the Korean and Japanese coasts in the Sea of Japan; (3) the Sea of Japan and Pacific coasts of Japan; and (4) coastal and offshore areas of the Pacific Ocean. The Committee welcomed this attempt to synthesise diverse types of non-genetic information that potentially can inform discussions of stock structure and found the idea of orienting the analyses around four key questions useful. The authors acknowledged that although they had attempted to be exhaustive, they might have missed some relevant biological information, particularly if it was reported outside the IWC context, and requested that any such information be forwarded to them. The Committee in particular supported the collation of information in table 3 in SC/62/NPM13 and **encourages** members to work together to complete this and provide it to the First Intersessional Meeting of the *Implementation Review*.

The Committee reconsidered Hatanaka and Miyashita (1997) that investigated feeding migration based on length data. It was pointed out that these data are consistent with the generic concept of an 'O' stock, and that the length data might be useful for mature/immature determinations to condition different migration patterns for one or more 'O' stocks. The Committee **agrees** to include these data in Annex D1, Appendix 2.

SC/62/NPM11 had two major objectives: (1) to determine the status of whales that could not be identified reliably to 'O' or 'J' stock based on analyses described in Kanda *et al.* (2009); and (2) to examine stock structure of the 'J' stock in the Sea of Japan and Yellow Sea. The Committee **appreciates** the efforts of the authors to respond to some of the suggestions for additional analyses made last year.

Two papers presented new analyses of mtDNA data. SC/62/NPM21 examined genetic variation at the mtDNA control region to evaluate the plausibility of proposed stock structure scenarios for the 'J' and 'O' stocks. SC/62/NPM20 reported on differences in mtDNA sequences and sex ratios in western North Pacific minke whales by combining information from samples collected in Korean market surveys with three Japanese datasets made available through the IWC Data Availability Agreement. SC/62/NPM27 commented on the analyses conducted in SC/62/NPM20. In discussion, it was clarified that although SC/62/NPM20 and SC/62/NPM27 largely considered the same group of samples, there were two important differences: (1) SC/62/NPM20 used market samples for Korean samples, while SC/62/NPM21 used bycatch; and (2) SC/62/NPM21 used mtDNA data that had been error-corrected subsequently whereas due to time constraints and the agreed deadlines for *pre-Implementation assessment*. SC/62/NPM20 used the original data and grouped haplotypes into haplogroups to minimize influence of the sequencing errors.

In further discussion of standards for establishing/rejecting hypotheses, the Committee **agrees** that it is important but challenging to try to find a balance between two potential errors: (1) interpreting minor differences that might be artefacts or not biologically meaningful as evidence for separate stocks; and (2) failing to recognise true stock structure because power to resolve closely related populations is low.

Discussion of these issues highlighted divergent opinions within the Committee regarding how best to deal with the inability to sample populations on their breeding grounds. In one view, the best way to approach this problem is to use results of the program *STRUCTURE* (Pritchard *et al.*, 2000) which is designed to deal with situations in which there are no reliable *a priori* ways of grouping individuals into putative populations. The other view was that this approach has elements of circularity and can result in a false sense of confidence in model results and that *STRUCTURE* has a documented inability to provide reliable results when dealing with mixtures of closely related populations. These issues have arisen previously regarding earlier versions of the genetic data analyses for North Pacific minke whales (IWC, 2010e).

The Committee **agrees** on the potential value of trying to collect samples in areas where a single stock is believed to occur, but recognises the difficulty in identifying the location of these.

Following presentation and discussion of new information, the Committee reviewed and discussed two independent attempts to generate plausible stock-structure hypotheses that synthesised both genetic and non-genetic information. The summaries of these papers and the ensuing discussion are below.

SC/62/NPM12 examined recent progress in the development of stock structure hypotheses for western North Pacific common minke whale ('O' and 'J' stocks), and conducted a preliminary evaluation of these hypotheses in the context of the available scientific information, mainly genetics, presented and discussed by the Committee in recent years. The aim was to identify stock structure scenarios that are consistent with the data. The authors of SC/62/NPM12 considered that the best available scientific evidence is consistent with the hypothesis that there is a single 'J' stock distributed in the Yellow Sea, Sea of Japan and Pacific side of Japan and a single 'O' stock in sub-areas 7, 8 and 9. They considered this hypothesis the most plausible. It is consistent with the pattern of mixing between 'J' and 'O' stocks along the Japanese coast as proposed by Kanda *et al.* (2009), the migration patterns of adult and juvenile 'J' stock whales as suggested by SC/62/NPM1, and the migration of 'O' stock whales as suggested by Hatanaka and Miyashita (1997). SC/62/NPM12 postulated three less plausible hypotheses which modify the most plausible scenario as follows:

(1) a W-stock sporadically intrudes into sub-area 9;
(2) a different stock (Y-stock) resides in the Yellow Sea and overlaps with 'J' stock in the southern part of sub-area 6; and
(3) a W-stock sporadically intrudes into sub-area 9 and a Y-stock resides in the Yellow Sea, and overlaps with 'J' stock in the southern part of sub-area 6.

These four hypotheses are further described and shown graphically in Annex D1, Appendix 3.

SC/62/NPM15 reviewed genetic and non-genetic data regarding stock structure; the authors summarised their conclusions in the context of addressing four key questions, as follows.

(1) Are whales in the Yellow Sea part of a population that migrates into the Sea of Japan?

SC/62/NPM15 summarised that migration north into the Yellow Sea, the presence of mature whales and cow/calf pairs there, and the fact that Yellow Sea whales have only autumn conception dates (*n*=124), provides evidence that a separate stock exists there. The Korean coast of the Sea of Japan showed some evidence for a mixture of two stocks, and microsatellite DNA showed seasonal differences that might be explained by a Yellow Sea stock moving along the Korean coast only in summer. In summary, the authors consider that the available data suggest that Yellow Sea whales may not be a part of the Sea of Japan stock.

(2) Are whales along the Korean coast part of the same population as whales along the western Japanese coast?

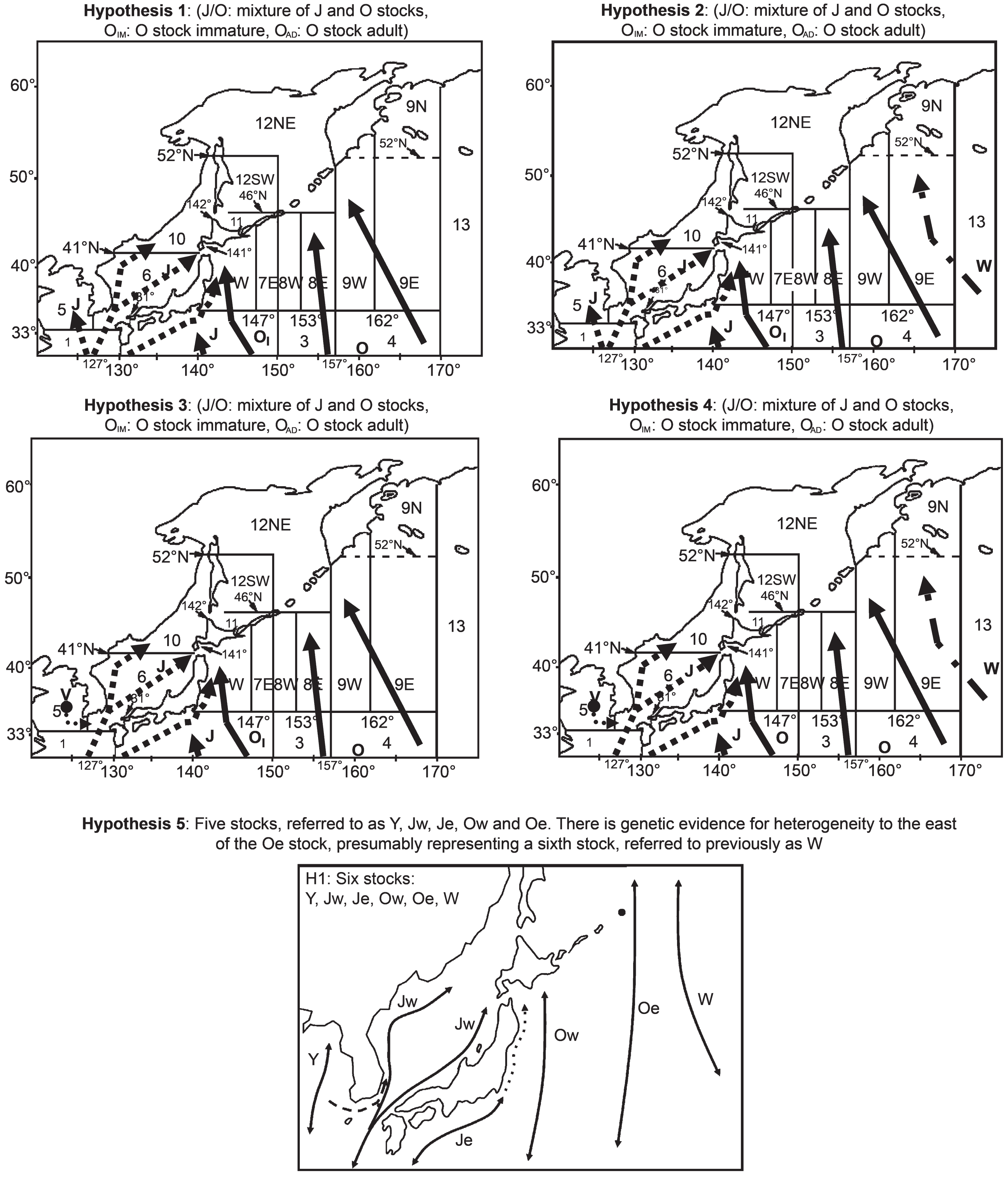
SC/62/NPM15 summarized that there is no obvious hiatus in distribution between the two coasts, and that genetic analyses showed mixed results (haplogroup and *STRUCTURE* found no difference, pair-wise mtDNA and microsatellite DNA found differences). A small sample (*n*=8) from the Sea of Japan showed a bimodal distribution of conception dates and a larger sample (*n*=63) showed two different flipper colour patterns, but these data could be explained by a mixture of whales coming into the northeast Sea of Japan from the Sea of Okhotsk. No sex bias or haplogroup-by-sex differences were found for Japanese Sea of Japan bycatch, suggesting a possible year-round presence of a non-migratory coastal stock. In summary, the authors consider that it is plausible there are different stocks on either side of the Sea of Japan, but the data are somewhat contradictory or are lacking in sufficient resolution or spatial extent to make definitive conclusions. Some genetic evidence suggesting a second stock could be most simply explained by whales from a Yellow Sea stock appearing along the coast of Korea in summer.

(3) Are so-called 'J-type' whales on the east coast of Japan the same population as on the west coast of Japan?

The majority of whales bycaught on the southern Pacific coast of Japan (sub-area 2) are assigned to be J-type and so are either part of a Sea of Japan stock or are a coastal stock separate from a Pacific Ocean ('O') stock. Whales caught in the Pacific Ocean, even from sub-area 7 coastal areas, only have winter conception dates (*n*=68) and a single flipper colour type (*n*=77); if coastal sub-area 7 had a mixture of stocks there should be autumn conception dates and a mixture of flipper colour types. There are differences in microsatellite DNA and mtDNA between the two coasts of Japan when all samples are used. Additionally, the southern Pacific coast bycatch (sub-area 2) is genetically different from bycatch along the northern Pacific coast of Japan (sub-area 7), suggesting a Pacific coastal stock might be distributed only in the Kuroshio current, and does not occur further north in the Oyashio current. In summary, the authors consider that it is plausible that there are different coastal stocks on either coast of Japan, and/or longitudinally along the Pacific coast.

(4) Is there a coastal population in Subarea 7 (east of Hokkaido and northern Honshu) that is different from offshore minke whales in the Pacific Ocean, even after accounting for Sea of Japan whales that might migrate into this area?

One hypothesis is that there is a 'pure' Sea of Japan stock (J-type whales) and Pacific Ocean stock (O-type whales). Under that hypothesis, genetic differences between Pacific coastal waters (sub-area 7W) and other areas have been interpreted to be a mixture of these two stocks. An alternate hypothesis is that this area contains a distinct stock characterised by intermediate haplotype frequencies, as seen in humpback whales, for example. Again, the lack of evidence of autumn conception dates (*n*=68) and a mixture of flipper colour types (*n*=77) in the Pacific Ocean argues


Hypothesis 1: (J/O: mixture of J and O stocks, O_{IM}: O stock immature, O_{AD}: O stock adult)

Hypothesis 2: (J/O: mixture of J and O stocks, O_{IM}: O stock immature, O_{AD}: O stock adult)

Hypothesis 3: (J/O: mixture of J and O stocks, O_{IM}: O stock immature, O_{AD}: O stock adult)

Hypothesis 4: (J/O: mixture of J and O stocks, O_{IM}: O stock immature, O_{AD}: O stock adult)

Hypothesis 5: Five stocks, referred to as Y, Jw, Je, Ow and Oe. There is genetic evidence for heterogeneity to the east of the Oe stock, presumably representing a sixth stock, referred to previously as W

Fig.1. Five plausible stock structure hypotheses for North Pacific minke whales.

against there being a mixture of stocks in coastal Pacific areas. Although it is possible that the haplotype frequencies of sub-area 7W could be explained by a complex seasonal, sex- and age-biased mixing of 2 stocks, e.g. a 'core J' and a 'core O', it is not as parsimonious as the hypothesis of a distinct stock with intermediate haplogroup frequencies. The absence of a strong haplogroup-by-sex interaction in coastal waters is inconsistent with the prediction of a sex-biased mixing of two stocks. SC/62/NPM30 concluded that there was genetic heterogeneity in the Pacific Ocean, with a strong signal in the coastal area east of Hokkaido. In summary, the authors consider that it is plausible that the unique genetic signals seen in coastal waters of the Pacific coast of Japan are due to the existence of a distinct coastal stock or stocks, rather than a mixture of a 'pure J' and a 'pure O' stock.

An additional stock-structure hypothesis based on consideration of the four questions posed above is that there are six stocks (Y, J_W, J_E, O_W, O_E, and W); this is described and shown graphically in Annex D1, Appendix 4.

In discussion, there was general agreement on answers to two of the key questions posed by SC/62/NPM15: (1) a separate J-like stock (denoted Y-stock) occurs in the Yellow

Sea and in at least some years some Y-stock whales are found in the Sea of Japan; and (2) minke whales on the east coast of Korea and on the west coast of Japan are generally part of a single stock.

In contrast, substantial disagreements remained concerning the other two questions. These disagreements centred on how to interpret results of statistical tests showing heterogeneity of allele frequencies. In one view, the results can be explained by overlapping distributions of 'O' and 'J' stock, which leads to different mixing proportions (and hence different allele and haplotypic frequencies) in different geographic areas. Under this hypothesis, it would not be surprising that comparisons of samples from areas having different fractions of the two stocks often produce statistically significant results. An alternative view to an explanation that requires complex mixing patterns is the hypothesis that the statistically significant differences reflect a distinct stock with intermediate gene frequencies.

In conclusion, in spite of the disagreements noted above, the Committee **agrees** that the set of stock-structure hypotheses based on the four proposed in Annex D1, Appendix 3 and the fifth proposed in Annex D1, Appendix 4 were inclusive and sufficiently plausible at least to take forward to the next step in the *Implementation* process (see Fig. 1).

6.3.1.2 CATCHES

The Committee noted that information was available on commercial catches for those countries that have taken the largest catches of western North Pacific minke whales. There are, however, limited data on catches for the People's Republic of China and no catch data for North Korea (if North Korea has taken western North Pacific minke whales).

The Committee reviewed information regarding incidental catches.

SC/62/NPM4 provided information on incidental catches of common minke whales off Japan and Korea. Some suggestions were made on how plausible estimates of future incidental catches can be made, as well as to how past series, now considered erroneous, can be constructed. The Committee noted that it would be useful if estimates were presented to the Preparatory Meeting for the First Intersessional Meeting of the *Implementation Review* (see Item 6.3.2 and Annex D1, item 11.2).

SC/62/NPM19 provided information on bycatch of minke whales in Korean waters from 1996 to 2008. The authors collected bycatch data from the 14 local branch offices of the Korea Coast Guard which investigates the bycatch of cetaceans. A total of 1,156 minke whales were bycaught of which 83.7% were bycaught in the East Sea; 363 animals were entangled or trapped by set nets, 316 and 303 were entangled by fish pots and gillnets, respectively.

SC/62/NPM26 provided information on incidental catches off Korea based on DNA profiling of market products (discussed under Annex J, item 9.4), which suggested that reported bycatch totals may be underestimated. The Committee was informed that the large majority of the incidental catch off Japan was taken in set nets; 119 common minke whales were bycaught in set nets and one animal in a gill net during 2009 (SC/62/ProgRepJapan).

The Committee **recommends** that available data on incidental catches and the associated effort should be analysed to develop CPUE series for possible use during the *Implementation Review*. The Committee **agrees** that sufficient information is available that alternative hypotheses regarding time-series of historical commercial and incidental catches can be developed during the *Implementation Review*. The Committee **agrees** that during the *Implementation Review* there is sufficient information to disaggregate the historical commercial and incidental catches to sub-areas and periods during the year.

The Committee received information on likely future whaling operations for minke whales in the western North Pacific. Japan aims to conduct land-based and pelagic whaling. Land-based whaling will be restricted to close to Japan while pelagic whaling will occur mainly in offshore areas. Temporal and spatial restrictions will be imposed on both types of whaling to try to reduce catching J-type animals. Korea intends to conduct land-based whaling to the east and west of Korea from March to November. These whaling plans will need to be elaborated further during the First Intersessional Workshop of the *Implementation Review*.

The work related to catches that needs to be completed prior to the Preparatory Meeting for the First Intersessional Workshop of the *Implementation Review* is:

(1) construction and GLM standardisation of CPUE series using the incidental catches and the associated fishing effort (see also Annex D1, item 8.3);
(2) development of a format for reporting incidental catches by Japanese and Korean scientists to the Secretariat and the provision of these data in the agreed format to the Secretariat; and
(3) development of alternative hypotheses regarding time-series of past and future commercial and incidental catches.

6.3.1.3 ABUNDANCE ESTIMATES

The Committee reviewed information available on abundance surveys and estimates of abundance.

SC/62/NPM2 provided estimates of abundance for the JARPN II survey area (sub-areas 7, 8 and 9, excluding the Russian EEZ) for the early (May and June) and late (July and August) seasons for 2006 and 2007. SC/62/NPM16 analyzed sightings data from recent surveys conducted by Korea in the Yellow Sea (sub-area 5) and the East Sea (sub-area 6) to estimate the abundance of common minke whales. Details are given in Annex D1, item 7.1.

SC/62/NPM24 reported on a sighting survey for minke whales and other cetaceans in the East Sea from 21 April to 30 May, 2009. An provided oversight on behalf of the Scientific Committee and the survey was undertaken in accordance with IWC guidelines. The plan had been presented to the 2008 Annual Meeting (Choi *et al.*, 2008) and was endorsed by the Committee. Details are given in Annex D1, item 7.1. The Committee expressed its appreciation to the Government of Korea for its continued commitment to surveys for minke whales in Korean waters, and to An for his role of oversight on behalf of the Committee. The Committee **agrees** that data from the 2009 survey off Korea are suitable for use in the RMP.

SC/62/NPM7 summarised the sighting surveys for minke whales in the western North Pacific conducted by Japan and Korea since 2000. The survey period for 'J' stock was April-June, and that for 'O' stock July-September. The areas covered were the Korean EEZ in sub-areas 5 and 6, the Japanese EEZ in sub-areas 6 and 10, the Russian EEZ in sub-area 10, the Sea of Okhotsk (sub-areas 11 and 12) and east of the Kurile archipelago and Kamchatka (sub-areas 8, 9 and 12), including the Russian EEZ. A total of 505 minke whale schools (560 animals) were sighted on 27,045 n.miles on primary search effort in 22 cruises.

SC/62/NPM8 updated the integrated abundance estimates for minke whales in sub-areas 5, 6 and 10 using new information on abundance and *g*(0). SC/62/NPM14 reviewed the proposed method in SC/62/NPM8 for integrating surveys for use in the *Implementation Simulation Trials*. Details are given in Annex D1, items 7.1 and 7.3.

The Committee **endorses** the method used to combine sightings data over time to estimate the extent of additional variance, but not necessarily the methods proposed for dealing with abundance across spatial areas in this case because of concerns over migration during the survey and extrapolation (see also Annex D1, item 7.3). The Committee did not review the abundance estimates in SC/62/NPM8 *inter alia* because it is unclear whether the sub-areas used for reporting abundance estimates will be used in the *Implementation Simulation Trials* developed during the First Intersessional Meeting. It was noted that although models can be used to interpolate abundance for unsurveyed regions, if a region has never been surveyed, the abundance estimate for that region should be set to zero when calculating catch limits under the RMP.

The Committee discussed possible migration patterns of 'J' stock minke whales in the Sea of Japan, as well as whether some component of the 'J' stock may not migrate to a substantial extent, in relation to how abundance estimates are computed and used in *Implementation Simulation Trials* and when applying the *CLA*. The Committee **agrees** that care needs to be taken to avoid double-counting animals when computing abundance estimates. In relation to animals in the Sea of Japan and the Yellow Sea, the Committee **agrees** that the *Implementation Simulation Trials* will capture hypotheses regarding the migration patterns of western North Pacific minke whales and that the models underlying these trials would be specified accordingly. The abundance estimates used for conditioning will be allocated to the appropriate time periods to avoid double counting.

The Committee **agrees** that there are several abundance estimates available for possible use when conditioning trials. Annex D1, table 1 provides a summary of the sightings surveys for the sub-areas used in the last set of *Implementation Simulation Trials* and those conducted since. The Committee did not discuss the acceptability or otherwise of the use of these surveys for conditioning the *Implementation Simulations Trials*.

The Committee noted that it was not necessary to select the abundance estimates for use in the *CLA* at the present meeting; this will take place during the First Intersessional Meeting of the *Implementation Review*. The selection of abundance estimates for use in *CLA* will need to take account of whether or not the surveys and their analysis followed the Requirements and Guidelines for Conducting Surveys and Analysing Data within the RMP (IWC, 2005c). Some of these surveys (e.g. those from JARPN II) have not been reviewed by the Committee for use in the RMP.

SC/62/NPM9 provided revised estimates of *g*(0) and abundance for western North Pacific common minke whales. The main changes from the previous analyses were the addition of new data, particularly for the Okhotsk Sea for 2003 and 2005. Details are given in Annex D1, item 7.5. The Committee welcomed this analysis which substantially reduced the previous range for *g*(0) but there was insufficient time for an in-depth review. The Committee **agrees** to review the method used to estimate *g*(0) and the resultant estimates further at the First Intersessional Workshop.

The Committee received information on plans for future sighting surveys by Korea and Japan (SC/62/NPM17 and SC/62/NPM4). Japan noted that it was not currently planning to conduct surveys in sub-areas 6 and 10, but may revise that decision in future. It was noted that the results of the *Implementation Simulation Trials* may provide information on which programme of surveys will lead to the best performance of the RMP, and that Japan and Korea may wish to modify their survey plans once the results of initial trials become available.

More specifically, SC/62/NPM25 described plans for a sighting survey in the Yellow Sea in April-May 2011, with the objective to obtain information on the distribution and abundance of minke whales. Details are given in Annex D1, item 7.6. The Committee was pleased to see that distance and angle estimation will be tested and **requests** that the results of analyses of these and previous data be presented to future meetings. It was noted that the survey could be conducted to eliminate the possible implications of migration during the survey. The Committee appointed An to provide oversight on behalf of the Committee.

SC/62/NPM23 described plans for a sighting and biopsy sampling survey for common minke whales in the Okhotsk Sea during summer 2010. The aim of the survey is to collect sightings data for abundance estimation and information on stock identification. To overcome CITES-related issues, genetic analysis using biopsied skin samples will be conducted on the research vessel. The Committee noted the importance of estimating the proportion of 'J' and 'O' stock animals in the survey area. It **recommends** that Japan explore ways that are not constrained by CITES to facilitate extracting relevant information from biopsy samples collected from the EEZ of Russia which could be used to examine stock structure and mixing. Specific suggestions for this are given in Annex D1, item 7.6. The Committee appointed Miyashita to provide oversight on behalf of the Committee.

6.3.1.4 OTHER ISSUES

Regarding information for estimating dispersal rates and mixing proportions, the Committee noted that SC/62/O30 outlined an approach for estimating mixing rates between stocks using microsatellite data.

Values for the biological parameters for use in *Implementation Simulation Trials* for the western North Pacific common minke whales had been assembled for the previous *Implementation* (IWC, 2004).

The previous trials were based on values for MSYR(mat) of 1% and 4%. These values should be used in any new trials unless the current review of MSY rates (Annex D, item 2) leads to a recommendation for a change to this range.

The Committee noted that CPUE data had been assembled and used to compare alternative stock structure hypotheses (Yasunaga *et al.*, 2009, Appendix II). It **recommends** that relevant commercial and incidental catch and effort data, along with the information identified by the 1987 CPUE Workshop (IWC, 1989), should be assembled, GLM standardised where possible, and be available at the First Intersessional Workshop of the *Implementation Review*. Data on flipper colour and conception dates should also be assembled and presented to the Preparatory Meeting of the First Intersessional Workshop of the *Implementation Review*. Initial discussions of future experimental and analytical ways to distinguish among competing hypotheses are given in Annex D1, item 10.

6.3.2 Recommendations

The Committee **agrees** that it has successfully addressed all of the items required for a *pre-Implementation assessment* and therefore **agrees** that the *pre-Implementation assessment* is completed.

The Committee **recognises** that there is a considerable amount of work that needs to be done to complete the *Implementation Review*. Specifically, there is a need: (a) to assemble the data so that they can be used when conditioning the operating models on which the *Implementation Simulation Trials* are based; (b) to specify and code the operating models themselves; and (c) to fit the operating models to the agreed data sets (conditioning).

The Committee **agrees** that it is infeasible to conduct all of the work in a single meeting (the First Intersessional Meeting). Rather, it **agrees** that the probability of completing the work during the first year of the *Implementation Review* will be maximised if two meetings occur. The main objective of the first (the Preparatory Meeting) would be to determine the structure (time-steps, sub-areas and population components) of the operating models so that all relevant data can be assembled at the appropriate spatial and temporal resolutions in time for the First Intersessional Workshop, and to start to specify the operating models and how they will be conditioned. The second step would be to complete work scheduled at the First Intersessional Workshop.

Annex D1, Appendix 9 outlines the work plan in more detail, including tentative dates for deadlines and holding the Preparatory Meeting and the First Intersessional Workshop.

6.4 North Atlantic common minke whales

6.4.1 New information on stock boundaries and abundance estimates

Some of the *Small Areas* boundaries for North Atlantic minke whales were changed during the 2003 *Implementation Review* but not all boundaries were fully specified. The Committee **recommends** that a point at 63°N, 12°W be introduced to fill the 'hole' between the CM and CIP *Small Area*, and that boundaries around the southern tip of Greenland be defined as shown in Annex D, fig. 1. It also **recommends** that the *Small Areas* in Annex D, fig. 1 be adopted for use when the applying the RMP for North Atlantic minke whales.

SC/62/RMP6 presented a method for estimating *g*(0) from single platform line transect data in which both the forward and perpendicular distances have been recorded. More details are given in Annex D, item 3.3.2. The Committee noted that attempts had been made in the past to estimate *g*(0) using data from a single platform. It **encourages** efforts to develop methods to achieve this. The Committee **recommends** that the robustness of the method proposed in SC/62/RMP6 to model structure uncertainty, measurement error, and diving pattern be examined.

SC/62/RMP7 summarised a sightings survey conducted in the North Sea area within *Small Area EN* during summer 2009. More details are given in Annex D, item 3.3.2. The Committee **welcomes** this information and noted that these data would be included in a future abundance estimate for the North Atlantic common minke whales.

SC/62/RMP5 presented estimates of abundance for common minke whales in the Central Atlantic from the North Atlantic Sightings Survey conducted by Icelandic and Faroese vessels during June/July 2007. More details are given in Annex D, item 3.3.2.

The Committee **agrees** that the methods in SC/62/RMP5 followed the relevant RMP Guidelines. Annex D, table 1 lists the estimates of abundance in SC/62/RMP5.

The Committee **agrees** to adopt the estimates of abundance for 2007 for the CG and CIP *Small Areas* presented in Annex D, table 1 for use in the RMP.

The Committee **endorses** abundance estimates for the CM *Small Area* and for the Eastern *Medium Area*, by *Small Area*, for use in the RMP given in Annex D, table 2.

6.4.2 Recommendations and work plan

The Committee **recommends** that the boundaries in Annex D, fig. 1 be adopted for use when applying the RMP for North Atlantic minke whales. It also **recommends** that abundance estimates in Annex D, tables 1 and 2 be adopted for use in the RMP. The Committee **agrees** that its work plan for the 2011 Annual Meeting will include the review of any new abundance estimates.

7. ESTIMATION OF BYCATCH AND OTHER HUMAN-INDUCED MORTALITY (BC)

The report of the Working Group on Estimation of Bycatch and Other Human-Induced Mortality is given as Annex J. This subject was introduced onto the Agenda in 2002 (IWC, 2003c) because as part of the Revised Management Procedure, recommended catch limits must take into account estimates of mortality due to *inter alia* bycatch, ship strikes and other human factors in accordance with Commission discussions at the 2000 Annual Meeting (IWC, 2001a), although of course such mortality can be of conservation and management importance to populations of large whales other than those to which the RMP might be applied. Subsequently, the issue of ship strikes has become of interest to the Commission's Conservation Committee (IWC, 2006a).

7.1 Collaboration with FAO on collation of relevant fisheries data

The effort to compile a comprehensive database of entanglement data in the national progress reports, an element of collaboration with FAO, has continued; the IWC Secretariat has now entered data from 2004-09.

7.2 Progress on joining the Fisheries Resource Monitoring System (FIRMS)

The information potentially to be developed in collaboration with FIRMS includes an inventory of fisheries, including gear characteristics and some indicators of fishing effort. The IWC will be eligible to move from observer status to full partnership in FIRMS after completion of the entanglement database (see Item 7.1, above). Details are provided in Annex J.

7.3 Estimation of bycatch mortality of large whales

7.3.1 Mortality in longline fisheries

The Committee received a global review of operational interactions between cetaceans and longline fisheries (SC/62/BC6). It reported deaths of humpback and Bryde's whales. In addition, mortality of southern right whales has been recorded elsewhere (Best *et al.*, 2001). Depredation by some species of cetaceans such as sperm and killer whales (Kock *et al.*, 2008; Kock *et al.*, 2006; Purves *et al.*, 2005) is of economic importance to some fisheries. Research to mitigate depredation and mortality can potentially contribute to estimating both fish and cetacean mortality rates.

7.3.2 Bycatches in Korea and Japan

Genetic analysis of samples of cetacean meat collected in markets in Korea in 2004-05 suggested that 90 common minke whales were represented (SC/62/NPM26). Details of the analyses are given in Annex J. The small number of samples from the same individuals suggests that the whales pass through the market rapidly. The reported bycatch for Korea for 2004 was 61. The detection of a minimum of 90 whales in the market indicates that the true bycatch was greater than reported. The reported bycatch for 2009 is 54. The results of the 2004-05 market survey analyses suggest that this is likely an underestimate.

The Committee welcomed publication of a recent paper describing incidental entanglement of minke whales in the Republic of Korea (Song *et al.*, 2010). This contained information that had been previously been requested of Korea by the Committee.

The Committee noted the need for time series of bycatch for the *Implementation Simulation Trials* for North Pacific common minke whales (see Item 6.3) for Japan and the Republic of Korea. The Committee reviewed the method presented in SC/62/NPM4 to estimate past incidental catches of minke whales in Japan (details are given in Annex J). Concern was raised regarding the multiplicative factor used to adjust reported catch figures for the period 1979-2000. It was noted that there was considerably more variability in the early reported figures, with CVs for the 1980s and 1990s three to six times higher than since 2001. For this reason, some members suggested that a multiplicative adjustment was not appropriate and that the reports of zero bycatch for some years, (which also resulted in zero estimates) were implausible. Other members considered that estimates in SC/62/NPM4 are an improvement compared to the previous assumption of 100 animals each year over a 100-year period. Butterworth commented that point estimates of zero for some years did not necessarily invalidate the method as a basis for estimating cumulative bycatch mortalities over time, which was the primary input required for *Implementation Simulation Trials*; nevertheless he encouraged refinement of the method presented.

In conclusion, the Committee **recommends** that additional analyses to arrive at time-series of bycatches in the region be undertaken for presentation to the preparatory meeting for the first intersessional workshop. In response to a suggestion from some members that bycatch in fisheries other than set nets warrants further examination, including historical information on past fisheries, e.g. the Japanese squid driftnet fishery of 1978-1992 (Yatsu *et al.*, 1994); it was noted that bycatches occur only rarely in types of gear other than set nets in Japanese waters, as reported in the national progress reports of Japan.

7.4 Estimation of risks and rates of entanglement

7.4.1 Report of intersessional workshop

The Committee noted relevant information on entanglement mortality in an advance copy of the report of the Commission's intersessional Workshop on Welfare Issues Associated with the Entanglement of Large Whales (IWC/62/15). The Workshop concluded that:

(1) all species of large whales are at risk of entanglement to varying degree, but common minke, humpback, right (both North Atlantic and southern) and gray whales are the most frequently reported;
(2) all types of stationary or drifting gear (i.e. not actively towed) pose potential risk to entangle, but pound, set and fyke-type nets, along with gill nets and various pot-type gear were most frequently implicated;
(3) entanglements can occur wherever this type of gear and large whales overlap in distribution, and isnot limited to feeding grounds but also includes breeding grounds as well as migratory pathways;
(4) given the cryptic nature of large whale entanglements in combination with the paucity of experienced observers and lack of formal reporting networks, entangled whales are severely underreported globally; and
(5) regional shifts in fisheries and gear types can produce major differences in the character of entanglements and reporting frequency (e.g. coastal versus offshore gear placement).

Based on these conclusions, the Workshop made the following relevant recommendations:

(1) that coastal nations establish adequate programmes for monitoring entanglement of whales; and
(2) that member countries improve reporting to the IWC through National Progress Reports.

The Committee **endorses** these recommendations. In addition it **recommends** that:

(1) all member countries which have coastal fishing operations be encouraged to more accurately report the occurrence and nature of large whale entanglements and establish entanglement response programmes where applicable;
(2) existing and new programmes communicate with each other to standardise the data collected to maximise their usefulness; and
(3) members be encouraged to facilitate thorough examinations of carcasses, at a minimum to record whether fishing gear is present, or fresh scars which might have resulted in mortality are visible, as well as facilitating necropsies on all large whales whenever possible. Such investigations should be conducted irrespective of population status, since this will be required to better estimate entanglement mortality rates including for species and populations that may be subject to whaling.

Additional details reported concerning the entanglement response networks of various nations are given in Annex J.

7.4.2 Entanglement mortality in Oman

An analysis of scars in the peduncle region indicates that 30-40% of whales observed in the isolated and severely depleted population of humpback whales in the western Arabian Sea (known as Breeding Stock X) were likely to have been involved in entanglements (SC/62/SH20). Of 10 stranded baleen whales, three were entangled in gill nets. Fishing effort, including use of drifting and set gillnets and fish traps, is increasing rapidly in the region. The Committee **welcomes** the establishment of a national stranding committee by the Government of Oman, and **recommends** that all member states that do not have national stranding networks to establish these. The importance of indications of fishing effort was also emphasised. The possibility of this population being considered as a candidate for a conservation management plan is discussed under Item 11.2.2.4.

7.5 Progress on including information in National Progress Reports

The data on entanglements and ship strikes reported in this year's National Progress Reports are summarised in Appendix 2 to Annex J. The Committee last year considered a proposal for developing a mechanism for online submission of the information; progress on issues related to online submission of bycatch and other information is discussed further under Item 3.2 and 25 and in Annex P.

7.6 Review of methods to estimate mortality from ship strikes

7.6.1 New data on ship strikes

The Committee received a report on ship strikes affecting southern right whales in Uruguayan waters (SC/62/BC2); between 2003 and 2007, seven whales were observed with large wounds due to collision and five were stranded dead. The Committee **welcomes** this information, noting that this is the type of information requested to be included in the national progress reports; in combination with data on shipping traffic, it may allow comparative analysis of ship-strike rates along the Atlantic coast of South America.

After consideration of a report of a 'near miss' between a humpback whale and a cruise ship in the Antarctic (see Annex J, item 10.1), it was **agreed** that a study of near-miss data (it is known that ferry operators in Hawaii collected such data) may yield additional insight into the dynamics of ship strikes and provide input for modelling risk (see below).

7.6.2 Progress in modelling risk

A report was received on progress in a series of winter and summer surveys of fin whale distribution and abundance in the Mediterranean Sea especially near the Italian coast and in the Pelagos Sanctuary. These surveys are in part intended to improve evaluation of population level effects of human-induced mortality including ship strikes. Details of the results are in Annex J. Plans to collect data on ship traffic were also detailed. The Committee **encourages** continuation of this effort that makes an important contribution towards the modelling of risk and assessing population level effects.

7.7 Progress in developing global database of ship strikes

This effort has been underway since 2007, with associated activities by IMO and ACCOBAMS. Tasks identified at last year's meeting have been completed or are nearly completed. Progress has relied on informal arrangements among the Secretariat, members of the data review group, and an external contractor. In view of the increasing workload and proposed intersessional tasks, detailed in Annex J, Appendix 3, the Committee **recommends** that consideration be given to the appointment of a dedicated coordinator; this is the practice for other similar successful databases of this scale. Funding requested to support intersessional work including data validation, the creation of a handbook and for work on data entry is discussed under Item 24.

The Committee **endorses** the policy on release of information in the database in response to requests from the public detailed in Annex J, Appendix 3. Information from nine fields in the database will be eligible for release on a down-loadable basis. Only data on confirmed ship strikes will be released. Requests for full access will be dealt with on an individual basis.

The Committee noted that IWC and ACCOBAMS will hold a joint workshop in Monaco from 21-24 September 2010 on reducing risk of ship strike and that some agenda items will be relevant to data gathering and estimating numbers of collisions. The IWC also continues to collaborate with IMO on efforts to minimise the risk of ships strikes and to reduce underwater noise from commercial shipping (Annex K, item 9.4).

7.8 Other issues

7.8.1 Methods for assessing mortality from acoustic sources

There was no new information on this topic. However, the Committee noted development of an improved method for handling and analysis of gas embolisms found in stranded cetaceans (Bernaldo de Quiros *et al.*, 2010); such embolisms may be linked with acoustic sources. A workshop entitled 'Diving marine mammals gas kinetics' was held in Woods Hole, MA, USA in April 2010 and the Committee looks forward to receiving the report at next year's meeting.

7.8.2 Methods for assessing mortality from marine debris

Methods used in a study modelling co-occurrence of debris and cetaceans (SC/62/BC5) have potential value for assessing mortality from debris. The Committee **recommends** that full necropsies be conducted on all stranded large whales, irrespective of population status, to detect incidents of mortality associated with ingested debris (and see the earlier recommendation on entanglement).

7.8.3 Other potential sources of human-induced mortality

The Committee noted that while there have been no confirmed reports of whale mortality due to collisions with marine renewable energy developments, the potential exists for such (SC/62/E7 and E8) and see Carter *et al.* (2008).

7.8.4 Actions arising from intersessional requests from the Commission

The Committee was asked to review Annex {DNA} of IWC/62/7rev. This contains a section on market sampling. Although the proposed scheme has the purpose of acting as a deterrent to illegal activity, the Committee noted that it might also potentially provide information for estimating bycatch. A workshop and simulation studies were conducted in the past by the Committee to assess the possibilities for developing a market sampling system to estimate bycatch (details in Annex J).

8. ABORIGINAL SUBSISTENCE WHALING MANAGEMENT PROCEDURE (AWMP)

This item continues to be discussed as a result of Resolution 1994-4 of the Commission (IWC, 1995a). The report of the SWG on the development of an aboriginal whaling management procedure (AWMP) is given as Annex E. The Committee's deliberations, as reported below, are largely a summary of that Annex, and the interested reader is referred to it for a more detailed discussion. The primary issues at this year's meeting comprised: (1) *Implementation Review* of eastern gray whales; (2) various aspects of providing management advice for Greenlandic hunts; and (3) review of management advice for the humpback whale fishery of St. Vincent and The Grenadines. This represented a significant workload. The Chair of the SWG noted that its work this year had been considerably assisted by the progress made at the intersessional Workshop on Greenland fisheries held in Roskilde, Denmark (SC/62/Rep3).

In addition, he recalled that two years ago (IWC, 2009c), the Committee had tested and agreed a safe method to provide interim advice (i.e. catch limits for up to two 5-year blocks) such that the catch limit is 2% of the lower 5th percentile of the most recent estimate of abundance.

8.1 Sex ratio methods for common minke whales off West Greenland

The Committee has been evaluating assessment methods for common minke whales off West Greenland that rely on the relationship between the observed sex ratio of catches and that inferred from population models parameterised in terms of carrying capacity, productivity and how the distribution of males may have changed relative to that of females. This concept was introduced in 2005 (IWC, 2006b; Witting, 2005). The major factor which suggests that sex-ratio data may be informative about population size is that catches have consistently been female-dominated. 'Best' estimates of population size from sex ratio based methods are infinite, in effect indicating that any level of past catches would not have impacted this population of minke whales. However, it is standard Scientific Committee practice, in accordance with a precautionary approach, to base management advice primarily on lower confidence bounds for such estimates. The Committee has therefore focussed attention on developing the novel assessment approach required to calculate these bounds.

Considerable technical work was undertaken by the SWG during the intersessional period with a view to being able to test the approach with an initial set of robustness trials as described in SC/62/Rep3. However, implementation of the new method is proving extremely difficult. The details of this are complex and can be found in Annex E, item 3.1.3 but in short can be said to be due to the continued difficulties the SWG has faced with the likelihood function that underlies the sex-ratio approach.

Several remedies were considered by the SWG. The most promising of these was to re-parameterise the analysis by replacing *K* (carrying capacity) with a suitable transformation. This can be thought of as a high-risk/high-reward option: it could provide an adequate basis for estimation thereby eliminating many of the intricacies that continue to plague the current framework, but it may introduce new difficulties.

The Committee **endorses** the SWG recommendation that this approach receive the highest priority during the next intersessional period. If a transformed analysis could be completed and agreed at the 2011 Scientific Committee meeting, the sex-ratio method could be used as a basis for abundance estimation and submitted to appropriate simulation trials to test performance and robustness. If these trials are passed, the approach could then be used for providing management advice and as a basis for a long-term *SLA* (Item 8.3).

The SWG also considered a number of other options which would not require such a drastic change but which it considered had less chance of being successful, as can be seen in Annex E. An option to try raising the current truncation point was shown not to solve the issue as a result of runs undertaken after the SWG had completed its work.

The SWG had agreed that the continued difficulties in successfully implementing a sex-ratio approach required a re-evaluation of its work plan. The original motivation for this work had been the Committee's inability to provide management advice for this hunt. Thus, reflecting the priorities of the Scientific Committee and the Commission, work on a sex ratio estimation of abundance for West Greenland common minke whales has been the dominant focus of SWG effort for a number of annual meetings and three intersessional workshops.The participants have devoted considerable research effort to this task, the work has been scientifically challenging and methodologically innovative and the potential gain in terms of providing adequate management advice extremely high. However, despite enormous effort, no satisfactory conclusion has been achieved to date. Last year, the Committee had agreed an abundance estimate for common minke whales off West Greenland that, in conjunction with the agreed approach to provide safe interim advice for up to two five-year blocks, meant that the Committee was able to provide satisfactory management advice for the first time.

Therefore, the SWG had concluded that it would no longer prioritise development of the sex ratio approach unless a comprehensive final analysis could be endorsed at the 2011 Scientific Committee meeting. Although it would be regrettable to abandon the sex ratio effort without obtaining an agreed abundance estimate, there are many other urgent issues to which the SWG must turn its focus. The Committee **concurs** with this view.

8.2 Conduct *Implementation Review* of eastern North Pacific gray whales

In 2004, (IWC, 2005d), the Committee presented the Commission with its recommended Gray Whale *Strike Limit Algorithm* (the *Gray Whale SLA*) and this was endorsed by the Commission. The scheduled 2009 *Implementation Review* had been postponed because a number of key analyses would not be ready in time.

The purpose of an *Implementation Review* is to update information on catch history and abundance and to determine whether any other new information that has become available in the intervening (normally) 5-year period indicates that the present situation is outside the region of parameter space tested during *SLA* development. If this is the case, additional trials will need to be developed to test the performance of the *SLA* in this new region. If performance is found to be unacceptable under these new trials, revisions to the *SLA* will be required.

Full details of the parameter space investigated in the development of the *Gray Whale SLA* can be found in IWC (2005d). In practical terms, the most important issues relevant to the present *Implementation Review* relate to the issues of stock structure and updated information on abundance/trends.

8.2.1 The issue of the DAA and the conduct of this Implementation Review

Implementation Reviews are subject to the Committee's Data Availability Agreement incorporating a timetable of events. Although many datasets and analyses were completed within the appropriate timelines, unfortunately, just before adoption of its report, the SWG had realised that the photo-id and genetics data central to its discussions of stock structure and movements had not formally been submitted to the IWC under the DAA (although the papers themselves had met the appropriate deadlines). The same is also true for the telemetry data that, while not central to the conclusions reached, was also discussed under that Agenda Item; in this case the paper also did not meet the appropriate deadline.

The Committee recognised that discussions of these data cannot be considered as part of the *Implementation Review.* Thus although the *Implementation Review* is considered complete with respect to the discussions involving the data properly made available under the DAA, it **recommends** that a new *Implementation Review* takes place at the next Annual Meeting. This is to enable the SWG to take properly into account the important new information received this year that had not met the DAA timeline and that could indicate that the original trial structure was not sufficiently broad (see Item 8.2.7). This issue is referred to, where appropriate, in other parts of this report. A mechanism to ensure that this unfortunate event does not happen again is discussed under Item 8.2.8.

8.2.2 Stock structure

In the development process for the *Gray Whale SLA*, the possibility of a summer feeding aggregation along the Pacific coast between California and southeast Alaska was noted (e.g. IWC, 2001h) but the Committee had agreed that a single stock scenario was the most appropriate (IWC, 2002d).

Considerable new information has been collected since that time on the animals feeding along the Pacific coast and the SWG received three papers of relevance to stock structure at this meeting (unfortunately, as noted above, these did not meet all of the DAA requirements). Although different names have been used in the past by different authors (e.g. the southern feeding group, the Pacific Coast Feeding aggregation), the Committee **agrees** to refer to the animals that spend the spring, summer and autumn feeding in coastal waters of the Pacific coast of North America from California to southeast Alaska as the Pacific Coast Feeding Group or PCFG.

SC/62/AWMP1 presented an analysis of the genetic differentiation between the PCFG (using samples from Vancouver Island) and the larger population (using samples from Baja California). The authors concluded that their results suggest that the matrilines of the southern feeding group are demographically independent from those of the rest of the population, and therefore require separate management consideration.

SC/62/BRG32 reported the results of an 11-year (1998-2008) photo-id study examining the abundance and the population structure of eastern gray whales that spend the spring, summer and autumn feeding in coastal waters of the Pacific Northwest. With respect to stock structure, it concluded that there is one group of whales that return frequently and account for the majority of the sightings in the Pacific northwest during summer and autumn (i.e. the PCFG) and a second group of whales are apparent 'stragglers' encountered in this region after the main migration.

The discussion was also informed by consideration of telemetry data (SC/62/BRG21) and the details can be found in Annex E, item 2.2.

The Committee thanked the authors for these comprehensive papers. There was considerable discussion of them and their implications for stock structure. Despite some differences in interpretation and recognising that further analyses could be carried out, the Committee **endorses** the SWG's conclusion that the hypothesis of a demographically distinct PCFG was plausible and warranted further investigation. The implications of this for the *Implementation Review* are discussed under Item 8.2.7.

Telemetry data may provide the best estimator of residency times for PCFG gray whales in order to evaluate their relative vulnerability with respect to the spatial and temporal characteristics being considered for the Makah hunt. Analogous data from non-PCFG whales may also help determine if there are differences between PCFG and non-PCFG whales with regard to their migrations (distances from shore, water depths or timing) or other behaviours. Therefore, the Committee **recommends** that the satellite tagging work should continue and that these data be analysed with the goal of providing input (e.g. as required in mixing matrices, etc.) for any future trials of the *Gray Whale SLA*.

8.2.3 Catch data

Allison informed the SWG that the catch series had been updated to incorporate new information. The complete series can be found in Annex E, table 1.

8.2.4 Abundance and trends

Two papers relating to calf counts were considered, one from migration and one from the breeding grounds.

SC/62/BRG1 presented calf counts from shore-based surveys of northbound eastern North Pacific gray whales that have been conducted each spring between 1994 and 2009 in central California. Estimates were highly variable between years, with no sign of a positive or negative trend. Calf production indices, ranged between 1.6 - 8.8% with an overall average of 4.2%. The authors hypothesised that a late retreat of seasonal ice may delay access to the feeding areas for pregnant females and reduce the probability that existing pregnancies will be carried to term.

SC/62/BRG36 reported on changes in the abundance of gray whales inferred from boat surveys at Laguna Ojo de Liebre and Laguna San Ignacio between the late 1970s to the present. There was a decrease in the numbers of cow-calf pairs in both lagoons during 2007 to 2009, similar to the results from shore-based surveys at Piedras Blancas during the northbound migration. The counts of cow-calf pairs in both lagoons in 2010 were the lowest over the last 15 years.

In discussion, it was noted that the calf production indices were particularly low (<3%) during two periods (1999-2001 and 2007-09). During the first period, calf counts were low and high numbers of strandings also occurred. However, although the calf counts were low during 2007-09, there is no evidence for higher numbers of strandings during these years. The Committee noted that the calf production indices are being used in its discussion of MSY rates (see Item 5.1). Although the time-series of calf counts is now 16 years long, this is only just long enough to allow estimation of these parameters.

The Committee therefore **recommends** that these data continue to be collected and are reviewed during future *Implementation Reviews*. The series of cow-calf counts in lagoons, which provide a relative index not absolute estimates, are consistent with the calf counts given in SC/62/BRG1.

The Committee noted that the calf count data had been used during the initial development and *Implementation* for eastern gray whales and **agrees** that the new information did not indicate a need to modify the trials structure.

The Committee had two new papers relating to total abundance estimates. The first, SC/62/BRG8 reported a promising new approach that has recently been adopted for the counts of southbound migrating whales at Granite Canyon, California, which form the basis of abundance estimation for the eastern gray whales. The authors recognised the need for new calibration data to evaluate the different biases of new counting methods and new observers before count data can be reliably rescaled to estimate abundance.

The Committee welcomed this report, noting the importance of ensuring comparability among years in any long-term monitoring effort. It **recommends** that data be collected to re-evaluate pod size bias given the change in survey protocol and that variance estimates for future survey estimates of abundance account for the uncertainty associated with calibration of abundance estimates computed using different survey protocols.

The second paper, Laake *et al.* (2009), re-evaluated the data from all 23 seasons of shore-based counts for the Eastern North Pacific stock of gray whales conducted throughout all or most of the southbound migration near Carmel, California using a common estimation procedure and an improved method for treatment of error in pod size and detection probability estimation.

In addition to these papers, the Committee noted that the telemetric information in SC/62/BRG21 provided the first confirmation of day/night migration rates since the original

Table 2

Time-series of agreed abundance estimates of eastern gray whales for use in the *Gray Whale SLA* (taken from Laake *et al.*, 2009).

Year	Estimate	CV	Year	Estimate	CV
1967/68	13,426	0.094	1979/80	19,763	0.083
1968/69	14,548	0.080	1984/85	23,499	0.089
1969/70	14,553	0.083	1985/86	22,921	0.081
1970/71	12,771	0.081	1987/88	26,916	0.058
1971/72	11,079	0.092	1992/93	15,762	0.067
1972/73	17,365	0.079	1993/94	20,103	0.055
1973/74	17,375	0.082	1995/96	20,944	0.061
1974/75	15,290	0.084	1997/98	21,135	0.068
1975/76	17,564	0.086	2000/01	16,369	0.061
1976/77	18,377	0.080	2001/02	16,033	0.069
1977/78	19,538	0.088	2006/07	19,126	0.071
1978/79	15,384	0.080			

radio tag information that has been used when estimating abundance from the southbound census. The Committee thanked the authors for this comprehensive and careful review of this extremely valuable time-series of absolute abundance estimates. It **recommends** that the estimates of abundance given in Table 2 be **adopted** for use in the *Implementation Review* and for use when applying the *Gray Whale SLA*.

SC/62/BRG32 referred to under Item 8.2.2, also used the photo-id data to estimate the abundance of the PCFG. Abundance estimates for whales present in summer and autumn were estimated using both open and closed population models. Methods were proposed to remove the 'stragglers' from both types of analyses, to estimate abundance only of regularly returning whales. Three methods and four geographic scales revealed the abundance of animals that regularly return to the Pacific Northwest to be at most a few hundred individuals.

The Committee **agrees** that these data will be extremely useful during the proposed 2011 *Implementation Review*, along with telemetry data, to determine the probability that animals from the putative feeding aggregation in the Pacific Northwest are at risk of being caught during hunts in that area (see Annex E, item 2.6). The estimates in SC/62/BRG32 will also be useful to condition any trials developed to examine the performance of *SLA* variants for this feeding aggregation.

8.2.5 Assessment

SC/62/AWMP2 fitted an age- and sex-structured population dynamics model to data on the catches and abundance estimates for the ENP stock of gray whales using Bayesian methods. The prior distributions used for these analyses incorporated the revised the estimates of abundance in Laake *et al.* (2009) and SC/62/BRG1, and account explicitly for the drop in abundance caused by the 1999-2000 mortality event. A series of sensitivity analyses were conducted. The baseline analysis estimated the population to be above MSYL and the 2009 population size (posterior mean of 21,911) to be at 85% of its carrying capacity (posterior mean of 25,808); conclusions were consistent across all the model runs. SC/62/AWMP2 only estimated an extra mortality parameter for 1999-2000 based both on calf and strandings data and the analysis of Brandon and Punt (2009a; 2009b) in which annual parameters were estimated for reproduction and survival.

The Committee thanked the authors of SC/62/AWMP2 for the updated assessment. It **agrees** that the results of the assessment are within the bounds considered during the *Implementation*. Although the base operating model used to estimate the *Gray Whale SLA* did not explicitly include the 1999-2000 event, robustness tests involving catastrophic mortality events were conducted and the *Gray Whale SLA* performed adequately for these tests.

8.2.6 Strandings data

SC/62/BRG25 provided a summary of all gray whale strandings in California, Oregon and Washington between 1 January 2010 and 31 May 2010. The Committee welcomes this information, **agrees** that it showed that stranding levels were now similar to 'normal' years, and **recommends** that these data continue to be collected and presented to the Committee.

8.2.7 Consideration of need for new trials (and, if applicable, results of those)

The Committee refers to its earlier comments on the situation with respect to the DAA and the need for an *Implementation Review*.

Although some of the papers/data available could not be considered in terms of the 2010 *Implementation Review*, the Committee **agrees** that the information provided on the PCFG was such that its existence represents a plausible hypothesis, not considered in the original *Implementation.* In accord with Committee guidelines for this process (IWC, 2005b), this is sufficient to trigger a new *Implementation Review* in 2011. The reason that this hypothesis is important from an AWMP perspective relates to the potential harvesting in this region by the Makah Tribe and thus the need for the SWG to provide advice/develop an *SLA* to fulfil both the 'conservation' and 'user' objectives given by the Commission. It noted that the situation for PCFG is not the same as for the Greenlandic feeding aggregation of humpback whales; the latter case involves a feeding aggregation that does not occur (even in the short-term during migration) with animals from other feeding aggregations in the waters where the hunt takes place. In the case of the proposed area for the Makah hunt, both PCFG and migrating whales from the other feeding areas co-occur at least some of the time. In fact the situation is more similar to that of Gulf of Maine humpback whales.

The Committee therefore **agrees** that the information on stock structure and hunting warranted the development of trials to evaluate the performance of *SLA*s for hunting in the Pacific northwest at the 2011 *Implementation Review*. The Committee also noted that the assessment work discussed above (Item 8.2.5) showed that the population as a whole is in a healthy state. It **agrees** that for the purposes of the 2011 *Implementation Review*, the primary focus should be the PCFG.

That being said, it also **agrees** that over the next few years (i.e. in time for an *Implementation Review* in about 2016), further work should be undertaken to investigate the possibility of structure on the northern feeding grounds, especially in the region of the Chukotkan hunts. It **recommends** that relevant information be collected from the Chukotkan region, in particular, where possible, including genetic samples and photographs from the hunt). In addition, the collation of information on the geographical and temporal distribution of the hunt will be valuable.

Annex E, item 2.6 provides some general guidance for the 2011 *Implementation* Review. The Committee **agrees** that any acceptable future *SLA* for the hunt in the Pacific northwest must include a feedback mechanism. It also requests that the Chair of the SWG discuss its requirements for need envelopes with the hunters and members of the

US delegation. The Committee **agrees** that the following would assist, but are not required for beginning, the trial development process:

(1) Collection/analysis of genetic data that would allow more robust comparison of such data from animals in the northern and southern feeding areas;
(2) Collection/analysis of genetic data from Kodiak Island to California to further examine the probable range of the PCFG;
(3) Collection/analysis of genetic data to compare further animals seen in only one year ('stragglers' in SC/62/BRG32) with animals that are frequently seen within the hunting area;
(4) Collection/analysis of additional information (including telemetry data) on the relative temporal 'availability' of PCFG animals within the hunting area (e.g. by month); and
(5) An updated analysis of any additional data to obtain the most recent abundance estimate for the PCFG at the time of the 2011 *Implementation Review.*

8.2.8 Conclusions and recommendations

In light of the DAA difficulties discussed earlier, the Committee **agrees** that it has completed the *Implementation Review* on the basis of the data that had been made available to it in accord with the DAA. However, given the new information available that did not meet the DAA conditions, it **agrees** that a new *Implementation Review* should occur in 2011 to take into account information provided on the PCFG which was presented outside the DAA as noted under Items 8.2.2 and 8.2.7. The Chair of the SWG **agrees** to ensure that all likely contributors to the review are made aware of the DAA requirements as well as the guidelines for genetic analyses and data. The draft guidelines for *Implementation Reviews* referred to under Item 8.4 will also assist this process. The Committee also **agrees** that preparatory discussions for the 2011 *Implementation Review* take place at the proposed intersessional workshop (see Item 21). Management advice for this population can be found under Item 9.2.2.

8.3 Continue work on developing *SLA*s for the Greenlandic fisheries

In 2009, the Committee agreed an approach for providing safe interim advice on catch limits that is valid for up to two five-year blocks. In doing so, this provides time for the SWG to develop long-term *SLA*s for the Greenlandic fisheries. Work on this has progressed in general terms (e.g. see discussion in SC/62/Rep3 and Annex E, items 3.3 and 4.2). However, particularly given the complexity of the multispecies hunt in Greenland, the Committee **agrees** that this must be given high priority for the future work of the SWG, such that suitable *SLA*s can be developed and tested before the interim advice expires.

Simulation evaluation of *SLA*s requires the development and parameterisation of a set of operating models. Unlike the situation for West Greenland common minke whales, the SWG has an assessment for West Greenland fin whales which means that it is in a better position to develop an *SLA* for fin whales. Last year, it was agreed that the set of RMP trials developed to evaluate variants of the RMP for North Atlantic fin whales would be an appropriate starting point for developing such trials and this year the SWG was presented with a summary of the stock structure hypotheses underlying those trials. These will need to be modified to focus more on the uncertainties pertinent to West Greenland if they are to form the basis for evaluation of *SLA*s for fin whales. Unfortunately, the SWG did not have time to consider this further at the present meeting.

With respect to common minke whales off West Greenland, the SWG had previously been awaiting the outcome of the evaluation of a sex ratio method approach before addressing the issue of long-term *SLA*s; the decision potentially to cease work on a sex-ratio abundance estimate in 2011 (see Item 8.1) does not affect the need to begin work on an *SLA* as soon as possible. As noted in SC/62/Rep3, consideration of existing RMP trials for North Atlantic common minke whales may again prove a useful starting point for discussions.

In conclusion, the Committee **re-emphasises** the importance of developing *SLA*s for Greenlandic fisheries as soon as possible. It **agrees** that this should form the primary item for discussion at the intersessional workshop.

8.4 Consider lessons learned from the bowhead whale *Implementation Review*

Two main issues arising from the bowhead *Implementation Review* relating to: (1) stock structure and in particular genetic samples; and (2) data availability. In relation to the first of these two issues, the Committee noted that there are now guidelines for DNA data quality (IWC, 2009h).

In relation to the general question of data availability, a number of issues were raised in the SWG (see Annex E, item 8). One reason for the difficulties encountered was the lack of explicit guidelines for conducting *Implementations* and *Implementation Reviews* for the AWMP process, noting how valuable these had proved for the RMP process. The Committee **agrees** that Donovan should develop a draft of such a document for consideration at next year's meeting.

8.5 Aboriginal Whaling Scheme (AWS)

In 2002, the Committee strongly recommended that the Commission adopt the Aboriginal Subsistence Whaling Scheme (IWC, 2003a, pp.22-23). This covers a number of practical issues such as survey intervals, carryover, and guidelines for surveys. The Committee has stated in the past the AWS provisions constitute an important and necessary component of safe management under AWMP *SLAs* and it **reaffirms** this view. It noted that discussions within the Commission of some aspects such as the 'grace period' are not yet complete.

8.6 Other

8.6.1 Conversion factors for edible products for Greenland fisheries

IWC/62/9 is the report of a Small Working Group (Donovan, Palka, George, Hammond, Levermann and Witting) established by the Chair of the Commission to provide advice on conversion factors for the Greenlandic hunt. The report of the group was presented to the intersessional Commission meeting to consider Greenlandic strike limits. In discussion of the report at that meeting, it was agreed that there was no need for the report to be reviewed in detail by the Scientific Committee but that individual scientists should send comments to the authors so that the report could be revised, if necessary, by the Commission meeting in Agadir. That request and the document itself was circulated to the Scientific Committee with a request for comments by 6 June 2010. However, it had been agreed that this issue would be added to the SWG agenda.

A short summary of the report, which has been available on the IWC website since February 2010, is given in Annex E, item 9.1[2].

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[2] The full 52 page report can be found at *http://www.iwcoffice.org/_documents/commission/IWC62docs/62-9.pdf.*

In discussion of IWC/62/9 during the present meeting, one member provided a number of comments on the underlying approach to calculating conversion factors, as well as to the quality of the data used by the authors. Points raised included whether conversion factors should be based only upon what product yield has been achieved in the past, or whether it should consider what could be achieved with significant improvements in processing efficiency. He also commented on the likely inaccuracy and unreliability of the hunter collected data. He suggested that Greenland be asked to come back next year with data of verifiable quality on length and product yield, and/or that the Committee be given details of the new data collection methods, together with information on the process by which the reliability of the product yield data is verified. In response, the authors noted that they had spent considerable time and effort in investigating the original data, recognising that it had not been collected by scientists for the purposes of estimating conversion factors. The large sample size and the consistency with edible product information collected by scientists in the North Pacific, revealed that the data for common minke whales were sufficient to calculate a robust conversion factor (as well as showing the flensing process to be efficient). The limitations of the conversion factors provided for the other species were recognised in the report and considered interim pending the recommended collection of additional data on length correction and edible products. They had offered to assist in appropriate experimental design. They also noted that it would take some time to obtain sufficient sample sizes for some species. They concluded that matters of efficiency were appropriate for discussion by the Commission.

The Committee endorsed the **recommendations** of the report. In particular, it supported the recommendations for further work that data on both 'curved' and 'standard' measurements are obtained during the coming season for common minke whales, fin whales and bowhead whales and that new data on edible products be collected using properly-design protocols, analysed appropriately and reviewed. It also supported the recommendation that the work be undertaken by scientists, hunters and wildlife officers since this would improve the ability of hunters, particularly those in remote areas, to obtain more accurate length and weight measurements. The Committee was informed that Greenland has already begun to implement some of the recommendations of the Small Working Group and they will be implementing all of them in the next season. There is now increased collaboration between hunters, scientists and managers and improved estimates of the three types of edible product should be possible by having each product stored in separate bins and weighed. It was also noted that collaboration between hunters from Alaska and Greenland was underway with the respect to flensing techniques for bowhead whales. Finally, the Committee **requests** Greenland to provide information on its sampling scheme and data validation protocols to next year's meeting.

9. ABORIGINAL SUBSISTENCE WHALING MANAGEMENT ADVICE

9.1 Eastern Canada and West Greenland bowhead whales

9.1.1 Assess stock structure and abundance of Eastern Canada and West Greenland bowhead whales

The Committee has agreed at the previous three Annual Meetings to consider a single stock of bowhead whales in this region as the 'working hypothesis' while acknowledging that there is still some uncertainty about the population structure of bowhead whales in eastern Canada and western Greenland (e.g. IWC, 2009d). Last year, the Committee had expressed some disappointment that the expected genetic analyses had not materialised to take discussions further. It had noted that use of the term 'working' hypothesis implies that alternative hypotheses can still be considered and thus there should be consideration of both one stock and two stock hypotheses. The Committee was therefore pleased to receive this year a number of stock structure papers, some of which include the use of genetic data.

SC/62/BRG26 presented work on genetic differentiation of bowhead whales in Eastern Canada and Western Greenland. The study included sequence data for 346 individuals from Baffin-Bay-Davis-Strait and 197 individuals from Hudson-Bay-Foxe-Basin. There was a slight but significant genetic difference between the two areas in terms of F_{ST} based on haplotype frequencies. However, there was no differentiation between Hudson Bay-Foxe Basin and Cumberland Sound, an area presumed to be within the range of the putative Baffin Bay-Davis-Strait stock. In the context of other biological information available (SC/62/BRG23 and SC/62/ BRG25), the authors consider the observed F_{ST} to be consistent with the one stock hypothesis.

SC/62/BRG25 reported on the re-identification patterns of genetic markers from bowhead whales sampled in Eastern Canada and West Greenland. From the total of 647 identified individuals, 91 were re-identified within the same location and year. Of the remaining 556 individuals (208 males and 348 females), the authors found 16 re-identifications between years. Three of these were between sampling areas and all three had moved from the Hudson Bay-Foxe Basin area to the Baffin Bay-Davis Strait area. In addition, of the 20 new satellite tags put out in 2009 in Disko Bay, four animals had crossed assumed boundaries between putative stocks. The authors concluded that: (i) the low number of re-identifications between years indicates that the population is relatively large; and (ii) the high proportion of re-identifications and movements of satellite tagged animals between areas indicate a high rate of movement between the areas. In the authors' view, these results indicate that there is only one stock of bowhead whales in Eastern Canada and Western Greenland.

SC/62/BRG23 reported on the sexual segregation of bowhead whales sampled in Eastern Canada and West Greenland. Genetic samples (the same as used in the previous two papers) were obtained from one location in West Greenland: Disko Bay (April-June 2000-09) and four locations in Eastern Canada: Pelly Bay (September 2000-02), Cumberland Sound (June-August 1997-2006), Foxe Basin (July-August 1994-2007) and Repulse Bay (September 1995-2005). The sex-ratio was significantly different from 1:1 in Disko Bay (76% females), but this was not the case in the remaining areas. The authors also reviewed available field observations and historical whaling records in the region, which provided further evidence of segregation. They concluded that Baffin Bay is mainly used by adult males and resting/pregnant females, whereas the Prince Regent, Gulf of Boothia, Foxe Basin and northwestern Hudson Bay areas are used by nursing females, calves and sub-adults. The Committee noted that the available information is consistent with some form of structured movement, but that this movement is still not well understood.

There was considerable discussion of these papers and their strengths and weaknesses in their ability to distinguish among stock structure hypotheses as can be seen in Annex F, item 4.2. Some members of the Committee interpreted the seasonal movements and resighting patterns between the two areas to mean that there is a single stock whilst others believed that these movements and the observed shallow population structure between some areas are still consistent with the two-stock hypothesis. The Committee **agrees** that the degree of population structure requires further work with additional molecular markers (nuclear loci) before a final conclusion can be reached and it also **recognises** the importance of the successful satellite tracking study. It **encourages** the continuation of work on structure in order to allow it to conduct a more in-depth analysis next year.

The Committee also received two papers on abundance (Annex F, item 4.2.2). SC/62/BRG28 reported the results of an aerial survey of the late-summer concentration of bowhead whales in Isabella Bay, Nunavut, Canada in September 2009. The resulting abundance of 1,105 (95% CI: 532-2,294) was corrected for whales that were submerged during the passage of the survey plane, but not for whales missed by the observers because >90% of the sightings were detected by both platforms.

SC/62/BRG34 summarised a preliminary evaluation of the potential to use photographs and capture-recapture analyses to estimate the size of the Eastern Canada-West Greenland stock(s) of bowhead whales. The large and often remote summer range of these animals makes it difficult to obtain an aerial survey estimate of abundance. On the other hand, photographic surveys benefit from mixing among the separate sampling areas and have been successfully used to estimate abundance of the B-C-B stock of bowhead whales. The authors proposed that photographic surveys be directed at areas of known summer aggregations. Photography methods and analyses for the proposed surveys would follow methods used for the 2004 B-C-B bowhead population estimate (Koski *et al.*, 2009), which has been accepted by the IWC. The Committee **welcomes** these papers and looks forward to further analyses at next year's meeting.

9.1.2 Review recent catch information

SC/62/BRG27 reported that two female and one male bowhead whales were taken in April-May 2009 and three females in April-May 2010 for subsistence purposes in Disko Bay, West Greenland (no whales were struck in 2008 and no whales were struck and lost in 2009 and 2010). In light of the uncertainties surrounding eastern Arctic bowhead stock structure and abundance, the Committee **requests** the Secretariat to contact Canada to try to obtain data on Canadian catches.

9.1.3 Management advice

In 2007, the Commission agreed to a quota for 2008 to 2012 of two bowhead whales struck annually off West Greenland but the quota for each year shall only become operative when the Commission has received advice from the Committee that the strikes are unlikely to endanger the stock. In 2008, the Committee was pleased to have developed an agreed approach for determining interim management advice (IWC, 2009c), that is valid for two five-year blocks. The Committee again **agrees** that the current catch limit for Greenland will not harm the stock (noting that this applies whichever stock structure hypothesis prevails)**.** It was also aware that catches from the same stock have been taken by a non-member nation, Canada. It **agrees,** as in previous years, that should Canadian catches continue at a similar level as in recent years, this would not change the Committee's advice with respect to the strike limits agreed for West Greenland.

The Committee reviewed the catch limits in Table 4 of the Report of 'Proposed consensus decision to improve the conservation of whales from the Chair and Vice-Chair of the Commission' (IWC/62/7rev). For Eastern Canada/West Greenland bowhead whales, the Greenland strike limit is 2 per year (plus a carryover provision of two unused strikes from the previous year). The Committee **agrees** that the strike limits for Eastern Canada/West Greenland bowhead whales that are listed in table 4 of IWC/62/7rev are in accord with its advice, recognising that the normal regular review is also intended as part of IWC/62/7rev. However, the Committee notes that Canada may allow for regular catches from this stock. If the size of Canadian catches increases then the Committee's advice may change in that the total number of removals may exceed the safe limit determined by the agreed approach. If the Canadian catch increases, then the Committee wishes to draw attention to the fact that the total number taken from the stock may be greater than what is safe. Given the importance of this issue, the Committee **recommends** that the Secretariat should contact Canada requesting information about catch limits for bowhead whales.

9.2 Eastern North Pacific gray whales

9.2.1 Summary of previous season's catch data

A total of 115 gray whales (58 males, 57 females) was harvested in Chukotkan waters in 2009 and 1 was lost. A total of 6 of the 115 individuals were considered as unfit for consumption in 2009 (samples were taken from all 6). Biological sampling was conducted on 61 gray whales.

9.2.2 Management advice

As noted under Item 8.2, the Committee **agrees** that it has completed the *Implementation Review* but that a new *Implementation Review* should take place next year. In this context, the Committee **agrees** that its position with respect to the provision of management advice was unchanged from last year, i.e. the *Gray Whale SLA* remains the appropriate tool to provide management advice for eastern North Pacific gray whales. This remains the case, at least until the 2011 *Implementation Review* is completed.

In line with the values in table 4 of the proposed consensus decision (IWC/62/7rev), the Secretariat ran the *SLA* using the updated information on catches and abundance agreed at this meeting. This confirmed that an annual strike limit of 145 animals will not harm the stock (note that 145 is the maximum catch that can be taken in any one year; the annual average catch is 129 whales). The additional five whales added to the annual maximum in any one year from that previously considered (140) was intended to account for 'stinky' whales (IWC/62/7rev). In providing its advice, the Committee **draws attention** to the need for a new *Implementation Review* next year with a focus on PCFG whales. It was noted that although the table included strike limits for 10 years, the proposed consensus decision envisages the usual periodic reviews of strike limits for indigenous whaling.

Borodin commented that the annual strike limit should include the actual number of struck-and-lost whales and 'stinky' whales (e.g. in 2009 the numbers were 1 and 6, respectively). If hunting is on large whales then the number of struck-and-lost whales will be higher. Within that context, he noted that the annual strike limit should not exceed 150 whales (the number included in the *Gray Whale SLA* trials for the early period of catches during the development process).

9.3 Bering-Chukchi-Beaufort (B-C-B) Seas stock of bowhead whales

9.3.1 Review catch information and new scientific information

The Committee was pleased to receive two papers dealing with broad-scale aerial surveys from the northeastern Chukchi (SC/62/BRG13) and Alaskan Beaufort (SC/62/BRG14) Seas respectively. Details can be found in Annex F, item 4.1.1.

SC/62/BRG13 presented preliminary analyses of broad-scale aerial surveys for large whales in the northeastern Chukchi Sea that were conducted in 2008 and 2009, and compared these with results from similar surveys conducted in that region from 1982-91. The distribution of bowhead whale sightings during the light ice years of the early period (1982, 1986, 1989 and 1990) was similar to the distribution of bowhead sightings during 2008-09. There did not appear to be any major shifts in cetacean distribution between the early and late surveys although there were unexpectedly no gray whale sightings in the offshore shoal areas during 2008-09. In general, it was noted that analysing cetacean distribution in relation to environmental factors like sea-ice was complicated with this data set because the timing of the surveys was not consistent between years.

SC/62/BRG14 presented a similar preliminary study for the Alaskan Beaufort Sea, using data from the Bowhead Whale Aerial Survey Project (BWASP) in 2000-09, with comparisons to historical data. Bowhead distribution was similar in 2000-09 compared with the observed distribution from earlier years with light ice cover.

The Committee **recommends** that these surveys continue on an annual basis in the future in light of their capacity to monitor the effects of climate change and other factors (including anthropogenic activities) on cetacean distributions in the Beaufort Sea.

SC/62/BRG17 provided information about acoustic monitoring during attempts to count migrating bowhead whales near Point Barrow, Alaska in 2009 and to test new acoustic equipment. Results demonstrated the efficacy of a new seafloor array procedure and indicate that it can be used in the future as the method for obtaining acoustic data for the bowhead census and population estimation process. The Committee **welcomes** this report and **encourages** the use of autonomous seafloor acoustic recorders when monitoring migrating bowhead whales.

The Committee also received information on summarised preliminary analyses on identifying yearling bowhead whales in aerial photographs (SC/62/BRG29) and recent efforts to estimate the population size of this stock of bowhead whales (Annex F, item 4.1.1). The Committee welcomed this new information and notes that a full survey effort is being planned again in 2011. In discussion, the importance of monitoring the tails of the distribution of migrating whales was noted in the light of information from this year's migration.

9.3.2 Management advice

SC/62/BRG18 provided information on the 2009 Alaskan hunt. A total of 38 bowhead whales were struck resulting in 31 animals landed). Challenging sea ice conditions and weather contributed to a poor spring hunt. Of the landed whales, 12 were males, 18 were females, while sex was not determined for one animal. Hunters mistakenly harvested two female calves (lengths of 6.2m and 6.6m) in the autumn thinking they were small independent whales. Autumn calves are close in body length to yearlings and it is difficult to determine their status when swimming alone. Other details are given in Annex F, item 4.1.2. It was reported that there were no catches of bowhead whales by Russia this year.

The Committee **reaffirms** its advice from last year that the *Bowhead SLA* remains the most appropriate tool for providing management advice for this harvest. The results from the *SLA* show that the present strike limits are acceptable.

The next *Implementation Review* for B-C-B bowhead whales is scheduled in 2012. The purpose of the *Implementation Review* is to evaluate new information which has become available since the last *Implementation Review* and assess whether the current state is outside the realm of plausibility covered by the *Implementation* trials. If so, it may be necessary to conduct further trials incorporating such information. Therefore, the Committee **encourages** researchers to present relevant papers and new information for consideration during next year's meeting, so that preparations for the next *Implementation Review* can proceed efficiently.

The Committee reviewed the catch limits in table 4 of 'Proposed consensus decision to improve the conservation of whales from the Chair and Vice-Chair of the Commission' (IWC/62/7rev). For B-C-B bowhead whales, the maximum strike limit is 67 per year (plus a carryover provision of 15 unused strikes from the previous year) for total landed of 560 (580 written in footnote 8 is a typo). The Committee **agrees** that the strike limits for B-C-B bowhead whales listed in table 4 are in accord with the management advice provided by the *Bowhead SLA*, noting that the normal regular review is also intended.

9.4 Common minke whale stocks off Greenland (AWMP)

9.4.1 West Greenland

9.4.1.1 SUMMARY OF PREVIOUS SEASON'S CATCH

In the 2009 season, 153 minke whales were landed in West Greenland and 11 were struck and lost. Of the landed whales, there were 105 females, 47 males, and one whale of unreported sex. Genetic samples were collected for 97 of the 153 minke whales landed in 2009.

9.4.1.2 MANAGEMENT ADVICE

In 2007, the Commission agreed that the number of common minke whales struck from this stock shall not exceed 200 in each of the years 2008-12, except that up to 15 strikes can be carried forward. Prior to last year, the Committee has never been able to provide satisfactory management advice for this stock. Last year, the Committee was for the first time able to provide management advice for this stock. It had adopted a new abundance estimate and agreed method for providing interim management advice. Such advice can be used for up to two five-year blocks whilst *SLAs* are being developed (IWC, 2009c). Based on the application of the agreed approach, and the lower 5th percentile for the 2007 estimate of abundance (i.e. 8,918), the Committee **repeats its advice** of last year that an annual strike limit of 178 will not harm the stock.

9.4.2 East Greenland

9.4.2.1 SUMMARY OF PREVIOUS SEASON'S CATCH DATA

Three males and one female common minke whale were struck (and landed) off East Greenland in 2009 (no animals were struck and lost; see SC/62/ProgRepDenmark). Genetic samples were obtained from two of these whales. Catches of minke whales off East Greenland are believed to come from the much larger Central stock of minke whales.

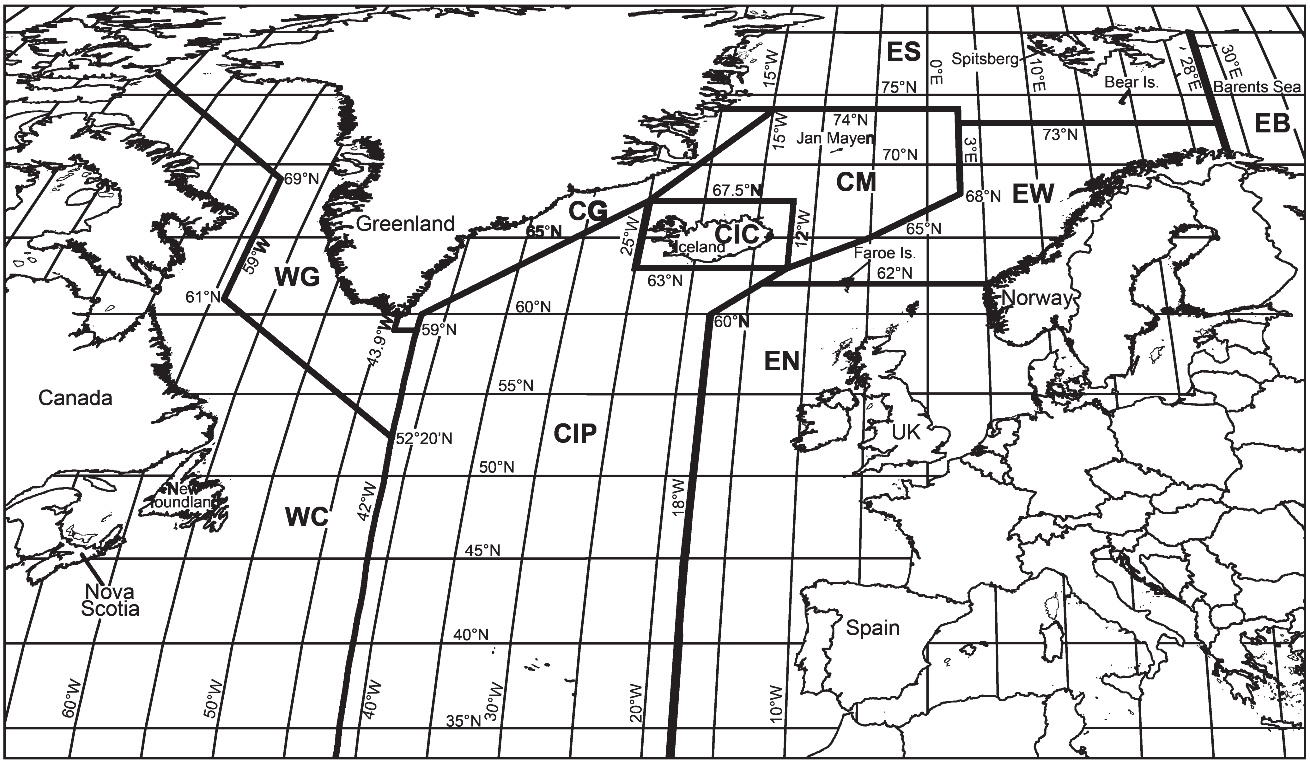

Fig. 2. The specifications for the Small Areas for the North Atlantic minke whales.

Table 3

Most recent abundance estimates for minke whales in the Central North Atlantic.

Small Area(s)	Year(s)	Abundance and CV
CM	2005	26,739 (CV=0.39)
CIC	2007	10,680 (CV=0.29)
CG	2007	1,048 (CV=0.60)
CIP	2007	1,350 (CV=0.38)

9.4.2.2 MANAGEMENT ADVICE

In 2007, the Commission agreed to an annual strike limit of 12 minke whales from the stock off East Greenland for 2008-12, which the Committee stated was acceptable in 2007. The present strike limit represents a very small proportion of the Central Stock (see Fig. 2 and Table 3). The Committee **agrees** that the present strike limit will not harm the stock.

9.5 Fin whales off West Greenland

9.5.1 Summary of previous season's catch data

A total of 8 (1 male; 7 females) fin whales were landed, and 2 struck and lost, in West Greenland during 2009 (SC/62/ProgRepDenmark). Genetic samples were collected for 5 of the 8 fin whales harvested during 2009.

9.5.2 Management advice

In 2007, the Commission agreed to a strike limit (for the years 2008-12) of 19 fin whales struck off West Greenland. The Committee agreed an approach for providing interim management advice in 2008 and this was confirmed by the Commission. It had agreed that such advice could be used for up to two five-year blocks whilst *SLA*s were being developed (IWC, 2009c). Based on the application of the agreed approach in 2008 (IWC, 2009c), the Committee **agrees** that an annual strike limit of 19 whales will not harm the stock.

9.6 Humpback whales off West Greenland

In 2007, the Committee agreed an approach for providing interim management advice and this was confirmed by the Commission. It had agreed that such advice could be used for up to two five year blocks whilst *SLA*s were being developed (IWC, 2009c). Using this approach, as last year, the Committee **agrees** that an annual strike limit of 10 whales will not harm the stock.

9.7 Humpback whales off St Vincent and The Grenadines

9.7.1 Summary of previous season's catch data

The Committee was advised that three females (lengths 34', 34'3" and 43'2") were taken during 2010. Neither genetic samples nor photographs were available for these animals. The Committee has encouraged St Vincent and The Grenadines to submit as much information as possible about any catches to the Committee via an Annual Progress Report.

The Committee **strongly recommends** collection of genetic samples for any harvested animals as well as fluke photographs, and submission of these to appropriate catalogues and collections. In respect of genetic samples, the Committee again **agrees** that the North Atlantic Whale Archive maintained by Per Palsbøll is an appropriate facility.

9.7.2 Management advice

In recent years, the Committee has agreed that the animals found off St Vincent and The Grenadines are part of the large West Indies breeding population. The Commission adopted a total block catch limit of 20 for the period 2008-12. The Committee **agrees** that this block catch limit will not harm the stock.

10. WHALE STOCKS

10.1 Antarctic minke whales (IA)

The Committee is currently continuing an in-depth assessment of the Antarctic minke whale. To complete this assessment, agreed abundance estimates from CPII and CPIII[3] are needed. Two different abundance estimation methods have been developed during the last few years, and although they give quite different point estimates, both are consistent in that they show an appreciable decline from CPII to CPIII. During the JARPA review in 2009, the quality of the Japanese ageing methods was questioned with implications for the catch-at-age analyses. During the present meeting, the priority topics discussed included: the two abundance estimation methods; the reasons for the differences between CPII and CPIII; age reading and the catch-at-age assessment models.

10.1.1 Produce agreed abundance estimates of Antarctic minke whales using IDCR/SOWER data

Skaug reported on work conducted by the Abundance Estimation Intersessional Working Group. Tasks to be considered by the group were directed towards elucidating possible causes for the difference in abundance estimates for Antarctic minke whales from the IDCR/SOWER data from the recent OK (Okamura and Kitakado, 2009) and SPLINTR (Bravington and Hedley, 2009) models. In completing most of these tasks, substantial progress had been made towards this in two regards: (i) development of a reference dataset for model comparisons; and (ii) Bravington had completed a non-spatial version of the SPLINTR model. For (i), a number of internal inconsistencies in the 'standardised' dataset were identified; as noted in IWC (2010f), it is essential that when comparing models, the data are identical. Since the purpose of this dataset is to allow appropriate comparisons between the models, the Committee **agrees** that this dataset is suitable for this purpose.

SC/62/IA14 provided results from applying the IWC 'standard' method (Branch, 2006), and the OK and SPLINTR models to simulated data, focussing on the latter two. In general, both models performed well, although when bias did occur, it tended to be positive for the OK model and negative for SPLINTR. The Committee thanked Palka for co-ordinating this extensive study. The simulated datasets have proved valuable in helping to develop and refine the models and for examining the differences between them. No simulated scenarios show the level of difference between the OK and SPLINTR estimates that the real data analyses reveal. This suggests either that the magnitudes of factors currently in the simulations do not cover the ranges found in the real data (either singly or in combination), or that there are additional factors not currently in the simulations that are important for modelling the real data.

During the pre-meeting and using the reference dataset, the OK and non-spatial SPLINTR outputs were compared. Estimated mean school sizes, effective strip half-widths, and encounter rates were combined using the simple line transect formula for estimating abundance. The resulting examination revealed that: (1) these estimated quantities from each model were being combined correctly to estimate abundance; (2) the effective strip half-widths for OK were about half of those of SPLINTR (i.e. the estimated abundances were approximately doubled, highlighting a need for further investigation); and (3) that the difference between the two models was not due to the data used and was probably not due to differences in mean school size. The Committee questioned whether sufficient progress had been made to determine whether further investigation was likely to determine the reason for the difference between the models. It **agrees** that if the Work Plan, including an intersessional workshop, is accomplished, there is a reasonable chance that this will be the case. It therefore **agrees** to proceed with these investigations until the 2011 Annual Meeting. The Committee also **agrees** a number of technical points related to this intersessional work (Annex G, item 5.1.8).

However, contingency plans (e.g. producing model-averaged estimates of abundance) will also need to be considered if it does not prove possible to resolve the difference in the estimates. Skaug compared estimates from OK, SPLINTR and a model-averaged estimate on the simulated data and found that the model-averaged estimator had smaller bias than either of the two individual models. There was some discussion on the appropriateness of using model-averaged estimates on the real data. However, as noted above, given the progress made this year, it is anticipated that the best outcome would be a resolution of the issue as a result of the intersessional work.

SC/62/IA3 and SC/62/IA12 presented the following 'survey-once' estimates (see Branch and Butterworth, 2001b) of abundance for the CPII and CPIII surveys from the OK and SPLINTR models respectively, as summarised in Table 4.

The Committee thanked both sets of authors for producing estimates and for the substantial amount of intersessional work, much of it collaborative. As last year, the issue is not that either set of diagnostics suggests not accepting the estimates, but rather that the estimates themselves are so different. This leads to the need to consider three – not necessarily unrelated – issues for next year: (1) pursuing the work to explain the differences; (2) the implications, if any, for future surveys; and (3) the procedural question of what the Committee should do if (1) does not succeed. As part of IWC/62/7rev, the Committee is expected to undertake an RMP *Implementation* for Antarctic minke whales in 2015 (and see Item 20). There is thus a pressing need for agreed absolute abundance estimates for the past surveys and an agreed method for analysing data from future surveys.

The Committee **strongly recommends** that the work plan and timeline set out in Annex G, Appendix 3 to finalise estimates be followed and completed. A workshop, to be held by February 2011 at the latest (see Item 21), is an essential component of this.

10.1.2 Conduct an analysis of aging errors that could be used in catch-at-age analyses

Lockyer presented the results of the Antarctic minke whale ageing exercise (SC/62/IA11) which she had carried out intersessionally following the 'blind' experimental design agreed by the Scientific Committee (IWC, 2009e, p.209). The study was assisted by staff from the laboratory at the Tokyo University of Marine Science and Technology, under the supervision of Kitakado. This had involved reading 250 earplugs from 1974/75-2005/06, i.e. including both Antarctic commercial and JARPA samples. The primary aim of the work was to determine whether evidence exists of a drift in reader performance, and, if so, to quantify it. A secondary aim was to quantify age-reading error variability.

The Committee thanks Lockyer and the Japanese graduate students who had assisted her, and for the professional manner in which they conducted the experiment. It also

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[3] CPII and CPIII refer to the second and third set of IWC cruises, referring to 1985/86-1990/91 and 1991/92-2003/04, respectively.

Table 4

Comparison of 'survey-once' estimates of abundance, by Management Area, from the OK and SPLINTR models. Estimates shown have been extracted from the papers SC/62/IA3 and SC/62/IA12 and rounded, with CVs incorporating additional variance given in parentheses.

	Area I	Area II	Area III	Area IV	Area V	Area VI	Total
CPII							
OK	209,000	261,000	187,000	104,000	635,000	90,000	1,486,000
	(0.35)	(0.38)	(0.42)	(0.37)	(0.29)	(0.39)	(0.17)
SPLINTR	117,000	141,000	87,000	61,000	282,000	59,000	747,000
	(0.38)	(0.39)	(0.55)	(0.36)	(0.34)	(0.40)	(0.19)
CPIII							
OK	65,000	93,000	126,000	79,000	244,000	105,000	712,000
	(0.34)	(0.37)	(0.33)	(0.45)	(0.33)	(0.34)	(0.17)
SPLINTR	35,000	56,000	59,000	36,000	140,000	57,000	382,000
	(0.33)	(0.35)	(0.31)	(0.33)	(0.31)	(0.33)	(0.17)

endorses the recommendation by Lockyer that a standard reference set of minke earplugs be maintained for age-reading training purposes.

SC/62/IA2 explored the impact of period/reader on age-determination by comparing age-estimates for the above 250 earplugs for the control reader (Lockyer) and three Japanese readers (Masaki, Kato and Zenitani). Overall, the results demonstrated that the Japanese readers and the control reader differed in terms of both expected age given true age and variance in age-estimates. The results also suggested that the expected age and random uncertainty in age-estimates differed among the Japanese readers although the differences were not severe. This work will assist in determining how catch-at-age data are used in the statistical catch-at-age analyses and in future virtual population analyses.

The Committee **welcomes** this study as an important advance. It was noted that: (a) Lockyer tended to report greater ages than the Japanese readers; (b) differences amongst the Japanese readers were slight; and (c) that there was no indication of a trend in bias in Japanese readings over the period examined (i.e. from commercial whaling to special permit whaling). It was also noted that SC/62/IA11 does not provide any information about the accuracy of the age readings in absolute terms, given the absence of known-aged individuals. The absence of known-aged individuals is also the general norm for fish populations although for a number of these there are indications that layers were formed seasonally. Similarly, studies of fin whales, as well as corpora counts and information from animals with known histories, all indicate that the growth layers groups used to estimate whale ages are laid down annually.

In conclusion, the Committee **agrees** that no further experiments or analyses on age reading errors are needed to resolve ageing related problems raised in e.g. the JARPA review.

The Committee also **recommends** that, where they do not already, national or other guidelines for dealing with stranded animals include encouragement to obtain samples which could provide information on the animal's age.

10.1.3 Continue development of the catch-at-age models

SC/62/IA6 examined the impact of allowing for ageing error based on the analyses of the above (Item 10.1.2) age-reading experiment when conducting assessments for Antarctic minke whales in Areas III-E, IV, V and V-W using statistical catch-at-age analysis by means of sensitivity tests. These sensitivity tests explored three scenarios: (a) no ageing error; (b) ageing error is modelled as in previous base-models; and (c) ageing error is based on the results from SC/62/IA2. Time-trajectories of total (1+) population size and recruitment were qualitatively the same, irrespective of how age-reading error was modelled.

In discussion, it was noted that while estimates from recent years of recruitment and abundance for the three different assessments were close, absolute values showed relatively large differences until the 1960s, and estimation variance would be expected to be much higher over this period.

Though the Committee **agrees** that no further experiments or analyses on age reading errors are necessary. This decision did not, however, imply that other issues associated with the data and analyses, such as reasons for the different length distributions at age for younger-aged commercial and JARPA, had been resolved.

Completion of the work on investigation of catch-at-age based assessments requires undertaking the tasks as detailed in Annex G, item 5.2.4. These investigations will require an extension of permission from Japan for use of their Antarctic minke whale catch-at-age data, and would be improved if data from the most recent JARPA cruises could also be made available. The Committee **recommends** that such an approach be made to Japan under Procedure B of the DAA. Kato indicated that corpora count data were available, and that these data would be provided if necessary. An intersessional steering group under Punt was established to co-ordinate this work (see Annex Q).

10.1.4 Continue to examine the difference between abundance estimates from CPII and CPIII

Estimates from the OK, SPLINTR and standard methods (Branch, 2006) were consistent in that they showed a decline from CPII to CPIII. Conclusions reached about the reasons for these changes should integrate information from other sources such as changes in ice coverage during the survey periods concerned. Until recently, there was little quantitative information on the number of Antarctic minke whales that might be present within the pack ice. This year the Committee was pleased to receive several papers reporting on, and analysing data from, surveys of whales within the pack-ice.

SC/62/IA4 investigated trends of sea ice in the period of IWC IDCR/SOWER circumpolar surveys from CPI to CPIII (1978-2004). The sea ice trends are fundamental information to understand the year-to-year sea ice variability. The authors concluded that the difference in abundance estimates between the CPII and CPIII surveys can be partly explained by the change in the amount of open sea areas within the sea ice field. The Committee **agrees** that further region-specific investigation is necessary to examine the extent of the role changes in sea ice may play in examining the change in abundance estimates between CPII and CPIII. In this context the Committee received a progress report from the intersessional working group established to examine this issue (SC/62/IA5). The authors have made progress importing satellite sea ice data from Area II into a GIS database but the work is not expected to be completed until the next Annual Meeting. The Committee **recommends** that every effort be made to complete this important work on time. Although the exact nature of any models relating minke whales densities in open water to those in the ice was not discussed, it is important to continue investigation of the relationships between whale density and ice characteristics.

This requires investigation of at least: (1) the relationship between whale density and days after sea-ice melt; and (2) the relationship between estimates of abundance and sea ice characteristics. The Committee **agrees** the detailed plan for this work given in Annex G, item 5.1.8. Bravington, Murase, Kitakado and Kelly will co-operate in this work.

This year, the Committee was pleased to receive reports (SC/62/IA8 and SC/62/O15) from two aerial survey programmes: the Australian East Antarctic programme (which co-ordinated in 2009/10 with the SOWER survey) using a fixed wing plane; and the German programme surveying the area in the Weddell Sea from a helicopter launched from the ice breaker vessel, the *Polarstern* (which was also used as a Platform of Opportunity for cetacean sightings). These programmes represent some of the first attempts to gather quantitative data to estimate densities of minke whales in the pack ice. Preliminary analyses from each programme can be found in SC/62/IA9 and SC/62/IA13.

The Committee **welcomes** this work and a full discussion can be found in Annex G, item 5.1.6.2. It thanked the governments of Australia, Germany and the Netherlands for supporting this research. It also was **pleased** to see the successful collaboration (both in collection of data, and in regular communications and data exchanges) between the Australian programme and the SOWER survey.

10.2 Southern Hemisphere humpback whales

The report of the Committee on the assessment of Southern Hemisphere humpback whales is given in Annex H. This assessment has been on the agenda of the Scientific Committee since 1992. The Committee currently recognises seven breeding stocks (BS) in the Southern Hemisphere (labelled A to G - IWC, 1998b), which are connected to feeding grounds in the Antarctic (Fig. 3). Preliminary population modelling of these stocks was initiated in 2000 (IWC, 2001g) and in 2006 (IWC, 2007a), the Scientific Committee completed the assessment of BSA (eastern South America), BSD (western Australia) and BSG (western South America). The assessment of BSC was completed in 2009 (IWC, 2010g). Since then, the completion of the assessment of BSB (western Africa) has been considered a priority by the Committee (IWC, 2010g, p.234).

10.2.1 Breeding Stock B

10.2.1.1 DISTRIBUTION

The Committee received several papers addressing the distribution, new records or habitat use of humpback whales along the central and northern Atlantic coast of Africa (Bamy *et al.*, 2010; Carvalho *et al.*, In review; Picanço *et al.*, 2009; Weir, 2010).

10.2.1.2 POPULATION STRUCTURE

It has been hypothesised that there may be two humpback whale sub-stocks in the eastern South Atlantic (IWC, In press). Breeding sub-stock B1 winters along the central West African coast and around the northern islands of the Gulf of Guinea and sub-stock B2 has been observed off the west coast of South Africa (WSA), in an area which appears to serve as a feeding site or possibly a migratory corridor. The breeding site of sub-stock B2 is unknown. A boundary between these two sub-stocks has been tentatively placed in the vicinity of 18°S (IWC, In press), see Fig. 4. At this meeting, the Committee further evaluated the evidence for BSB substructure, in light of new information.

SC/62/SH30 presented three stock structure hypotheses that were used in the assessment models. These hypotheses included: (1) a single, fully-mixed stock; (2) two breeding stocks that mix only on the feeding grounds and (3) two breeding stocks with partial migratory overlap along the west coast of Africa. SC/62/SH8 described temporal population structure in humpback whales on the west coast of Africa using maternally (mitochondrial DNA control region) and bi-parentally (10 microsatellites) inherited markers. Results showed significant genetic differentiation, low gene flow and

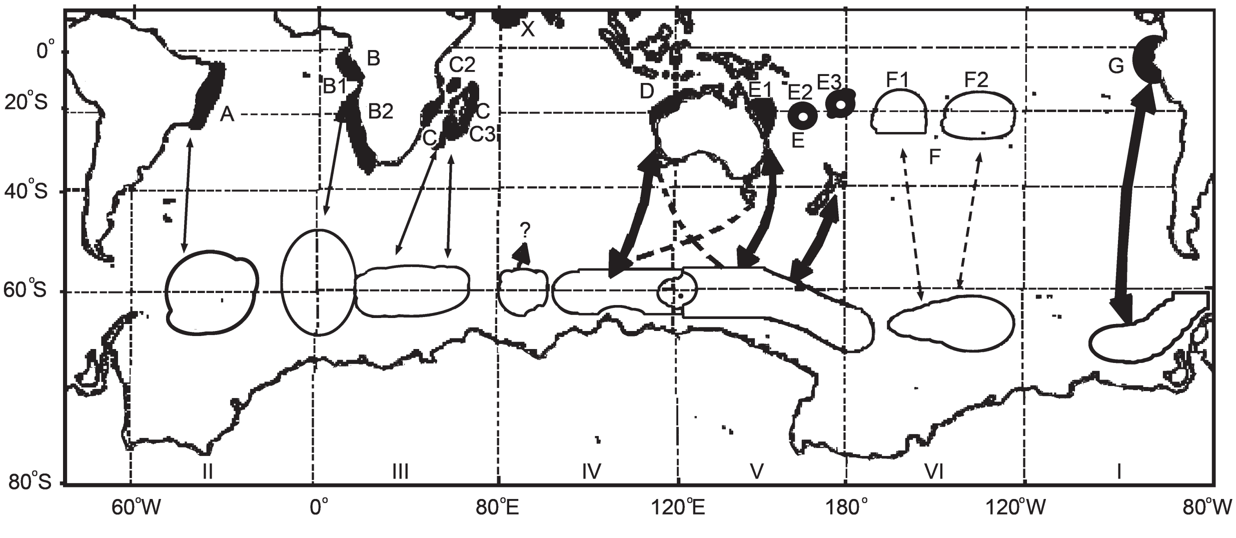


Fig. 3. Southern Hemisphere humpback whales, breeding stocks and feeding grounds (IWC, in press).

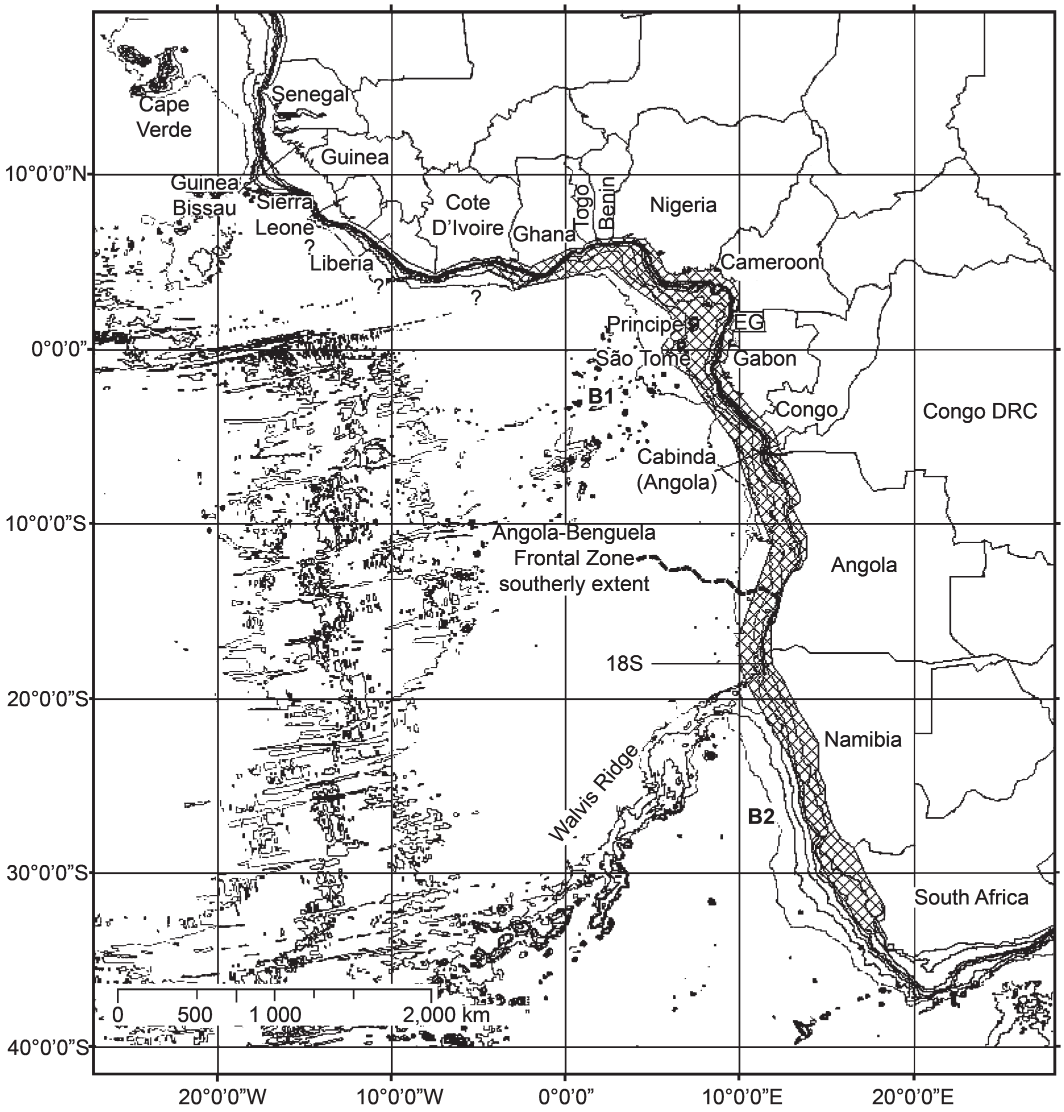


Fig. 4. Distribution of humpback whales in west Africa. The boundary between B1 and B2 has been proposed to be near 18°S (IWC, in press).

seasonal differences between WSA and Gabon. Movements of genetically identified individuals, both males and females, indicate that interchange occurs between these two region, with all movements to date being from north to south.

SC/62/SH15 examined humpback whale genetic structure in the Antarctic and evidence of connectivity to breeding grounds using biopsy samples collected during the 2006/2007 SOWER cruises. An updated analysis of the mitochondrial DNA (mtDNA) data presented in this paper was received during the meeting. Population structure was evaluated for the feeding grounds associated with BSB and BSC, under the catch allocation Hypotheses 1 and 2 developed by the Committee last year (Findlay *et al.*, 2010, fig.1). Under Allocation Hypothesis 1, Gabon was found to be significantly different from the Nucleus feeding areas of both BSB (10°W to 10°E) and BSC (30°E to 60°E). For Allocation Hypothesis 2, samples from Gabon were found to differ significantly from the BSB Nucleus (10°W to 10°E) and BSB/BSC Margin (10°E to 40°E). WSA was significantly different from BSB and BSC Nucleus, as well as the BSB/C margin area. Feeding grounds of BSB and Margin of B/C were found to be significantly different from the Nucleus area associated with BSC under Allocation Hypothesis 1. No significant differentiation was found across feeding areas under Allocation Hypothesis 2.

An analysis of mtDNA on feeding grounds (10°W-10°E) by latitudinal gradient revealed that no significant difference between Gabon and samples collected north of 60°S. WSA differed from samples obtained both north and south of 60°S on the basis of F_{ST} but significance was only found for samples obtained north of 60°S. These results were interpreted as indicative of some type of latitudinal variation in the distribution of whales from BSB in the Antarctic.

The Committee welcomed the genetic studies described above; this research is relevant to the assessments of Southern Hemisphere humpback whale stocks. The Committee **recommends** that a mixed stock analysis be performed to better inform stock structure assumptions and to increase the available data for population dynamics modelling.

The Committee also considered new photo-id matching results relevant to the stock structure of BSB. SC/62/SH10 presented preliminary results of photographic matching between Gabon, WSA and Antarctic Areas II and III. A total of three matches were found between Gabon and WSA. SC/62/

SH31 reported no matches resulted from the comparison of a photo-id catalogue from WSA and another from the south coast of east South Africa and southern Mozambique (BSC1). It was noted that a substantial number of images held by Oceans and Coast (the South African governmental agency from BSC1) have not been compared to WSA. In this regards, the Committee **recommends** comparisons of the WSA fluke photographs to the Oceans and Coast catalogue and **requests** that the relevant photographs and associated information be made available.

Barendse *et al.* (2010) described the results of shore-based observations on humpback whales off Saldanha Bay, WSA. This area was presumed to be a migration corridor for whales from the postulated BSB2 breeding sub-stock. The authors concluded that the area off WSA is not strictly a migration corridor, but also a primary or supplementary feeding ground. Discussion of this paper is given in Annex H, item 2.1.2.

SC/62/SH5 reviewed the catch history, seasonal and temporal trends in availability and the migrations of humpback whales along the west coast of southern Africa. After the initial decline in availability in all areas pre World War I, the catch history in Gabon differed markedly from those in the three southern grounds, especially off South Africa. This suggests some degree of stock sub-structure within BSB. A hypothesis of a single breeding ground (in the Gulf of Guinea) but separate, maternally-directed migratory routes to and from different feeding grounds was proposed.

The Committee concluded that the following points were relevant to the development of stock structure hypotheses based on its extensive review of information:

(1) there is probably more than one genetically distinct humpback whale population in the eastern South Atlantic;
(2) Gabon is a breeding ground and WSA exhibits characteristics of both a feeding ground and a migratory corridor;
(3) at least some of the animals sampled at Gabon migrate to the Antarctic to feed and that migration may follow an inshore route (via WSA), an offshore route or both (if the latter individual migrants maintain fidelity to a particular route or maintain alternate routes);
(4) some of the whales that breed at Gabon may maintain maternal feeding site fidelity to west South Africa, such that they do not migrate to the Antarctic; and
(5) individuals observed at WSA may migrate to an unidentified breeding site that is distinct from Gabon (if so, some fraction of those individuals may pass by Gabon, *en route* to that breeding site) or the breeding ground of these individuals may lie between Gabon and WSA.

In light of the new information presented above, the Committee indentified new stock structure hypotheses and progressed with exploratory population dynamics model runs. Results of these analyses are presented under Item 10.2.1.4 below. A minority statement in relation to item (5) above is found in Annex H, item 2.1.2.

10.2.1.3 ABUNDANCE ESTIMATES

The Committee received two papers with abundance estimates based on capture-recapture data. SC/62/SH2 reported on within-region photo identification and genotypic matching for WSA. Resightings between six different time-periods and five different datasets (three from photo-id data, one from microsatellite data and one combined) resulted in estimates of abundance ranging from 223 (CV=0.35) to 939 (CV=0.38) individuals. SC/62/SH11 presented estimates of abundance for humpback whales in Gabon for the period 2001-06 using photographic and genotypic data. While the estimates themselves provided in this paper were not discussed, the capture-recapture data were used in preliminary assessment models presented at the meeting (SC/62/SH30). Details of these papers and the data therein are presented under item 2.1.3 in Annex H.

10.2.1.4 POPULATION ASSESSMENT

After initial discussion of the assessment models in SC/62/SH30, the Committee developed additional stock structure hypotheses on the basis of the new information presented in Item 10.2.1.2. Additional model runs were then undertaken to inform the Committee about possible implications of various stock structure hypotheses and input data selection for population model outputs. Preliminary results suggested that the assessment model parameter estimates were relatively robust across the proposed stock structure hypotheses and input data for sub-stock B1 (Gabon). However, the population trajectories varied widely for sub-stock B2 (WSA). Based on these results, the Committee concludes that additional modelling was required and **agrees** upon a suite of stock structure hypothesis that would probably be used in the assessment of BSB (Annex H, item 2.1.4). The Committee selected three priority hypotheses that it **recommends** should be used in further population assessment (Fig. 5).

The Committee also discussed model input data and possible sensitivity analysis when evaluating the results of the stock assessment models (details in Annex H, item 2.1.4). Input data included allocation of breeding and feeding ground catches, values for minimum past population sizes (N_{min}), type of capture-recapture data (photo-id, genotype), proportions of whales migrating to breeding and feeding grounds, and rate of struck and lost whales. The Committee **agrees** to a selection of input data to be used as the reference cases and sensitivity scenarios in the population dynamic models, as presented in Table 5.

The Committee **agrees** that considerable progress was made during the meeting. However, there was insufficient time to complete the assessment of BSB. In this regard, the Committee notes that last year it had agreed to complete the assessment of BSB as a single stock if an assessment at the sub-stock level was not possible. However, in light of the new information brought forward this year, the Committee **agrees** that a considerably more robust assessment could be finalised if additional work was conducted intersessionally. The Committee **agrees** that the completion of the assessment of BSB by 2011 is a matter of the highest priority for the sub-committee on other Southern Hemisphere humpback whales. It **strongly recommends** that the strict work plan outlined in Table 6 be followed to facilitate completion at next year's meeting. Regular progress on these tasks will be monitored and reported by Zerbini to an intersessional group (Annex Q). The Committee **recommends** a pre-meeting to the Annual Meeting to ensure the timely completion of this work.

The modelling required to complete the assessment has financial implications for the Committee and this is discussed under Item 24.

The Committee **agrees** that it will conclude the assessment of BSB humpback whales at next year's meeting. Therefore, the Committee **recommends** that assessments of BSE and BSF humpback whales should be initiated and a progress report be presented at SC/63. An intersessional e-mail group was established under Jackson to assemble all the relevant

Table 5

Input data reference cases and sensitivities selected for use in population modelling for the assessment of BSB.

Data category	Population	Reference case	Sensitivity analysis
Capture-recapture	Gabon	Microsatellites, males-only* (see note below)	Flukes; microsatellites (both sexes)
Capture-recapture	WSA	Microsatellites* (see note below)	Right dorsal fin; flukes
Minimum past population	Gabon	$N_{min} = 68$	None
Minimum past population	WSA	$N_{min} = 24$	None
Catch allocation (north of 40°S)	Gabon	Congo and 50% Angola	Congo and Angola; Congo only
Catch allocation (north of 40°S)	WSA	50% Angola, Namibia and WSA	Namibia and WSA; Angola, Namibia and WSA
Catch allocation (south of 40°S)	Gabon	Allocation Hypothesis 1 developed last year	None
Catch allocation (south of 40°S)	WSA	Allocation Hypothesis 1 developed last year	None
Migration to unknown breeding ground	Gabon	25%	None
Migration to Antarctic	WSA	50%	100%; 0% (does not migrate)
Struck and loss rate	Both	0.15 (as presented in SC/62/O2)	0

*Microsatellite data will only be used as a reference case for capture-recapture data if genotyping errors can be incorporated into assessment models. Otherwise flukes will be used.

Table 6

Intersessional tasks to finalise the assessment of BSB humpback whales.

Task	Responsible persons	Final deadlines: Circulation to group for consideration	Final deadlines: Decision regarding use in model
Work on data inputs to model and possible refinements to stock hypotheses			
Inspection of mark-recapture data within and between Gabon and WSA for consideration in stock structure hypothesis refinement.	Barendse and Collins	15/12/10	31/01/11
Investigate and update estimates of potential and realized error in genetic and photo-identification data.	Carvalho, Collins, Rosenbaum, Cerchio	15/12/10	31/01/11
Re-analyse mark-recapture data from WSA using multi-year Program MARK (or equivalent) models to examine the effects of heterogeneity (for fluke data), tag loss (for dorsal fin data) and genotype error on abundance estimates, and assess the most appropriate data on interchange.	Barendse, Cerchio, Best	15/12/10	31/01/11
Conduct feeding-breeding ground mixed-stock analysis in order to estimate stock mixing proportions between Gabon and WSA and the Antarctic in order to further refine stock structure hypotheses for assessments.	Rosenbaum, Carvalho, Loo	15/12/10	31/01/11
Examine catch data for incorporation in population models, which should be sex-disaggregated, if possible.	Best and Butterworth	15/12/10	31/01/11
Comparison of WSA catalogue to South African government Oceans and Coast Catalogue (advantageous but not critical).	Barendse, Findlay and Meyeo	01/12/10	31/01/11
Modelling work			
Development of assessment models consistent with stock structure hypotheses selected by the Committee. Highest priority is for the models in Annex H, table 2. To the extent time permits variants of these models will be considered as sensitivities (Annex H, table 3).	Butterworth, Muller, Johnston	Some initial runs for highest priority stock hypotheses	Final runs for at least highest priority stock hypotheses
The assessment models should use the input data identified as the reference cases and sensitivities in table 2 above. Data output should include the posterior median and the 90% probability interval for the year for which the abundance prior corresponds.		15/01/10	One week before pre-meeting
Present results for at least highest priority hypotheses.			

data needed for these assessments. The assessment of BSD humpback whales (western Australia) had been completed at the SC meeting in 2005 (IWC, In press), but because of extensive mixing in the feeding grounds with other stocks (e.g. BSE) this stock might needed to be re-assessed along with BSE and BSF. The intersessional group will also consider the inclusion of BSD humpback whales in the assessments of the two other stocks.

The Committee **agrees** that a new item will be added to its agenda to consider new information on the Arabian Sea humpback whale population.

10.2.2 Review new information on other breeding stocks

10.2.2.1 BREEDING STOCK A

The Committee welcomed two papers with new information relevant to BSA. SC/62/SH27 reported a photographic match of a female humpback whale between Abrolhos Bank, Brazil (BSA) and the east coast of Madagascar (BSC3), which represents a new mammalian distance record. SC/62/SH28 presented a new line-transect abundance estimate of 9,330 whales (95% CI=7,185-13,214; %CV=16.13) for the coast of Brazil in 2008. This stock appears to be undergoing a steady growth, but further studies are necessary to reduce uncertainties associated with *g*(0) estimation and other potential sources of bias. Further details are described in Annex H, item 2.2.1.

10.2.2.2 BREEDING STOCK D

Two papers provided information relevant to Breeding Stock D. These are summarised below, with additional details provided in Annex H, item 2.2.2. SC/62/SH21 reported on the deployment of 23 satellite tags on southward migrating whales off Kimberley coast, northwestern Australia. In total, 263 days of location data tracked whales over a total distance of nearly 20,000km. This work has provided the most detailed movement data off northwestern Australia to date and revealed an unexpected 1,200km movement from the coast into the Indian Ocean.

SC/62/SH24 described an unusual peak in recorded mortalities (n=47) of humpback whales in Western Australia

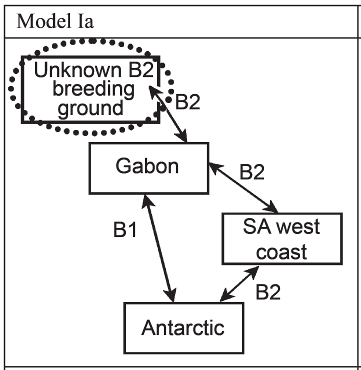
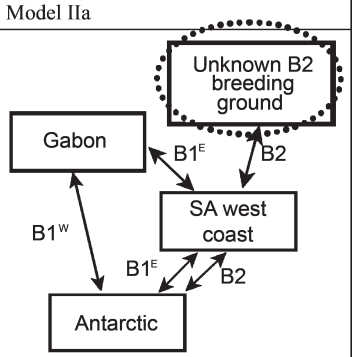
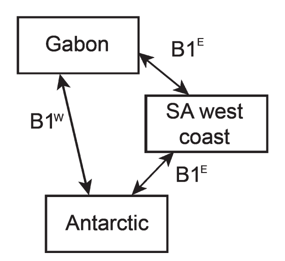
Model Ia	Model IIa	Model III
		
Model description: model assumes two independent breeding sub-stocks which can mix on Antarctic feeding grounds. Whales from breeding sub-stock B1 feed in the Antarctic and migrate to Gabon for breeding. Whales from breeding sub-stock B2 feed off WSA and migrate along the West African coast through Gabon to a separate unidentified breeding ground. Additionally, some portion of B2 animals migrate to Antarctic feeding grounds. Variants on this model were not considered priority for the assessment of BSB.	*Model description:* model assumes two breeding sub-stocks, B1 and B2. B1 has two migratory components, B1E and B1W. Whales from B1W migrate from Antarctic feeding grounds directly to Gabon while whales from B1E migrate through waters off west South Africa before continuing on to the Gabon breeding grounds. Whales from sub-stock B2 feed primarily off WSA, do not migrate past Gabon and migrate to a separate unidentified breeding area. In addition, some portion of animals from sub-stock B2 migrates to Antarctic feeding grounds. Variants on this model were not considered priority for the assessment of BSB.	*Model description:* model assumes a single breeding stock, B1, with two migratory components B1W and B1E. B1W migrates directly to Gabon from Antarctic feeding grounds while B1E migrates through waters off west South Africa before continuing on to the Gabon breeding grounds. The proportion of animals using each migratory route may change over time.

Fig. 5. Stock structure hypotheses selected as priority for use in the BSB assessment.

in 2009. Only a few mortalities have been reported per year in previous decades. The authors hypothesised that this event could represent:

(1) an artefact of searching effort and coastal oceanography;
(2) a temporary increase in mortality rates; or
(3) the start of an increasing trend in mortality.

They considered the latter two hypotheses to be the most plausible, but noted that additional research would be required to discriminate between them. The Committee noted the importance of continued stranding monitoring to clarify the cause of such unusual events.

10.2.2.3 BREEDING STOCKS E AND F

The Committee welcomed papers on Breeding Stocks E and F and noted these will be relevant for the forthcoming assessment of these stocks. Two papers provided new information on the distribution and habitat use of humpback whales along the east coast of Australia (BSE1).

SC/62/SH21 described results from 13 satellite tags from northward migrating humpback whales off Evans Head, eastern Australia. In total, 371 days of location data tracked whales for nearly 21,000km. The results represent the first detailed movement data of this species in their proposed calving area around the southern Great Barrier Reef.

SC/62/SH25 described the first on-water photo-id study of humpback whales in the Great Barrier Reef Marine Park Cairns/Cooktown Management Area. Thirty percent of the 28 groups observed contained young calves, indicating that this may be an important nursery area for BSE1. Seven individuals were matched to sightings in other areas of east Australia in previous years. Group size, composition, distribution and behaviour were also discussed. Further work is planned and data are available for collaborative research.

Three papers provided new information on the population structure and dynamics of BSE and BSF. SC/61/SH14 presented annual realised growth rates and survival of post-yearling BSE1 humpback whales off New South Wales, Australia (1994-2009). Several caveats were noted and suggestions for further analysis of these data are described in Annex H, item 2.2.2.

SC/62/SH7 reported on a large collaborative comparison of microsatellite genotypes from the migratory corridor along eastern Australia (n=734), the South Pacific Islands (n=1,086) and Antarctic feeding Areas I-VI (n=175). Breeding ground interchange was detected between Eastern Australia-New Caledonia (n=11) and Eastern Australia-Tonga (n=1). The only matches made to feeding grounds were between Eastern Australia and Antarctic Area V (n=3), despite larger sample sizes from Areas IV and VI. The authors concluded that breeding sub-stocks may be mixing on both their breeding and feeding grounds.

They also highlighted the feasibility of this type of collaborative research for studying migratory interchange on a large-scale. SC/62/SH18 reported photographic and genotypic mark-recapture estimates of abundance for humpback whales breeding at the South Pacific Islands (BSE2, BSE3 and BSF) for the period 1999-2003 and concluded that total combined abundance for these breeding stocks likely lies between 2,361 and 3,520 whales. No significant trend in abundance for this population was detected.

Additional details on the discussion of papers on BSE and BSF can be found in Annex H, item 2.2.3.

10.2.2.4 BREEDING STOCK X (ARABIAN SEA POPULATION)

The Committee received two papers with new information on the status of breeding stock (BSX). It had been given this name at a 2006 workshop on Southern Hemisphere humpback whales (IWC, In press). The population is believed to be resident to the Arabian Sea, is currently estimated at 82 individuals (95% CI=60-111) (Minton *et al.*, In press) and recently listed by the IUCN as endangered (Minton *et al.*, 2008). The Committee **agrees** to henceforth call this the Arabian Sea population.

SC/62/SH6 reported on the genetic distinctiveness and current population status of the Arabian Sea population. Genetic analyses based on 11 microsatellite markers and mtDNA sequences revealed significant differentiation between whales sampled off the coast of Oman (n=67), relative to the North Pacific and four Southern Hemisphere regions. Estimated levels of differentiation are among the highest recorded for humpback whale populations worldwide.

It is very unlikely that there is currently any exchange between the Arabian Sea and the Southern Indian Ocean stocks. Tests of population expansion suggest that the population has not yet started recovering and may still be in decline. SC/62/SH20 discussed the anthropogenic threats facing this population and challenges faced in monitoring this endangered population. Baleen whales in this region are potentially vulnerable to impacts from fishing, coastal development, shipping and noise and impacts. At least one live humpback whale entanglement in a gillnet is known to have occurred during the period 2007 and 2009. Research effort has been severely limited in recent years.

The Committee thanked the authors for this new information, noting its **great concern** over the status of this population. The Committee **strongly recommends** the continuation of research on humpback whales in the Arabian Sea in light of the small population size and escalating threats (see also Annex J, item 9.3). It further recognised the difficulty of undertaking such studies for small populations in remote areas.

The Committee also makes the following **recommendations** (in order of priority) for this population:

(1) studies that enable identification and quantification of threats to the Arabian Sea population should be initiated, including an in-depth investigation into the impact of bycatch;

(2) studies and surveys in Oman should be continued and expanded in scope to include more detailed genetic, acoustic and behavioural studies, as well as satellite telemetry studies;

(3) surveys should be encouraged in additional locations in confirmed range countries (Kuwait, India, Iran, Iraq, Oman, Pakistan, Sri Lanka, United Arab Emirates, Yemen), with particular focus on those countries with large coastal regions, such as Pakistan and India - in this regard, abundance surveys should be repeated on a regular basis in order to enable determination of population abundance and trend;

(4) further investigation into humpback whale occurrence in suspected/potential range countries (Bahrain, Maldives, Qatar, Saudi Arabia) should also be conducted; and

(5) studies and surveys to determine the population identity of whales in the Seychelles Exclusive Economic Zone should be performed.

The Committee further noted that given that this is a small population with known anthropogenic threats, it may well benefit from the development of a conservation management plan, following the model for western gray whales described under Item 10.4 and based upon Donovan *et al.* (2008). The Committee **agrees** that this should be explored further, perhaps within the context of conservation management plans being discussed by the IWC Conservation Committee

Further discussion of the Arabian Sea population is found in Annex H, item 2.2.4

10.2.2.5 FEEDING GROUNDS

SC/62/SH3 described a pilot study of cetacean distribution off Adélie Land that was launched by the French Polar Institute (IPEV) as part of the Southern Ocean Research Partnership (SORP). One photo-id match supported a migratory link between BSE and Area V. The Committee **recommends** the continuation of this programme, noting its relevance and utility for the forthcoming assessments of BSE and BSF.

SC/62/O12 presented a preliminary report of a joint Australian-New Zealand Antarctic Whale Expedition. Thirty humpback whales were satellite tagged on the Southern Ocean feeding grounds, and over 60 biopsy skin samples and approximately 60 individual fluke photographs were also collected. The Committee welcomed this research, which will make an important contribution to forthcoming assessments, and **recommends** its continuation. It also **recommends** that photo-id, biopsy sampling and satellite tagging research be conducted in other poorly surveyed areas of the Southern Hemisphere. The Committee **appreciates** the data sharing that has occurred post-expedition; this has been very productive with respect to matches identified with the East Australian breeding region and it **recommends** the continuation of such open collaborations. Finally, the Committee further **recommends** that long-term studies of humpback whales be undertaken and continued in the Southern Hemisphere.

SC/62/SH19 reported molecular genetic species identification of 281 whale bones collected between 2006 and 2007 in South Georgia. The prominence of humpback, fin and blue whale bones correspond to the early catch record in this area. Historical and contemporary humpback whale mtDNA haplotype diversity will be compared to measure the extent of the 'exploitation bottleneck' of stocks around South Georgia. The Committee **welcomes** this work and strongly **encourages** the continuation of bone collection for 'historical' DNA analysis. It further noted that this research will be important for the comparison of historic and current population abundance and diversity.

10.2.2.6 PRELIMINARY MULTI-STOCK ASSESSMENT

SC/62/SH33 reported preliminary results from the development of a population model that aimed to include all seven Southern Hemisphere humpback whale breeding stocks in a single joint assessment, with the purpose of allowing high-latitude historic catches to be allocated to breeding stocks in proportion to abundance, rather than on set ratios. The Committee **encourages** the further development of this model and the presentation of results in future meetings.

10.2.3 Antarctic Humpback Whale Catalogue

SC/62/SH17 described the progress of the Antarctic Humpback Whale Catalogue (AHWC). A total of 899 photographs of 721 individuals were catalogued from Antarctic and Southern Hemisphere waters for the interim period. Images were submitted by 21 individuals and research organisations. These submissions bring the total number of catalogued whales identified by fluke, right dorsal fin/flank and left dorsal fin/flank photographs to 3,665, 413 and 407, respectively. New inter-area matches were as follows: BSG-Antarctic Peninsula (19), BSG-Chile (3), BSA and BSC3 (1; see SC/62/SH27) and BSE-Antarctic Peninsula (2; see Robbins *et al.*, 2008). Re-sightings were also made at the Antarctic Peninsula (3) and within BSG (11). Progress continues to encourage contributions from researchers and eco-tourism. A new on-line catalogue using Flickr is in development and can be viewed at *http://www.flickr.com/ahwc*. The Committee noted the importance of this IWC-supported work and **recommends** its continuation.

10.3 Southern Hemisphere blue whales

In 2002, the Committee recommended that the assessment of blue whales be started in 2005, after the completion of the IDCR/SOWER review (IWC, 2003a, p.41). In 2008, the Scientific Committee completed a circumpolar assessment of Antarctic blue whales (IWC, 2009f) and recommended that area-specific analysis be examined to evaluate whether separate assessments can be done for each IWC Management Area (IWC, 2009f). The Committee also recommended gathering data relevant for the assessment of non-Antarctic (pygmy-type) blue whales. Detailed discussions from this year can be found in Annex H, item 3.

10.3.1 New information

The Committee welcomed new abundance estimates of blue whales off Chile. A new analysis of line transect data collected as part of the 1997/98 SOWER cruise off Chile (Williams *et al.*, 2009b) resulted in an estimate of 303 individuals (95% CI=217-455). Aerial line transect surveys conducted off Isla Chiloé in 2007, 2009 and 2010 resulted in estimates of 97 (CV=0.51), 154 (CV=0.32) and 163 (CV=0.39) individuals, respectively. Further details of these surveys are presented in Annex H, item 3.1.

At last year's meeting, the Committee noted that available line transect estimates probably do not represent the total size of the population(s) present and recommended other approaches be used to estimate blue whale abundance. Progress was reported on the Alfaguara Project's field season off Isla de Chiloe (southern Chile), and particularly its continuing blue whale photo-id research. A preliminary mark-recapture abundance estimate was also presented for pygmy blue whales at the Perth Canyon, Western Australia. Further description of that on-going work is provided in Annex H.

The Committee **recommends** that new or revised estimates of abundance be provided to next year's meeting; specifically from Chile (Galletti and Hucke-Gaete). For Western Australia (Perth Canyon) the level of research necessary to improve the mark recapture data (which is currently very sparse in recaptures) for updated abundance estimates is unlikely to be affordable in the coming year. The Committee also **recommends** that the intersessional e-mail group under Bannister continues to work toward providing new estimates of mark-recapture abundance of blue whales and to report new information at next year's meeting.

The Committee was informed of progress on the development of a cooperative Southern Hemisphere blue whale photo-identification catalogue (SHBWC). Nine groups have joined the SHBWC, including researchers in Chile, the Eastern Tropical Pacific, Australia, Sri Lanka, and Antarctica. Photo-id data from the Japanese Institute for Cetacean Research (ICR) Whale Research Program under special permit in the Antarctic (JARPA 1987/88-2004/05 seasons) has also been submitted to the IWC Secretariat and will be added to the SHBWC through the appropriate data availability channels. The Committee **welcomes** the update on the work of the SHBWC and **recommends** its continuation. It **recommends** that the photographs from the ICR catalogue should be compared to those already held at the Southwest Fisheries Science Center.

SC/62/SH29 reported on archiving and matching of blue whale photographs collected by the IDCR/SOWER cruises between 1987/88 and 2008/09. Over 23,000 photographs were obtained from all six IWC Management Areas, with 219 individual whales identified. Results suggest some degree of residency within a summer feeding season.

The Committee **recommends** that work on the Southern Hemisphere Blue Whale Catalogue (SHBWC) be continued. Over the next two years this will require completion of the matching from the three regions. Budget implications are given under Item 24.

SC/62/SH21 reported on satellite tagging of pygmy blue whales off southwestern Australia. Three tags were deployed (two males, one female) and the whales were tracked for over 8,000km. The tag with greatest longevity (137 days) provided definitive evidence of a link between whales that feed offshore of the Perth Canyon and those that occur around eastern Indonesia, such as the Banda Sea where reports of blue whales appear to be increasing.

The Committee welcomed a number of studies on blue whale acoustics. SC/62/SH26 described the migratory patterns and estimated population sizes of pygmy blue whales traversing the Western Australian coast. An analysis of passive acoustic data estimated that 662-1,559 pygmy blue whales passed the sampling instrument during the 2004 southbound migration. The Committee noted that the acoustic approach to estimating population size reported here represents an important theoretical development, but noted that a number of assumptions of this method needed to be explored in more detail before it could be considered to produce robust estimates of abundance. The Committee also encouraged the continuation of this work.

Gedamke and Robinson (2010) reported the results of an acoustic survey for whales and seals in eastern Antarctic waters (30-80°E) between January and February 2006. Blue whales were the most commonly recorded species identified. They were detected in large concentrations where relatively extensive sea ice remained off the continental shelf and the more eastern waters off the Prydz Bay region. Two detections of pygmy blue whales represent the most southerly recordings of these species.

SC/62/SH13 described results from passive acoustic monitoring for the presence of baleen whales off the coast of Northern Angola, off the Congo River outflow. A series of pygmy blue whale calls were detected by two marine autonomous recording units deployed between March and December 2008, 15km and 24km offshore. This represents the first confirmed modern documentation of this sub-species in Southeast Atlantic waters north of 60^{o}S since the cessation of commercial whaling for blue whales in the region. The calls were of the type attributed to the Sri Lanka population of pygmy blue whales, and not previously recorded outside of the Indian Ocean. Antarctic blue whale calls were not detected. The recording of Sri Lanka pygmy blue whale calls in the Atlantic Ocean was considered to be of great interest.

Progress was reported on a genetic study of Antarctic blue whales, which has been carried out with access to 218 IDCR/SOWER biopsy samples provided by the IWC. More than half of the haplotypes detected thus far have not previously been described. Analysis of the samples is ongoing and the results will be used to estimate the minimum historical population abundance of the Antarctic blue whale. The Committee welcomed this work and **recommends** its continuation. It was observed that this study expands on the haplotype data originally reported by LeDuc *et al.* (2007); the additional haplotypes reported here likely originated from IWC Management Areas II and III (Donovan, 1991), which were under-sampled in the previous study.

The Committee welcomed information on an upcoming study of the global taxonomy of blue whales using mitogenomic and nuclear sequence data. This work aims to conduct a comprehensive genetic assessment of blue whale taxonomy using next-generation sequencing methods to sequence whole mitogenomes and a large number of nuclear regions, for phylogenetic analysis. The project will particularly focus on determining the sub-specific status of blue whales in the North Pacific. The Committee **strongly encourages** continued collaborative efforts to acquire blue whale samples globally, and welcomed further updates on the results of the study

Four blue whale genetic projects are currently in progress: (1) genetics of blue whales in Geographe Bay, Western Australia, as part of a southern Australian study (11 samples collected, 11 analysed and archived, Möller, see SC/62/ProgRepAustralia); (2) a genetic population structure study of blue whales in the southeast and Eastern Tropical Pacific regions (Flores-Torres); (3) a global taxonomy study of blue whales (Lang); and (4) a genetic analysis of the diversity of IDCR/SOWER Antarctic blue whale biopsy samples and South Georgia whalebones (Sremba). The Committee **encourages** continuation of this research and **recommends** that results from these studies be reported when they become available.

10.4 Western North Pacific gray whales (BRG)

10.4.1 New scientific information

Considerable information was presented, and this is discussed in Annex F, item 6.1. Only a brief summary of that work is given here.

In SC/62/BRG11, data generated using a panel of 13 microsatellite loci were combined with updated information from mtDNA control region sequences to further assess the population structure of gray whales in the North Pacific. The results are consistent with the possibility that there may be some dispersal between two populations but that observed genetic differentiation is supportive of two populations.

SC/62/BRG10 presented the results of a paternity analysis conducted on the western gray whale population. The results suggest that some males that contribute to reproduction in this population may not regularly use the primary Sakhalin feeding ground. This highlights the need to collect genetic samples from animals recorded in other areas of the western gray whale's range. The results also provide evidence of interbreeding among animals that show fidelity to the Sakhalin feeding ground.

SC/62/BRG5 presents the first analysis of genetic (mtDNA) data obtained from the gray whales migrating along the Japanese coast (n=6) and incorporated comparison of these with a sample of animals from the Chukotkan hunt in 2008 (n=7). In summary, while recognising the small sample size: (a) all of the mtDNA haplotypes found had been previously reported; (b) the level of genetic diversity within samples was surprisingly high; (c) no genetic heterogeneity in haplotype frequencies was detected between the two samples; and (d) phylogenetic analysis of the haplotypes detected no distinct cluster for the Japanese whales.

The Committee **welcomes** these analyses. It **encourages** the collection of more samples from areas outside Sakhalin feeding ground when they are available and **recommends** a more detailed analysis of samples currently available and a number of suggestions are given in Annex F, item 6.1.

The Committee also received a number of papers on distribution and abundance. A number of points of interest were raised by these papers including:

(1) the potential for western gray whales to reoccupy parts of their former range if the currently small population expands (SC/62/BRG3);
(2) significant annual variation in whale densities among years within the Piltun and offshore feeding areas (SC/62/BRG4);
(3) updated information on an industry-sponsored monitoring programme using photo-id included the movement of animals between Sakhalin and Kamchatka and mother-calf pairs in Olga Bay, Kamchatka (SC/62/BRG9);
(4) updated information from the 2009 collaborative Russia-U.S. research programme (SC/62/BRG6);
(5) comparison of age at sexual maturity in western and eastern gray whales suggesting that the range 6-12 yrs is appropriate for both populations although further data would be welcome (SC/62/BRG2); and
(6) updated information on research and conservation in Japan including information on skeletal studies and an educational programme for fishermen (SC/62/O7).

The Committee **welcomes** all of the new information on this critically endangered population. It **encourages** further work and as in previous years, re-emphasises the importance of continued long-term monitoring. The Committee **recommends** that, if the observed density of gray whales in the Piltun feeding area continues to decline or remains lower than in previous years, future studies should investigate whether this reflects natural variation (e.g. in prey availability), industrial disturbance or some other factors.

Donovan reported on progress with the telemetry programme on western gray whales that has been recommended by the Committee (e.g. see IWC, 2010c). He reported that the programme is progressing and that all involved are grateful to Ilyashenko and his colleagues at IPEE for their work to try to ensure that this project goes ahead, particularly at this stage with respect to the permit issue. An overall administrative and scientific structure has been agreed between the participating institutions and companies, the IWC and IUCN. The scientific steering group is continuing to work on finalising the protocols that will ensure that the IWC Scientific Committee safeguards and guidelines are met as it has been tasked by the Committee; the final protocols will be drawn up in co-operation with IPEE and OSU. IWC, IUCN and the funding companies are also working hard on difficult budgetary issues. It is hoped that it will be possible for the programme to take place this summer.

10.4.2 Conservation advice

The Committee again **recognises** that the problem of net entrapment of western gray whales is a range-wide issue. It **welcomes** the efforts of Japan to reduce mortality, including the educational programme, and notes that net entrapments could occur in other range states. Brownell summarised plans for seismic surveys off Sakhalin Island in 2010. There is concern that anthropogenic sound, especially from seismic surveys, will negatively affect western gray whales in their primary feeding area. Previously, the Commission expressed concern and passed resolutions on this topic. Two seismic surveys in or near the feeding area are planned for 2010. It was noted at the recent meeting of the IUCN Western Gray Whale Advisory Panel that the company (Rosneft) planning the later survey has not followed the same procedures in regard to monitoring and mitigation as the company planning the first survey (by Sakhalin Energy). As currently planned, the Rosneft survey will occur while the highest number of feeding gray whales, including cow and calves, are present. The Committee is **extremely concerned** about the potential impact on western gray whales and **strongly recommends** that Rosneft postpone their survey until at least June 2011 The Committee also **recommends** that Rosneft use monitoring and mitigation measures similar to those used by Sakhalin Energy (see Annex F, Appendix 4), which have been independently reviewed by experts, and that all energy companies operating in the feeding areas of western gray whales should use comprehensive monitoring and mitigation measures to protect western gray whales.

As in previous years, the Committee **acknowledges** the important work of the IUCN Western Gray Whale Advisory Panel (WGWAP). This year's update on the panel's activities is given in Appendix 4 of Annex F. Noting that the WGWAP's present contractual five year life span ends after December 2011, the Committee **re-emphasises** its view that its work is important and should be **continued** if at all possible, and the Committee **requests** the Secretariat to send a letter to IUCN in this regard.

In 2009, the Committee welcomed the report of the IUCN range wide workshop (IUCN, 2009). An important conclusion of that workshop was the need for the development of a conservation plan for western gray whales and this recommendation was endorsed by the Scientific Committee.

This year, the Committee was extremely pleased to receive the first draft of this important Plan (SC/62/BRG24). It **commends** the authors, who include scientists from range states as well as elsewhere, for this important document. The Plan follows the guidelines developed for such plans by Donovan *et al.* (2008) that were endorsed by the Committee (IWC, 2009a). Much of it is based on the report and recommendations of the IUCN rangewide workshop that have also been endorsed by this Committee. The Committee emphasised that the Plan should be supported and endorsed by many stakeholders, including national and local governments, industry, and non-governmental organisations, as well as international organisations such as IWC and IUCN. The overarching goal of the Plan is to reduce mortality related to anthropogenic activities to zero as quickly as possible. The Plan includes 11 focussed actions (related to co-ordination, public awareness, conservation research, monitoring and mitigation) of high importance for the conservation of this critically endangered population. The most immediate, in terms of ensuring the success of the Plan is the appointment of a Steering Committee and of finding funds for and appointing a full-time Co-ordinator. This is also critical to the need, identified by the authors, to engage broad stakeholder participation in the Plan as soon as possible.

The Committee **strongly endorses** this Plan and **commends** it to the Commission and range states. It also **recommends** that it is broadly distributed, including being posted on the IWC and IUCN websites. Consideration is being given to it being published by the *JCRM*. The Committee **recommends** the Plan as a model for the development of other conservation plans for cetacean populations.

10.5 Southern Hemisphere right whales

10.5.1 Australian and New Zealand areas

The Committee received a number of papers on southern right whales from these areas. Details can be found in Annex F, item 5.3. A number of points of interest from these are given below:

(1) genetic comparison of animals around the subantarctic Auckland Islands and the main islands of New Zealand provided documented evidence for the first time of the movement between the two regions and, along with other available data, is most consistent with either the one stock or the extirpation/recolonisation hypotheses (SC/62/BRG16);
(2) results from satellite telemetry provided data on migratory movements of three whales tagged at the Auckland Islands revealed that animals from this nursery area/breeding ground can move north to their feeding ground - the reverse of the generally accepted migratory pattern for southern right whales (SC/62/BRG19);
(3) information on acoustic contact calls from southern right whales near the Auckland Islands (SC/62/E13); and
(4) updated information on long-term aerial survey monitoring programme along the southern Australian coast results in an annual increase rate for cow/calf pairs of around 7.5% (95%CI 3.2, 12.0) for the period 1993-2009 and a minimum population size of 2,530, with a total Australian population of about 3,000.

Difficulties or complications experienced in obtaining permits for biopsy sampling of right whale calves were discussed. Although there were legitimate concerns over possible disturbance to mother-calf pairs, no adverse effect had been shown on subsequent calving interval in a study of the effects of biopsying over 100 cow-calf pairs off South Africa, although the statistical power was low (Best *et al.*, 2005). Given the potential value of such sampling, particularly in establishing issues of paternity the Committee **recommends** that permitting authorities should view requests for biopsy sampling of cow-calf pairs on their scientific merit and apply appropriate safeguards to limit the degree of disturbance where necessary.

10.5.2 South America area

The primary item discussed under this item was the report of a workshop (convened by Brownell) held at the Centro Nacional Patagónico (CENPAT) in Puerto Madryn, Argentina from 15-18 March 2010. The goal of the workshop was to investigate the causes of the high mortality of southern right whales around Península Valdés, Argentina. Participants included experts on the ecology and marine environment of the Península Valdés region, scientists studying right whales in the South Atlantic and international experts on whale strandings and mortality.

Small numbers of strandings have been recorded in the region since 1971. However, since 2003, when the Southern Right Whale Health Monitoring Program (SRWHMP) was established, a total of 366 right whale deaths have been recorded, with peaks in 2003 (31), 2005 (47), 2007 (83), 2008 (95) and 2009 (79). Over 90% of the deaths have been of first-year calves. After investigating thoroughly a range of possible causes for these first year deaths, the workshop agreed three leading hypotheses (it was not possible to determine which was most likely and some combination of factors may have occurred, at least in some years): (1) reduced food availability for adult females; (2) biotoxins; and (3) infectious disease.

The workshop recommended a number of steps to build a better understanding of the cause or causes as listed in Annex F, item 5.3.2.

Of these, continuation of the long-term aerial photo-id programme, other complementary monitoring effort and the SRWHMP are highest priority. The workshop agreed that cooperation and collaboration among research groups is essential for addressing complex questions concerning the die-offs. A western South Atlantic right whale consortium (the North Atlantic right whale consortium) could be used to establish and maintain links among researchers and to share information (this should also include researchers in different parts of the range). Efforts to improve such cooperation and collaboration should be a high priority for local and national governments, NGOs and INGOs.

It was also agreed that the absence of conclusive information regarding the cause(s) of exceptional right whale mortality should not preclude authorities from proceeding with some management measures, particularly in relation to kelp gulls, where gull lesions are clearly harmful to the whales, especially the calves.

The workshop also recognised: (1) the considerable efforts of the researchers in Argentina (and abroad) to investigate the die-offs in the face of fiscal and logistical constraints; and (2) the importance of governmental commitment to the long-term conservation of right whales in Argentina.

The Committee thanked Brownell for his presentation and **endorses** the workshop report. The Committee **welcomes** the announced intention of the Argentine authorities to introduce this year a pilot plan for the control of nuisance gulls.

As in previous years, the Committee **recognises** the value of the long-term photo-id programme of right whales at Península Valdés that had now lasted 40 years, particularly in being able to describe the significance of the recent die-off events and test certain causation hypotheses. It **strongly recommends** its continuation. It also noted that this year emergency funding had been provided by the US Marine Mammal Commission to enable the necropsy programme to take place and strongly **recommends** the continuation of this programme to investigate the reason(s) for the die-off.

The Committee also considered SC/62/BRG15, a preliminary assessment of the genetic structure of the southern right whales from Península Valdés, Argentina. A number of comments to assist in future analyses were raised in discussion (Annex F, item 5.3.2) and the Committee looks forward to an updated analysis next year.

The Committee was pleased to receive information on the 2009 flights of an aerial survey programme off Brazil and it **recommends** the continuation of the surveys.

10.5.3 South Africa area

The Committee was pleased to receive updated information on demographic parameters obtained from the long-term monitoring programme of South Africa (SC/62/BRG30). The results are discussed in Annex F, item 5.3.3 but key features include an annual growth rate of about 7% (95% CI 6.5%, 7.5%); a mean calving interval of about 3.2 years; and a population size in 2006 as about 4,100 animals. SC/62/BRG31 examined the possibility of changes in some demographic parameters for right whales off South Africa through the analysis of re-sighting data for females with calves over the 1979-2006 period. No statistically significant change in adult survival rate or population growth rate was found but a reduction in mean calving interval from 3.2 to 3.1 years was detected.

SC/62/BRG33 reported on the recent announcement of the intention to drill exploratory boreholes for natural gas in eight districts of the coastal region of the southwest coast of South Africa, three of which included nearshore waters that were home to the largest concentration of cow-calf pairs on the African coastline. About 75% of cow-calf pairs on the southern African coast occur in this region in spring, some of which are resident for up to three months, while the westward coastal movement seasonally means that an even larger proportion of the population almost certainly uses the region.

The Committee viewed this potential development with concern, noting the current lack of information available on the proposed activities. It **recommends** to the South African government that all permits issued for exploratory activities should contain mandatory mitigation measures to avoid disturbance to right whales, including confining all marine drilling activity to the season when right whales are absent (January to May). It also **recommends** that if gas production is ultimately planned for the region, the use of closed areas or the development of further mitigation measures such as directional drilling should be considered.

The Committee **endorses** a proposal for the establishment of a Southern Ocean Right Whale Photo-identification Catalogue (the Antarctic Humpback Whale Fluke catalogue). The intention is to provide a resource that could be consulted when researchers holding images taken in coastal waters wished to establish linkages with feeding grounds in pelagic waters (see Appendix 2 of Annex F for detail). It was confirmed in discussion that this would be supplementary to such coastal catalogues. The Committee looks forward to receiving a progress report at its next meeting. Funding is dealt with under Item 24.

10.5.4 Plans to review southern right whales

Brownell reported on progress in preparing for the Southern Right Whale Assessment Meeting, planned to be held at Puerto Madryn, Argentina, in September 2011. Given that this meeting would be held very shortly after next year's IWC meeting a budget would have to be prepared at this meeting (and reserved until 2011). A small group was set up to draw up the budget and draft the Terms of Reference for the meeting (see Annex F, Appendix 3). The Committee **agrees** that this should be funded next year.

10.5.5 Other

The Committee recognises the importance of long-term studies, to provide biological information from photo-id and information on trend and population size from sighting and mark-recapture analyses. It **strongly recommends** the continuation of such long-term studies in relevant areas.

10.6 Other stocks of right whales and small stock of bowhead whales

10.6.1 North Atlantic right whales

An update was provided on North Atlantic right whales for the period May-October 2009, as an addendum to information presented in Pettis (2009). The summary reflects the work of the North Atlantic Right Whale Consortium (NARWC). A shared photographic catalogue was used to produce a 'best' estimate of population size of 438 for 2008. This total did not explicitly account for unphotographed whales in the population and may change slightly as additional data are incorporated into the catalogue. One right whale death was documented during the report period, but the cause was not determined. Additionally, there were three new entanglement cases and eight previous entanglement cases that had not yet been resolved.

The Committee **agrees** that the documented growth in the catalogue plus successive years of improved calf production gave grounds for cautious optimism over the future status of this population. However, while welcoming the management measures that have been taken to date, the Committee **repeats its previous recommendations** on this population that it is **a matter of absolute urgency** that every effort be made to reduce anthropogenic mortality to zero.

10.6.2 North Pacific right whales

SC/62/BRG3 reviewed past sightings of North Pacific right whales off western Kamchatka from spring to autumn. A number of sightings of these whales were made during Japanese-led surveys from 1989 to 2003; these were mostly restricted to the southern portion of study area. However, there were also a few sightings in earlier years by Soviet scientists, including in the northern part of the area. These sightings also highlight the need for directed research and monitoring of right off western Kamchatka in areas overlapping with fishery and oil and gas development activities.

SC/62/NMP22 provided results of observations of North Pacific right whales during the common minke whale sighting and biopsy survey conducted in the Okhotsk Sea in summer 2009. The research area was set north of 46°N, south of 57°N and west of 152°E in the Okhotsk Sea including the Russian EEZ. 17 schools (29 animals) of North Pacific right whales were found, mainly in the offshore waters deeper than 200m. Of these, 16 schools were targeted for photo-id research and 22 animals in 15 schools were individually identified (there are no re-sightings among them).

The Committee welcomes the sighting and photo-id information from these cruises and **encourages** continuing these studies in the area.

Wade *et al.* (2010) used photographic and genotype data to calculate the first mark-recapture estimates of abundance for right whales in the Bering Sea and Aleutian Islands. The estimated abundance data reveal this to be an extremely small population of perhaps around 30 animals. The results will be updated using more samples and images from another survey planned in the eastern North Pacific this year and the Committee looks forward to receiving this information.

Noting the extremely small size of this population, and also the potential for disturbance and ship-strike mortality from greatly increased ship traffic resulting from the likely opening of the northeast or northwest Passages due to sea ice retreat, the Committee considers it **a matter of absolute urgency** that further research be conducted on eastern North Pacific right whales, and **recommends** that this research focus on assessing status and identifying any current sources of anthropogenic mortality.

10.6.3 Small stocks of bowhead whales

SC/62/BRG3 summarised sightings of bowhead whales off western Kamchatka from existing published literature and other available sources. Okhotsk Sea bowhead whales were recorded only a few times in the study area during the spring-autumn period, with one sighting during winter; however it is known from historical whaling data that this species was abundant in the area, particularly in the northern regions during periods of open water.

SC/62/BRG20 reported the results of a survey for bowhead whales conducted in the Fram Strait during 29 March-14 April 2010. Two observations were made, but it was determined based on identifiable scars that both encounters were of the same individual.

Witting reported that 12 sighting of bowhead whales were made in the Northeast Water Polynia off Northeast Greenland during an aerial survey for walrus during August 2009. He also reported that a female with a calf was seen off Norske Island, Northeast Greenland in July 2009. In discussion, it was noted that two passive acoustic recorders were deployed in the Fram Straight during 2008-09 and that these instruments detected numerous bowhead sounds including songs.

The Committee welcomes the above information and **encourages** future updates and research.

10.7 Antarctic cruises

10.7.1 General review of 2009/10 cruise

The planning meeting for the 2009/10 IWC/SOWER cruise was held in Tokyo, Japan in September 2009 (SC/62/Rep6). The cruise took place in Area IV and had two main objectives: (1) to undertake a sightings survey in collaboration with an Australian Antarctic Division aerial survey; and (2) to continue research on the priority species (southern right, blue, fin, and humpback whales). The total number of minke whales sighted in the research area was 83 groups, comprising 152 animals; humpback whales were the most frequently sighted species (174 groups comprising 322 animals). Biopsy samples and individual identification photographs were taken from 21 and 45 humpback whales and 22 and 26 southern right whales, respectively. A total of 28 groups of southern right whales (38 animals) were sighted (SC/62/IA1).

The Committee thanks the Government of Japan for generously providing the vessel and crew for this survey, and also thanks the Cruise Leader for her efforts. Noting that this was the last IDCR/SOWER cruise, the Committee also extended its appreciation to all member nations and researchers who had contributed to this extensive programme, and particularly to the governments of Japan and the former Soviet Union, for providing the survey vessels. The data collected during the programme provide an unparalleled source of information on Antarctic cetaceans. The experience gained from these surveys will continue to be of use in planning future studies, in the Southern Ocean and elsewhere. The Committee **agrees** that a Special Issue of the *JCRM* on the IDCR/SOWER surveys is warranted and re-establishes the working group to progress this idea (see Annex Q).

10.7.2 Plans for cetacean sighting surveys in the Antarctic in the 2010/11 season

SC/62/O17 described a dedicated, systematic cetacean sighting survey which was being planned to take place from December 2010 to February 2011 in order to obtain estimates of abundance for use in the RMP. The research area will be south of 60ºS in Area V and the western part of Area VI (130ºE-145ºW), including the Ross Sea. This survey will be conducted in relation with the Japanese Whale Research Programme under special permit in the Antarctic (JARPA II). Two dedicated, sighting survey vessels, *Shonan-Maru No.2* and *Yushin-maru No.3*, will be used and the survey procedures will be based on the standard

SOWER search modes; closing (NSC) mode and passing with the independent observer (IO) mode.

In order to minimise difficulties associated with survey design, an intersessional Working Group was established under Matsuoka (Annex Q). The Committee **agrees** that Matsuoka is responsible for IWC oversight.

10.8 North Pacific cruises

10.8.1 Recommendations for 2010 cruise and short term objectives

During the last year's Scientific Committee meeting, Japan presented a proposal for a medium- to long-term research programme involving sighting surveys to provide information for cetacean stock management in the North Pacific. The Scientific Committee welcomed the initiative and agreed the value of a large-scale, medium-long term integrated research programme in the North Pacific and encouraged this in the context of international collaboration under IWC auspices.

A meeting to discuss the North Pacific survey programme was held in Japan in September, 2009 (SC/62/Rep3). The meeting agreed four terms of reference:

(1) review the Scientific Committee's issues in the North Pacific;
(2) review the past and ongoing survey activities and available data in range states;
(3) consider possible line transect survey plans and additional data collection (e.g. photo-id and biopsy) for the 2010 season; and
(4) prepare a proposal for an intersessional workshop (to be held between SC/62 and SC/63) on future surveys beyond 2011.

SC/62/IA15 was provided in response to the first term of reference from the meeting and provided a summary of the Scientific Committee issues relating to North Pacific sei, common minke, Bryde's, right and blue whales. The distributions of these whale species were described and requirements for further surveys, in order to estimate abundance and investigate stock structure, were considered.

SC/62/IA10 presented the research plan for an IWC/Japan whale sighting survey taking place in summer 2010. The plan had been drawn up following guidelines agreed at the North Pacific programme intersessional meeting. The research area (170°E-170°W) had been chosen because for some species it spans proposed stock boundaries and has been poorly covered by previous surveys, representing an important information gap for several large whale species. The cruise will collect line transect data to estimate abundance, and biopsy/photo-id data contributing to the work of the Scientific Committee on the management and conservation of populations of large whales in the North Pacific. It will provide:

(1) information for the proposed future in-depth assessment of sei whales in terms of both abundance and stock structure;
(2) information relevant to *Implementation Reviews* (e.g. common minke whales) in terms of both abundance and stock structure;
(3) baseline information on distribution and abundance for a poorly known area for several large whale species/populations, including those that were known to have been depleted in the past but whose status is unclear; and
(4) biopsy samples and photo-id photos to contribute to discussions of stock structure for several large whale species/populations, including those that were known to have been depleted in the past but whose status is unclear.

The cruise will last about 60 days (including transit time) between July and August. In order to adequately cover the longitudinal range, the latitudinal range is restricted between a southern boundary at 40°N and a northern boundary at the Aleutian Islands chain. Four researchers can be accommodated on this cruise; US and Korean scientists will participate. The cruise will follow the requirements for reports and documentation developed for cruises that could provide data for use under the RMP and will be the responsibility of the Japanese scientists.

The Committee thanked the Government of Japan for its generous offer of a vessel for this survey. Matsuoka was assigned responsibility for IWC oversight.

Brownell reported that a scientist from SWFSC had now been identified for the cruise, but major problems regarding CITES permits remain; these issues are similar to those described in SC/62/NPM22 that were encountered between Japan and Russia for the collection of minke whale biopsy samples in the Russian EEZ. There are CITES issues for both inside and outside the US EEZ, because samples collected outside the US EEZ have to enter US waters and then all samples must be exported to Japan. A possible solution (institutional permits) has been proposed to Japan and it is being considered. If these problems are not worked out, it will not be possible to collect any biopsy samples (inside or outside the US EEZ) during this cruise. This would be a major scientific loss to advancing our understanding of the stock structure of baleen whales in the North Pacific, specifically sei whales. The Committee **recognises** the importance of the CITES issue and agreed that it should be resolved among parties concerned expeditiously. The Committee **endorses** the working group's report, and **recommends** that the investigations regarding the use of Institutional permits to exchange biopsy samples proceed as soon as possible, with the results of the investigations being reported to the Planning Meeting scheduled for October 2010.

SC/62/O16 described two sighting surveys for cetaceans, taking place in the North Pacific in 2010, to examine the distribution of sei, Bryde's and minke whales and to estimate abundance for use in the RMP. Both surveys are in the middle part of the Western North Pacific. The main target species are sei and minke whales for the first survey and Bryde's whale for the second survey. The Committee assigned responsibility to Matsuoka for IWC oversight.

10.8.2 Mid- to long-term plans for the North Pacific Survey Programme

In addition to plans for a 2011 cruise, the Committee **recommends** that a coherent multi-year plan be developed for the survey programme in accordance with the discussion given in SC/62/Rep3. A Steering Group to oversee the IWC North Pacific surveys was established under Kato (Annex Q). It was proposed that a meeting of the Steering Group should be scheduled immediately prior to the Planning Meeting for the 2011 cruise, in order to develop the programme of research to be undertaken over the next few years.

10.9 Other

The precise taxonomic relationships and species delineations within the Bryde's/Eden's whale complex are currently uncertain. In South Africa, 'inshore' and 'offshore' forms of Bryde's whale have been described (Best, 1977), and there has been some uncertainty as to whether they should be referred to as *B. edeni* and *B. brydei* respectively. The Committee received a proposal for opportunistic collection of biopsy samples of Bryde's whales during a forthcoming research cruise between the Strait of Gibraltar and Cape Town, South Africa. These samples would be used to facilitate more in-depth genetic analysis of the relationship between the 'offshore' form and other more well sampled Bryde's whale species. The Committee **recommends** this proposal, assuming that relevant permits will be acquired. The Committee also **recommends** that biopsy samples from other whales be obtained, where legally permitted to do so.

11. STOCK DEFINITION (SD)

This Agenda Item was established in 2000, and has been handled since then by a Working Group; see IWC (1999d, p.83) for the original Terms of Reference. The term 'stock' has been used with different meanings in different contexts at different times, both within IWC and in other management and conservation contexts. These multiple meanings have sometimes hindered the Committee's ability to provide management advice. The Working Group was set up to clarify the issue of 'stocks' in a management context (see Item 11.3), to create a bridge between IWC and the expertise of the wider population genetics community (see Items 11.2 and 11.3), to develop software that evaluates the management utility of various population genetic analyses (see Item 11.2), and to develop guidelines for preparation and analysis of genetic data within an IWC context (see Item 11.1). These issues are of fundamental importance to the Committee's discussions on assessments and to the development of management advice. The Report of the Working Group is given as Annex I.

11.1 Statistical and genetic issues related to stock definition

11.1.1 Guidelines on DNA data quality

The Committee has previously endorsed a general set of guidelines for ensuring sufficient quality in genetic data used for management advice (IWC, 2009g; *http://www.iwcoffice.org/sci_com/handbook*). These guidelines constitute a 'living document' that will be updated as necessary. Since the issues involved are complex, the guidelines currently lack any numerical reference points, and the Committee again **encourages** suggestions accordingly. The intersessional e-mail group established in 2008 (Annex Q) was unable to report back this year, but will be continued in the coming year. The item remains on the agenda for the 2011 Annual Meeting.

11.1.2 Guidelines on genetic and statistical analysis

In parallel with the development of data quality guidelines, the Committee is developing guidelines for some of the more common types of statistical analyses of genetic data that are employed in IWC management contexts. These guidelines, which are being developed through another intersessional working group, are at an earlier stage of development than the DNA data quality guidelines. The proposed structure of the document, including a motivating example, was shown last year (IWC, 2009h).

This year, the Committee reviewed a preliminary version of the guidelines (SC/62/SD1), with drafts of several of the sections. Some further work is required, but after one further iteration, the guidelines should be able to appear on the IWC website. Following review of the text so far, a number of suggestions were made for the next iteration, including an 'FAQ' and the possible use of simulated datasets from TOSSM (see Item 11.2) as worked examples. The full list may be found in Annex I. This document will entail a great deal of effort, but should be of lasting importance. It deserves to be published, both online via IWC and in peer-reviewed literature.

11.1.3 Other approaches to stock identification

The Committee has previously considered the utility of acoustic data in questions of stock definition (IWC, 2005e, pp.248-49). Acoustics may be an efficient tool for proposing stock distinctions and boundaries, but interpretation can be difficult unless *inter alia* the stability of individual acoustic behaviour over time is known. This year, paper SC/62/SD2 presented results from acoustic monitoring of fin whales in different seasons and regions of the Mediterranean. The Strait of Gibraltar and Alborán Sea areas experience an influx, during the breeding season only, of fin whales that are acoustically consistent with Icelandic or Norwegian animals, but distinct from other Mediterranean fin whales. The results suggest a possible explanation for the low levels of gene flow that have been found between Mediterranean and North Atlantic fin whale populations. The Committee noted the value of these new data in suggesting rather precise areas where stock mixing and/or separation may occur, and consequently in assisting development of economical sampling design. It **encourages** plans to follow up this study with biopsy sampling.

11.2 TOSSM (Testing of Spatial Structure Models)

The aim of the TOSSM project is to facilitate comparative performance testing of population structure methods intended for use in conservation and management planning. From an IWC perspective, the TOSSM software package allows evaluation of methods for detection of genetic structure, in terms of how well the methods can be used to set spatial boundaries for management. As noted last year, the framework is now complete and the software is available for all to use; simulated datasets exist for three of the five stock-structure archetypes previously proposed by the Committee (IWC, 2009a, p.51). To date, ten methods have been tested on datasets from the two simplest Archetypes (single-stock panmixia, and two populations with limited migration sampled and harvested on the breeding grounds). No new results were received this year. Just as last year, though, the Committee noted the relevance of Archetype IV to North Pacific common minke whale discussions, where program STRUCTURE (Pritchard *et al.*, 2000) is receiving extensive use. It may well be possible to use TOSSM datasets to investigate the likely performance of STRUCTURE in a North Pacific minke whale-like setting, not merely in terms of overall 'boundary setting' but also in terms of specifics such as ability to assign individuals to specific stocks.

Mark-recapture data are another powerful tool for investigating stock issues. These have not yet been considered in TOSSM; next year, the Committee will consider the feasibility of incorporating mark-recapture data into TOSSM datasets. Another potentially powerful tool is the suite of coalescent-based methods but no coalescent-based approaches to boundary-setting have yet been considered in TOSSM. The Committee hopes to consider results of a TOSSM on the coalescent-based software MDIV next year.

There has been much discussion of how to interpret results from the program STRUCTURE, specifically in assigning individuals either to a smaller number of stocks which mix to a different extent in different places, or to a larger number of ‘new’ stocks that are less mixed. The Committee **encourages** the submission of papers investigating the performance of STRUCTURE for this question, and noted that datasets from TOSSM (existing ones, or new ones if necessary) might be a good starting point for such investigations.

11.3 Unit-to-conserve

‘Unit-to-conserve’ is a standing item on the SD Working Group agenda. It provides for discussion of potential ‘definitions of stock’ in a management context, including their operational implications for measurement and management. No new proposals were considered this year.

12. ENVIRONMENTAL CONCERNS (E)

The Commission and the Scientific Committee have increasingly taken an interest in the possible environmental threats to cetaceans. In 1993, the Commission adopted Resolutions on research on the environment and whale stocks and on the preservation of the marine environment (IWC, 1994a; 1994b). A number of resolutions on this topic have been passed subsequently (IWC, 1996a; 1997; 1998a; 1999b; 1999c; 2001c). As a result, the Scientific Committee formalised its work on environmental threats in 1997 by establishing a Standing Working Group that has met every year since then. Its report this year is given as Annex K.

12.1 State of the Cetacean Environment Report (SOCER)

The SOCER aims to provide Commissioners and Scientific Committee members with a non-technical summary of events, developments and conditions in the marine environment relevant to cetaceans. The report is compiled annually, in response to IWC (2001c), with a focus on one pre-selected region each year plus a global section.

The 2010 SOCER was focused on the Arctic and based on peer-reviewed papers published between 2008 and 2010. The overwhelming issue for the Arctic was climate change – e.g. rate of ice loss and ecosystem shifts – but many of the papers in the review period had already been summarized in previous Committee reports because of their global significance. There were few pollutant studies specifically on cetaceans in 2008-10, but the Arctic Monitoring and Assessment Programme (AMAP) 2009 Assessment of Arctic Pollution Status (*http://www.amap.no/*) provides a comprehensive review of pollutant levels in the Arctic. Globally, the environmental issue that received the most attention over the past year was underwater noise, especially disturbance from boat traffic, impacts of sonar on beaked whales and the acoustic impacts of wind farms. Of note, a bibliometric analysis showed that there has been a shift in focus in the cetacean research literature from basic biology topics, which were prevalent in the literature in the 1970s, to conservation topics in recent years. Next year the SOCER will focus on the Southern Ocean.

12.2 Review progress in planning for POLLUTION 2000+, Phase II

The IWC-Pollution 2000+ programme was initiated to investigate pollutant cause-effect relationships in cetaceans, and arose from a Workshop on chemical pollution and cetaceans held in Bergen, Norway in 1995 (Reijnders *et al.,* 1999). Following the Bergen workshop, a planning meeting was held in 1997 (Aguilar *et al.,* 1999a) and a workshop was held in 1999 (Aguilar *et al.*, 1999b), where Phase I of the POLLUTION 2000+ programme was launched. Phase I had two objectives: (1) to select and examine biomarkers for exposure to and/or effects of PCBs; and (2) to validate/calibrate sampling and analytical techniques. The results of Phase I were reviewed and a general framework for POLLUTION 2000+ Phase II was outlined (IWC, 2008a). Discussion for Phase II studies since that time has determined the need to: (1) produce a framework for modelling the effect of pollutants on cetacean populations; (2) identify cetacean populations to be studied under Phase II; and (3) develop a protocol for validating biopsy samples and applying this protocol to any large whale species selected.

Last year, the Committee had proposed the following modified goals for the Phase II programme:

(1) develop an integrated modelling and risk assessment framework to assess cause-effect relationships between pollutants and cetaceans at the population level, building on the progress made during Phase I and on recent research, using modification of a tiered risk assessment paradigm;
(2) extend the work to new species and contaminants as appropriate; and
(3) validate further biopsy sampling techniques for use in addressing issues related to pollution, including legacy contaminants and new contaminants of concern and associated indicators of exposure or effects.

In February 2010, an expert workshop (with expertise in chemical contaminants, toxicology, cetacean biology, veterinary medicine and biomarkers) was held to further develop proposals for Phase II of the programme (SC/62/Rep4). Presentations were made on risk assessment frameworks, chemicals of emerging concern, contaminant exposure, modelling approaches and case studies. Biomarkers of chemical exposure and effects were also discussed, with the workshop purposefully selecting those that have been validated in cetaceans. An international prioritisation survey for chemical contaminants was developed and will be distributed to subject matter experts, with a final report on survey results to be presented at the 2011 IWC Scientific Meeting.

The Committee **endorses** four **recommendations** made at the Workshop:

(1) to improve existing concentration-response (CR) function for PCB-related reproductive effects;
(2) to derive additional CR functions to address other endpoints (i.e., survival) in relation to PCB exposure;
(3) to integrate improved CR components into a population risk model (e.g., individual-based model) for one or more case study species (e.g. bottlenose dolphin and/or humpback whale); and
(4) to develop new biomarkers and improve the linkages between lower and higher levels of organisation (molecular - individual - population). The highest priority for biomarker development should include those with direct relevance to population-level endpoints such as reproduction and survival.

A plan to make progress on Phase II can be found in Annex K. The Committee noted data gaps and research needs identified at the Workshop, specifically noting that progress on this topic will require initiating new studies or additional support of existing efforts

The ICES Working Group on Marine Mammal Ecology (WGMME) met in April 2010 in part to ‘Review the current contaminant loads reported in marine mammals in the ICES area, the cause-effect relationships between contaminants and health status, and the population-level effects of environmental impacts.' The SWG had reviewed recommendations made by the WGMME with regard to pollutants in marine mammals (*http://www.ices.dk/reports/ACOM/2010/WGMME/wgmme_final_2010.pdf*). and the Committee **endorses** these recommendations.

The Committee received new information (SC/62/E9) on the development of a suite of sensitive biomarkers from non-lethal sampling to evaluate the toxicological status of Bryde's whale in the Gulf of California. A 'multi-trial-biomarker-tool' was developed, combining protein biomarkers with concentrations of organochlorines and polycyclic aromatic hydrocarbons. A second biomarker study (SC/62/E10) examined a multi-response *in vitro* method to detect toxicological effects of contaminant mixtures on skin samples from cetaceans in the Mediterranean Sea. Preliminary findings indicate that the combination of protein biomarkers, gene expression levels and tissue contaminant levels may be a useful tool in determining 'multiple toxicological stress' in free-ranging cetaceans. The Committee **welcomes** these studies but **emphasises** the importance of standardisation of contaminant concentration reporting.

The Committee received an overview of the oil spill that followed the explosion on board and subsequent loss of the drilling structure 'Deepwater Horizon' on 20 April 2010, approximately 50 miles southeast of Louisiana in the Gulf of Mexico. The incident claimed the lives of 11 workers. Immediately after the spill, response networks for marine mammals, sea turtles, and birds were established, including four facilities for de-oiling of manatees, dolphins, and sea turtles.

As of 4 June, 31 dead dolphins and 277 dead sea turtles had been documented, with numerous accounts of large and small cetaceans seen swimming in oil-contaminated waters. The Committee **commends** all groups that are responding to impacted marine mammals and turtles in the region.

It also **agrees** that it is extremely important to learn as much information as possible from this tragedy in order to accurately assess impacts and be better prepared for potential future oil spills. In this regard, the Committee **strongly recommends** that the government of the USA, range states of the Gulf of Mexico and the responsible parties:

(1) search for and examine as many cetacean carcasses as possible that may have been impacted by the spill through detailed necropsies and thorough tissue sampling;
(2) analyse tissues for contaminants specifically related to spilled oil (i.e. polycyclic aromatic hydrocarbons, dispersants and mixtures of the two);
(3) provide detailed chemical composition of the dispersants that have been used in the Gulf of Mexico;
(4) develop and examine a suite of biomarkers that will be useful for understanding impacts from the spilled oil and use of dispersants in the Gulf of Mexico; and
(5) conduct biomarker studies of cetacean populations in the Gulf of Mexico, especially bottlenose dolphins, sperm whales and Brydes whales.

The situation in the Gulf of Mexico also emphasises the need for adequate environmental baseline data *before* oil and gas exploration, development, or production occurs in any region and for these data to inform mitigation and management decisions. Therefore, for member governments with on-going or planned offshore oil and gas activities within their territories the Committee **strongly recommends** the collection of baseline data to include:

- contaminant levels in cetaceans, their prey, and in sediments, especially polycyclic aromatic hydrocarbons (PAHs) and other contaminants that may interact with PAHs;
- biomarker levels in cetaceans and their prey;
- abundance and distribution of cetaceans and their prey; and
- condition of cetacean habitats (i.e. water quality, sediment quality, etc.).

Finally, the Committee **strongly recommends** contingency planning and training for oil spill responses in areas of oil and gas development. It looks forward to receiving an update on the studies into the effects of this spill at future meetings.

12.3 Review progress of CERD Working Group

The CERD working group was established in response to the report of a workshop on infectious and non-infectious diseases of marine mammals and impact on cetaceans that was held in 2007 (IWC, 2008d). The Committee received an update on its intersessional accomplishments and plans (Annex K, item 8), which are summarised in five categories: (1) skin disease; (2) diagnostic laboratories and veterinary experts; (3) prioritization of pathogens; (4) emergency response; and (5) enhancement of capacity and communications among stranding networks. With regard to the last category, capacity building workshops were held in four regions: West Africa, Caribbean, Brazil and India. Drawing information from the ICES working group and the IWC Ship Strike Working Group, a global inventory of stranding networks has been developed and the CERD working group is developing recommendations to maintain and provide access to the inventory.

The Committee also noted a prioritisation of cetacean pathogens developed on behalf of the US Working Group on Marine Mammal Unusual Mortality Events, from a survey that evaluated 76 pathogens based upon five factors. Of the pathogens included in the survey, most were potentially zoonotic, while others were associated with emerging/re-emerging human diseases in the United States. The ten highest priority pathogens among small cetaceans were morbillivirus, parapoxvirus, *Brucella* spp. anisakis, calicivirus, herpesvirus, nasitrema, *Clostridium* spp., and toxigenic *Escherichia coli*. Although the CERD WG is not tasked to compare cetacean-borne pathogens to those in terrestrial species, the Committee expressed interest in this broader approach, which is consistent with the global *One Health* approach to medicine (*http://onehealthinitiative.com/index.php*). Specifically, *One Health* highlights the importance of integration of surveillance systems in wildlife, domestic animals, public health and environmental health. The Committee **commends** projects that integrate a *One Health* approach to build capacity in countries that are responding to diseases that are shared by people and wildlife. Further, it **recommends** that marine species be considered by all organisation that are implementing the *One Health* approach. Finally, the Committee **commends** the many and varied accomplishments of the CERD WG and **endorses** the work plan for 2011 (Annex K, Appendix 3).

12.4 Review new information on anthropogenic sound: focus on 'masking sound'

The Committee's SWG on environmental concerns has included an item on underwater sound on its agenda each year since 2004 (IWC, 2005f, p.268). In 2009, a presentation on low-frequency 'masking sound' precipitated adopting it as a focal-topic. Low-frequency (LF) ocean noise has increased substantially in recent decades, concomitant with a three-fold increase in commercial shipping and other offshore industrial activities. The Committee reviewed a mechanistic model that dramatically demonstrates the reduction in the 'communication space' of baleen whales that now occurs, especially near shipping lanes and busy ports (Annex K, item 9). It then reviewed a variety of evidence with regard to the masking sound and its possible effects on whales, including: (1) altered calling patterns and frequency in the presence of LF sound from shipping and seismic airguns shown by fin whales in the western Mediterranean Sea and humpback whales off the coast of Northern Angola; (2) chronic exposure of the small population of humpback whales in the Arabian Sea to LF sound from construction, shipping and seismic surveys; and (3) the elevation of LF sound levels at distances from 450 to 2,800km from a seismic survey area south of Tasmania in the Southern Ocean. Based on the aggregate information presented to the SWG with regard to masking sound from anthropogenic sources, the Committee **recommends** that:

(1) seismic surveys be regulated in the same legal frame, whether for scientific or commercial purposes;
(2) baseline data be collected, satisfactorily analysed and modelled using appropriate techniques, regarding the seasonal and spatial distribution of whales in areas of interest to the geophysical community (scientific and commercial) before survey operations;
(3) the masking potential of anthropogenic sources be quantified and acoustic measurements be standardized to ensure that datasets among researchers are comparable; and
(4) in studies examining potential changes in whale acoustic behaviour, the ability to detect whale calls during periods of exposure and non-exposure to anthropogenic LF sound be quantified.

Further, the Committee **strongly recommends** that further research be conducted on the Arabian Sea humpback population (and see Item 10.2.2.4), including studies directed at quantifying the impacts of acoustic disturbance and masking to support conservation planning and protection for this small population.

The SWG had reviewed available information on plans for seismic surveys in support of oil and gas development planned for the Russian Far East, including the Sea of Okhotsk, Anadyr Gulf, the East Siberian and Chukchi Seas (Annex K, item 9.1). The scale of these activities is 'matched' by plans for broad-scale seismic surveys in the US Chukchi and across the US-Canadian Beaufort sea region. At least six endangered whale species (e.g. North Pacific right whales and Okhotsk Sea bowhead whales) occur in low numbers in waters offshore western Kamchatka, where seismic surveys are anticipated during summer 2010.

In light of this, the Committee **recommends** that additional surveys to provide baseline information on cetaceans be conducted in waters off western Kamchatka, and that seismic surveys and other potentially disturbing industrial activities should be conducted during times of lower cetacean abundance in all ocean regions whenever possible (e.g. see the mitigation and monitoring plan for a seismic survey in the Sakhalin region developed under the auspices of IUCN's Western Gray Whale Advisory Panel, and information regarding other seismic survey issues specific to western gray whales under Item 10.4 above). When informed that industry has initiated research into alternative (quieter) technology (vibroseis), the Committee **strongly encourages** this research and **recommends** continued development of such methods.

The conclusions from the workshop on 'Cumulative Impacts of Underwater Noise with Other Anthropogenic Stressors on Marine Mammals' were reviewed (Annex K, item 9.3). That workshop had agreed that cumulative impact assessments (CIAs) are needed to account for sub-lethal effects of human disturbance. The Committee **recommends** that member governments work to develop a quantitative approach for assessing cumulative impacts, including ways that anthropogenic sounds might impact cetaceans and their prey.

In regard to reducing LF sounds from shipping, the SWG (Annex K, item 9.4) had noted rapid progress, especially in the past three years, towards addressing this issue, including both the formation of a Correspondence Group within the Marine Environment Protection Committee (MEPC) of the International Maritime Organization (IMO) and the granting of IMO 'observer status' to the IWC (IWC/62/4). With reference to the IWC's awareness of the critical nature of acoustic communication to whales and that interference, or masking, of this communication is to some extent preventable, the Committee **strongly recommends** that:

(1) the goal of noise reduction from shipping advanced in 2008 (i.e., 3dB in 10 years; 10dB in 30 years in the 10-300Hz band) be actively pursued;
(2) new and retro-fit designs to reduce noise from ship propulsion be advanced within the goals of the IMO, when and wherever practicable; and
(3) the IWC and IMO continue to work collaboratively to advance the goal of worldwide reduction of noise from commercial shipping when and wherever practicable including reporting progress on noise measurements and implementing noise reduction measures.

12.5 Review progress on work from the 2nd Climate Change Workshop

The 2nd Climate Change Workshop (IWC, 2010j) resulted in a series of recommendations summarised under three headings corresponding to working groups established at the workshop: Arctic; Southern Ocean; and Small Cetaceans (and see Annex K, item 10). With regard to the Arctic, three study themes were established: (a) Single Species-Regional Contrast; (b) Trophic Comparison; and (c) Distribution Shift. With reference to theme (a), planning discussions have been completed for a comparison of physical indicators of climate change and available data on population dynamics and behavioural ecology of the Bering-Chukchi-Beaufort Seas and Hudson Bay-Davis Strait populations of bowhead whales. In the Southern Ocean, the SWG was provided an update on the responses of the southern right whale population of Península Valdés, Argentina to climate driven changes on their feeding grounds off South Georgia. As was reported in the Southern Right Whale Die-Off Workshop (SC/62/Rep1 and see Item 10.5 above), one of three possible hypotheses to explain recent peaks in calf mortalities is a decline in food availability for adult females on their feeding ground during the year or two prior to calving. This hypothesis will be explored by updating an analysis on the relationship between changes in sea surface temperature and calving success. The Committee reviewed a draft agenda for a Small Cetaceans and Climate Change Workshop planned for November 2010, where the main focus will be: (1) restricted habitats – estuaries, reefs, environmental discontinuities, rivers and shallow waters; and (2) range changes – i.e. evidence of changes in distributions, reasons and consequences; and (3) with a review planned for small cetaceans in the Arctic Region and suggested that the definition of restricted habitat be broadened (Annex K, item 10). Noting that last year the Committee had recommended that countries should pay more attention to tertiary concerns arising from climate change, the Committee noted that Alter *et al.* (2010) provide arguments suggesting that tropical, coastal and riverine cetaceans are particularly vulnerable to those aspects of climate change that are mediated by changes in human behaviour.

12.6 Other habitat related issues

There has been a rapid expansion of marine renewable energy devices (MREDs) in European seas as governments strive to meet renewable energy commitments. Today there are some 89 such sites in various stages of development (most of these are wind farms), representing a five-fold increase in numbers since 2000, with a concomitant major increase in the size of planned developments. The SWG reviewed concerns associated with the construction, operation, maintenance and (ultimately) decommissioning of wind, tidal and wave renewable energy technologies (Annex K, item 11.1) and the Committee **strongly recommends** that countries co-operate to limit impacts on marine wildlife from these sources. The SWG subsequently discussed the ICES WGMME recommendations with regard to the effects of wind farm construction and operation on marine mammals (Annex K, item 11.1) and the Committee **endorses** those recommendations.

The French Agency for Marine Protected Areas (AAMP) has initiated the REMMOA project, a series of surveys across the French EEZ to identify hotspots of abundance and diversity. Extensive surveys have been conducted across the EEZ of Martinique and Guadeloupe, off Guiana and in the southwest Indian Ocean region. The South Pacific regions will be surveyed during 2010-11 (French Polynesia) and 2011-12 (southwest Pacific Ocean around New Caledonia and Wallis and Futuna) and the Atlantic survey is planned for 2012-13. The Committee also received information on systematic monitoring of density and abundance of the most common cetacean species of the Pelagos Sanctuary and in the seas surrounding Italy. The aim of this work, funded by the Italian Government, is to inform conservation measures throughout the Mediterranean Basin. It also responds to priority actions in a number of other international bodies (e.g. the Sanctuary Management Plan, ACCOBAMS, the Specially Protected Areas and Biodiversity Protocol under the Barcelona Convention, the EU Habitat Directive and the Convention on Biological Diversity). The Committee **commends** both of these studies and encourages their continuation. It noted the impressive advancements of current methods giving the authors the ability to correlate cetaceans with specific habitat features as well as other megafauna.

Finally, there has been limited progress since the update on the Madagascar Mass Stranding Event (MMSE) given in 2008 (IWC, 2009a, p.71). Two potential scenarios to move forward with an Independent Scientific Review Panel (ISRP) were identified: (1) a National Office of the Environment (ONE) to request and oversee an ISRP; or (2) the Environmental Governance Commission to serve as an intermediary body between the Government and/or ONE to promote the need for an ISRP to assess the results of the MMSE. The Committee welcomed this update and thanked The Wildlife Conservation Society and its partners' continuing efforts to bring the results of the MMSE to an appropriate conclusion through an ISRP process, as well as keeping the SWG updated on the current challenges and progress.

13. ECOSYSTEM MODELLING

The Ecosystem Modelling Working Group was first convened in 2007 (IWC, 2008c). It is tasked with informing the Committee on relevant aspects of the nature and extent of the ecological relationships between whales and the ecosystems in which they live. This advice is important to other responsibilities of the Committee: it can be used to simulate an ecosystem framework in which to evaluate management strategies; it can provide a bio-physical context within which to try to understand spatial or temporal (e.g. interannual, interdecadal, or long-term climate-driven) variability in cetacean population dynamics, distribution, behaviour, and health; it can provide insight into interactions between whales and fisheries; and it may inform the prioritisation and design of future IWC research projects by identifying critical information gaps and offering recommendations of when, where and how field efforts should be conducted to successfully collect new data that are necessary for providing insight into key questions. The Commission has stated their interest in such work in a number of resolutions (IWC, 1999a; 2001c; 2002a). Each year the Working Group reviews the progress in developing ecosystem models relevant to the work of the IWC, which is a broad task encompassing the evaluation of model inputs, assumptions, structure and outputs. In addition, the Working Group has placed a priority on discussions and collaborations with institutions outside of the IWC to facilitate the exchange of information on the state of the science of ecosystem modelling and, where applicable, to collaborate to achieve a common goal. No primary ecosystem modelling papers were received this year, so the Working Group dedicated its time to three general tasks: (1) reviewing ecosystem models and modelling approaches that were developed outside of the IWC; (2) learning about the Climate Impacts on Oceanic Top Predators (CLIOTOP) project; and (3) discussing and planning the future role of this Working Group within the Scientific Committee. The report of the Working Group is given as Annex K1.

13.1 Review ecosystem models relevant to the Committee's work

This year, Lehodey introduced the CLIOTOP project and in particular the ecosystem model that he and his colleagues developed to analyse and predict the spatio-temporal dynamics of tuna populations under the influence of environmental and fishing pressures (Lehodey *et al.*, 2008). The model has been applied to skipjack, bigeye, yellowfin and albacore tuna in the Pacific Ocean (Lehodey and Senina, 2009) and also been used to investigate potential influences of climate change on tuna population dynamics (Lehodey *et al.*, 2010).

CLIOTOP is a global project implemented under two International Geosphere-Biosphere Programme (IGBP) international research programmes: Global Ocean Ecosystem Dynamics (GLOBEC) and Integrated Marine Biogeochemistry and Ecosystem Research (IMBER). Its general objective is to enhance the understanding of oceanic top predators in their ecosystems in the context of both climate change and fishing, and to develop new tools leading to the evaluation of management strategies. CLIOTOP and the IWC share many common scientific interests, including: studying the behaviour, movement patterns and habitat of large predators; developing and applying technology for animal tracking; estimating food consumption rates; understanding and modeling predation by, and competition among, large predators; modelling and acoustic monitoring of prey fields; investigating various approaches to ecosystem modelling; and addressing issues of bycatch. The Committee **encourages** the establishment of collaborations between the IWC and CLIOTOP.

As part of its remit to preview general developments in ecosystem modelling to identify new modelling approaches and develop an evaluation framework that may be of benefit to the Committee's work, four recently published papers were reviewed (A'Mar *et al.*, 2009; Allen and Fulton, 2010; Buckley and Buckley, 2010; Hannah *et al.*, 2010). These covered issues of model structure, assumptions, complexity and validation. In discussion, it was noted that some existing research suggests that management strategies relying on empirical data through fisheries statistics performed better than those that incorporated ecological information; however, ecological data are valuable for constructing and constraining the range of ecosystem models that could be used to evaluate management strategies within the Scientific Committee.

13.2 Recommendations on the role of this Working Group within the Committee

SC/62/EM1 motivated discussions about the future of the Ecosystem Modelling Working Group. It provided background into the initial objectives and the history of the Working Group; reiterated the distinction between 'tactical' models (those used to set catch limits or to make other management advice) and 'strategic' models (those used to simulate an environment in which to test simpler models); listed some of the ecological and analytical issues that have been recurrent in Committee discussions to date; and introduced several recommendations to help the Committee evaluate ecosystem models, given the numerous uncertainties inherent in the modelling process. As did the Working Group, the Committee **agrees** to the following recommendations, based on those in SC/62/EM1:

(1) standardised templates should be developed for documenting metadata and analytical techniques;
(2) performance criteria should be established, including testing model fit to historic or present data and assessing its ability to generate ecologically reasonable predictions into the future;
(3) sensitivity analyses should be conducted to quantify and provide insight into the importance of model inputs (which can guide data collection priorities) and assumptions on model outputs;
(4) Scientific Committee members should be given access to relevant background information (such as the full mathematical specification) used in any presented ecosystem models that may inform management decisions (via the Secretariat);
(5) the Scientific Committee should explore various ecosystem modelling approaches for a system in order to compare performance across models;
(6) intersessional meetings should be used, when necessary, to allow in-depth examination of competing models; and
(7) the EM Working Group should continue to convene every year at the annual meetings to address issues relevant to the Scientific Committee and to remain informed about new developments in the ecosystem modelling field.

The Committee **emphasises** that the Working Group is an important forum for evaluating ecosystem model inputs, structure, assumptions and predictions related to its work. *Inter alia*, it is also the appropriate sub-group within the Committee for reviewing the ecosystem aspects of ongoing special permit whaling programmes.

The Committee **recognises** the need to involve outside experts in the Working Group. Work is underway to establish an avenue for exchanging information about new developments in ecosystem modelling and its feedback into management, and to solicit feedback on how ecosystem models could inform IWC management decisions.

The Committee **agrees** that the activities of the Working Group should be structured around the timetable of RMP assessments and *Implementations*, enabling ecosystem models relevant to a specific stock being assessed to be reviewed prior to the assessment; the North Pacific is the appropriate region for 2011. The Working Group will take efforts during the intersessional period to engage researchers involved in the North Pacific Marine Science Organization (PICES) and the North Pacific Research Board (NPRB) to collaborate on primary papers for next year's meeting on how North Pacific ecosystem models can be used to inform the RMP process. Two additional issues were highlighted for discussion next year, if primary papers can be prepared in advance. One is a review of functional responses, and the second is a review of methods for evaluating ecosystem models. It is expected that the latter will result in a framework that the Committee will use to guide future ecosystem model evaluations, providing model developers specific details regarding the information required to determine whether the input data and parameters, the model and the resulting predictions should be considered acceptable to inform the work of the Committee.

13.3 Work plan

The work plan is detailed under Item 24. The Working Group requests no funds for the upcoming year.

14. SMALL CETACEANS (SM)

The Committee has been discussing issues related to small cetaceans since the mid-1970s (IWC, 1976). Despite the differences of views over competency (IWC, 1993), the Commission has agreed that the Committee should continue to consider this item (IWC, 1995c). The report of the sub-committee on small cetaceans is given as Annex L.

14.1 Review taxonomy, population structure and status of small cetaceans of northwestern Africa and the Eastern Tropical Atlantic (ETA)

The priority topic this year was the review of the status of small cetaceans of northwestern African and eastern tropical Atlantic waters (Fig. 6), a region with a variety of ecosystems and coastal habitats. The review was greatly assisted by the availability of published review papers and documents prepared for this meeting by scientists working in Canary Islands (Spain), Mauritania, Cape Verde, Guinea, Ghana, Togo, Benin, Nigeria, São Tomé and Príncipe, Cameroon, Gabon, Congo and Angola.

The following sections represent a short summary of the extensive review. Details can be found in Annex L.

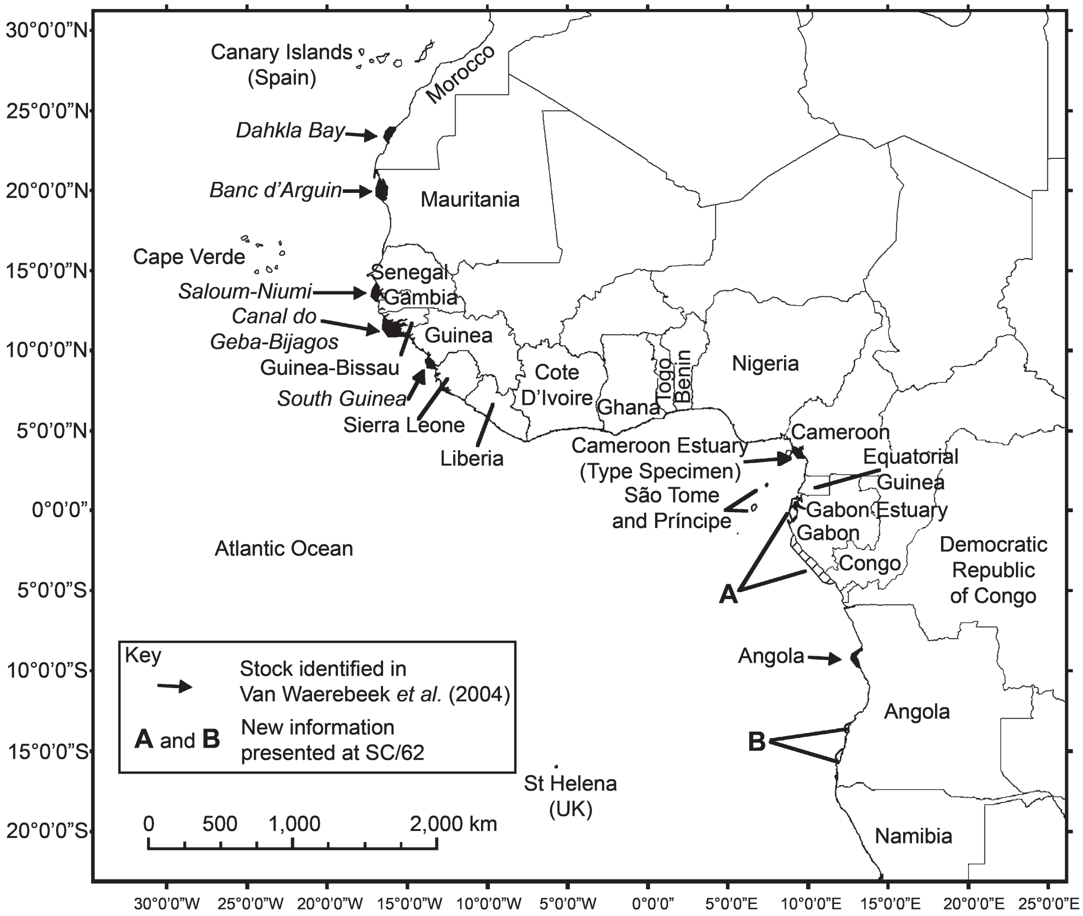


Fig. 6. Map of the northwestern and western African countries relevant to the cetacean distribution review. A=Information from SC/62/SM9. B=Information from SC/62/SM6.

Weir (2010) reviewed cetacean occurrence (sightings, strandings, direct captures, bycatch) in West African waters from the Gulf of Guinea to Angola, updating Jefferson *et al.* (1997). At least 21 odontocetes (including at least 17 delphinids) have been documented in the region. The author stressed that the region's cetaceans face several threats including bycatch, direct capture (e.g. in Ghana and Togo) and threats to them and their habitat, e.g. due to oil and gas development. Moore *et al.* (2010) reported information on cetacean bycatch from interview surveys in 2007 and 2008 in fishing communities of seven countries: Sierra Leone, Cameroon, Nigeria, Tanzania, Comoros, Malaysia and Jamaica They provided information on reported cetacean bycatches in Sierra Leone and Cameroon.

Further information on the region's cetaceans came from a number of papers focussing on country reports.

SC/62/SM9 reviewed recent information on Atlantic humpback dolphins in Gabon and Republic of Congo. Both countries have large and diverse national park systems that include protected coastal habitat. Given the low human population densities and the extent of relatively undisturbed habitat in Gabon and northern Congo, this region may represent a stronghold for the species. However, bycatch and evidence of dolphins in the bushmeat trade give cause for concern, particularly as the demand for fish in cities increases. The Committee commends the authors for their efforts in the region and **recommends** that research, monitoring and conservation efforts for humpback dolphins along the coast of Gabon and Congo continue.

The Committee received two papers covering Nigeria (SC/62/SM12 and SM1). Cetaceans occur throughout Nigerian coastal waters in the Gulf of Guinea, although there has been little directed cetacean research. Potential threats include: bycatches (a reported zero bycatch rate for Nigeria obtained in an interview survey by Moore *et al.* (2010) is not credible, probably due to low sample size); direct catches of delphinids (SC/62/SM1) for sale as 'marine bushmeat' (Clapham and van Waerebeek, 2007) which may be widespread; and habitat degradation (e.g. uncontrolled trawling operations, indiscriminate dumping of non-biodegradable nylon and plastic products and household items). The absence of monitoring may explain the lack of detailed information on direct catches. SC/62/SM1 reiterated the suggestion by Van Waerebeek *et al.* (2004) that Atlantic humpback dolphins inhabited the Niger Delta before large-scale oil exploration and extraction altered the coastal environment.

Information on Ghana was provided in SC/62/SM10 with an emphasis on the captures of small cetaceans in artisanal fisheries, mainly using drift gill nets. Cetaceans have been documented from three fish landing ports since 1995 but these landings do not represent the total for the country. It is often unclear if 'bycaught' cetaceans in Ghana are the result of unintentional or intentional taking. The species most frequently 'bycaught' are the clymene dolphin (24.5%), pantropical spotted dolphin (12.3%) and common bottlenose dolphin (12.3%). SC/62/SM10 suggested an increasing trend in the scale of landings between 1999 and 2010, and particularly since 2002-03. Once the practice of catching and marketing cetacean products becomes established, it can escalate rapidly as implied in the existing catch series. Although aquatic mammals are protected by law, there are no explicit regulations concerning the use of cetaceans killed in nets and the use of dolphin meat as bait in shark fisheries and for human consumption is not considered illegal. This means that catches are not concealed for fear of sanctions and therefore catch statistics can be obtained. This makes it feasible to study trends and carry out biological studies based on carcass sampling protocols.

As stated in SC/62/SM10, traditional taboos against catching dolphins are rapidly eroding in the Volta Delta region. This seems to happen in some areas of Nigeria as well. One important development is that the monetary value of a small cetacean is now roughly equivalent to that of a similar-sized large billfish. In fact, more money can be earned by selling the cetacean carcasses for shark bait as the export market in Asia for shark fins is lucrative and growing.

The Committee thanks the researchers working in Ghana for their efforts and notes that the evidently close cooperation with fisheries officials is encouraging.

Tchibozo summarised the current knowledge on small cetaceans along the 124km coastline of Benin (Tchibozo and van Waerebeek, 2007). The presence of four species has been confirmed: Atlantic spotted dolphins, common bottlenose dolphins, false killer whales and *Delphinus* sp. There have been no systematic studies on the distribution, abundance or ecology of small cetaceans in Benin. Although bycatch of cetaceans is known to occur in fisheries along the entire coast, no monitoring programme is in place.

SC/62/SM11 confirmed the presence of four small cetaceans in Togo's coastal waters: pantropical spotted dolphins, common dolphins, pilot whales and killer whales. However, there is no information concerning abundance, natural history or ecology. The main potential threats are:

(1) bycatch in fisheries, with the possibility that this has led or soon will lead to directed taking as has been observed elsewhere; and
(2) severe chemical pollution due to the mining of phosphorites and discharge of phosphate-rich mud into coastal waters.

Bamy *et al.* (2010) reported that four odontocetes occur along Guinea's 300km coastline: common bottlenose dolphins, Atlantic humpback dolphins, Atlantic spotted dolphins and pygmy sperm whales. It is probable that short-finned pilot whales, rough-toothed dolphins and common dolphins also occur there. This information comes mainly from observations during irregular, largely opportunistic surveys of fishing communities in 2001-03 by personnel from Guinea's Centre National des Sciences Halieutiques de Boussoura (CNSHB). There is no evidence of substantial directed or incidental takes (e.g. at the scale reported in Ghana) but monitoring and reporting have been limited. There is evidence that bycaught small cetaceans and a stranded whale were used for human consumption. The authors expressed concern about even occasional catches of Atlantic humpback dolphins.

During discussion, reference was made to the study by Brashares *et al.* (2004) on the relation between declining fish supplies in West African waters and the increase in hunting for 'bushmeat' and consequent declines in wildlife populations.

SC/62/SM8 updated Picanço *et al.* (2009) with information on small cetaceans off São Tomé and Príncipe. At least four species of small cetaceans are known to occur there with the common bottlenose dolphin and pantropical spotted dolphin being the most numerous.

Several species of small cetaceans were hunted historically in the Cape Verde Islands using hand harpoons. Despite protective legislation, cetaceans are still captured occasionally and their meat is sold and consumed (Hazevoet and Wenzel, 2000; Reiner *et al.*, 1996).

Vely summarised cetacean occurrence in Mauritania between 1987-95 based on dedicated surveys in two main areas: (a) between the southern border with Senegal and the village of Nouamghar at the northern entrance of the National Park of Banc d'Arguin (PNBA); and (b) within the PNBA. Species observed at sea were common bottlenose dolphins, Atlantic humpback dolphins and killer whales. Stranded specimens included harbour porpoises, clymene dolphins, common dolphins, Risso's dolphins, melon-headed whales, short-finned pilot whales, pygmy sperm whales, dwarf sperm whales and Cuvier's and Gervais' beaked whales.

Smit *et al.* (2010) summarised information on the presence and distribution of small cetaceans off the coast of La Gomera (Canary Islands), where a total of 21 species were observed at sea. The five most abundant species (87% of sightings) were common bottlenose dolphins, short-finned pilot whales, Atlantic spotted dolphins, short-beaked common dolphins and rough-toothed dolphins.

The Committee thanks all of the contributors but noted that its review was characterised by rather scarce information from the northwest African countries (see Annex L). However, enough new information was available from West Africa to update and make some corrections to the existing state of knowledge on cetaceans along the west African coast (see table 1 of Annex L).

IUCN Red List status for 21 out of 22 species is either Least Concern or Data Deficient (2008). The Atlantic humpback dolphin is listed as Vulnerable. There is a general lack of relevant information on many of the species, not only for western African waters but also globally, on taxonomy, population structure, abundance, life history and ecology.

The scarcity of information prevented the Committee from being able to make a reliable evaluation of the status of any of the species in the region. That being said, the information available in the review showed that nearly all species are taken either intentionally or unintentionally (SC/62/SM1, SM10 and SM11; see also Bamy *et al.*, 2010; Van Waerebeek *et al.*, 2008; and Weir, 2010). Especially for one species, the clymene dolphin, the Committee **expresses serious concern** about the ongoing observed landings in Ghana.

The Committee then reviewed two species on which there was a little more information.

Killer whales

Killer whales observed off Angola, Gabon and São Tomé were similar in external appearance to, and their appearance was consistent with, the Type A 'nominate' killer whale form described by Pitman and Ensor (2003). Weir *et al.* (2010) summarised published records from Liberia, Côte d'Ivoire, Ghana, Annobón Island (Equatorial Guinea) and Gabon as well as 31 sightings from Angola, Gabon and São Tomé, and a single record from Cameroon. De Boer (2010) provided an additional record of killer whales in the offshore waters of Gabon. Most sightings have been recorded since 2001, corresponding with the onset of dedicated survey work in the region. Bamy *et al.* (2010) found no confirmed records for the stretch of coast from southern Senegal (Casamance) to Liberia. They also questioned whether killer whales venture into the shallow waters of Guinea-Bissau, Guinea and Sierra Leone.

No information was received regarding recent intentional takes although one killer whale was recorded as landed in Ghana between 1998 and 2000 (SC/62/SM8).

The killer whale can be considered a regular component of the cetacean community off Angola and in the Gulf of Guinea. However, more survey work is required throughout the region to clarify its status and biology off tropical West Africa (Weir *et al.*, 2010). The IUCN Red List status of the species is Data Deficient.

Atlantic humpback dolphin

The Atlantic humpback dolphin - an endemic species for this region - was a priority species in 2002 (IWC, 2003b) but at that time the review focused on the Indo-Pacific humpback dolphin.

The taxonomy of the genus *Sousa* remains largely unresolved. Although three putative or nominal species have been widely discussed (*chinensis*, *plumbea* and *teuszii*), the IWC presently recognises only two, the Atlantic species *S. teuszii* and a geographically widespread Indo-Pacific species *S. chinensis*. Although the Committee was informed by Rosenbaum of a collaborative study to clarify the taxonomy of *Sousa*, the Committee **agrees** to retain its present nomenclature until formal publication of this information. It also **recommends** that samples from *S. teuszii* be provided to Rosenbaum as soon as possible so that they can be included in the ongoing efforts described above, which are essential for resolving questions questions concerning taxonomy and population structure.

Van Waerebeek *et al.* (2004) reviewed the state of knowledge on Atlantic humpback dolphins and proposed eight provisional management stocks based on the fragmentary information available to them. Six were confirmed as extant based on recent records: Dakhla Bay (Western Sahara), Banc d'Arguin (Mauritania), Saloum-Niumi (Senegal, Gambia), Canal do Gêba-Bijagos (Guinea-Bissau), South Guinea and Angola. The other two – Cameroon Estuary and Gabon – were considered historical. Those authors also noted the 'potential existence' of a western Togo stock. They concluded that there were nine confirmed range states: Morocco (including Western Sahara), Mauritania, Senegal, The Gambia, Guinea-Bissau, Guinea-Conakry, Cameroon, Gabon and Angola.

Van Waerebeek *et al.* (2004) stated that the species was limited to tropical and subtropical waters very near shore from Western Sahara in the north to Angola in the south; the distribution is patchy and limited to particular stretches of coastline separated by gaps of absence or very low density. In many cases, it was unclear whether the absence of records from an area means the species naturally does not occur there, or it has been extirpated in the area, or search effort and reporting have been insufficient.

Bamy *et al.* (2010) considered as uncertain the degree of distributional continuity and gene flow between the provisionally defined 'South Guinea stock' and other provisionally defined stocks (Van Waerebeek *et al.*, 2004). As in Guinea-Bissau, most of Guinea's coastline has features suitable as humpback dolphin habitat: warm and shallow waters on a shelf extending up to 200km from shore, with extensive mangrove creeks around four main river mouths. The lack of sighting records is probably partly due to the small amount of near-shore survey effort. Ghana represents a confirmed gap (SC/62/SM10).

Although much remains unknown about distribution and the extent to which it has changed over time as a result of human activities (e.g. bycatch, habitat degradation), current understanding is that there are regional pockets of relatively high density, such as in Senegal-The Gambia-Guinea-Bissau-Guinea-Sierra Leone, Gabon-Congo and Cameroon-Angola-Namibia.

Although its typical habitat was thought to be shallow coastal waters, especially estuaries, mangrove systems and sheltered bays (Van Waerebeek *et al.*, 2004), new information on the presence, distribution and behaviour of Atlantic humpback dolphins was received from Flamingos (southern Angola), Gabon and Congo (SC/62/SM9), also see Weir *et al.* (2009). In Gabon, Congo and elsewhere in the southern range of the species, humpback dolphins are regularly observed on open coastlines.

The loss and fragmentation of habitat due to expanding coastal communities, coastal development, dredging, trawling, deforestation, mangrove destruction, pollution, eutrophication and oil spills also threaten this species. Its preference in many areas for shallow, nearshore and estuarine habitat would render it particularly vulnerable to ubiquitous inshore set gillnets, beach seines and disturbance.

The Committee **agrees** that there is ample evidence for serious concern about the conservation status of this species (SC/62/SM1; SM6; SM9-SM11, and see also Bamy *et al.*, 2010). Although quantitative data or even good qualitative data (e.g. confirmation of species presence/absence) are lacking for much of the known or suspected range, the information available from areas where cetaceans have been consistently studied (e.g. Ghana, Guinea) indicates that the overall population is fragmented, bycatch (if not also directed catch) is occurring, and habitat conditions are deteriorating. Populations in Gabon and northern Congo appear healthy, but recently documented bycatches and utilisation in Congo may be indicative of a growing reliance on non-fish marine wildlife, including dolphins, as food.

In view of the growing concern (e.g. summarised in SC/62/SM6) that the Atlantic humpback dolphin faces some of the same threats that led to the extinction of the baiji and caused the vaquita to become critically endangered, the Committee **recommends** that IUCN reassess the Atlantic humpback dolphin's status in the light of new information.

It also **recommends** the following items for further conservation and research action for Atlantic humpback dolphins, taking into account *inter alia* the CMS regional action plan for the conservation of West African small cetaceans[4].

(1) Coordinated data collection should be facilitated in order to improve knowledge of the abundance, distribution and conservation status of *S. teuszii* throughout its known range. Specifically:
    (a) estimates of abundance and distribution are urgently required (including where feasible photo-id);
    (b) tissue samples should be obtained at every opportunity from stranded or bycaught Atlantic humpback dolphins. These need to be appropriately preserved and provided to scientists for genetic analyses investigating population structure;
    (c) critical habitats should be identified, including areas of high density and regular occurrence ('hotspots') and migratory pathways (if such exist), as candidates for focused conservation effort; and
    (d) overviews of existing knowledge, national species lists, specimen collections, research centres and protected areas should be compiled.

(2) Identify and mitigate known and potential threats to *S. teuszii*, particularly entanglement in fishing gear, and directed take and anthropogenic noise. Specifically this should include:

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[4] Action Plan for the Conservation of Small Cetaceans of Western Africa and Macronesia, ratified in 2008 by West African member nations of CMS.

(a) improving the understanding of the causes, levels and impacts of bycatch on *S. teuszii*;
(b) assessment of the causes, level and intensity of directed small cetacean takes;
(c) efforts should be made to minimise the ecological impacts of fisheries on, and direct takes of, *S. teuszii* through the implementation of explicit fisheries management measures; and
(d) ensure that all littoral developments and activities take into account their potential for having negative effects on small cetaceans and the environment.

(3) The designation and management of national and transboundary marine protected areas that include *S. teuszii* habitat based on scientific data and broad stakeholder involvement should be encouraged.

The Committee also specifically **recommends** that regional or sub-regional research projects be conducted that would allow the preparation of management plans for the conservation of Atlantic humpback dolphins in particular areas. Candidate areas are: (a) off Flamingos, Angola; (b) along the coasts of Gabon-Congo; (c) Senegal-The Gambia-Guinea-Bissau-Guinea-Sierra Leone where the humpback dolphin population(s) may be transboundary and where bycatch is a serious concern; and (d) Mauritania where humpback dolphins were observed regularly in Banc d'Arguin National Park and environs over many years, but may have declined recently (Van Waerebeek and Perrin, 2007).

The Committee **strongly encourages** scientists in the range states to submit collaborative proposals for funding so that transboundary problems can be addressed in a comprehensive way, possibly cooperating with the staff of National Parks.

General recommendations relevant to all species

In general, the Committee **acknowledges** that the failure to manage industrial fisheries sustainably has often caused coastal artisanal and subsistence fisheries to suffer and, in turn, has led local people to seek alternative resources for consumption, including cetaceans.

Given the observed threats and the existing knowledge, the Committee makes the following general **recommendations** applicable to all small cetacean species in the west and northwestern Africa.

(1) The tallying of cetacean landings should be implemented as a standard procedure for fisheries observers at the national level, including the collection of photographic material, recognizing that small cetaceans are a *de facto* exploited marine living resource and therefore need to be monitored on a permanent basis.
(2) An intensive biological sampling programme based on fresh carcasses, collecting data on morphological variation, reproduction, growth, feeding, stock identification, genetics, migratory habits, etc. of cetacean species should be implemented.
(3) Use of platforms of opportunity should be intensified to collect data on distribution, relative abundance and behaviour of cetaceans.
(4) Further assessment of the links between declining fish catches and increasing takes of small cetaceans in West Africa should be made.

In at least three west African countries, Ghana, Togo and Guinea, the ongoing activities represented good examples of how the first two of these recommendations could be realised. The Committee **acknowledges** the contributions already being made by scientists in Nigeria and Benin and recognised that there is a great need for capacity building and financial support before such programmes can be implemented. The same is true for São Tomé and Príncipe where the status of small cetacean populations has not been fully assessed and for the Cape Verde Islands, where no study of small cetaceans has ever been conducted. With regard to the third recommendation, the Committee noted and commended the published work by Weir (2007; 2010) and de Boer (2010), much of which was based on data from platforms of opportunity (e.g. seismic survey vessels, oceanographic research vessels); these are seen as excellent examples of how this recommendation can be realised in more areas.

In conclusion, the Committee **recommends** international collaboration for funding and capacity building to support programmes for monitoring, management and conservation of coastal marine living resources in this region.

14.2 Review report from the working group on climate change and small cetaceans

The Committee received a summary on the ongoing plans for an IWC workshop on the effects of climate change on small cetaceans. The workshop plan (10-12 invited participants meeting for 3 days) was agreed last year but the workshop was not held in the last intersessional period as the final *tranche* of funding was only confirmed late in the year. The steering group and convener (Simmonds) are now finalising plans for the workshop, which will probably be held in Vienna in November 2010 (see Appendix 2 of Annex L). The focal topics are: (a) restricted habitats; (b) range changes; and (c) the Arctic region. During discussion it was suggested that pathogens should also be discussed.

The Committee **re-confirms** its support for the meeting and looks forward to receiving a full report of this workshop at the next annual meeting in 2011.

14.3 Review progress on previous recommendations

IWC Resolution 2001-13 (IWC, 2002b) directs the Scientific Committee to review progress on previous recommendations related to critically endangered species and stocks of cetaceans on a regular basis and the Committee noted that its previous recommendations stand until new information is received and considered.

14.3.1 Vaquita

The Committee reviewed new information on the critically endangered vaquita. SC/62/SM3 reported on a survey in the Upper Gulf of California that was conducted from mid-September, through October and November 2008 in a joint effort between the governments of Mexico and the US. The primary objective was to test alternative acoustic detection technology as a means of monitoring trends in vaquita abundance. Total abundance (based on both acoustic and visual data) was estimated as 250 animals (95% CI 110, 564). The estimate for waters inside the Vaquita Refuge was 123 (95% CI=64-239). The total estimate for 1997 had been 567 (95% CI=177-1,073). Analyses strongly support a population decline over the 11 years from 1997 to 2008. The overall distribution did not change between the two surveys, indicating that the apparent decline was not an artifact of a distributional shift. Approximately half of the population appears to be present inside the Vaquita Refuge area at any time, with individuals moving freely into and out of the refuge. Hence, they are at risk of interaction with fishing operations when outside of the refuge, and this means that protection from bycatch is only partial. Fishermen consider waters inside the Refuge to be a prime shrimping area and thus fishing activity is very intensive immediately outside its borders. The buyout programme begun by the Mexican government in 2007 has reduced the fishing effort by about 40%, but over 600 artisanal boats (*pangas*) are still fishing and those fishermen who remain active are strongly committed and unlikely to accept the buy-out offers from the government. This makes it crucial to develop alternative fishing methods that do not involve the risk of vaquita bycatch.

The Mexican government made a commitment to reduce the vaquita bycatch to zero within three years starting in 2008. There are no data to confirm that the bycatch rate has been reduced apart from an inference from the reduction in fishing effort; because of the regulatory situation, fishermen generally no longer report and deliver bycaught vaquitas to authorities. This makes the implementation of regulations particularly challenging.

SC/62/SM5 reported on the development of a monitoring plan to assess trends in vaquita abundance based on acoustics using C-POD. It is anticipated that the scheme will be in operation by the end of this year (2010). Jaramillo-Legorreta acknowledged the financial support provided to this work by a number of agencies and organisations in addition to the Mexican government: National Marine Fisheries Service, WWF, the Cousteau Society, Ocean Foundation, US Marine Mammal Commission and International Fund for Animal Welfare.

The Committee thanks Jaramillo-Legorreta for this update and commends those involved for their hard work and commitment to saving the vaquita. The Committee **agrees** that it would be useful to document (in working papers or publications) all of the costs of the vaquita conservation and monitoring efforts for future reference for other Countries with similar bycatch problems.

The Committee **remains gravely concerned** about the fate of the vaquita and it **reiterates its previous recommendation** (IWC, 2010h, p.324) that, if extinction is to be avoided, all gillnets should be removed from the upper part of the Gulf of California. The Committee further **recommends** intensified development and testing of alternative fishing gear (e.g. through a smart-gear competition) that fishermen can use in place of entangle gears. It **strongly encourages** Mexico to continue and intensify its efforts to conserve the vaquita.

14.3.2 Harbour porpoise

No primary papers on harbour porpoises were presented at this meeting.

A joint workshop of ASCOBANS/ECS recommended a revision of EU regulation 812/2004 on monitoring and mitigation of cetacean bycatch in gillnet and pelagic trawl fisheries, as at present it does not include small vessels of less than 15m length. The Committee **recommends** that the EU regulation should be reviewed if realistic total estimates of bycatch are to be provided.

Available information for the German North Sea and Baltic from 2003 to 2009 suggests an increasing trend in bycatch. As last year, the Committee **expresses concern** about the ongoing evidence of large-scale bycatch in this region, including the western Baltic (as discussed last year when the Committee called for more research). The Committee **notes**, in particular, that the harbour porpoise population in the Baltic proper is considered Critically Endangered. Better information on both the scale of incidental mortality and the stock affinities of the affected porpoises is essential.

Attention was drawn to the vulnerability of the recently identified a isolated Iberian population of harbour porpoises. The Committee **recommends** further study of this population.

14.3.3 Franciscana

The franciscana, endemic to the eastern coasts of Brazil, Uruguay and Argentina, is regarded as one of the most threatened small cetaceans in South America due to high bycatch levels as well as increasing habitat degradation throughout its range. It is classified as Vulnerable by IUCN. Secchi *et al.* (2003) proposed four management stocks (known as Franciscana Management Areas or FMAs): three in Brazil (FMA I-III), one in Uruguay (FMA III) and one in Argentina (FMA IV).

Mendez *et al.* (2010) stressed that considering all franciscana genetic analyses to date, there is strong evidence for the existence of at least three populations in Brazil (FMAs I, II and III), one in Uruguay (FMA III) and three in Argentina (FMA IV).

The Committee welcomes the new information concerning franciscana stocks in Argentina and encourages the continuation of research and conservation efforts on the species there, particularly in light of the high bycatch rates. It **recommends** that the possibility of further population structure within the range of the franciscana be investigated.

SC/62/SM7 presented information on distribution and provided the first estimate of abundance of franciscanas in FMA II (Brazil) from aerial surveys conducted in December 2008 and January 2009. Coverage included an area believed to correspond to a hiatus in the distribution between FMA I and FMA II. Sightings were confined to the coastal stratum, but offshore effort was low due to poor weather conditions. Corrected abundance was estimated to range between 8,000 and 9,000 individuals (CVs=0.32-0.35) although some additional sources of possible bias require investigation. Current estimates of incidental mortality in FMA II correspond to 3.3-6.2% of the estimated population size presented here, which is likely unsustainable.

The Committee **welcomes** this paper that addresses recommendations from previous years (IWC, 2005g, p.309). It notes that the estimates of abundance were probably negatively biased because of limited coverage of the offshore stratum and because estimates of group size from aircraft are consistently smaller than those from boats and land observation sites.

With regard to the aerial surveys in FMA II, the sub-committee commends Zerbini and his co-workers for their excellent work and **recommends** that further studies be carried out to:

(1) improve estimates of visibility bias;
(2) evaluate potential biases in the estimation of group sizes; and
(3) estimate franciscana diving parameters in areas where such information is not available.

The Committee also **recommends** that bycatch be estimated in additional areas and assessments be carried out of other possible threat factors such as underwater noise, chemical pollution from coastal development and industrial and human waste discharge, oil and gas exploration activities and vessel traffic.

14.3.4 Narwhal

Last year (IWC, 2010h, p.325), the Committee noted that new estimates of narwhal abundance had recently become available. Subsequently, the results of aerial surveys in Canada indicating total abundance greater than 60,000 narwhals were published (Richard *et al.*, 2010). The NAMMCO Scientific Committee considered new estimates from Greenland in its management advice given in April 2009 (IWC/62/4). At its 2009 meeting, the NAMMCO Council (NAMMCO Annual Report 2009, pp.96-97) considered the new information on narwhal abundance and revised its management advice accordingly. The 2005 NAMMCO assessment had concluded that narwhals in West Greenland were highly depleted and that annual sustainable harvest levels would be as low as 15-75 animals. However, population modelling with the new survey data from 2007 and 2008 indicated that overall abundance was at 51% (95% CI: 27-79%) of carrying capacity, with a 2009 modelled abundance of 12,000 (95% CI: 6,200-26,000), and NAMMCO concluded that its management objectives would be met at 70% probability with annual total removals of 310 (West Greenland) and 85 (East Greenland).

The Committee **thanks** the NAMMCO observer for providing information and **encourages** closer links between the NAMMCO and IWC Secretariats in sharing information, e.g. catch data. The possibility of a joint special meeting or workshop on monodontids (involving IWC, NAMMCO, Canada-Greenland Joint Commission on Narwhal and Beluga) should be considered in the near future, assuming that a data availability agreement can be established in advance. The next meeting of the Joint NAMMCO SC and JCNB scientific working group on narwhal and beluga will probably be in 2012, leaving adequate time to explore the potential of a joint meeting/workshop. The Committee **agrees** that an e-mail working group convened by Bjørge will follow up this possibility during the intersessional period and report back next year.

14.3.5 Irrawaddy dolphin

The freshwater population of Irrawaddy dolphins in the Mekong River is Critically Endangered (Smith and Beasley, 2004).

SC/62/WW4 reported on dolphin-watching tourism in the Mekong where photo-id studies indicate dolphins exhibit high site fidelity to particular deep-water pool areas that are very limited in size (1-2 km^2). The authors argued that an adaptive, precautionary approach is essential to managing tourism that targets small, closed, resident communities of cetaceans such as in this case. SC/62/WW4 recommended a range of management interventions, all aimed at decreasing the exposure of dolphins to dolphin-watching vessels.

The Committee received information from World Wide Fund for Nature (WWF)-Cambodia indicating that there are fewer than 100 dolphins based on a photographic mark-recapture analysis. At least 92 dolphins (>63% of them classified as calves) died in the period 2003-09, likely due primarily to entanglement in fishing gear and conservation efforts have focussed on the elimination of gill nets in the core habitat for dolphins in the 200km stretch of the Mekong between Kratie town and the Lao border. The conservation of dolphins in the Mekong is primarily the responsibility of the Commission on Dolphin Conservation and Ecotourism Development (Dolphin Commission). Despite its efforts, the mortality rate has remained high and the population apparently is continuing to decline. Dolphin conservation efforts in Cambodia reportedly have been hindered by inadequate funding for the Dolphin Commission and the lack of regulations that could help to reduce or eliminate the use of gill nets. There is also a need for much better cooperation among the Dolphin Commission, the Fisheries Administration and WWF. WWF and the Fisheries Administration are currently working to develop protected areas and other regulatory tools to protect dolphins. WWF and local NGOs are also working with local communities to reduce gill net use and to develop alternative livelihoods in order to reduce fishing pressure in core dolphin habitat.

The Committee **expresses grave concern** about the rapid and not fully explained decline of this riverine population. It commends the efforts by Cambodian government agencies and WWF-Cambodia to diagnose the cause(s) of the decline, and **strongly recommends** that every effort be made to stop and reverse it, e.g. by immediately eliminating entangling fishing gear in the pool areas used most intensively by the dolphins and by taking immediate steps to reduce the exposure of the dolphins to tour boat traffic.

14.3.6 Other

The Committee received an update (SC/62/SM2) of Amaral *et al.* (2009), the goal of which is to revise the model of worldwide population structure of common dolphins, genus *Delphinus,* using a multilocus approach. It has become clear that the long-beaked population in the northeastern Pacific is highly differentiated from all other populations based on both nuclear and mitochondrial markers. The differentiation between short-beaked populations occurring in different oceans is even higher than suggested in Amaral *et al.* (2009). Future analyses will estimate divergence times and migration rates between the different populations. This study also highlighted the difficulty of obtaining informative molecular markers other than mitochondrial DNA and microsatellites, due to the low overall level of polymorphism in the nuclear genome of common dolphins.

The Committee **encourages** the continuation of this global study of the genus. It also **recommends** that efforts should be made to obtain samples from regions where both short-beaked and long-beaked forms occur, as is the case in West Africa and the southeastern Pacific.

14.4 Other information presented

SC/62/BC6 presents a preliminary global review of operational interactions between odontocetes and the longline fishing industry and potential approaches to mitigation. This is a global problem for both cetaceans and fishermen. Mitigation strategies are needed to ensure the sustainability of both the odontocete populations and the longline fisheries. Bycatch occurs in many longline fisheries and involves at least 13 species but there are few quantitative data. The inadequacy of life history and population data adds to the difficulty of assessing the sustainability of the bycatch in most cases. Considerable effort has been devoted to solving the depredation problem and potential solutions have included acoustic and physical tools. Acoustic approaches to mitigation have proven problematic but recent trials using physical depredation mitigation devices have yielded promising results.

In discussion it was noted that longline fisheries for halibut and Greenland halibut in the northern North Atlantic have increasingly experienced problems with depredation of catches by northern bottlenose whales (*Hyperoodon ampullatus*).

New information was presented on the ongoing commitment of the Italian government (Ministry of the Environment) to conduct systematic abundance aerial surveys of small cetaceans in Italian waters (Ligurian, Tyrrhenian, Sardinian and Ionian seas) and in the Pelagos Sanctuary. Initial scientific and technical support was provided by the IWC Head of Science. The surverys are a priority action common to the Sanctuary Management Plan, ACCOBAMS and RAC/SPA UNEP. Among the preliminary conclusions from the completed surveys were: (1) the Sanctuary does not cover the full population range of striped dolphins; and (2) there is substantial seasonal variation in the density and abundance of striped dolphins (higher in summer). These density and distribution data from the surveys will be instrumental to the proposed ACCOBAMS basin-wide survey and will help guide the development of a long-term monitoring programme. The Committee also **welcomes** news of a complete survey of the Adriatic Sea funded by the Italian Government in July-August 2010.

The ACCOBAMS observer reported that a basin-wide survey of cetaceans in the Mediterranean and Black Seas remains one of ACCOBAMS' highest priorities. Activities are underway with the aim to start such a survey in the next triennium (2011-13).

The Committee **welcomes** the new information and **supports** continuation of such efforts in the Mediterranean Sea and adjacent areas. It specifically **endorses**, as it has in the past, implementation of the ACCOBAMS basin-wide survey, as soon as possible.

14.5 Review of takes of small cetaceans

At the last meeting, the sub-committee discussed various problems associated with the compilation of data on takes of small cetaceans including both direct catches and bycatch (IWC, 2010h, pp.326-28). It recommended a series of changes in how the data should be compiled, reported and interpreted. The process of setting up a system for direct electronic submission of these data by national representatives is still ongoing. The information retrieved by the Secretariat from national progress reports was reviewed. Data on bycatch of small cetaceans was presented in 12 National Progress Reports (Annex L, table 2).

The Committee **reiterates** the importance of having these data submitted and **encourages** all countries to do so.

The observer from NAMMCO advised that catch data from member countries are routinely published in the NAMMCO Annual Reports that are available on the website *http://www.nammco.no*.

Concern was expressed about the information from 12 West African countries indicating human consumption of cetaceans, exchange of cetacean meat in markets or direct capture of cetaceans (see Annex L, table 1); consumption and exchange can lead to targeted and unregulated direct hunting.

Information was received on small cetacean interactions with fishing gear in Machalilla National Park, Ecuador. Four species of cetaceans were caught incidentally: common bottlenose dolphins, dwarf sperm whales, Risso's dolphins and pantropical spotted dolphins. The Committee **expresses concern** about the implications of the bycatch documented in this preliminary study and looks forward to a more detailed report next year on the scale of the fisheries involved and therefore the implied magnitude of the cetacean bycatch.

14.6 Voluntary Fund for Small Cetaceans Conservation Research

The Committee discussed a proposed mechanism and procedure for allocating project support for high priority conservation projects (e.g. improving status of threatened species, capacity building) from the IWC Small Cetacean Research Fund. Australia's recent contribution to the fund is intended to support high priority research that demonstrably links to improving conservation outcomes for small cetaceans globally, particularly those that are threatened or especially vulnerable to human activities. Preference for funding will be based on a determination of need, the quality of the research application and the demonstration of links between research and conservation outcomes. Proposals that demonstrate a capacity building legacy will be viewed favourably.

In order to maximise the number of projects supported by the fund, and hence enhance conservation outcomes for small cetaceans, any single proposal will be limited to a maximum of £34,000. Other IWC member governments will also be encouraged to provide additional voluntary donations to the fund to further support small cetacean research.

A funding application form is being developed and made available via the IWC Secretariat. Applications should be received by the Secretariat at least 60 days prior to the start of the Committee's Annual Meeting. A Review Group will be appointed by the Convenor of the Small Cetacean sub-committee to review proposals in accord with agreed criteria. The group will make recommendations for funding to the Small Cetaceans sub-committee. It may suggest improvements to proposals where appropriate and can solicit the assistance of other researchers in the review process if necessary.

The recommended projects and budgets will be reviewed by the Small Cetacean sub-committee and the full Scientific Committee. Recommended proposals will be added to the Committee's budget as a specific request to the Voluntary Research Fund for Small Cetaceans. The Secretariat will organise contracts for the projects that are approved for funding by the Commission.

The Committee **emphasises** the importance of ensuring that proposal review and project selection meet the criteria and priorities of the sub-committee on small cetaceans. In addition to a call for proposals via a circular from the IWC Secretariat to all members of the Scientific Committee, a broader announcement mechanism will be developed.

The Committee **expressed** its gratitude to the Government of Australia for its generous contribution to the Voluntary Fund for Small Cetacean Conservation Research, which will make a significant difference to the Fund's ability to pursue its conservation priorities.

The Committee also **emphasises** the importance of building the Fund by obtaining donations from other sources. It was noted that good outcomes from the funded research should encourage more countries to contribute.

14.6.1 Project Proposal for the Voluntary Fund for Small Cetacean Conservation Research

A proposal for funding by the Small Cetacean Conservation Research Fund entitled '*Threatened Franciscanas: Improving Estimates of Abundance to Guide Conservation Actions*' was presented (Annex L, Appendix 3). The proposed work is directly linked to previous recommendations of the sub-committee, and responds directly to recommendations made at the present meeting based on consideration of SC/62/SM7 (see Annex L).

The sub-committee **strongly supports** the proposal, based on the following considerations:

(1) the franciscana is threatened by a variety of human activities in the region, particularly artisanal fishing;
(2) the proposal addresses a clear conservation need as expressed in present and previous recommendations; and

(3) more robust estimates of franciscana abundance (along with improved, more nearly complete estimates of bycatch as well as assessments of other threat factors) are needed to assess the status of populations and develop appropriate mitigation efforts.

The proponents have a strong track record (e.g. as reflected in the quality of the work described in SC/62/SM7).

The Committee therefore **recommends** that the proposal be funded by the Voluntary Fund for Small Cetacean Conservation Research and that a full report on the results be provided for consideration at a future meeting.

14.7 Work plan

The sub-committee on small cetaceans reviewed its schedule of priority topics which currently includes:

(1) systematics and population structure of *Tursiops*;
(2) status of ziphiids worldwide; and
(3) fishery depredation by small cetaceans.

The Committee **agrees** that the priority topic for the next annual meeting will be the status of ziphiids (beaked and bottlenose whales) worldwide.

Further discussion of potential future topics can be found in Annex L. As part of the discussion it was agreed to establish an intersessional correspondence group convened by Ritter to consider whether the issue of the consumption of cetaceans ('marine bushmeat') as some type of substitute for other resources that are becoming scarce should be added to the priority topic list. The group will collate information intersessionally and report back at the next annual meeting.

The Committee will also review the report from the Workshop on climate change and small cetaceans.

15. WHALEWATCHING (WW)

The report of the sub-committee on whalewatching is given as Annex M. Scientific aspects of whalewatching have been discussed formally within the Committee since a Commission Resolution in 1994 (IWC, 1995b).

15.1 Proposal for a large-scale whalewatching experiment (LaWE; including reports from the intersessional steering group and the advisory group)

The Committee received a proposal from the large-scale whalewatching experiment (LaWE) intersessional steering group. The report elaborated on the objectives, aims, methodology, design, management and funding considerations for this initiative (Annex M, Appendix 2).

Three options were presented for procedural mechanisms to manage the different components of the LaWE project, ranging from top-down (in which the IWC would play a steering group role) to decentralised (in which the IWC would play a coordinating role (Annex M, item 5.1, fig. 1). After discussion, the Committee **agrees** that a transitional process is preferable, with a top down approach (hierarchical structure) at the initial stage of the project progressing into a mechanism where the IWC would play more of a coordinating role (network structure). Discussions are detailed in Annex M, item 5.1.

IWC member nations will be able to use the results of the project as the basis for appropriate scientific management of whalewatching. The information collected during LaWE will also provide data on general biology and life history parameters of cetaceans that are relevant to other aspects of the Committee's work. There are a variety of potential funding sources for the LaWE effort including:

(1) IWC membership: funding derived from fees/contributions from member nations;
(2) national/regional initiatives: funding derived from national or regional governments involved in the support/promotion of whalewatching;
(3) NGOs: funding derived from national/international NGOs involved in the conservation of cetaceans;
(4) whalewatching operators: funding derived from whale/dolphin-watching operators; and
(5) hybrid model: targets key operators in high profile whalewatching areas with additional funding sought from host countries, IWC, NGOs, and other sources.

The Committee **recommends** that an e-mail correspondence group be formed to further develop the budget for the LaWE, although it noted that until power analyses are completed and species and sites are chosen, only approximate budgets can be created.

The Committee **agrees** to combine the two previous LaWE intersessional groups into one 'steering group' to maximise collaborative discussions (see Annex M, item 5.1).

The budget request to assist the LaWE intersessional work to develop procedural mechanisms to centralise data received from research groups relevant to LaWE with the Secretariat and commence power analysis for key parameters depending on data received is discussed under Item 24. In addition, funding is requested for a pre-meeting of the LaWE steering committee to review and advance intersessional progress on all aspects of the project, including reviewing data received, advancements in power analysis, and the selection of appropriate study species and sites.

There was no formal report from the advisory group, as the LaWE is not yet at the point of selecting research sites.

15.1.1 Other

SC/62/WW5 presented a summary of progress from a working group tasked with developing a formal mathematical structure from the US National Academy of Sciences Population Consequences of Acoustic Disturbance (PCAD) conceptual framework. The working group decided to develop three statistical models to provide the linkages from disturbance to population dynamics. Work has focused on the first models (disturbance to physiological conditions). First implementations with simple systems (southern elephant seals at-sea movement) proved extremely successful and body condition time series could be estimated and validated against body weight when the seals returned to the colony. A similar, albeit more complex, model was developed for coastal dolphin population case studies and will be implemented over the next year.

Discussions on the motivational state-space approach to the PCAD model and concern about the restrictions on the remit of the PCAD project are detailed in Annex M, item 5.1.

15.2 Review of whalewatching off North Africa

SC/62/SM8 reported on cetacean sightings, local human activities and conservation off São Tomé (São Tomé and Príncipe), Gulf of Guinea, West Africa. This region seems to be an important area for cetaceans; however, the status of species or populations has not been assessed due, in part, to lack of information and effort. A similar situation may exist in the Cape Verde Islands where there are resorts and a significant number of tourists. It was noted that several measures regarding the conservation of natural populations of cetaceans are needed for these areas (including international standards of operation, educational programmes and research) to reinforce a change to a more conservation-oriented perspective with direct involvement of local communities.

The Committee welcomed the report and noted the lack of information on whalewatching activities in western and northern Africa. Furthermore, it **expresses concern** at the potential for expansion of whalewatching activities in the region without sufficient scientific information on cetaceans and called for an assessment of the scope of activities to be made by relevant authorities as soon as possible.

An overview of whalewatching activities in the Mediterranean will be prepared under ACCOBAMS. More information is available on the Agreement's official website, *http://www.accobams.org*.

15.3 Assess the impact of whalewatching on cetaceans

SC/62/WW4 reported on the critically endangered Irrawaddy dolphin population inhabiting the Mekong River. Studies indicate dolphins exhibit high site fidelity during the dry season, have low genetic diversity and a high mortality rate. The locations of dolphin-watching areas are at two of the critical habitats for the remaining population in the river, numbering less than 100 individuals. Initially, at both locations, the dolphin-watching industry was land-based, with a few row-boats occasionally taking tourists into the pool to view dolphins. By the early 2000s this expanded to approximately 15 larger motorised boats that offered dolphin tours. Now it numbers more than 20. The authors believe that an adaptive, precautionary approach is essential to managing tourism that targets small, closed, resident communities of cetaceans and that for this Critically Endangered population, a 'no vessel-based dolphin tourism' policy is desirable. It was noted that the issues associated with Cambodian cetacean-watching tourism may be generic to developing countries.

The Committee reiterated **its concern** over the critically endangered Mekong River Irrawaddy dolphin population. In 2006, it had noted that there was compelling evidence that the fitness of individual odontocetes repeatedly exposed to tour vessel traffic can be compromised and that this can lead to population level effects (IWC, 2007b). It also stated that, in the absence of data, it should be assumed that such effects are possible until indicated otherwise – particularly for small, isolated and resident populations. Accordingly, the Committee **strongly recommends** that the Cambodian government and relevant agencies make every effort to reduce the exposure of dolphins to vessel-based tourism in deep-water pools in the Mekong River.

SC/62/WW1 reported on behavioural responses of southern right whales to human approaches in Bahia San Antonio, Rio Negro, Argentina. Results are listed in Annex M, item 6. The Committee noted the small sample size but commended the before-during-after experimental design.

SC/62/WW2 summarised recent advances in whale-watching research. Noren *et al.* (2009) investigated the prevalence of 'surface active behaviours' (e.g. spy hops, breaches) in the vicinity of boats in southern resident killer whales; Arcangeli and Crosti (2009) conducted a study on an Australian common bottlenose dolphin (*Tursiops truncatus*) population in the coastal waters of Bunbury; Christiansen *et al.* (2010) used a Markov chain analysis to investigate changes in Zanzibar Indo-Pacific bottlenose dolphin (*T. aduncus*) behavioural states in relation to boat traffic; Scarpaci *et al.* (In press) reported on the impact of swim-with-cetacean tourism on bottlenose dolphins within a 'sanctuary zone' in Port Phillip Bay, Australia; Sousa-Lima and Clark (2009) used automated acoustic recordings to monitor and track the singing behaviour of male humpback whales in Abrolhos Marine National Park, Brazil, a major humpback whale breeding ground; Stamation *et al.* (2010) monitored the behaviour of groups of humpback whales off Queensland Australia from both whalewatching vessels and land-based platforms; Filla and Monteiro (2009) investigated various types of whalewatching on estuarine or 'guianensis' dolphins (*Sotalia guianensis*) in Cananéia, southeast Brazil; and Jensen *et al.* (2009) found that common bottlenose dolphin and pilot whale (*Globicephala macrorhynchus*) communication calls could be masked substantially by small outboard engine noise. Summaries are presented in Annex M, item 7.

The Committee **welcomes** this review and encouraged the author to prepare a similar review for the next meeting. It was clarified that these reviews are not critiques of methods or results but rather a compilation of new research results of interest.

SC/62/WW3 reported on the US National Oceanic and Atmospheric Administration's efforts to develop management plans to reduce the exposure of resting spinner dolphins (*Stenella longirostris*) to human activity in Hawaiian waters. One management approach under consideration focuses on time-area closures to reduce the number and intensity of interactions between humans and dolphins during critical rest periods in particular bays. Research will combine boat-based and land-based visual observations with passive acoustic monitoring and is an international collaboration between researchers from American, Australian and Scottish universities. Time area closures will not be implemented until a full year of pre-closure data collection has been completed. The authors highlighted this study as a possible candidate project for inclusion in the Large-scale Whalewatching Experiment (LaWE) initiative, as it incorporates many facets that the LaWE initiative strives to achieve.

The Committee **commends** this study and deems it relevant to the LaWE initiative.

SC/62/WW8 presented a precaution on interpreting the results of impact study data analysis. The paper discussed the possibility of confounding variables when interpreting correlations between whalewatching exposure and reproductive parameters of female humpback whales (see Weinrich and Corbelli, 2009). Discussion is presented in Annex M, item 7.

The Committee **welcomes** this paper as an important consideration in impact analyses. It was noted that this contribution clarifies that whalewatching is essentially another habitat variable, and should be treated as such in multivariate models.

Parrot *et al.* (2010) report on an agent-based simulation platform to assess the characteristics of interactions between whales and vessels under different scenarios. The simulation is composed of a spatial environment in which a whale individual-based model and a boat agent-based model can evolve. It simulates the spatiotemporal movement of marine mammals and vessel traffic in the St Lawrence Estuary. It estimates movement parameters from long-term data collected using both onboard GPS and vessel monitoring systems for vessels and a variety of land-based and boat-based focal follows as well as sightings for marine mammals from whalewatching boats.

This platform can be used to inform decision-making by simulating different vessel and whalewatching traffic scenarios.

This project is highly relevant to the LaWE objectives and offers an avenue to simulate boat interaction consequences for cetaceans using behavioural statistical models of disturbance effects. The Committee **welcomes** this effort.

The Committee noted that its work on whalewatching has been influential with other research initiatives to understand effects of disturbances on cetacean populations.

At last year's meeting, there was discussion on the impacts of aerial whalewatching (IWC, 2010i). Groch noted that she was not able to analyse behavioural data collected in previous years during southern right whale photo-id surveys from a helicopter in Brazil. Sironi reported that a trial was conducted to record before-during-after behavioural observations during the 2009 southern right whale photo-id aerial survey in Argentina from a fixed-winged aircraft. Dedicated flights are required to obtain more accurate behavioural data.

15.4 Review reports of intersessional working groups

15.4.1 Online database for worldwide tracking of commercial whalewatching/associated data collection

Robbins summarised the status of an online database for tracking whalewatching operations and associated data collection programmes. This database was originally described in Robbins and Frost (2009) and is intended to facilitate studies of whalewatching impact as well as to allow better assessments of the scientific value of data collection programmes. Database development has made considerable progress intersessionally and should be available to go online prior to next year's meeting. The Committee **recommends** that the intersessional working group continue and report back next year (see Annex Q).

15.4.2 Swim-with-whale operations

Rose reported that due to time constraints, no progress was made intersessionally on field-testing a questionnaire to further assess the extent of swim-with-whale operations. However, a draft questionnaire is ready to be distributed and plans are in place to do so in the Dominican Republic and possibly Australia before next year's meeting. The Committee welcomes the commitment of funding for this effort by the Pacific Whale Foundation and **recommends** that the intersessional working group continue and report back next year (see Annex Q).

15.5 Other issues

15.5.1 Consider information from platforms of opportunity of potential value to the Scientific Committee

Progress continues in efforts to stimulate submission of opportunistic data from ecotourism cruise ships in the Southern Ocean to the Antarctic Humpback Whale Catalogue (AHWC). The availability of these data has broadened understanding of the exchange between areas and in some cases provided information that was previously not available. Ritter (2010) reported on a near-miss event involving a large vessel and humpback whales off Antarctica (see Annex M, item 9.1).

Smit *et al.* (2010) reported on opportunistic research off the coast of La Gomera, Canary Islands (Annex M, item 9.1). The study highlights the importance and the potential of mutual long-term co-operation between whalewatching operators and scientists. The Committee welcomes the reports and reiterated the value of collaboration between researchers and whalewatching operations and other platforms of opportunity.

15.5.2 Review of whalewatching guidelines and regulations

The compendium of whalewatching guidelines and regulations around the world is in the process of being updated and will be available on the IWC's website in August. SC/62/WW2 described several papers relating to guidelines and compliance including Noren *et al.* (2009), Williams *et al.* (2009a); Stamation *et al.* (2010); Sousa-Lima and Clark (2009); and Jensen *et al.* (2009).

Summaries of the reports are found in Annex M, item 9.2.

15.5.3 Review of risk to cetaceans from collisions with whalewatching vessels

No new information was brought to the meeting this year. Some members indicated that papers on this item would be submitted to next year's meeting. The Committee noted that this issue will be discussed at a joint workshop with ACCOBAMS in Monaco from 21-24 September 2010.

15.5.4 Future of the sub-committee on whalewatching

The Committee took note of IWC/62/CC8 and the possible interface between the Conservation Committee's work and its own work on whalewatching. The Conservation Committee has established a Standing Working Group on Whalewatching and intends to develop a draft strategic plan for five years (2010-15). IWC/62/CC8 made reference to the work of the Committee and various scientific issues and the section on Capacity Building and Development states that actions 'may include… provision of expert assistance through the Scientific Committee's sub-committee on whalewatching'.

The Committee requests clarification on the mechanism by which this expert assistance will inform the work of the Standing Working Group. It welcomes the opportunity to liaise with the Conservation Committee and Commission, but noted its own terms of reference, and believes that the advice it offers should be within that framework. One possible mechanism, for example, would be to designate a representative from the Committee to work directly with the CC on this issue, thereby providing a formal interface.

The Committee is also seeking clarification on the envisioned management objectives for whalewatching, as IWC/62/CC8 states both 'growth' and 'sustainability' objectives. Clarification will guide the scientific work of the Committee for Objective 7 of the LaWE project ('Develop an integrated and adaptive management framework for whalewatching that accounts for uncertainties, and includes monitoring and feedback mechanisms').

The Committee draws the attention of the Conservation Committee to the definitions of whale ecotourism developed at previous meetings (IWC, 2006c) and considered it important that the Conservation Committee takes a strategic view of what it might achieve in the five years. It also **stresses** the importance of a good scientific basis for the work that it is recommending to the Commission.

It was noted that it would be valuable to increase communication with and explore possibilities for collaborate with the UN World Tourism Organisation, as its remit complements the work of the sub-committee in a number of aspects. Lusseau agreed to liaise for this purpose.

15.5.5 Other

Eisfield *et al.* (2010) reported on the behaviour of a female solitary sociable dolphin studied on the southeast coast of England in 2007, previously addressed by the Committee. The report is summarised in Annex M, item 9.5.

The Committee **reiterates its recommendation** of 2008: habituation of solitary dolphins can make them vulnerable to harm, including being killed, and should be avoided.

16. DNA TESTING (DNA)

The report of the Working Group on DNA is given as Annex N. This particular Agenda Item has been considered since 2000 (IWC, 2001d; 2001e; 2001h) in response to a Commission Resolution (IWC, 2000).

16.1 Review genetic methods for species, stock and individual identification

No new documents were submitted under this Item this year. Last year, the Committee had reviewed Cipriano and Pastene (2009), which provided a comprehensive review of current knowledge of techniques to extract DNA from 'difficult' samples.

16.2 Review results of the amendments of sequences deposited in GenBank

During the first round of sequence assessment (IWC, 2009i, p.347), some inconsistencies were found for some sequences assigned to right and minke whales. These appeared to have been due to a lag in the taxonomy recognised by *GenBank* or uncertainty in taxonomic distinctions currently under investigation (e.g. the number of species and appropriate names for recently described species of 'Bryde's whales').

Last year, the Committee noted that the original submitter would be notified of the inconsistencies and a suggestion made that an amendment be made to the entry. Pastene reported that he had contacted *GenBank* officers to make the above indicated amendments. He was informed that only the original submitters of the sequences can make amendments to their submissions. In view of this he contacted the relevant scientists encouraging them to make the relevant amendments. As a result, the notification regarding Bryde's whale taxonomy (IWC, 2010c, p.73) was made. Amendment work by the original submitters of right and minke whale sequences is ongoing and this work will be completed during the next intersessional period.

The Committee thanked Pastene for his work in this regard.

16.3 Collection and archiving of tissue samples from catches and bycatches

The collection of tissue samples in Norway is from the commercial catches of North Atlantic common minke whales from 1997 to 2009. A total of 484 whales were landed in 2009 (see Annex N, Appendix 2).

The collection of samples in Japan is from special permit whaling in the Antarctic (JARPA II) and North Pacific (JARPN II), bycatches and strandings. The collection includes complete coverage for 2009 and the 2009/10 Antarctic season. A total of 506 genetic samples of the Antarctic minke whale and one of the fin whale were collected from the 2009/10 austral summer survey of JARPA II. From JARPN II in the western North Pacific (NP) samples stored in 2009 were: NP common minke whale, n=162; NP Bryde's whale, n=50; NP sei whale, n=100; and NP sperm whale, n=1. The samples from bycatch stored in 2009 were: NP common minke whale, n=119; NP humpback whale, n=3. Genetic samples were stored for the following stranded whales in 2009: NP common minke whale, n=3; NP humpback whale, n=1 and NP sperm whale, n=1 (see Annex N, Appendix 3).

The collection of samples from Iceland in 2009 was from commercial catches of North Atlantic common minke whales (n=81) and fin whales (n=125). Samples are currently in hand for all whales taken in 2003-09 (see Appendix 4 of Annex N).

The Committee welcomes this information from Norway, Japan and Iceland.

16.4 Reference databases and standards for diagnostic registries

Genetic analyses have been completed and data on mtDNA, microsatellites and sex entered in the Norwegian register for years up to 2007. The laboratory work on the 2008 samples is completed but has not yet been analysed. Laboratory work is ongoing for the 2009 samples (see Annex N, Appendix 2).

For the Japanese register, the genetic analyses based on mtDNA have been completed for North Pacific common minke, Bryde's, sei and sperm whales taken by special permit whaling up to 2009. Laboratory work on microsatellites for these samples is ongoing.

The genetic samples of Antarctic minke whales obtained by JARPA II have not yet been analysed, except for sex and for microsatellites of 190 samples taken in 2006-07 (six loci) and 551 taken in 2007-08 (six loci). For bycatch samples, genetic analyses based on mtDNA have been completed for all samples up to 2009. Laboratory work on macrosatellites for these samples is ongoing. Laboratory work is ongoing for stranded animals in 2009 for both mtDNA and STR (see Annex N, Appendix 3).

For the Icelandic register, genetic analyses (mtDNA and microsatellites) have been completed for common minke whales taken by special permit whaling in 2003-07. Laboratory work of samples taken under commercial whaling in 2006-09 is ongoing. Genetic analyses were completed for fin whale commercial samples collected in 2006 and 2009 (see Appendix 4 in Annex N). It was noted that only whales intended for export from Iceland were currently being genotyped for inclusion in that country's registry and that other whale samples will be genotyped as soon as possible.

The Committee **recommends** the adoption of a standard format for the updates of national DNA register to assist with the review of such updates in the future and agrees that the format used by the Norwegian registry update provides a suitable model. Pastene will work intersessionally with colleagues from Norway, Japan and Iceland to agree on the standard format. In addition, the Committee **agrees** that it would be useful to add a 'per cent completed' column for genetic analysis of tissue samples to assist in the annual review.

Whilst agreeing with these recommendations, Víkingsson reminded the Committee that Norway, Japan and Iceland are providing updates of their registries to the Committee on a voluntary basis.

The Committee noted that full technical specifications for the Japanese and Icelandic DNA registries have not been received or reviewed. Although such information is provided voluntarily, such a review would be helpful for the Committee's annual review of the status of DNA registries under its standing agenda items. The Committee recalled that updates of registers should include a list of references including the relevant documents on protocols used.

16.5 Other

SC/62/O19 describes a proposal to the IWC DAG under Procedure B, requesting access to the Japanese DNA register for the purposes of evaluating the technical aspects of traceability/trackability of sei, fin and Antarctic minke whale products purchased at commercial outlets in Santa Monica, USA and Seoul, South Korea. SC/62/O19 requested that the proposal be considered for endorsement by the Group.

The Committee could not reach an agreement on whether or not to endorse the proposal in SC/62/O19 of the current policy of Japan, Norway and Iceland regarding DNA registers access and market survey, although it recognised that the matching exercise proposed would, in principle, be valuable for testing functionality of DNA registers for identifying and tracking whale products.

16.6 Work plan

Members of the Committee were encouraged to submit papers in response to requirements placed on the Committee by the IWC Resolution 1999-8 (IWC, 2000). Results of the 'amendments' work on sequences deposited in *GenBank* will be reported next year.

17. SCIENTIFIC PERMITS (SP)

This Agenda Item was discussed by the Working Group on Special Permits in an evening session to enable all Committee members who wished to do so to attend. Bjørge was elected Chair of the Working Group. Reeves acted as Rapporteur, and the report has been directly incorporated here.

17.1 Review of activities under existing permits

All cruise reports from Japanese scientific permits from 1987 to the present are publicly available on the website of the Institute for Cetacean Research[5]. As in recent years, documents describing activities carried out in the preceding year were received by the Committee but not presented or discussed, except for points of clarification. Authors' summaries are included below. Full discussions will occur during the periodic reviews (see Item 17.3).

17.1.1 JARPN II

SC/62/O4 presented the results of the eighth full-scale survey of the Japanese Whale Research Program under Special Permit in the Western North Pacific-Phase II (JARPN II)-offshore component-, which was conducted from 10 May to 29 July 2009 in sub-areas 7, 8 and 9 of the western North Pacific. A total of five research vessels was used: one trawl survey vessel equipped with scientific echo sounder (TSV), one dedicated sighting vessel (SV), two sighting/sampling vessels (SSVs) and one research base vessel. A total of 6,374n.miles was surveyed. During that period 63 common minke, 482 sei, 93 Bryde's and 287 sperm whales were sighted. A total of 43 common minke, 100 sei, 50 Bryde's and one sperm whales was caught by the SSVs. All whales caught were examined on board the research base vessel. A total of 53 kinds of samples and data were obtained from each whale. A total of 16 skin biopsy samples were collected from blue (6), sei (9) and sperm (1) whales. As in previous surveys, common minke whales fed mainly on Pacific saury (*Cololabis saira*) and Japanese anchovy (*Engraulis japonicus*). Bryde's whales fed mainly on Japanese anchovy and oceanic lightfish. Sei whales fed mainly on copepods, Japanese anchovy and mackerels. Dominant preys in the stomach of one sperm whale were various kinds of squids, which inhabit the mid- and deep-waters. Qualitative and quantitative data on stomach contents will be used in the development of ecosystem modelling.

SC/62/O5 outlined the results of the sixth JARPN II survey (coastal component), conducted off Sanriku, northeastern Japan (i.e. the middle part of sub-area 7). The survey was carried out from 22 April to 21 May 2009 using four small sampling vessels and one echo sounder-trawl survey vessel. The research area was set within 50n.miles of Ayukawa port in the Sanriku district. The prey species survey was also conducted by the echo sounder-trawl survey vessel. A total of 4,756n.miles (464 hours) was surveyed and 111 schools (112 individuals) of common minke whales were sighted. No other large cetacean species was sighted. A total of 60 common minke whales were caught (27 males and 33 females) and landed at the JARPN II research station for biological examination. Only one individual in each sex was sexually mature. In addition the female was pregnant. The dominant prey species found in the forestomach was adult Japanese sand lances (*Ammodytes personatus*). The Japanese anchovy (*Engraulis japonicus*) and krill (*Euphausia pacifica*) were also observed but their frequency of occurrence was much lower. The prey species survey revealed high density of Japanese anchovy in the sampling area for common minke whale. These results suggest that during the 2009 survey common minke whales had prey preference for Japanese sand lance.

SC/62/O6 reported the results of the seventh JARPN II survey (coastal component), conducted off Kushiro, northeastern Japan (i.e. the northern part of sub-area 7). The survey was conducted from 5 September to 17 October 2009 using four small sampling vessels. The research area was set within 50n.miles of Kushiro port. The total searching effort by the sampling vessels was 5,136n.miles (494 hours) and 106 schools of common minke whales (107 individuals) were sighted; 59 animals were caught (36 males and 23 females) and landed at the research station. Of the males, 12 were sexually mature. None of the females sampled had attained sexual maturity. The walleye pollock (*Theragra chalcogramma*) was the most dominant prey species in the forestomach, followed by krill (*Euphausia pacifica*), Japanese anchovy (*Engraulis japonicus*), and Japanese common squid (*Todarodes pacificus*). Pacific saury (*Cololabis saira*) was not observed this year. All the animals feeding on walleye pollock were sexually immature. These results were almost the same as in the previous coastal surveys off Kushiro. The results suggest differences in feeding habits between immature and mature common minke whales off Kushiro in autumn. During the survey, other baleen whales were also sighted: 51 fin, 5 sei, and 22 humpback whales. They were observed in the vicinity of sampling positions of common minke whales that were feeding on krill.

17.1.1.1 POINTS OF CLARIFICATION

In response to a question regarding what new information of value in ecosystem modelling could be learned from the taking of one sperm whale last year (relative to the large number that had been caught and examined, with similar results regarding prey, in previous commercial whaling), the proponents stated that previous data on sperm whale diet from commercial catches were non-quantitative and did not consistently identify prey items to species level. They stated that this limited their utility in models such as ECOSIM and ECOPATH, and that data obtained from JARPN II were effectively used for ecosystem modelling. Others considered that this was not the case, and reiterated their view, and that of the JARPN II Review Panel (IWC, 2010a), that the catch of sperm whales in JARPN II is not scientifically justified.

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[5] *http://www.icrwhale.org/CruiseReportJARPA.htm* and *http://www.icrwhale.org/CruiseReportJARPN.htm*.

17.1.2 JARPA II

SC/62/O3 presented the results of the third full-scale survey of the Japanese Whale Research Program under the Special Permit in the Antarctic-Second Phase (JARPA II), which was conducted during the 2009/10 austral summer season. Two dedicated sighting vessels (SVs), two sighting and sampling vessels (SSVs) and one research base ship were engaged in the research for 97 days from 14 December 2009 to 20 March 2010 in Areas III East (35°E-70°E), IV (70°E-130°E), V West (130°E-165°E) and part of Area V East (165°E-175°E). The total searching distance was 8,232n.miles. Eleven species including six baleen whales (Antarctic minke, blue, fin, sei, humpback and southern right whales) and two toothed whales (sperm and southern bottlenose whales) were identified during the research period. A total of 986 groups (2,242 animals) of Antarctic minke whales were sighted. It was the dominant species in the research area followed by the humpback whales (603 groups, 1,187 animals), and fin whales (56 groups, 186 animals). The number of sightings of the Antarctic minke whales was about 1.9 times higher than that of humpback whales in this survey. A total of 506 Antarctic minke whales and one fin whale were caught. All whales caught were examined on board the research base vessel. A total of 55 kinds of samples and data were obtained from each whale sampled. A total of 8 blue, 110 humpback and two southern right whales was photographed for natural marks. A total of 86 skin biopsy samples were collected from fin (1), humpbacks (84) and southern right (1) whales. To investigate vertical sea temperature profiles oceanographic surveys were conducted at 57 points using TDR. The main results of this survey were as follows: (1) whale composition in the research area was stable compared to previous JARPA II surveys in this area; (2) the ice-free extent of the research area was substantially larger than in past seasons and high density areas of Antarctic minke whales were observed near the continental shelf; (3) mature females of Antarctic minke whale were dominant in Prydz Bay; and (4) humpback whales were widely distributed in the research area and its density index was higher than that of the Antarctic minke whales in Areas IV West and V East. The 1994/95 IWC/SOWER cruise was conducted in similar areas and periods as in the present survey. In 1994/95 Antarctic minke whales were the most dominant species. The number of sightings of Antarctic minke whales in 1994/95 was about five times higher than that of humpback whales. According to the authors of SC/62/O3, comparison of whale abundance between these two surveys suggests that humpback whales were increasing and expanding into the research area.

17.1.2.1 POINTS OF CLARIFICATION

In response to a question on information on whether vomiting and faecal observations (SC/62/O3 table 7) referred to ‘natural’ events or were due to harpooning, the proponents explained that the recording of such observations was for the purpose of helping to evaluate the relative merits of lethal versus non-lethal sampling, and thus that there was no value in including observations of vomiting due to harpooning.

17.1.3 Planning for final review of results from Iceland’s scientific take of North Atlantic common minke whales

Víkingsson summarised the status of Iceland’s analytical work on the 200 common minke whales taken as part of its scientific research programme between 2003 and 2007; annual reports had been provided while the programme was still active. Last year it had been expected that most analyses would be completed and available in 2011; this would have allowed a formal review of the programme in 2012 following the Committee’s guidelines (IWC, 2009j) provided the appropriate deadlines had been met. He reported that most of the laboratory analyses are either completed or in a final stage (see SC/62/ProgRepIceland). There had been changes and delays in some components, particularly those involving outsourced chemical analyses that required CITES permits. In addition, the serious economic difficulties experienced by Iceland in recent years have affected the programme and delayed completion of some analyses. Nonetheless, the necessary adjustments had been made to the workplan and he remained optimistic that the work would be completed on schedule.

In discussion, Víkingsson clarified that some of the analyses indicated in SC/62/ProgRep Iceland concerned species and specimens other than the 200 minke whales caught and sampled under Special Permit. Iceland’s Special Permit programme had ended when the last of the 200 minke whales was taken in 2007.

In summary, an update on progress will be provided at the next Annual Meeting and approximately three months later a document will be submitted by Iceland that initiates the process leading to external review of the final results of this programme.

17.2 Review of new or continuing proposals

The Chair noted that both JARPA II and JARPN II are continuing on the basis of plans already submitted and reviewed in the Scientific Committee. There was no further discussion of this item. However, a statement in relation to this Agenda Item was received and can be found in Annex U. This statement reflects the view of many members. The response to this statement can be found in Annex U.

17.3 Procedures for reviewing Scientific Permit proposals

The Chair recalled that the Scientific Committee had spent considerable time in the past discussing this matter, and agreement on a process had been reached in 2009 (IWC, 2009j, colloquially known as ‘Annex P’) that had been used for the review of results of JARPN II. He noted that criticism by some members following the JARPN II review centred on how the procedures in ‘Annex P’ had been implemented rather than on the adequacy of the procedures themselves. Specifically, concerns had been expressed about the ‘independence’ of the specialists who served on the review panel, the Chair’s decision not to request panel members to submit a conflict-of-interest declaration and the Chair’s decision not to allow additional observers to attend the specialist workshop. The Chair noted in that regard that he also had not allowed scientists affiliated with the JARPN II programme to attend the deliberations of the expert panel.

Last year, it had been agreed to revisit at this meeting the question as to whether changes are needed to ‘Annex P’. However, the Chair identified two factors weighing against the idea of having a full discussion at this time. First, given the ongoing discussions of the ‘consensus package’ prepared by the Commission Chair and Vice-Chair, it would be sensible to wait for outcome of those discussions before further discussion of ‘Annex P’. Secondly, he believed that the dissatisfaction of some with the performance of the procedures for reviewing JARPN II was related to how these were implemented, rather than the wording of procedures themselves. In any event, Bjørge stressed that if the Committee decides to open ‘Annex P’ to revision, in his view such revision should be limited to only those aspects that have been controversial, i.e. the selection of experts to the review panel and the admission of observers. In discussion, it was further noted that given the schedule for reviewing the Iceland programme (as summarised under Item 17.1.3), there should be no need to implement 'Annex P' during the upcoming intersessional period. The Committee **agrees** that no further discussion of the procedures was needed at this time.

Childerhouse asked whether the adoption of a 'consensus package' would mean that Special Permit whaling would therefore end and preparations for reviews should begin. Bjørge replied that he was not in a position to advise on that, but he assumed that if the Commission reaches a decision that includes Special Permit whaling, it would then be incumbent on the Commission to provide guidance to the Scientific Committee on how permit reviews should be handled in the future.

18. WHALE SANCTUARIES

In the major discussion about sanctuaries in 2004, the Committee recommended procedures to facilitate the review of future proposals and future sanctuary reviews (IWC, 2005a, pp50-51). No new proposals for Sanctuaries were received this year. The item will remain on the Agenda for future meetings.

19. SOUTHERN OCEAN RESEARCH PARTNERSHIP

The Southern Ocean Research Partnership (SORP) was proposed by the Australian Government to the IWC in 2008 (IWC/60/16) with the aim of developing a multi-lateral, non-lethal scientific research programme that will improve the coordinated and cooperative delivery of relevant scientific information to the IWC. A framework and set of objectives for SORP were presented, discussed and endorsed last year (IWC, 2010c, pp.80-82).

At this year's meeting it was agreed to hold discussions at an evening session to allow all members who wished to attend to be able to do so without conflict with other sub-group meetings; that session was chaired by Gales and rapporteured by Childerhouse. It was agreed that the report of those discussions would be incorporated directly into the Plenary report.

19.1 Intersessional progress

SC/62/O9 reported on the intersessional progress on SORP. Progress was made on the following major items:

(1) establishment of a SORP Steering Group (SSG) with associated terms of reference;
(2) the holding of a Workshop further develop the SORP in Seattle in December 2009 (SC/62/O8);
(3) identification of seven proposed projects that will form the basis for SORP work into the future (SC/62/O10);
(4) the development of a funding mechanism for SORP projects (see below); and
(5) the holding of a first cruise of the joint Australia-New Zealand Antarctic Whale Expedition, AWE (SC/62/O12).

These items are covered in more detail below. It was noted that a full discussion of SC/62/O12 had taken place in the sub-committee on Southern Hemisphere whales (Annex H). The brief discussion under the present item focussed on suggested improvements in future cruises related to estimating abundance, the representativeness of the study area, the use of faecal sampling, the effect of satellite tagging on animals and some comments on the ability of the project to meet its objectives.

19.2 Report of the SORP Workshop, Seattle, December 2009

The SORP workshop (SC/62/O8) was hosted and supported by the Government of the USA and attended by 15 people from five nations. Its main aims were to continue developing the mechanism by which SORP would conduct its business and achieve its objectives. The workshop agreed that a focused approach to the research was required and this was best achieved through the development of research projects that were consistent with both the agreed SORP objectives and priority issues identified by the IWC Scientific Committee. To address this latter issue, a summary document of recommendations relevant to the Southern Ocean had been compiled. The proposed draft SORP projects that were developed at the workshop are described below.

19.3 Summary and consideration of proposed SORP projects

Several draft research projects were presented to the Committee in order to obtain comments and advice (SC/62/O10). The selection process had followed a lengthy consultation process starting at the Sydney SORP workshop (Southern Ocean Research Partnership, 2009) where broad themes were developed and these themes were endorsed by the Committee last year (IWC, 2011). *Inter alia* these draft projects developed at the Seattle SORP workshop are those that were considered to benefit from large scale, multi-regional participation and were consistent with both SORP objectives and IWC priority issues. The purpose of presenting these draft projects to the Committee this year was to seek initial comments and perhaps general endorsement of the overall approaches. The intention is that the project leaders will take any comments made into account when developing the projects intersessionally. It was clarified that there was no intention for the Committee to approve the draft budgets appended to the projects at this stage. These and other aspects of the proposals would require further development and should be re-submitted using the agreed funding mechanism (see Item 19.4) at the 2011 Annual Meeting.

19.3.1 Killer whales in the Southern Ocean

A short project description of 'Distribution, relative abundance, migration patterns and foraging ecology of three ecotypes of killer whales in the Southern Ocean' was presented. There are three ecotypes of killer whales described from Antarctic waters. Little is known about these ecotypes and it is important to understand these populations as killer whales play a key role in the Antarctic marine ecosystem. This is especially true with respect to the impacts that they have on prey populations including marine mammals, fish and penguins.

This project will investigate factors related to their ecosystem impact in Antarctica and adjacent waters, by focusing on their systematic relationships, abundance, distribution, movement patterns and prey preferences. It will include analyses of lipid, isotopes and contaminants from biopsy samples. Collaborators are from USA, Brazil, France and Brazil/Canada.

In discussion, it was agreed that this was an ambitious and valuable project outline. It was noted that the proposal required considerably more detail on the proposed analytical methods before it can be properly evaluated and that this was true for most of the draft projects presented. It is also important that any final proposal includes information on the conceptual and analytical and framework linking the sub-projects together. Suggested additional potential collaborators included Lauriano from the Italian Antarctic Programme and Bester from South Africa who is undertaking related work at Marion Islands.

19.3.2 Foraging ecology and predator prey interactions of whales and krill

A short project description of 'Foraging ecology and predator/prey interactions between baleen whales and krill: a multiscale comparative study across Antarctic regions' was presented. Little is known about the dynamics of predator-prey interactions and the response of baleen whales to the distribution of their prey in the Antarctic. As an important marine ecosystem (e.g. with respect to issues of climate change impacts as well as international management of marine living resources), research focused on cetacean foraging ecology in the Antarctic should help to fill a critical data gap. The project will use novel tagging technologies combined with traditional scientific hydroacoustic methods to quantify the types and frequency of prey consumed and daily consumption rates of poorly understood yet ecologically integral and recovering krill predators in the Antarctic: the humpback whale and the Antarctic minke whale. Collaborators are from USA and Australia for phase 1 and potentially Brazil, South Africa and Germany for phase 2.

In discussion, it was noted that this was an ambitious and valuable project. In addition, the proposal generally provides a good example of the level of detail required to allow for a full scientific evaluation. There were some methodological issues that required additional thought, including how the results from detailed studies collected at a fine spatial scale would be expanded to the medium and large scale, and also about the reliability of the method for estimating gulp volume. In response, it was noted that this project represents a step along the line in estimating consumption rates and that moving out from very fine to middle to large scale will be represent a challenge and needs further consideration. The similarity between aspects of this project and the Committee's SOWER 2000 project (IWC, 2000) developed but never implemented was noted and it was suggested that this may provide some useful additional ideas and information for the developers of the current project.

19.3.3 Oceania humpback mixing

A short project description of 'What is the distribution and extent of mixing of Southern Hemisphere humpback whale populations around Antarctica? Phase 1: East Australia and Oceania' was presented. An improved understanding of the movements and mixing of humpback whales around Antarctica has been identified as a priority for the Committee as part of its Comprehensive Assessment of Southern Hemisphere stocks. This information is integral to assessing the recovery of depleted populations. A key step in assessing recovery is estimating pre-exploitation size which requires knowledge of stock identity and appropriate allocation of historic catches to correct stocks. An improved understanding of the migratory and feeding behaviour of humpback whales should allow an appropriate allocation of catches made in this region to breeding stocks, which will improve the accuracy of recovery assessments and estimates of pre-whaling population sizes. Collaborators include New Zealand, Australia, USA, France, Samoa, Tonga and Chile.

In discussion, it was noted that when exploring allocation of past catches to breeding stocks, additional information would need to be considered given the potential temporal and spatial mixing of different breeding stocks and sexes on the feeding grounds and given the relatively small number of SOWER/IDCR samples available from this region. Similar work was being undertaken by other researchers (e.g. low to high latitude matches from Japanese and SOWER/IDCR data sets) which would help broaden the context for this work. It was noted that the outline study presented represents only Phase One; the focus is on Oceania and will include all the SOWER/IDCR data available. Future work is already being planned and there are plans to collaborate with researchers across the Southern Hemisphere (e.g. Africa, Chile, Brazil, Australia) using both mitochondrial and microsatellite data. It was suggested that the telemetry component of the study would be better structured if animals were tagged on the feeding rather than breeding grounds as this would provide more information on mixing. In response, it was noted that this had been the plan of the AWE but due to technical failure with the tags this had not been achieved. The issue of collaboration and inclusiveness was raised (as it had been at the IWC workshop on Southern Hemisphere humpback whales held in 2006) and it was noted that the proposal did not include all potentially valuable datasets. The Committee agreed that it was important that SORP projects are open to all researchers who hold appropriate datasets.

19.3.4 Fin and blue whale acoustics

A short project description of 'Acoustic trends in abundance, distribution, and seasonal presence of Antarctic blue whales and fin whales in the Southern Ocean' was presented. This initiative aims to implement a long term acoustic research programme that will examine trends in Southern Ocean blue and fin whale population growth, distribution, and seasonal presence through the use of passive acoustic monitoring techniques. Current understanding of blue and fin whale life history characteristics, population abundance, and any post-whaling recovery is extremely limited. While obtaining accurate absolute abundance estimates is currently beyond the reach of passive acoustic methods, measures of relative abundance and trends are more easily obtainable and can be conducted in a consistent manner. Comparison of relative abundance estimates from individual locations across many years collected by acoustic surveys can provide a precise measure of population growth. Comparison of relative abundance estimates within and between locations and years can further be used to assess trends in distribution and seasonal presence over time. Collaborators are from Australia, France, USA and Germany.

In discussion, it was noted that the primary focus was on the Indian Ocean. The Committee agreed that it would be useful to consider including similar acoustic data from other sources (e.g. the GLOBEC acoustic data that had been collected for six years at the Antarctic Peninsula) and was pleased to hear that the inclusion of such data is planned and that GLOBEC researchers will be approached soon. The plan to develop less expensive acoustic loggers was welcomed as an excellent step forward in the use of acoustics as a tool for monitoring. There was some thought that the timetable to complete the feasibility stage of the project (one year) may be too ambitious. As for other projects, more detail of the analytical methodology was requested. In terms of assessing the extent to which the project would meet its objectives (i.e. estimation of trends), it was noted that it would be helpful to see the detection range of the loggers as the small number of loggers planned to be deployed would cover a relatively small part of the Southern Ocean. It was recognised that complete coverage of the South Ocean was not possible given logistical constraints (i.e. the limited number of vessels in the area and where they go) but part of the future planning was to consider the best sites for deployment to maximise the usefulness and representativeness of those sites and to try and capture representative variability. It was suggested that it would be useful for the loggers to collect environmental as well as acoustic data which would help to provide context for any variability seen, provided this could also accommodate the objective of keeping the units small and affordable. The Committee noted that using such data to estimate absolute abundance is a long term and extremely ambitious objective of the project. The project leaders acknowledged that this would not be easy, noting that the project would start by estimating relative abundance to quantify trends and work towards absolute abundance. With respect to the long-term aim, it was suggested that the developers of the programme approach scientists such as Len Thomas (University of St Andrews) who had made some progress in the development of new analytical approaches to estimate density from acoustic data.

19.3.5 Year of the Blue Whale 2013/14

As one of the major initiatives within the SORP, the Committee discussed a proposal for a multi-vessel, circumpolar research project to focus on Antarctic blue whales in the austral summer of 2013/14. The proposed objectives for this 'Year of the Blue Whale' would be to:

(1) provide a circumpolar abundance estimate of Antarctic blue whales based on data collected during a single-season, multi-vessel survey design that incorporates acoustic localisation of blue whales and traditional sightings surveys;
(2) improve our understanding of Antarctic blue whale stock structure through the collection of genetic, photographic and acoustic data;
(3) improve understanding of linkages between blue whale feeding and breeding grounds using satellite telemetry; and
(4) characterise foraging habitat of blue whales on the basis of sightings surveys and satellite telemetry data.

It was recognised that any research effort to satisfy these ambitious objectives in a single year of field work will require substantial methodological development (e.g. to determine how to combine visual and acoustic survey techniques) as well as a need to build in provisions for substantial 'off-survey' activities (e.g. satellite tagging, biopsy sampling and individual photo-id). The project will also require substantial logistical planning to access and coordinate shipping and research activities around Antarctica within a single season. It had been proposed that a small scientific steering committee be established with the task of: (1) developing a full research proposal for the Year of the Whale; (2) determining the optimal scale of shipping and research effort required to fulfil the objectives; (3) initiate processes towards accessing these shipping resources; and (4) reporting back to the 2011 Annual Meeting.

In discussion, there was broad agreement about the general concept and draft proposal and several members expressed an interest in participating in planning for the SORP Year of the Whale. There was a short discussion of a suggestion that fin whales could be included in the proposal but it was noted that high density areas of blue and fin do not always overlap and that to include fin whales might dilute the effort with respect to blue whales. The Committee agreed that the inclusion of other species, while desirable, must be considered in light of the primary objective of assessing blue whales. Recent experience during the AWE had demonstrated that acoustics was a practical method of finding blue whales and that this would allow a blue whale cruise to minimise the amount of time searching and maximise the amount of time spent with blue whales. Recognising the ambitious nature of the project, it was suggested that the timeframe of 2013/14 was optimistic and that a delay in 1-2 years might be considered, given the enormous coordination and organisational effort required to ensure the success of such a large project. Consideration may also need to be given to spreading effort out over two years. The Committee **agrees** that until the proposal is more fully developed, it will not be possible to assess the logistical requirements necessary to complete the work. It was suggested that a small group of survey and other specialists, including those familiar with organising large multi-vessel multinational projects, should work together to further develop the proposal and report back to the SSG and the Committee next year (see Item 21); Gales agreed to co-ordinate this. Their task would *inter alia* be to determine the level of resources required, provide an outline of research methods (and analyses) and survey design, and assess the feasibility and timeframe of the project (if that group deemed it necessary, a short workshop might be considered).

19.3.6 Whales and climate change

This project has been identified as a potential project since the Sydney SORP workshop and it has been further discussed at the second IWC climate change workshop (IWC, 2010c), last year's Scientific Committee meeting and the recent Seattle SORP workshop. Long-term southern right whale datasets have been identified as the most likely existing data for correlation with long term climate changes. Leaper *et al.* (2006) demonstrated the utility of the long-term Argentinean study for assessing correlations with climate variables. It has been proposed that a project along these lines could be developed using a common method that can be applied to the Australian, South African and Brazilian long-term datasets, provided an initial examination revealed them suitable for this purpose. In this regard, consideration should be given to the development of recommendations about how existing programmes/datasets could be improved/modified to make them more suitable for future work along these lines.

As the Committee has previously recognised, an understanding of these issues requires long-term data on prey and/or climate as well as long-term whale data; this will require incorporation of relevant experts in these fields in the project. The Committee also agreed that it was worth examining the potential use of time series of whale oil production, provided that suitable climate data over the same period can be found. Investigation of long-term datasets from other species in the same ecosystem could also be valuable. The Committee **agrees** that formal proposals for work under a climate change project would be welcome for consideration at the 2011 Annual Meeting.

19.3.7 Non-lethal research techniques workshop

This proposal is for a technical conference/workshop to review the strengths and weaknesses of available non-lethal research methods for studies of living whale in the Southern Ocean and their ecological roles in the Southern Hemisphere. The objectives are to advance the synergies of non-lethal methods for investigations addressing a range of research themes. Presentations at the workshop will focus on methodological or technological advances to non-lethal methods, including those that are still under development, or with specific applications to populations in the Southern Hemisphere. Preliminary planning has been undertaken and it is likely to be held in Chile in late 2011.

It was suggested that the workshop could take place in association with the proposed Assessment workshop on southern right whales planned for Argentina in September 2011. A draft Agenda for this workshop can be found in Annex R.

19.4 Funding mechanism for SORP

The Committee **endorses** the process for evaluating requests for funding under the IWC/SORP research fund given in Annex R. It agrees that the IWC Head of Science and Chair of Scientific Committee should be included in the SORP Steering Committee.

20. ACTIONS ARISING FROM INTERSESSIONAL REQUESTS FROM THE COMMISSION

As part of the Commission's work on the Future of the IWC, the Chair and the Vice-Chair of the Commission, based on discussions within the Chair's Support group and the Small Working Group on the Future of the IWC, developed the 'Proposed Consensus Decision to Improve the Conservation of Whales'. The Committee received a short PowerPoint presentation explaining the background to the document, focussing on issue of relevance to the Scientific Committee. In particular, the Committee was asked, via the Small Working Group on the Future of the IWC, to provide scientific advice on a number of aspects of the proposed Consensus Decision; the Terms of Reference for our work are given in Annex G of IWC/62/6 rev. They are also given as Annex S to this report.

The parts of the report requiring review and advice, along with the sub-groups of the Committee that took the initial review can be summarised as follows:

(1) Review of Annex {DNA} on DNA registers and market sampling – jointly by the Working Group on DNA and the Working Group on the estimation of bycatch and other human induced mortality – see Annex N, item 9;
(2) Reviews of Annex {SI} on scientific information required from the catch and Annex {OI} review of operational information – the sub-committee on the RMP – see Annex D;
(3) Review of the potential workplan for the Scientific Committee – relevant sections were reviewed by the sub-committee on the RMP and the sub-committee on in-depth assessments (Annexes D, and G, respectively); and
(4) Review of the report of the Scientific Assessment Group (IWC/M10/SWG6) in the light of the numbers in table 4 of IWC/62/7rev (the table of catch limits) - relevant sections were reviewed by the sub-committee on the RMP, the working group on the *pre-Implementation assessment* of common minke whales in the western North Pacific, the sub-committee on in-depth assessments, the sub-committee on other Southern Hemisphere whale stocks (Annexes D, D1, G, and H, respectively).

The discussions within the sub-committees form the basis of the Committee's advice given below.

With respect to tasks (1)-(3) above, the complete Annexes incorporating our recommendations are included in Annex T, as is an updated timetable.

20.1 Review of Annex {DNA} on DNA registers and market sampling schemes

The Committee was requested to review Annex {DNA} of IWC/62/7rev for clarity and completeness. Annex {DNA} of IWC/62/7rev is based on the report of an earlier specialist workshop held from 7-9 March 2005 (IWC/M05/RMSWG 5). The objective of the review is to ensure that the Annex remains a cost-effective, robust, independent and transparent system in conjunction with the other monitoring and control measures.

To address the above objectives, the Committee **recommends** that the text given in Annex S replaces Annex {DNA} of IWC/62/7rev. Here follows a summary of the recommended changes.

1. SPECIFICATIONS FOR THE ESTABLISHMENT/ MAINTENANCE OF A DIAGNOSTIC DNA REGISTER/ TISSUE ARCHIVE
1.1 Laboratories
1.1.1 Minimal laboratory requirements

1.1.1 (6)	to clarify the length of time that archived samples were to be stored;
1.1.1 (7)	to clarify requirements that a variety of error-checking procedures should be followed and that sample quality should be checked routinely prior to genetic analysis.
1.1.1 (9)	to take into account several different factors in calibration exercises.
Footnote text	a more comprehensive definition of 'diagnostic DNA register'.

1.2 Sample collection
1.2.1 Size of the samples
1.2.2 Preservations

1.2	to specify training of and information to be collected by persons who may be involved in the collection of genetic samples for DNA registries other than commercial, scientific and indigenous catches (e.g. bycatches or stranded animals).
1.2.1 and 1.2.2	to clarify the sample preservation requirements.

1.4 Markers and methods of analysis
1.4.1 Mitochondrial DNA
1.4.2 Microsatellites
1.4.3 Sex identification

1.4.1, 1.4.2 and 1.4.3	to clarify that the analytical methods adhering to the quality standards as specified in the IWC genetic data quality guidelines must be approved by the international expert group.

1.7 External audit of DNA registers

1.7	to specify that the international expert group shall submit an annual report to the Secretariat of the IWC for distribution to contracting governments and the Commission (and, if necessary subsidiary bodies of the Commission) at least two months before it must be considered.

1.8 Submission procedure for samples for comparison with registers

The Committee considered all of section 1.8 in light of the stated objective of Annex {DNA}: 'to ensure a robust, independent and transparent system'. Item 1.8 makes a crucial contribution to these objectives, by providing a mechanism for sample verification that is not reliant on national market sampling schemes, and is also not reliant on the international expert panel, whose role is to audit the system rather to focus on individual samples. The Committee **agrees** that the current wording of item 1.8 does not fully make clear the intent of the mechanism and has thus provided new clarifying wording (including in the heading).

It also **agrees** to a new item 1.9, to specify the submission of DNA profiles to the IWC' central register from contracting governments under whose jurisdiction whales and whale products may be legally marketed.

2. SPECIFICATIONS FOR THE ESTABLISHMENT/ MAINTENANCE OF MARKET SAMPLING SCHEME
2.2 Development of appropriate market sampling schemes including audit

New 2.2 (4)	to take into account that some 'degraded' and/or 'processed' samples from market surveys could not be analyzed using exactly the same procedures as those currently used for 'fresh' and 'unprocessed' samples, but that methods could be developed to allow accurate comparison of such samples with profiles in DNA registries.

2.4 Reporting

2.4	a slight revision of the text concerning reporting to the IWC by the international expert group: the international expert group shall submit an annual report to the Secretariat of the IWC for distribution to contracting governments and the Commission (and, if necessary bodies of the Commission) at least two months before it must be considered.

20.2 Review of Annex {SI} to IWC/62/7rev – scientific information requirements

The draft Annex was based on previous recommendations of the Committee in the context of RMS discussions (IWC, 1995d). The Committee reviewed the Annex. In discussion it was recalled that the Committee has previously agreed that bulla do not provide a reliable means for estimating age (IWC, 2002c, p.12). It also noted that earplugs do not provide reliable age estimates for North Atlantic common minke whales. Walløe and Víkingsson reported that lengths could not always be recorded for minke whales in North Atlantic in the manner specified, although estimates of length are reported to the Secretariat.

Given the above the Committee **recommends:**

(1) reference to 'bulla' be removed from point 2(b); and
(2) the following footnote be added to point (a) 'Onboard small coastal whaling vessels such as those participating in Norwegian and Icelandic operations, it may be difficult to obtain accurate length measurements because whales are handled on a limited space. It is recognised that measurements in these cases may not be as accurate as those taken in ideal situations.'

The full revised Annex is given as Annex T.

20.3 Review of Annex {OI} to IWC/62/7rev – operational information requirements

The Committee **endorses** the operational information requirements as given in the proposed Annex.

20.4 Review of proposed timetable for future *Implementations* and *Implementation Reviews* (IWC/62/7rev Appendix B, p. 37)

The Committee **concurs** with the SAG that the schedule in Section 5 of IWC/62/7rev, updated following its deliberations as Table Y below, is ambitious. It noted that *Implementations* and *Implementation Reviews* can (and do) involve considerable time and resources from national scientists and, especially in cases when *Implementation Simulation Trials* are required, the Secretariat. Moreover, delays can occur when conducting *Implementations* given that the same members of the Committee are involved in many of the *Implementations* and *Implementation Reviews*.

The Committee has previously agreed that it can only conduct one *Implementation* at a time. The schedules for Western North Pacific Bryde's whales, and for North Atlantic common minke and fin whales given in IWC/62/7rev match the schedules expected from the *Implementations* for these species in terms of the Committee's agreed guidelines (IWC, 2005b). The Committee has previously been able to complete an *Implementation Review* during a single meeting, provided that no *Implementation Simulation Trials* are required.

The Committee therefore cannot conduct *Implementations* for Western North Pacific sei and Antarctic minke whales at the same time. The SAG had considered it more important to conduct an *Implementation* for Western North Pacific sei whales first given the size of current catches and the estimates of abundance for this stock. However, the Committee noted that there are also reasons to conduct an *Implementation* for Antarctic minke whales starting in 2012. After discussion of the relative amount of preparatory work required for *In-depth* and *pre-Implementation assessments* of North Pacific sei whales compared to Antarctic minke whales, the Committee **recommends** to deal with North Pacific sei whales before minke whales, as in IWC/62/7rev, and further **recommends** the schedule given in 20.5.3.4 below.

The Committee **recommends** that two years should be allowed for the *pre-Implementation assessment* for Antarctic minke whales irrespective of when the *Implementation* for these whales starts (under the current schedule, the first year of the *pre-Implementation assessment* would be 2014). It was also recognised that the current *Implementation* for these whales is sufficiently dated (1993) that it was unreasonable to expect that this 1993 *Implementation* can simply be reviewed after almost 20 years of developments in how to *Implement* the RMP.

The Committee therefore **recommends** that '/IR' (for *Implementation Review*) be deleted from the box for 2015 for Antarctic minke whales.

20.5 Review of the Scientific Assessment Group (SAG) Report

As part of the Commission's discussions on the Future of the IWC, the Commission's Chair and Vice-Chair developed the document 'Proposal Consensus Decision to Improve the Conservation of Whales' (IWC/62/7rev). During the development process but before finalisation of IWC/62/7rev, a small Scientific Assessment Group (SAG) was established to provide a report (IWC/M10/SWG6) of a concise scientific review on whether proposed catches were such that the long-term status of the populations concerned would be negatively affected. The numbers in table 4 of the proposed consensus decision (i.e. proposed whale catches for the period 2010/11-2019/20) are below those considered by the SAG. The terms of reference developed by the Small Working Group on the Future of the IWC (SWG) for the Committee's review of the SAG report in the light of the numbers in table 4 of IWC/62/7rev are given in Annex S and summarised below.

The Committee shall follow the terms of reference of the SAG (IWC/M10/SWG, Annex B), recognising:

(a) the need to be concise;
(b) the fact that there are a number of different approaches to evaluating short-term catches and no single method will be appropriate in all circumstances; and

(c) that the report should provide an integrated, pragmatic view on whether or not the proposed short-term catches (i.e. before the RMP can be used) are likely to negatively affect the long-term (i.e. RMP simulation framework timeline of 100 years) status of the stock *given* the timetable for RMP work.

It had also been requested that the Chair of the Scientific Committee should ensure that the time spent on this review should be such that it does not interfere with the Committee's focus on completing RMP-related work as soon as possible.

The SAG had noted that there were two categories of stocks for which advice was required: those for which the RMP could be applied immediately, and those for which it could not. The report below follows a similar pattern, focussing initially on the application of the RMP (western North Pacific Bryde's whales, North Atlantic common minke whales, North Atlantic fin whales) and then turning to those stocks for which it cannot immediately be applied (Antarctic minke whales, Southern Hemisphere fin whales, western North Pacific common minke whales, and western North Pacific sei whales).

20.5.1 General issues related to using the RMP

20.5.1.1 CATCH LIMIT CALCULATIONS (ACTIVATION, YEARS, INPUTS AND OUTPUTS)

As part of the SAG process, the RMP was applied to three species-Region combinations (western North Pacific Bryde's whales; North Atlantic minke whales; and North Atlantic fin whales) upon instruction from the Chair of the Commission. The calculations reported are therefore the results of applying the RMP itself, although results are also shown for tunings other than the Commission-agreed 0.72 tuning (the 0.6 tuning). The Committee repeated the RMP catch limit calculations for these stocks. Differences from the SAG's calculations are documented in the following sections. When applying the *CLA*, the phase-out rule was applied for each *Small Area* after the catch limit was cascaded to the *Small Areas* from the *Medium Area* rather than applying the phase-out rule before cascading the *Medium Area* catch limit to *Small Areas*, in accordance with RMP specifications (RMP specification 3).

20.5.1.2 TUNING LEVELS

The SAG report (and Annex D, Appendix 8) provides results for the 0.72 and 0.6 tunings of the RMP because the whaling countries in the Commission's support group had requested the latter tuning. This issue is discussed more fully in the SAG report.

The Committee noted that although the 0.6, 0.66 and 0.72 tunings of the *CLA* were recommended to the Commission by the Committee, having been subjected to testing during the development of the RMP, the *Implementation Simulation Trials* have only been conducted by the Committee for the 0.72 tuning of the RMP. Norwegian scientists have run the *Implementation Simulation Trials* for minke whales in the Northeast Atlantic for the 0.6 tuning of the RMP, but these calculations were not undertaken nor reviewed in detail by the Committee. In addition, which RMP variants are 'acceptable' may change if the tuning level is changed. The Committee **agrees** that the tuning level which was used when calculating catch limits using the *CLA* should be that which is tested in *Implementation Simulation Trials*; in this case only the 0.72 tuning. In principle, the *Implementation Simulation Trials* could be repeated for a new tuning if requested by the Commission. However, the criteria used to evaluate whether performance of an RMP variant is 'acceptable', 'borderline' or 'unacceptable' is linked to the 0.6 and 0.72 tunings of the RMP. The present criteria may need to be investigated if the Commission requested that a different tuning of the RMP should be considered.

20.5.1.3 OTHER ISSUES

The Committee notes that its advice is based on the schedule of RMP *Implementations* proposed in Appendix B of the Chair's and Vice-Chair's proposal (IWC/62/7rev). The Committee brings to the attention of the Commission its concern that delays in completion of these implementations may increase risks to whale populations. Attention is drawn to the two-year schedule for completion of an *Implementation* as set out in the Committee's agreed guidelines (IWC, 2005b) - proposals made in this report follow from the Committee's intent to progress work in terms of this schedule.

On a more general issue, the Committee draws the Commission's attention to the fact that the RMP and AWMPs are designed to provide advice on catch and strike limits for periods of up to 6 years. Further work may be needed to assess the risks associated with setting catch limits for longer periods than 6 years.

20.5.2 Application of Stocks/Regions for which the RMP can immediately be applied

The Committee reviewed the specifications (provided by the Secretariat) of how the RMP was applied during the SAG meeting to western North Pacific Bryde's whales, North Atlantic minke whales, and North Atlantic fin whales. The following items summarise the modifications to the initial applications by the Secretariat made by the Committee in reaching its agreed applications: these primarily involve clarifications with respect to time-stamps of abundance estimates and the addition of newly agreed abundance estimates. Table 7 lists the resulting catch limits from the 0.72 and 0.6 tunings of the *CLA*. The format used to document the input and present the results (see Annex D, Appendix 8 for the final format) illustrates the calculations made, and emphasises the results calculated using the Commission-agreed 0.72 tuning.

20.5.2.1 WESTERN NORTH PACIFIC BRYDE'S WHALES

The application of the RMP to western North Pacific Bryde's whales was based on a single abundance estimate for the *Region* (time-stamped at 2000). The Committee requested that the time-stamps for the *Small Areas* when applying catch cascading be set to the effort-weighted years.

It was noted that survey data were available for 1988-96 and some of these data were used when computing the additional variance for the 1998-2002 surveys (Shimada *et al.*, 2008). An abundance estimate can be computed for 1988-96, but the Committee has only accepted the estimate from the 1998-2002 surveys (IWC, 2009b). Although abundance estimates could be calculated using the 1988-96 data, account would need to be taken of the correlation of these estimates with those for 1998-2002 if they were included in RMP calculations of catch limits. However, the presently-coded version of the RMP does not allow input of a variance-covariance matrix for the abundance estimates. The Committee therefore **recommends** that:

(1) the program for the *CLA* be modified to allow variance-covariance matrices to be input (Annex D, item 2.4); and
(2) the data and resulting abundance estimates from the 1988-96 surveys should be reviewed for possible use in the RMP during the next *Implementation Review*.

Table 7

Summary of the application of the RMP (full details of the inputs to the RMP as well as relevant intermediate calculations are given in Annex D, Appendix 8). Phaseout has been applied where applicable.

Year	WNP Bryde's whales	North Atlantic fin whales		North Atlantic minke whales					
Sub-area	1W+1E	WI (variant 6)	WI (variant 2)	CIC	CM	ES	EB	EW	EN
Catch limits based on the 72% tuning (Commission's agreed value)									
2010	**5**	**46**	**87**	**224**	**135**	**58**	**92**	**152**	**70**
2011	**3**	**46**	**87**	**224**	**135**	**58**	**92**	**152**	**70**
2012	**1**	**46**	**87**	**224**	**135**	**46**	**92**	**152**	**70**
2013	**0**	**46**	**87**	**224**	**135**	**35**	**92**	**152**	**56**
2014	**0**	**46**	**87**	**224**	**108**	**14**	**92**	**152**	**42**
Catch limits based on the 60% tuning									
2010	33	90	155	345	208	122	195	322	148
2011	19	90	155	345	208	122	195	322	148
2012	4	90	155	345	208	97	195	322	148
2013	0	90	155	345	208	73	195	322	118
2014	0	90	155	345	166	29	195	322	89

The final specifications for how the RMP was applied to these whales are listed in Annex D, Appendix 8A.

20.5.2.2 NORTH ATLANTIC MINKE WHALES

The Committee **recommends** the following changes to the abundance estimates for minke whales in the Central North Atlantic:

(1) use the estimates in Annex D, Table 1 to construct an abundance estimate for *Small Areas* CG+CIP and include this abundance estimate in that for the C *Medium Area* for 2006;
(2) use the estimate for the CM *Small Area* in 2005 of 12,043 (CV 0.28) in place of the estimate of 6,174 (CV 0.36) because the former estimate is based on surveys which covered more of the CM *Small Area*; and
(3) use the revised version of the estimate of abundance for 2005 of 26,739 (CV 0.39) in place of the estimate of 24,890 (CV 0.45);

Allison recalculated the CVs for the abundance estimates for the C *Medium Area*.

The Committee **recommends** that the catch limits for the minke whales in the eastern North Atlantic be based on the latest sex ratio data (i.e. 2005-09) rather than 2004-08 as was used for the SAG report. The final specifications for how the RMP was applied to North Atlantic minke whales are listed in Annex D, Appendix 8B.

20.5.2.3 NORTH ATLANTIC FIN WHALES

The Committee had no changes to the application of the RMP used in the SAG report. The specifications for how the RMP was applied to North Atlantic fin whales are listed in Annex D, Appendix 8C. As noted under Item 6.2.1, the Scientific Committee has already confirmed that *Variant 2* would be acceptable for 10 years, followed by *Variant 1*, if accompanied by an acceptable research programme. No final research proposal to distinguish between stock structure hypotheses has yet been adopted. Therefore, *Variant 2* is not an available option at this time. However, a preliminary proposal was submitted and discussed at this meeting. The Scientific Committee made two specific recommendations for improvement. The proposal will be modified accordingly, in consultation with an advisory committee appointed by the Scientific Committee, and submitted to the next Annual Meeting for adoption.

20.5.3 Advice on Stocks/Regions for which the RMP cannot immediately be applied

20.5.3.1 ANTARCTIC MINKE WHALES

Information on the timetable for undertaking an *Implementation* of Antarctic minke whales is given under Item 20.4. If this timetable can be met, it is expected to be completed in 2016.

20.5.3.2 SOUTHERN HEMISPHERE FIN WHALES

Section 2.6 of IWC/M10/SWG6 considered Southern Hemisphere fin whales. It is proposed that catches would be taken alternately in the Indian Ocean (between 35°E-130°E) and Pacific Ocean (between 130°E and 145°W) sectors of the Antarctic. A total of 10 annual catches would be taken in the period 2010/11-2012/2013, starting in the Pacific Ocean sector. Catches would be reduced from 10 to 5 individuals from 2013/14 until 2019/2020.

The Committee noted that in the past there was extensive exploitation (nearly 750,000 fin whales were killed in the 20th Century), and that recent information on fin whales in the Southern Hemisphere is poor. The Committee also noted that there were additional abundance estimates for this population, derived from IDCR/SOWER surveys, which had not been considered by the SAG (e.g. Branch and Butterworth, 2001a; Butterworth and Geromont, 1995). Branch and Butterworth (2001) estimated that the circumpolar abundance of fin whales south of 60°S was 2,100 (CV=0.36), 2,100 (CV=0.45) and 5,500 (CV=0.53) for CPI, CPII and CPIII respectively. These estimates are negatively biased since the areas north of 60°S were not covered[6].

It is unlikely that sufficient information will become available in the interim period (up to 2020) for an RMP *Implementation* to occur. Nevertheless, some members noted that if the *CLA* of the RMP was used it would result in a catch limit of 0. The Committee **concurs** with the general conclusions of the SAG, i.e. that it is unlikely that the proposed catches will affect the long-term status of the stock[s]. Some members were concerned about providing *ad-hoc* advice on catch limits without any likelihood of a formalised procedure being available in the foreseeable future. They did not want this exercise to set a precedent for providing *ad-hoc* advice.

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[6] IWC (1996b) reports IDCR estimates extended to south of 30°S by using Japanese Scouting Vessel survey results to provide an index of relative abundance.

20.5.3.3 WESTERN NORTH PACIFIC COMMON MINKE WHALES

Information on the timetable for undertaking an *Implementation Review* of western North Pacific common minke whales is given under Item 20.4. Given the progress made at this meeting (see Annex D1), it is expected that this will be completed in 2012.

The Committee noted that it was not possible to apply the RMP to the data for these minke whales owing to the considerable changes to the understanding of stock structure in recent years. It **agrees** that the present uncertainty precludes giving adequate advice regarding the catches in Table 4 of IWC/62/7rev The Committee generally **agrees** with the conclusions of the SAG; the Committee summarised its conclusions as follows.

(1) The *Implementation* process should be completed as quickly as possible. Completing the *Implementation Review* will allow advice on catches to be based on the RMP, which has been selected to ensure that catches are sustainable.

(2) A high priority should be accorded to research to determine the proportions of 'O' and 'J' stock in sub-area 12 because the implications of any proposed catches for both 'O' and 'J' stock clearly differ depending on this proportion. In this respect, the Committee welcomed the survey of sub-area 12 planned for summer 2010 and **emphasises** the importance of collecting as much data as possible to estimate stock proportions in sub-area 12.

(3) The proposed catches by coastal whalers in Table 4 of IWC/62/7rev may not help to improve the status of 'J' stock compared to current JARPN II catches. The incidence of 'J' stock in the catch decreases with distance offshore. The Committee received an analysis which estimated the number of 'J' stock animals under catch levels of 150 inshore and 70 offshore (Annex G1, Appendix 8). The Committee recognised the value of analysis such as those in Annex G1, Appendix 8 and **recommends** that further analyses be conducted using a finer spatial resolution and quantifying the uncertainty associated with the predictions, including the likely level of inter-annual variation in catches of 'J' stock animals.

(4) The Committee was unable to agree on the impact of the proposed catches on the 'O' stock. However it **agrees** that the risk to the 'O' stock will be minimised if the *Implementation Review* is completed as soon as possible so that advice can be based on the RMP and hence also **agrees** that catches of 'O' stock should not exceed present levels.

Table 8

Scientific Committee work plan for RMP *Implementations.*

	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	202
Western North Pacific Bryde's whales				IR					IR		
NA common minke whales - eastern and central medium areas					IR						IR
NA fin whales - central medium area					IR					IR	
Western North Pacific common minke whales	PIA		RMP	[RMP]					IR		
Western North Pacific sei whales		IDA		PIA	RMP	[RMP]					IR
Antarctic minke whales					PIA	PIA		RMP			

IR= *Implementation Review* (often possible to complete in one year). PI = *pre-Implementation assessment* (may take more than one year). RMP completed *Implementation* (takes two years once the PIA is completed IDA= in-depth assessment, usually takes two years or more and feeds in a *pre-Implementation assessment.* As explained in the text, the plan ambitious and it may not be possible to achieve all of the work by t years indicated. Square brackets are used to express possible but perhap less likely dates.

20.5.3.4 WESTERN NORTH PACIFIC SEI WHALES

Information on the timetable for undertaking an *Implementation* of western North Pacific sei whales is given under Item 20.4. If the *Implementation* turns out to be as simple as suggested there, it is expected to be completed by 2014.

The SAG report was based on the assumption that the In-depth Assessment for North Pacific sei whales would be conducted in 2010 as planned last year. This year, the Committee has concluded that in view of the relatively simple information available on the population, the In-depth Assessment and *pre-Implementation assessment* could most efficiently be combined into a single exercise, and **agrees** a compromise date of 2013 for the combined assessment, with RMP catch limits to be set the following year if no complications arise. The Committee **concurs** with the SAG that priority for the Committee should be to complete the RMP *Implementation* as soon as possible rather than to develop formal interim management advice. The Committee was unable to agree on the impact of the proposed catches on sei whales. The Committee **recommends** that as a minimum there should be no increase in the present level of catches until the RMP *Implementation* has been completed. Catches for North Pacific sei whales resumed in 2002 and the annual catch since 2004 has been 100 animals.

Table 9

Workshops and intersessional meetings planned for 2010/11.

Subject	Agenda item	Venue	Dates	Steering Group
North Pacific sighting survey workshop	Item 10.8.1; Annex G	Tokyo	28-30 September 2010	Q15
North Pacific 2011 cruise: planning	Item 10.8.2; Annex G	Tokyo	24-26 September 2010	Q15
Small cetaceans and climate change workshop	Item 12.5; Annex K	Vienna	28 November- 1 December 2010	Q24
Abundance of Antarctic minke whales workshop	Item 10.1.1; Annex G	Bergen?	January 2011	Q13
North Pacific minke whale preparatory meeting	Item 6.3; Annex D1	Tokyo	25-27 September 2010	Q4
North Pacific minke First Intersessional Workshop	Item 6.3; Annex D1	Korea	14-17 December 2010	Q4
Workshop on AWMP	Items 8.2; 8.3; Annex E	TBA	March 2011	Q1

Possible pre-meetings immediately before SC/63 depending on intersessional progress: AWMP gray whale *Implementation Review*; western North Pacific common minke whale *Implementation Review;* assessment of humpback whale Breeding Stock B.

21. RESEARCH AND WORKSHOP PROPOSALS AND RESULTS

Table 9 lists the proposed intersessional meetings and workshops. Financial implications and further details are dealt with under Item 24.

Results from last year's intersessional IWC workshops are dealt with under the relevant Agenda Items.

21.1 Review results from previously funded research proposals

Results from IWC funded projects are dealt with under the relevant agenda items.

21.2 Review proposals for 2010/11

No unsolicited research proposals were received. The Committee has **agreed** mechanisms for reviewing proposals under the SORP programme (Item 19) and the Small Cetaceans Voluntary Fund (Item 15).

22. COMMITTEE PRIORITIES AND INITIAL AGENDA FOR THE 2011 MEETING

Revised Management Procedure (RMP)

The following issues are high priority topics:

GENERAL MATTERS

(1) complete review of the range of MSYR values for use in the RMP;
(2) finalise approach for evaluating proposed amendments to the *CLA*;
(3) evaluate the Norwegian proposal for amending the *CLA*;
(4) consider implications that the phase-out rule in the RMP is applied by *Small Area* when catch cascading is applied and the abundance estimates are based on multi-year surveys; and
(5) modify the Norwegian 'CatchLimit' program to allow variance-covariance matrices to be specified for the abundance estimates.

***IMPLEMENTATION REVIEW* FOR NORTH PACIFIC COMMON MINKE WHALE**

(1) review results of intersessional workshops; and
(2) complete the work assigned to the 'First Annual Meeting' in accord with our guidelines.

***IMPLEMENTATION* FOR THE WESTERN NORTH PACIFIC BRYDE'S WHALES**

(1) review the research proposal for the 'variant with research'.

***IMPLEMENTATION* FOR THE NORTH ATLANTIC FIN WHALES**

(1) review revised research proposal for the 'variant with research'; and
(2) review abundance estimates for use in the *CLA*.

***IMPLEMENTATION* FOR THE NORTH ATLANTIC MINKE WHALES**

(1) review any new abundance estimates.

Aboriginal Whaling Management Procedure (AWMP)

The following issues are high priority topics:

(1) work on developing appropriate long-term management advice for the Greenlandic fisheries with the primary focus on:
    (a) completing work on a sex-ratio based assessment of common minke whales off west Greenland; and
    (b) progress on developing *SLA*s for West Greenland fin and common minke whales;
(3) the *Implementation Review* for the eastern North Pacific gray whales; and
(4) consider any new scientific information related to conversion factors for edible products for Greenland fisheries.

Bowhead, right and gray whales (BRG)

The following issues are high priority topics:

(1) perform the annual review of catch information and new scientific information for B-C-B stock of bowhead whales and prepare for the 2012 *Implementation Review*;
(2) review stock structure and abundance for Eastern Canada and West Greenland bowhead whales;
(3) review scientific information on North Pacific and North Atlantic right whales;
(4) review progress towards southern right whale workshop;
(5) review new information on western gray whales;
(6) review information on other stocks of bowhead whales; and
(7) review new information on eastern gray whales (not relevant to *Implementation Review*).

In-depth assessment (IA)

The following issues are high priority topics:

(1) resolve the reasons for the differences between estimates of abundance of Antarctic minke whales between the OK and SPLINTR models;
(2) continue development of the catch-at-age models of Antarctic minke whales, including sensitivity tests to examine various assumptions regarding ageing errors and age-length keys; and
(3) continue examination of the differences between minke abundance estimated from CPII and CPIII, by further investigation of the relationship between sea ice and minke whale abundance.

Bycatch and other human-induced mortality (BC)

The following issues are high priority topics:

(1) collaboration with FAO on collation of relevant fisheries data and joining FIRMS;
(2) review progress in including information in National Progress Reports;
(3) continue development of the international database of ship strike incidents;
(4) consider methods for estimating risk and rates of bycatch and entanglement;
(5) consider methods and data sources for establishing time series of bycatch;
(6) review methods to estimate mortality from ship strikes; and
(7) review methods for assessing mortality from acoustic sources and marine debris.

Stock definition (SD)

The following issues are high priority topics:

(1) furtherance of guidelines for genetic analyses;
(2) updates on guidelines for DNA Data Quality;
(3) statistical and genetic issues concerning stock definition;
(4) TOSSM; and
(5) unit-to-conserve.

DNA (DNA)

The following issues are high priority topics:

(1) review genetic methods for species, stock and individual identification;

(2) review of results of the 'amendments' work on sequences deposited in GenBank;
(3) collection and archiving of tissue samples from catches and bycatches; and
(4) reference databases and standard for diagnostic DNA registries.

Environmental concerns (E)
The following issues are high priority topics:

(1) SOCER;
(2) review progress on POLLUTION 2000+;
(3) review new information impact of oil and dispersants on cetaceans;
(4) review progress of the CERD Working Group;
(5) review progress on recommendations from 2010 focus sessions on masking sound;
(6) review approaches as available from other international forums with regard to mitigation of effects of anthropogenic sound on cetaceans;
(7) review progress on work from the 2nd Climate Change Workshop; and
(8) review of marine renewable energy development.

Ecosystem modelling (EM)
The following issues are high priority topics:

(1) review ecosystem models from the North Pacific that may be relevant to assessments and RMP *Implementations*;
(2) review other issues relevant to ecosystem modelling within the Committee; and
(3) review ecosystem modelling efforts undertaken outside the IWC.

Southern Hemisphere whales other than Antarctic minke whales (SH)
The following issues are high priority topics:

(1) humpback whales-complete the assessment of breeding stock B;
(2) blue whales (Antarctic and pygmy): population estimates and continue work on the Southern Hemisphere blue whale catalogue;
(3) prepare for assessment of humpback whale breeding stocks D, E and F;
(4) review new information on the Arabian humpback populations.

Small cetaceans (SM)
The following issues are high priority topics:

(1) the status of status of Ziphiidae (beaked and bottlenose whales) worldwide;
(2) directed takes of small cetaceans;
(3) review report from climate change-small cetaceans workshop;
(4) other topics e.g. marine bushmeat; and
(5) review of progress on previous recommendations.

Whalewatching (WW)
The following issues are high priority topics:

(1) assess the impacts of whalewatching on cetaceans;
(2) review reports from intersessional working groups:
    (a) large-scale whalewatching experiment (LaWE) Steering Group;
    (b) LaWE Budget Development Group;
    (c) on-line database for world-wide tracking of commercial whalewatching and associated data collection; and
    (d) swim-with-whale operations;
(3) consider information from platforms of opportunity of potential value to the Committee;
(4) review of whalewatching guidelines and regulations; and
(5) review of collision risks to cetaceans from whalewatching vessels.

Scientific Permits
The following issues are high-priority topics:

(1) Review of activities under existing permits.
(2) Review of new or continuing proposals.
(3) Procedures for reviewing scientific permit proposals.
(4) Planning for final review of results from Iceland's scientific take of North Atlantic common minke whales.

23. DATA PROCESSING AND COMPUTING NEEDS FOR 2010/11

The Committee identified and agreed the requests for intersessional work by the Secretariat given in Table 10.

Table 10

Computing tasks/needs for 2010/11.

RMP – preparations for *Implementation*
Run a full set of trials using the Norwegian 'CatchLimit' program for North Atlantic fin whales, Western North Pacific Bryde's whales; and North Atlantic minke whales and place the results on the IWC website (Item 5.3).

AWMP
Work in preparation for/arising from the proposed workshop (Item 21).

NPM
Update the control program for North Pacific minke whales and undertake any work arising from the Preparatory Meeting and the First Intersessional Workshop including assembling the catch data at the appropriate spatial and temporal resolutions and coding and conditioning the operating models themselves (Item 6.3.2).

In-depth assessment
Validation of the 2009/10 SOWER cruise data for incorporation into the DESS database; complete validation of the 1995-97 blue whale cruise data and incorporate into the DESS database; prepare a catch series for North Pacific sei whales (Item 10.9.1).

Southern Hemisphere whale stocks
Documentation of the catch data available for Antarctic minke whales in preparation for the *pre-Implementation assessment* (Item 20.4).

Bycatch
Input bycatch data from the last season (2009) and for previous seasons (from 2003 back) into the bycatch database (Item 7.1).

24. FUNDING REQUIREMENTS FOR 2010/11

Table 11 summarises the complete list of recommendations for funding made by the Committee. The total required to meet its preferred budget is £316,700. The Committee **recommends** all of these proposed expenditures to the Commission. This is slightly above the projected amount available for funding (£315,750). The Committee **agrees** that the final column given in the table represents a budget that will allow progress to be made by its sub-committees and Working Groups in its priority topics.

A summary of each of the items is given below, by sub-committee or standing Working Group. Full details can be found in the relevant Annexes as given in Table 11.

The Committee was pleased to note that procedures have been agreed to review proposals for funds from the Small Cetaceans Voluntary Fund and the Southern Ocean Research Partnership (Items 14 and 19). One proposal under the former has been recommended (see Item 14.6.1). The Committee was also pleased to note that funding has been found for the Workshop on Small Cetaceans and Climate Change (see Item 12.5).

Table 11

Summary of budget requests.

	Annex	Short title	Requested (£)
RMP			
1	Annex D	Analysis and use of time-series of data on calving rates and intervals for use in the MSYR review.	7,000
NPM			
2	Annex D1	Pre-meeting and 1st Intersessional Workshop towards *Implementation Review* for WNP common minke whales.	25,000
AWMP			
3	Annex E	AWMP Workshop on Greenlandic fisheries and preparing for gray whale *Implementation Review.*	12,000
4	Annex E	AWMP developers fund.	8,000
BRG			
5	Annex F	Southern Ocean right whale photo-id catalogue.	3,800
IA			
6	Annex G	Investigate the relationship between sea-ice characteristics and Antarctic minke whale abundance estimates.	5,000
7	Annex G	Resolving differences in minke whale abundance estimates.	15,000
8	Annex G	Import of 2009/10 SOWER data and assist abundance working group.	3,000
9	Annex G	North Pacific sighting cruise.	58,000
10	Annex G	Workshop to plan medium-long term North Pacific sighting survey programme.	7,000
11	Annex G	Statistical catch-at-age estimators for Antarctic minke whales.	2,500
SH			
12	Annex H	Southern Hemisphere Blue Whale Catalogue Project.	18,900
13	Annex H	Modelling of Southern Hemisphere humpback whale populations.	3,000
14	Annex H	Antarctic humpback whale catalogue.	15,000
BC			
15	Annex J	Further development and maintenance of the IWC ship strike database.	5,000
16	Annex J	Development of an online submission database for Progress Reports.	5,000
E			
17	Annex K	Risk assessment modelling to determine the impact of pollutants on cetacean populations.	52,500
18	Annex K	State of the Cetacean Environment Report (SOCER).	3,000
WW			
19	Annex L	Data compilation and power analyses for the LaWE.	4,000
ALL			
20		Invited Participants to the 2011 Annual Meeting.	64,000
Total			**316,700**

Revised Management Procedure

(1) ANALYSIS AND USE OF TIME-SERIES OF DATA ON CALVING RATES AND INTERVALS FOR USE IN THE MSYR REVIEW

The Committee is conducting a review of the range of MSYR values to include in simulation trials when selecting among variants of the RMP. The third intersessional workshop on the review of MSYR assembled a number of datasets on calving rates and calving intervals for baleen whales. Efforts were made following the workshop to fit models which accounted for both process and observation error to the data on calving rates and calving intervals. However, numerical problems were encountered when implementing these models. Funding is required for researchers to overcome these problems to provide the inputs needed to apply the Bayesian hierarchical method adopted by the Committee for computing a posterior distribution for r_0.

North Pacific minke whales

(2) PREPARATORY MEETING AND FIRST INTERSESSIONAL WORKSHOP TOWARDS THE IMPLEMENTATION REVIEW FOR WESTERN NORTH PACIFIC COMMON MINKE WHALES

The schedule for an *Implementation Review* specifies that between the finalisation of the *pre-Implementation assessment* and the following annual meeting of the Scientific Committee, an intersessional workshop shall be held to address a number of issues. Given the complexity of this *Implementation Review*, it is important to hold a preparatory meeting before the First Intersessional Workshop.

Aboriginal Whaling Management Procedure

(3) WORKSHOP ON GREENLANDIC FISHERIES/PREPARATION FOR GRAY WHALE IMPLEMENTATION REVIEW

The Committee has a number of priority areas related to Greenlandic fisheries and an intersessional Workshop is required to address:

(1) progress on developing *SLAs* for West Greenland fin and common minke whales;
(2) progress on the development of the sex-ratio method; and
(3) preparation for the *Implementation Review* for eastern North Pacific gray whales.

(4) AWMP DEVELOPERS FUND

The developers fund has been invaluable in the work of *SLA* development and related essential tasks of the SWG. It has been agreed as a standing fund by the Commission. The primary development tasks facing the SWG are for the Greenlandic fisheries. These tasks are of high priority to the Committee and the Commission. The fund is essential to allow progress to be made.

Bowhead, right and gray whales

(5) SOUTHERN OCEAN RIGHT WHALE PHOTO-ID CATALOG

For several decades, extensive photo-id surveys have been carried out for southern right whales in the coastal waters of South America, southern Africa and Australia during winter and spring, and much valuable data on the demographics of these populations has been collected. Together with genetic information, these data also provide the opportunity to investigate interchange and mixing between the coastal populations. However, because of its geographic limitations it is uninformative about the links between these populations and those found (generally at higher latitudes) in summer where extensive catches were taken in pelagic whaling. Funding is requested to address this gap by compiling images of southern right whales taken away from coastal waters of the continents, in a catalogue and associated database.

In-depth assessments

(6) INVESTIGATE THE RELATIONSHIP BETWEEN SEA ICE CHARACTERISTICS AND ANTARCTIC MINKE WHALE ABUNDANCE ESTIMATES

No conclusions have yet been reached on the reasons for the appreciable decline in abundance estimates from CPII and CPIII. Changes in sea ice characteristics, such as its extent and configuration, have been considered as one of the most likely influential factors. In order to investigate this carefully, funding is required to enable the preparation of the following sea ice related data sets:

(1) timing of the ice melt index for the entire time series of CPII and CPIII; and
(2) sea ice characteristics (e.g. area of sea-ice-field) in the south of ice edge for the entire time series of CPII and CPIII.

(7) RESOLVING DIFFERENCES IN MINKE WHALE ABUNDANCE ESTIMATES

Over the past two years, two methods have been presented to estimate abundance from the CPII and CPIII IDCR/SOWER cruise data. However, there are large differences between the estimates. These differences are much greater than statistical uncertainty, and than generally seen in the simulated datasets. Following intersessional work by correspondence a workshop is required to attempt to finally resolve the difference between the two approaches.

(8) IMPORT 2009/10 SOWER DATA AND ASSIST ABUNDANCE WORKING GROUP

Funds are required to enable the 2009/10 IWC/SOWER data to be incorporated into DESS and to provide general support to the IWC Secretariat regarding DESS. Errors will be corrected in the 'standard' and IDCR/SOWER datasets before the 2010 Scientific Committee meeting.

(9) AND (10) 2011 NORTH PACIFIC SIGHTING CRUISE AND ASSOCIATED MEETINGS

A new medium- to long-term research programme involving sighting surveys to provide annual information for cetacean stock management in the North Pacific is scheduled to commence in 2011. The cruise will last a total of about 60 days between July and August and the vessel *Kaiko Maru* will generously be provided by the Japanese Government. A two-day planning meeting for the 2011 cruise will be held in Tokyo. It will be preceded by a three-day workshop to develop the medium to long term objectives of the research programme and associated fieldwork.

(11) STATISTICAL CATCH-AT-AGE ESTIMATORS FOR ANTARCTIC MINKE WHALES

The Committee is trying to understand the reasons for the apparent large declines in abundance indicated by estimates produced from these surveys. Several of these reasons can be explored by population dynamics modelling. In 2005, Punt and Polacheck developed the statistical catch-at-age (SCAA) model, which has been refined over the last few years and is considered the most appropriate modelling framework for addressing these issues. Funding is requested for Committee's researchers to implement the recommendations so that in 2011 it will be in a position to apply the SCAA model to the most recent datasets.

Other Southern Hemisphere whale stocks

(12) SOUTHERN HEMISPHERE BLUE WHALE CATALOGUE PROJECT

Little is known about the present-day migration of blue whales, population structure and abundance or the level of interchange among populations. In 2008, the IWC supported the creation of a Southern Hemisphere blue whale catalogue and Centro de Conservacion Cetacea in Chile was tasked with developing a central web-based system by which Southern Hemisphere blue whale photo-id matching could take place. Matching will be conducted during the next two years through this platform by researchers from three Southern Hemisphere regions. Comparisons of blue whale photo-id and the significant number of individuals catalogued will be time consuming and researchers will not have enough free time to dedicate to the matching process. Therefore funding is required to ensure the matching process is completed. This will be a two-year project and a further request for funding (£11,200) will be submitted next year.

(13) MODELLING OF SOUTHERN HEMISPHERE HUMPBACK WHALE POPULATIONS

(1) Deliberations at the 2010 Annual Meeting have led to a number of proposed variants of stock-structure models for breeding stock B. Computer software needs to be developed to implement these models to take account of tag-recapture data.
(2) Simultaneous analysis of all 7 breeding stocks using the current age-aggregated model is desirable so that:
    (a) the catch allocation uncertainty is taken into account in a consistent and even-handed manner;
    (b) uncertainties in the boundaries for such allocations can be properly included in the analysis; and
    (c) likely similarities in intrinsic growth rate parameters for the different stocks can be properly factored into the analyses.

Development of this model has commenced but still needs further development. A contribution towards the salaries of researchers is requested to enable progress to be made with (1) and (2).

(14) ANTARCTIC HUMPBACK WHALE CATALOGUE

The Committee is already committed to funding this project, which represents only a partial cost of running the catalogue and is of great benefit to its in-depth assessment of Southern Hemisphere humpback whales. The funds are required to continue the cataloguing of submitted photographs and further develop and enhance the system for on-line access. The work will be carried out by Carlson and Allen.

Bycatch and other human-induced mortality

(15) FURTHER DEVELOPMENT AND MAINTENANCE OF THE IWC SHIP STRIKE DATABASE

Development of the IWC ship strike database has continued intersessionally. Funding is required for: (1) completing work on public summaries; (2) the development of a handbook; (3) data entry and validation; and (4) annual ongoing work by the data review group. The need for a global database of incidents involving collisions between vessels and whales has previously been recognised by the Committee, as well as other bodies such as the International Maritime Organization (IMO) and ACCOBAMS.

(16) DEVELOPMENT OF AN ONLINE SUBMISSION DATABASE FOR PROGRESS REPORTS

In 2009 the possibility of developing an online form/ database for submission of national Progress Reports was discussed as part of work on bycatches and small cetaceans, in addition to the general work of the Committee. Due to time constraints it was not possible to progress this further. A small group met this year to design an initial template and the Committee is now in the position to start trialling such a database. Funding is required for an expert to work with the IWC Secretariat to create this database and an initial version will be available at the next Annual Meeting.

Environment

(17) RISK ASSESSMENT MODELING TO DETERMINE THE IMPACT OF POLLUTANTS ON CETACEAN POPULATIONS

The report of the Phase II Intersessional IWC Pollution 2000+ Workshop (SC/62/Rep4) recommends that a number of modelling exercises be undertaken. This will involve the development and implementation of two demonstration projects, using the risk assessment framework (based on an individual based model approach). Funding is required to employ a post-doctoral research assistant to conduct this work under the direct supervision of Schwacke and Hall, with input and guidance from the Pollution 2000+ Steering Committee. This will be a two-year project and a further request for funding (£70,750) will be submitted next year.

(18) STATE OF THE CETACEAN ENVIRONMENT REPORT (SOCER)

The Committee regards SOCER to be a useful document that provides a 'snapshot' of environmental developments relevant to cetaceans that was requested by the Commission. Money is requested to support the production of this report.

Whalewatching

(19) DATA COMPILATION AND POWER ANALYSES FOR THE LAWE

The LaWE initiative aims to understand the possible effects of whalewatching on the demographic parameters of cetacean populations. In order to develop procedural mechanisms to centralise relevant data and to commence power analysis for key parameters, funding is required to employ a research assistant for 6 weeks.

Other

(20) INVITED PARTICIPANTS (IPs) FUND

The Committee **draws attention** to the essential contribution made to its work by the funded IPs. The IWC-funded IPs play an essential role in the Committee's work, including the critically important roles of Chairs and rapporteurs. They represent excellent value as they receive only travel and subsistence costs and thus donate their time, which is considerable. As was the case for previous meetings, where possible, effort will be made to accommodate scientists from developing countries.

25. WORKING METHODS OF THE COMMITTEE

25.1 Citation of Scientific Committee documents

SC/62/SCP1 was produced in response to the discussion last year about the Committee's policy with respect to the citation of Scientific Committee documents (IWC, 2010c, p.92). At that time the Committee had noted that *inter alia* its policy must ensure transparency with respect to advice provided by the Committee and to respect the rights of scientists to first publication of data.

The authors of SC/62/SCP1 had examined both the policy of the *Journal* and that of the Committee with respect to the question of including 'Not to be cited (or used) without the permission of the author(s)' at the top of a paper. They noted that there was some ambiguity in the present rules that required clarification and suggested that the ability to include a 'not to be cited....' restriction to a paper should be removed and replaced by a 'please inform authors when citing outside an IWC meeting' header.

There was considerable discussion of this proposal. The Committee, as before was concerned to:

(1) ensure transparency;
(2) respect rights to first publication; and
(3) avoid the possibility that authors may refuse to submit papers of value to the Committee's work.

Recognising the sensitivities involved and the need to find an appropriate balance amongst items (1)-(3) above, the Committee **agrees** that in future, all papers presented to the Scientific Committee contain the following header (this information will also be included in the Scientific Committee Handbook and when providing information on document submission to meetings and workshops):

> 'Papers submitted to the IWC Scientific Committee are produced to advance discussions within that Committee: they may be preliminary or exploratory. It is important that if you wish to cite this paper outside the context of an IWC meeting, you notify the author at least six weeks before it is cited to ensure that it has not been superseded or found to contain errors.'

The Scientific Committee List of Documents attempts to keep track of papers that have been presented to Scientific Committee meetings and can be found on the IWC website[7]. Authors who are aware of particular problems with any of their past papers are invited to inform the Secretariat who will keep an updated compilation.

25.2 Working papers, late papers and related issues

As a result of discussions during the meeting, the Committee **agrees** on the need to clarify certain issues with respect to working papers and primary papers that arrive late. The definitions and rules regarding these (and other categories of paper including 'For Info' papers) can be found in the Scientific Committee Handbook[8].

Primary papers must be submitted by the end of the first day of the Annual Meeting. Considerable flexibility has been shown by the Chair and Head of Science in the way they have dealt with papers for which a title has been submitted but which for one reason or another, arrive late. Formally, they can be called working papers because they have missed the deadline and then immediately be 'upgraded' to primary papers to minimise copying. Unfortunately, this flexibility is tending to be abused as a larger number of papers are being submitted past the deadline. For this reason, the Committee **agrees** that in future only in exceptional circumstances will late papers be accepted. In addition, Chairs will be very strict on the criteria for accepting working papers i.e. they must arise from discussions and be requested and/or be likely to expedite resolution of disagreements or stimulate debate within the meeting.

Notwithstanding the question of late papers, the Committee **agrees** that there may be circumstances in the future where it is appropriate for certain working papers to be 'elevated' to the status of a primary paper during the meeting. The Chair and Head of Science will apply the following two criteria:

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[7] *http://www.iwcoffice.org/publications/pubmain.htm.*

[8] *http://www.iwcoffice.org/sci_com/handbook.htm.*

(1) the working paper has been presented and discussed within a sub-group or the plenary, such that an opportunity to comment on it has been given; and

(2) the text of the sub-group or plenary report would be significantly improved, streamlined or clarified by the ability to reference the paper as a primary document.

26. ELECTION OF OFFICERS

The Committee **agrees** that there was no need for elections this year.

27. PUBLICATIONS

Donovan reported on issues relating to the production of the *Journal*. Unfortunately, the year has been plagued by a series of problems with respect to getting the *Journal* published, due to internal problems at the printers that the IWC has used for many years. Sadly, after attempts to secure further investment, they are no longer trading but the Secretariat had very little notice in terms of finding an alternative. We have managed to find another company that we are using on a trial basis, and thanks to the page-setting abilities of Andrea Cooke, we managed to at least get the large *Supplement* out on time. We are now dealing with a different company and the *Journal* and Supplements should once again appear promptly. That being said, the Secretariat is in the process of examining a number of companies for ability and price. It is expected that the resultant backlog of papers will be reduced or eliminated in the coming year. In addition, the possibility of including electronic subscriptions is being investigated. The most efficient and cost effective way to digitise earlier reports is also being investigated. The Committee, as in previous years, **reiterates** the importance of the *Journal* to its work and encourages members to urge their institutes to subscribe.

28. OTHER BUSINESS

This is the final meeting for Nicky Grandy, Secretary of the Commission. The Scientific Committee rose in appreciation of her dedicated work in organising its meetings over the last decade. It noted the calm, efficient, good humoured way that she (and the team she ran) had assisted the Scientific Committee, even in the face of its sometimes unreasonable demands. On behalf of the Committee, its elder statesman, John Bannister, presented her with a specially painted card and a beautiful Moroccan rug, wishing her the very best for the future – she will be greatly missed.

29. ADOPTION OF REPORT

In closing the meeting, Palka thanked the Secretariat for carrying out its work in the usual efficient manner. The report was adopted at 17:20 on 11 June 2010. As is usual, final editing was carried out by the Convenors after the meeting.

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Report of the

Scientific Committee

Tromsø, Norway, 30 May to 11 June 2011

Annex E: Standing Working Group on an Aboriginal Whaling Management Procedure (AWMP)

This report is **CONFIDENTIAL** until
the opening session of the Commission's Plenary
at **10.00am** on **Monday 11th July 2011**

International Whaling Commission, Tromsø and Jersey, 2011

Annex E

Report of the Standing Working Group on the Aboriginal Whaling Management Procedure (AWMP)

Members: Donovan (Convenor), Acquarone, Allison, Baker, Bickham, Borodin, Brandão, Brandon, Breiwick, Broker, Brownell, Butterworth, Childerhouse, Cipriano, Dupont, Fadeev, Givens, Gunnlaugsson, Heide-Jørgensen, Hiruma, Ilyashenko, Iñíguez, Jaramillo, Johnston, Kanda, Kitakado, Lang, Lockyer, Mate, Moore, J., Nukulina, Palka, Punt, Reeves, Roel, Rose, Schweder, Scordino, Suydam, Swindoll, Thomas, Tyurneva, Uoya, Walløe, Weller, Witting.

1. INTRODUCTORY ITEMS

1.1 Convenor's opening remarks

Donovan welcomed the participants to the meeting. He noted that given the logistics of the intersessional workshop, it had not been possible to dedicate sufficient time to consideration of Greenlandic issues related to future *SLA* development (SC/63/Rep2). Given that the focus of the pre-meeting was to provide time for that discussion to begin, he noted that that the relevant agenda items 2 and 3 would be completed during the normal SWG sessions.

1.2 Election of Chair

Donovan was elected chair.

1.3 Appointment of rapporteurs

Givens and Punt acted as rapporteurs, with assistance from the Chair.

1.4 Adoption of Agenda

The adopted agenda is given in Appendix 1.

1.5 Documents available

The new primary documents available to the SWG were SC/63/AWMP1-5 and SC/63/Rep2.

2. CONCLUSIONS ON THE SEX RATIO METHOD

Witting (2005 [SC/57/AWMP4]; 2006 [SC/58/AWMP3]) proposed that the abundance of West Greenland minke whales could be estimated using time series data on the sex ratio of past catches. Since then, the proposed method and subsequent improvements to estimate only the lower confidence bound on the abundance (starting with Witting and Schweder, 2007 [SC/59/AWMP6]) have been evaluated by the SWG to determine if they could provide reliable, accurate, and precise estimates at Annual Meetings and Workshops. Last year, the SWG agreed that despite considerable effort, it was still not possible to confirm whether a sex-ratio-based method was appropriate and effective. It agreed that it would no longer prioritize development of this technique unless a comprehensive final analysis could be endorsed at the 2011 Annual Meeting.

In response to the problems seen in the sex ratio method, SC/63/AWMP5 described a possible remedy involving transformation of a key parameter in the model. An illustrative example used a transformation which operates in a way that for population sizes much greater than are realistic, the impact of catches of females on abundance is damped. This leads to finite estimates of carrying capacity *K* even in circumstances where the trend over time in the proportion of whales in the catch that is male is decreasing (as is the case for West Greenland minke whales). The example was shown to produce positively biased estimates of the lower 5% confidence interval for current population size. However the degree to which this bias warrants concern is difficult to assess since the estimator is positively biased even in circumstances where the proportion of the catches that are male does not trend downwards over time.

The SWG thanked the authors of SC/63/AWMP5 for their efforts to resolve the problems. Although SWG members offered the authors a variety of technical suggestions and comments on the method, it was clear that exploratory work in SC/63/AWMP5 was not the comprehensive final analysis sought by the SWG. The most obvious limitation of the method was that estimation of abundances appeared to be strongly positively biased. This is problematic in relation to abundance estimation, but it was noted that the approach in SC/63/AWMP5 might still prove useful in a future *SLA* if, for example, the bias was corrected for, or the *SLA* was tuned to adapt suitably to the bias.

The SWG thanked Witting, Schweder, Brandão and Butterworth for their considerable effort over the last several years in developing a novel and scientifically interesting estimation approach for sex ratio data. Despite their outstanding contributions to the work of the SWG, no final solution had yet been developed to remedy the previously expressed concerns. The SWG also noted that the original motivation for the work, the need to obtain a satisfactory abundance estimate has been superseded by the aerial survey (Heide-Jørgensen *et al.,* 2010) that had resulted in an agreed abundance estimate (16,600; 95% CI:7,170-38,500) that was suitable for assessment. Discussion of how to proceed with the development of an operating model to evaluate candidate *SLA*s for this stock is provided under item 3.2.

3. CONSIDERATION OF WORK REQUIRED TO DEVELOP *SLA*S FOR ALL GREENLANDIC HUNTS BEFORE THE END OF THE INTERIM PERIOD

In Greenland, a multispecies hunt occurs and the expressed 'need' is for 670 tonnes of edible products from large whales for West Greenland; this involves catches of common minke, fin, humpback and bowhead whales. The flexibility among species is important to the hunters and satisfying 'subsistence need' to the extent possible is a critical component of management. Last year, the SWG noted that the development of a combined approach to calculate strike limits for more than one species has not been previously attempted (IWC, 2011).

The SWG **endorsed** the views of the intersessional Workshop that this matter should be deferred until single-species management approaches had been developed further. These would provide the necessary basis to extend to multi-species considerations, such as need being expressed on a species-combined rather than a species-specific basis.

For a number of reasons, primarily related to stock structure issues, the SWG noted that development of *SLA*s for Greenland aboriginal hunts (especially for common minke and fin whales) will be more complex that any implementation the SWG had previously considered. The Committee endorsed an interim safe approach to setting catch limits for the Greenland hunts in 2008 (IWC, 2009), noting that this should be considered valid for two five-year blocks i.e. the SWG target will be for agreed and validated *SLA*s, at least by species, for the 2017 Annual Meeting (assuming that the Commission sets 5-year block quotas in 2012 as scheduled). Given the complexity of the development process, this work is high priority and the SWG **emphasised** that it will be necessary to hold intersessional workshops (see item 10) to expedite progress.

3.1 and 3.2 Fin whales and common minke whales

At its 2011 intersessional workshop, the SWG noted that the first step toward *SLA* development for West Greenland fin whales and common minke whales will be to define the operating model(s) that are to be used to test the performance of candidate *SLA*s.

The SWG noted that both of these species have been the focus of RMP *Implementations* and *Implementation Reviews*, even though the focus has not been on Greenland. It is clearly essential that the operating models used to develop *SLA*s for the Greenland hunts are based on those used in the RMP *Implementations.* These should be based on the existing *Implementation Simulation Trial* framework for the North Atlantic common minke (IWC, 1994, 2005, 2009) and fin whales (IWC, 2010). Given the SWG's focus on Greenland, it is clear that the review of the RMP operating models and specifications will probably identify refinements and modifications to the existing trials structure to properly account for the West Greenland case, particularly with respect to stock structure; it is important that ultimately these discussions are held in collaboration with the sub-committee on the RMP to ensure consistency with operating models to the extent possible. In addition, the *SLA* development process will have to take into account catches made under the RMP.

As part of the conceptual discussions held within the SWG, Witting and Heide-Jørgensen produced some initial ideas on the better integration of the West Greenland situation with the existing RMP operating models. They agreed to develop these ideas further and present a paper to the proposed intersessional meeting.

3.3 Humpback whales

The Scientific Committee has previously agreed to provide management advice on the West Greenland feeding aggregation of humpback whales by treating this as an independent stock (IWC, 2008, p.21). The SWG welcomed new work presented this year on the development of a stock assessment model for these whales (SC/63/AWMP2).

SC/63/AWMP2 used recent abundance estimates, historical catches starting from 1664, and an age- and sex-structured population model to perform Bayesian assessments of West Greenland humpback whales. The historical catches included the West Greenland catches as a lower bound on the catch history, and the West Greenland plus 10% of the West Indies catches as an upper bound. Prior distributions for life history parameters had been constructed from studies on humpback whales in the North Atlantic to account for the uncertainty associated with the parameters. The abundance data included a fully-corrected West Greenland humpback abundance estimate of 3,270 (CV: 0.50) individuals in 2007 (Heide-Jørgensen *et al*., 2008), a time-series of relative abundance estimates from aerial surveys (Heide-Jørgensen *et al*., 2008), and a time-series of relative abundance estimates from mark-recapture analysis (Larsen and Hammond, 2004).

SC/63/AWMP2 examined whether the long-term dynamics (from 1664) is best described by density-regulated growth, with perturbed populations returning monotonically towards an equilibrium state, or by inertia dynamics, where populations typically return through damped cycles. There was substantial statistical support for inertia dynamics and rejection of density-regulated growth. It was estimated that the abundance declined from a population dynamic equilibrium of 2,900 (90% CI:1,800-5,900) individuals in 1664 to a minimum of 1,300 (90% CI:230-5,100) individuals in 1927. The depletion ratio for 2011 was estimated to be 1.4 (90% CI:0.68-3.1), and the model projected that the population will increase to 5,200 (90% CI:2,400-9,000) individuals in 2020 (assuming yearly post 2010 catches of 10).

The SWG noted that a key element of SC/63/AWMP2 was the comparison of three alternative dynamics models: exponential growth (E), density regulated (D), and inertia dynamics (I). Model E fitted the available abundance data well, but was not appropriate to use without modification over time spans longer than a few decades because it included no regulation of abundance or density feedback mechanism. Model D explicitly included density regulation, but did not fit the data well over the long time period that started in 1664. However, it could be made to fit the abundance and catch data over a shorter period of time. In other applications (e.g., for eastern Pacific gray whales), model misfit over similarly long time periods has been addressed by starting the model recently and estimating its status relative to carrying capacity at that time. Such an approach may be applicable to the West Greenland humpback case, too. Additional calculations during the meeting applied a density-regulated model over a short time-period starting in 1980, and this fitted the data as well as the exponential model. In this case, however, the data were not informative about an upper bound for the carrying capacity.

Model I led to a good fit to the abundance data when the model was started in 1664, but may be questionable for use as operating model because the inertia dynamics over long time periods will be quite sensitive to parameterization. This sensitivity could also render the parameterization of future projections (i.e., as an operating model to test *SLA*s) difficult.

SWG members offered several comments on these assessment methods. It was suggested that the prior distributions for the bias parameters should be changed to be uniform on a log scale because this would mean that the relative abundance indices would not provide information on absolute abundance. It was noted that only one of the abundance estimates used in the analysis was an estimate of absolute abundance, so the fitted abundance curve should pass right through that point. This result was not seen, but calculations during the meeting using log uniform priors on the abundance parameters and the bias in the relative surveys did achieve this result.

It was noted that models E, D, and I used 7, 8, and 9 parameters, respectively, to fit 9 data points. One member expressed concern about the very low number of degrees of freedom in these models because (i) posterior distributions for some of the parameters (survival and birth rates, and age of sexual maturity) could be misleading (see below), and (ii) in an over-parameterized model, nearly any predicted outcome can be achieved from a variety of parameter combinations. The SWG noted that when dynamics models are sex- and age-structured, it is common to find that the data provide information about only a few parameters (e.g., carrying capacity and MSYR or the inertia parameter) while the posterior distributions for the remaining parameters differ little from the priors because the abundance data do not provide much signal for these parameters. This was found in SC/63/AWMP2. In the present application, the data were also informative about the parameters specifying bias in the relative abundance estimates. For parameters about which the abundance data contain little information, incorporating prior distributions (as done in SC/63/AWMP2) can be interpreted as a strategy to incorporate additional uncertainty into the results. The priors on the life history parameters of SC/63/AWMP2 were based on studies of humpback whales in other areas of the North Atlantic than West Greenland.

Over-fitting can sometimes be identified using the correlation and strength of nonlinear relationships among posterior parameter estimates. A supplement to SC/63/AWMP2 listed the parameter correlation matrix for each model. Correlations ranged from zero to strong (~0.90), yet it is important to realize that correlations among parameter estimates can also reflect the underlying constraints established by the structure of the dynamics model. The SWG **agreed** to carefully monitor for signs of problems associated with over-fitting when it conditions operating models for *SLA* development and testing.

In conclusion, the SWG recognised that the development process of an *SLA* for Greenland humpback whales would focus on consideration of the West Greenland feeding aggregation as a management unit. This may allow less attention on the overall North Atlantic humpback whale stock structure and may also avoid attempting to incorporate the long time series of catch data and the attendant catch allocation problems noted during the comprehensive assessment (e.g. IWC, 2002; 2003).

3.4 Bowhead whales

Discussion within the Committee in recent years has focussed on stock structure and associated abundance estimates. The present working hypothesis is that bowhead whales in eastern Canada - West Greenland comprise a single stock; the alternative hypothesis is one of two stocks: one in Hudson Bay - Foxe Basin and another in Baffin Bay - Davis Strait.

SC/63/AWMP3 used recent abundance estimates, historical catches starting from 1719, and an age- and sex-structured population model to conduct Bayesian assessments of bowhead whales in eastern Canada - West Greenland. It also included a model for a Baffin Bay - Davis Strait stock, given the alternative two stock hypothesis. The historical catches were based on Higdon (2010), with a lower bound on the catch histories being given by the high and medium quality catch data, and an upper bound being given by all available data. An agreed abundance estimate of 6,340 (CV: 0.38) for 2002 (IWC, 2009a) was available to represent either the abundance of the entire eastern Canada - West Greenland population, or the Baffin Bay - Davis Strait stock. A time series of five estimated sighting rates covering the range from 1981 to 1998 for the Disko Bay area (Heide-Jørgensen *et al.*, 2007) was also used when fitting the model.

SC/63/AWMP3 examined whether the long-term dynamics (from 1719) are best described by density-regulated growth or by inertia dynamics. For eastern Canada - West Greenland bowhead whales there was substantial statistical support for inertia dynamics and for rejection of density-regulated growth. It was estimated that abundance declined from a population dynamic equilibrium of 30,000 (90% CI:24,000-35,000) individuals in 1719 to a maximal depletion of 1,700 (90% CI:510-4,900) individuals in 1888. The depletion ratio in 2011 was estimated to 0.29 (90% CI:0.15-0.58), and the population was projected to increase to 10,000 (90% CI:5,200-20,000) individuals in 2020 (assuming yearly post-2010 catches of 5). For the Baffin Bay - Davis Strait stock under the two stock hypothesis, it was estimated that abundance declined from a population dynamic equilibrium with 34,000 (90% CI:23,000-40,000) individuals in 1719 to a maximal depletion of 3,400 (90% CI:590-8,500) individuals in 1888. The depletion ratio in 2011 was estimated to 0.25 (90% CI:0.13-0.52), and the population was projected to increase to 9,100 (90% CI:4,500-18,000) individuals in 2020 (assuming yearly post 2010 catches of 3).

In discussion, it was noted that this approach was very similar to the method used for humpback whales discussed under Item 3.3. However, in the bowhead case, limitations of the available data presented greater problems and raised concern for SWG members.

Most importantly, the SWG noted that 5 of the 6 abundance estimates used as data were rough indices of relative abundance (as opposed to absolute abundance) pertaining to a small area and hence may be questionable as indices of total abundance. These estimates were based on a total of only 11 sightings from aerial surveys of the spring aggregation of bowhead whales in the Disko Bay area. Data on body length suggest that it is primarily large and mature bowhead whales without calves that occur in the Disko Bay area (Heide-Jørgensen *et al*., 2010), and it may be expected that the time series of sighting rates relate to a local age/sex aggregation. It was further noted that problems with over-parameterisation were more likely here than for West Greenland humpbacks. For these reasons, the SWG was sceptical that the available index data could be used to fit a dynamics model reliably.

It was noted that the posterior distribution for adult mortality appeared to be bounded above by approximately 1%, whereas analysis of the Bering-Chukchi-Beaufort Seas bowhead populations had supported values half as large and even smaller. The analysis did not include an explicit prior on adult mortality. Instead, values for adult mortality were calculated from sampled values from the priors on the other life history parameters and the prior on the population growth rate. Thus, it was not clear whether this result was an artifact of the prior distributions for the other parameters or driven by the data (through the likelihood function). If desired, the assessment could place a prior on the adult mortality rate rather than the growth rate, with the growth rate being calculated from the values of the other parameters. The SWG did not consider whether it was most desirable to control the growth rate or adult mortality using an explicit prior.

The analysis in SC/63/AWMP3 assumed a prior for the growth rate parameter that supported only positive values. However, Witting reported that negative values would have received some posterior probability had they been given some prior probability. During the meeting, a version of the analysis that fitted the mature component of the population to the sighting data from Disko Bay using a uniform prior from -0.07 to 0.07 on the growth rate of the exponential model was presented. The posterior estimate (3.8%, 90% CI: -2.7% - 6.1%) was less accurate, but with a point estimate rather similar to the estimate from the Bering-Chukchi-Beaufort Seas population of bowhead whales (3.4%, 95% CI: 1.7%-5%, Zeh and Punt, 2005).

The SWG recalled that a primary purpose for this bowhead assessment is the development of an *SLA*. In this context, a high degree of precision appears unnecessary. The agreed abundance estimate for 2002 is 6,340 (CV: 0.38; IWC, 2009a), yet the need envelope is probably likely to be around five strikes per year, to which probably less than five additional removals would be added to reflect takes by native communities in Canada, at least on present information (Annex F). Compared to the abundance estimate, this level of removals would seem to have only limited impact. The SWG noted that it might be therefore possible to establish a simple *SLA* because these circumstances suggested that the need to develop a more sophisticated approach appeared to be a low priority. Furthermore, a simple method would still be subject to an *Implementation Review* if the approach appeared inadequate or if the need envelope or level of Canadian takes increased. Development of a simple method would require the determination of a need envelope, and the Chair of the SWG was asked to discuss need envelopes with the hunters.

4. IMPLEMENTATION REVIEW OF GRAY WHALES WITH EMPHASIS ON THE PCFG

At the 2010 Annual meeting (IWC, 2011), it had been agreed that the information on stock structure and hunting presented, although some of it had not met the Data Availability Guideline requirements (IWC, 2004) for the 2010 review, warranted the development of trials as part of a new *Implementation Review* in 2011 to evaluate the performance of *SLA*s for hunting in the Pacific Northwest, with a primary focus on the PCFG (Pacific Coast Feeding Group). It also agreed that the 2010 *Implementation Review* had shown that the population as a whole was in a healthy state, but that over the next few years, further work should be undertaken to investigate the possibility of structure on the northern feeding grounds, especially in the region of the Chukotkan hunts.

4.1 Summary of intersessional Workshop

Donovan summarised the report of the intersessional workshop held in La Jolla, California from 28 March – 1 April 2011. With respect to gray whales, the focus of the workshop was preparing to complete an *Implementation Review* of eastern gray whales at the 2011 Annual Meeting, with the focus on the proposed Makah hunt and the PCFG. Most of the effort centred on reviewing the available information in the context of developing an operating model and trial structure such that conditioning and trial runs could be completed before and at the Annual Meeting.

The SWG received new and updated information on stock structure and movements (including information, some preliminary, on movements of gray whales between the western and eastern North Pacific), abundance and trends (including estimates for the PCFG and for the 'total'), catch data (including bycatches) and feeding ecology.

The Workshop agreed that the trials would consider three geographic regions. The north area is north of 52^0N (roughly northern Vancouver Island), the PCFG area is between 41°N and 52°N, and the 'south' area is south of 41°N. The trials will consider two stocks ('PCFG' and 'north'). Some PCFG whales will be found outside of the PCFG area at various times during the year. However, this is not problematic since the historical catches north of 52°N occurred well north of 52°N and future catches will either occur in the Bering Sea or in the Makah U&A[1].

The discussions of trial structure were greatly aided by the presentation of SC/M11/AWMP1 in which an age- and sex-structured operating model was presented that could form the basis of operating models for the *Implementation Review.* The *SLA* to be considered was provided by the Makah Tribal Council (details are presented in SC/63/Rep2, Annex D). Its implementation in the operating model is included in Appendix 3 to this report as part of the overall trial specifications, as are details of catches, bycatches, abundance, biological parameters including MSYR and performance statistics, including updates from the present meeting.

Unlike previous *Implementations*, the PCFG was for a 'small' population (previously referred to as a 'Type 3 Fishery'). Based on the work of Punt and Breiwick (2002), it was agreed that demographic uncertainty would be largely inconsequential even for a population of 200. However, it also agreed (1) that the lowest number of mature females during the 100-year projection period should be included in the standard set of summary statistics so that an evaluation of the potential for depensation could be made; and (2) the set of trials will include cases in which there is environmental variability in the form of mortality events.

The Workshop agreed to the following specifications for the base-case trials:

(1) Two stocks (PCFG, non-PCFG)

(2) Four spatio-temporal strata (south, north, PCFG [Dec-May], CPFG [June-Nov])

(3) Split of catch to stock

  (a) South: 1% PCFG; 99% non-PCFG

  (b) PCFG [Dec-May]: 20.3% PCFG; 79.7% non-PCFG

  (c) PCFG [Jun-Nov]; 100% PCFG

  (d) North: 0% PCFG

(4) The split of the catch to stock is deterministic in the past, but stochastic in the future.

(5) The probability of a PCFG whale being classified as non-PCFG is 0.

(6) The probability of a north whale being classified as PCFG is 0.01.

(7) 50% of struck animals are lost.

(8) Selectivity is to be 1+.

(9) All catches occur prior to May[2].

(10) $MSYL_{1+} = 0.6$; $MSYR_{1+}$=4.5%.

From this, the Workshop developed an initial set of *Evaluation* and *Robustness Trials* (SC/63/Rep2, Tables 4 and 5) and reviewed and modified the performance statistics from the 2004 *Implementation.* The revised set of statistics can be found in Appendix 3 to this report.

A number of intersessional tasks were set and progress with these is discussed under Item 4.3.

4.2 Review of information on the PCFG

SC/63/AWMP1 presented a review of published and gray literature on PCFG gray whales. The objective of the paper was to familiarize the AWMP SWG with the biology of the PCFG whales and to draw attention to important components of the PCFG as it relates to management. The first issue for management consideration is the range of the PCFG. The IWC currently defines PCFG whales as gray whales observed in multiple years between 1 June and 30 November between 41N and 52N (IWC, 2011). This definition is based on research that does not uniformly survey the potential range of PCFG gray whales; the northern and southern extents of the range are poorly sampled. Gosho *et al.* (2011) found that 17.5% of gray whales photographed during surveys at Kodiak Island, Alaska matched to whales in

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[1] 'usual and accustomed fishing grounds' – NB although these include the Strait of Juan de Fuca the hunt will be prohibited there due to the large portion of PCFG whales photographed in that area. The hunt will be limited to 1 December - 30 May to minimise the likelihood of PCFG whales.

[2] This is assumption is conservative because it will lead to the highest assessed risk to the PCFG stock. In principle, it would be desirable to model to relative probability of strikes by month but no data are available to make any estimates. Sensitivity is explored to the assumption that all of the catches occur in April.

the Cascadia Research Collective catalogue of whales in the PCFG area. If Kodiak Island were included in the PCFG range then the population estimate for the PCFG would be biased low by 100-200 whales. The second issue for management consideration is immigration. Recently Frasier *et al.* (2011) and Lang *et al.* (2011) have found small but significant differences in mitochondrial DNA haplotype frequencies between PCFG whales and samples thought to be representative of the overall Eastern North Pacific (ENP) population and high genetic diversity in both PCFG and ENP whales. Lang *et al.* (2011) suggested that the high observed genetic diversity and low level mtDNA differentiation is consistent with the PCFG either being a recently founded group or a group exhibiting filopatry recruitment with low level recruitment. Photo-identification surveys show recruitment into the PCFG at rates thought to be greater than the potential calf production of the PCFG (Calambokidis *et al.* 2010; IWC 2011). The newest time series of abundance estimates for PCFG whales indicates that there was an average recruitment of 25.8 whales into the PCFG between 1999 and 2002, coinciding with the observed mortality event of ENP whales (IWC, 2011). Ethnographic records presented by Scordino suggest gray whales have been hunted off the coast of Washington in the 1 June through 30 November timeframe since at least the 1850s. Stable isotope findings are less conclusive, but may show that the PCFG has existed for the past 1500 years in which Makah whaling has been documented. Together, these results strongly suggest that some level of immigration is occurring to the PCFG. As a result, when setting up implementation trials, some degree of immigration from the ENP must be considered and there should be recognition of potential negative bias to population estimates of the PCFG.

Scordino also provided an overview of the Makah Tribe’s proposed hunt (Annex D of SC/63/Rep2). The SWG noted that unlike the *SLA*s for the BCB bowhead and the ENP gray whales, the *SLA*s to be evaluated for the hunt in the Makah U&A were not developed by the SWG, but are rather based on the proposed hunt and variants thereof developed by the Makah Tribe.

4.3 Progress with intersessional tasks

4.3.1 Finalise the specifications for the trials

4.3.1.1 PROVIDE UPDATED ABUNDANCE ESTIMATES AND THE ASSOCIATED VARIANCE-COVARIANCE MATRIX

Jeff Laake provided the updated abundance estimates for inclusion in the trials (see Annex H of SC/63/Rep2). The SWG thanked Laake for providing this information before the agreed deadline.

4.3.1.2 SPECIFY HOW TEMPORAL AUTOCORRELATION IN THE ABUNDANCE ESTIMATES WILL BE MODELLED

The inter-annual correlation between the PCFG abundance estimates is generally small (maximum 0.215 between the abundance estimates for 2007 and 2008). The SWG **agreed** that this level of correlation is sufficiently low that it is not necessary to take it into account in trials.

4.3.2 Refine the estimates of PCFG / north mixing based on the 2009 photo-ID data

Weller notified the SWG that the 2009 and 2010 photo-ID data were not available for use during the current meeting.

4.3.3 Coding and validation

4.3.3.1 TRIALS

The trials specified during the March 2011 AWMP Workshop focused on the performance of *SLA*s for the proposed hunt in the Makah Tribe’s U&A, because, except for the proposed Makah hunt and the associated possibility of a stock in the PCFG area, the *Implementation Review* for the ENP gray whales had been completed during the 2010 Annual Meeting. The trials developed during the Workshop considered a number of major hypotheses, including those related to: (a) MSYR, (b) levels of immigration, (c) the level of mixing between PCFG and northern whales when the Makah hunt is likely to take place, and (d) aspects of the hunt including struck and lost rates.

SC/63/AWMP4 showed how the trials specified during the March 2011 AWMP Workshop led to poor residual patterns for the fits to the revised abundance estimates for the PCFG. It provided a set of revised trials which include a pulse of immigration from the northern into the PCFG stock, in 1999 and 2000. In general, the operating models on which the revised trials are based are able to mimic the abundance data adequately. However, a subset of the trials (e.g. with high annual rates of immigration) are unable to mimic the abundance data well.

The SWG thanked Punt for conducting this intersessional work. The SWG noted that the abundance estimates exhibit a high rate of increase during the early years which is biologically implausible. Pulse immigration was one way to allow the operating model to mimic the abundance data. However, pulse immigration is not the only way to achieve consistency between the operating model and the data. Specifically, an alternative explanation is that the trend in abundance from 1998 to 2002 is not due to immigration, but is instead due to a change in survey bias. It was recognized that neither model adjustment was developed independently of the abundance data. Thus, it was not surprising that models including a change in survey bias or pulse immigration fit the abundance data better than models which have neither effect, and which exhibit a residual pattern as noted in SC/63/AWMP4. Regardless, the SWG recognized the need to explore a plausible range of hypotheses with respect to the biologically implausible rates of increase in the abundance estimates. The predicted abundance trajectories (historical and future) for the three types of model differ, reinforcing the need to include alternative scenarios for changes in underlying abundance. Witting noted that models based on inertial dynamics were unlikely to be able to mimic the change in abundance estimates better than the other models considered by the SWG due to the short time period of the phenomenon discussed above.

The SWG emphasized that the set of operating models used to test *SLA*s need to cover the plausible range. The SWG discussed the relative plausibility of a change in survey bias. It was noted that there is no direct evidence for such a change, such as marked changes in survey effort and its spatial distribution (although changes in survey effort have occurred) [Appendix 2]. Moreover, the trend in abundance for the more intensively surveyed area from Oregon to Northern British Columbia shows the same trend as the entire PCFG area. However, there may be reasons other than a simply change in effort for a change in survey bias. For example, consider the case when individual PCFG whales have very heterogeneous detection probabilities. This would cause a downward bias in estimated abundance. Over several years, the accumulated data might begin to dominate and average away any such bias, leading to the pattern used in the SWG's survey bias model (Fig. 1). Another possible contributor to the (artificial) appearance of survey bias is the approach used for the capture-recapture abundance estimation that an animal is defined as being part of the PCFG only if it is seen in at least two years in the PCFG area.

The SWG considered how to best move forward given the concerns with the trials structure established during the March 2011 workshop and with that in SC/63/AWMP4. Furthermore, although software which could be used to condition and run trials during the meeting was available, the programs have yet to be validated by the Secretariat.

In order to establish a workplan, the SWG identified four 'broad' base-case models which captured hypotheses for the trend in the abundance data for PCFG area:

(1) The 1998 abundance estimate is biased due to 'discovery' and 20 whales immigrated into the PCFG stock from the northern stock in each of 1999 and 2000 (hypothesis E).

(2) There has been no pulse immigration into the PCFG stock; rather the abundance estimates are subject to time-varying bias (Fig. 1a) (hypothesis A)

(3) There has been no pulse immigration into the PCFG stock and the abundance estimates are unbiased (hypothesis X).

(4) 10 whales immigrated into the PCFG stock from the northern stock in each of 1999 and 2000 and the abundance estimates are subject to time-varying bias (but not the extent as for hypothesis A; Fig. 1b) (hypothesis Y).

The SWG then identified a subset of the evaluation trials in SC/63/AWMP4 which cover a range of the factors which might impact eventual performance and could help the SWG select which trials to focus on (Table 1). The factors considered were: (a) $MSYR_{1+}$; (b) need in the Russian hunt; (c) the probability of harvesting a PCFG whale during an April hunt in the PCFG area; (d) the struck and lost rate in the PCFG hunt; (e) low-level (non-pulse) immigration into the PCFG stock from the northern stock; (f) episodic events; and (g) the sex-ratio of future catches in the PCFG area.

The SWG also selected a number of diagnostic plots and tables to help it understand the behaviour of the models and trials, in order to narrow down the SLA testing framework. Among the items considered were:

(1) Time-trajectories of 1+ population size (northern and PCFG stock) in absolute terms and relative to carrying capacity, along with the fits to the abundance estimates. This plot allows an evaluation of whether conditioning has been achieved satisfactorily.

(2) Histograms of the 100 parameter vectors for each trial. This plot allows an evaluation of whether and how conditioning has impacted the priors for these parameters.

(3) Individual time-trajectories of 1+ population size for the northern and PCFG stocks, individual time-trajectories of strikes for the northern and PCFG area, a summary (median and 95% intervals) for the depletion of the PCFG stock, and a summary (median and 95% intervals) for the time-trajectories of 1+ population size when (a) there are no future catches, (b) there are only incidental catches, and (c) there are incidental catches and catches due to hunts in the PCFG and northern area.

(4) Tables showing the statistics selected during the March 2011 Workshop.

The SWG noted that the time-trajectories of strikes for the PCFG area are uninformative, but that the 'ray plot' developed during the March 2011 Workshop was not more informative. The SWG requested that in thefuture, the number of strikes of PCFG-stock animals be added to the tabular summary. It was also not possible to condition all of the 'X' and 'Y' trials during the meeting and owing to very strong posterior correlations. Specifically, it was not possible during the meeting to obtain 100 unique parameter vectors for the trials in which $MSYR_{1+}$ is 4.5% for the northern stock and 1% for the PCFG stock without adjusting the priors.

The SWG noted that carrying capacity varied among the hypotheses (a wide range for the 'E', 'X' and 'Y' trials and a relatively narrow range for the 'A' trials). The SWG also noted that the results for both the northern and PCFG stocks differed between the various hypotheses even when the remaining specifications were the same (e.g. the final depletion for the northern stock for trials GA03 and GE03). The SWG emphasized the need to fully understand the results before drawing any final conclusions about the relative merits of the four operating models or any changes to the list of evaluation and robustness trials, with the exception that the SWG agreed to move the trial with $MSYR_{1+}$=2% and all future Makah hunting takes PCFG animals to the evaluation set (this is reflected in table 1).

The SWG established a Steering group (Donovan (Convenor), Allison, Brandon, Butterworth, Givens, Punt, Scordino) to further review the trials structure before the proposed intersessional workshop. The SWG **strongly recommended** that the abundance estimates for the PCFG be updated to include data for 2009 and 2010. A paper presenting all of the abundance estimates should be provided to the SWG.

4.3.3.2 PARAMETER VECTOR GENERATION

This issue will be considered during the next *Implementation Review*.

4.4 Review of results, conditioning and work plan

The SWG was unable to fully review the conditioning because the full set of trials have yet to be completed. Similarly, the SWG did not review the results of the trials.

The SWG **agreed** that its work plan for the 2011 Annual Meeting and associated interessional period would be as follows:

(1) Update the output from the control program to include the number of struck PCFG whales [Punt, June 30, 2011] (item 4.3.3)

(2) Validate the control program and the code for implementing the PCFG hunt (item 4.3.3).

(3) Refine the set of trials (Steering Group, item 4.3.3).

(4) Condition all of the trials and conduct all of the projections before the Workshop (item 4.3.3).

(5) Conduct a Workshop, probably in March 2012 with a focus on the completion of the *Implementation Review* (item 4), and an initial consideration of operating models for West Greenland fin whales (although progress on all species will be considered).

5. IMPLICATIONS OF NEW INFORMATION ON GRAY WHALE STOCK STRUCTURE

5.1 Summary of relevant BRG discussions

Kitakado summarised the discussions in the BRG sub-committee related to the implications of western gray whales being seen off the U.S. west coast: (1) there is now more uncertainty regarding Pacific gray whale stock structure; (2) there is no need to revise stock structure assumptions for Pacific gray whales at present; and (3) range-wide studies need to be undertaken to better understand the situation.

5.2 Conclusions with respect to *Implementation Review*

Given the information under Item 5.1, the SWG **agreed** that formally there was no need to modify the existing trials structure which had been designed to evaluate the *SLA*s for the northern and PCFG areas in the context of eastern gray whales. However, this structure does not incorporate conservation implications for western gray whales. Therefore, the SWG **stresses** that the new information on movements of gray whales described under Item 5.1 highlights the importance of further clarification of the stock structure of North Pacific gray whales. In particular, the matches of western gray whales with animals seen in the PCFG area and other areas along the west coast **emphasises** the need for efforts to estimate the probability of a western gray whale being taken in aboriginal hunts for Pacific gray whales. It **strongly endorses** the research programme developed by the BRG sub-committee that focuses on photo-identification, genetics and telemetry (see Annex F), incorporating both further analysis of existing data and collection of new data. The results of the research may require further trials for future *SLA* testing; this will certainly be a matter for the next *Implementation Review* if not before. The SWG will continue to monitor discussions within BRG and is willing to respond to any guidance or requests for further information from the Commission.

Final dates for the 2012 meeting are not yet, known but likely deadlines for the DAA process are:

Final datasets available (6 months): 30 November 2011.

Papers using novel methods (3 months): 28 February 2012.

Papers using standard methods (2 months): 31 March 2012.

Papers responding to those above (1 month): 30 April 2012.

6. ANNUAL REVIEW OF MANAGEMENT ADVICE

The SWG recognises the logistical difficulties in collecting samples in remote areas but in order to assist in its work, it **recommends** that biological information and material be collected from as many whales as possible.

6.1 Common minke whales off West Greenland

6.1.1 New information

In the 2010 season, 179 minke whales were landed in West Greenland and 7 were struck and lost (SC/63/ProgRepDenmark). Of the landed whales, there were 122 females, 53 males, and four whales of unreported sex. Witting noted that there are plans to tag minke whales in the coming years to establish correction factors to be applied to future surveys.

6.1.2 Management advice

In 2007, the Commission agreed that the number of common minke whales struck from this stock shall not exceed 200 in each of the years 2008-12, except that up to 15 strikes can be carried forward. In 2009, the Committee was for the first time ever able provide management advice for this stock based on a negatively biased estimate of abundance of 17,307 (95% CI 7,628 – 39,270) and the method for providing interim management advice which was confirmed by the Commission. Such advice can be used for up to two five-year blocks whilst *SLA*s are being developed (IWC, 2009b, p.16). Based on the application of the agreed approach, and the lower 5th percentile for the 2007 estimate of abundance (i.e. 8,918), the Committee repeats its advice of last year that an annual strike limit of 178 will not harm the stock.

6.2 Common minke whales off East Greenland

6.2.1 New information

Nine common minke whale were struck (and landed) off East Greenland in 2010 (no animals were struck and lost) (SC/63/ProgRepDenmark). Of the landed whales, there were two females, four males, and three whales of unreported sex. The SWG noted that catches of minke whales off East Greenland are believed to come from the large Central stock of minke whales.

6.2.2 Management advice

In 2007, the Commission agreed to an annual quota of 12 minke whales from the stock off East Greenland for 2008-2012, which the Committee stated was acceptable in 2007. The present strike limit represents a very small proportion of the Central Stock (see Table 1). The SWG agreed that the present strike limit would not harm the stock.

6.3 Fin whales off West Greenland

6.3.1 New information

A total of four fin whales (all females) were landed, and one struck and lost, in West Greenland during 2010 (SC/63/ProgRepDenmark). An acoustic study on fin whales in Davis Strait between Greenland and Canada found that call frequencies peaked in November–December, and continued until the area was covered by ice in January (Simon *et al*., 2010).

6.3.2 Management advice

In 2007, the Commission agreed to a quota (for the years 2008-2012) of 19 fin whales struck off West Greenland. The Committee agreed an approach for providing interim management advice in 2008 and this was confirmed by the Commission. It had agreed that such advice could be used for up to two five-year blocks whilst *SLA*s were being developed (IWC, 2009b). Based on the application of the agreed approach in 2008 (IWC 2009b), the SWG agreed that an annual strike limit of 9 whales will not harm the stock.

6.4 Humpback whales off West Greenland

6.4.1 New information

A total of nine (three males; five females; one unreported sex) humpback whales were landed (none were struck and lost) in West Greenland during 2010 (SC/63/ProgRepDenmark). Genetic samples were obtained from five of these five whales.

6.4.2 Management advice

In 2007, the Committee agreed an approach for providing interim management advice and this was confirmed by the Commission. It had agreed that such advice could be used for up to two five year blocks whilst *SLA*s were being developed (IWC, 2009b, p.16). Using this approach, as last year, the SWG agreed that an annual strike limit of 10 whales will not harm the stock.

6.5 Humpback whales off St Vincent and The Grenadines

6.5.1 New information

The SWG received no information on 2010-2011 catches by St Vincent and The Grenadines. The SWG **strongly recommended** that catch data, including the length of harvested animals, be provided to the Scientific Committee. It also **strongly recommended** that genetic samples by obtained for any harvested animals as well as fluke photographs, and that this information be submitted to appropriate catalogues and collections.

6.5.2 Management advice

In recent years, the Committee has agreed that the animals found off St. Vincent and The Grenadines are part of the large West Indies breeding population. The Commission adopted a total block catch limit of 20 for the period 2008-12. The SWG **agreed** that this block catch limit will not harm the stock.

7. ABORGINAL WHALING MANAGEMENT SCHEME

7.1 Draft guidelines for *Implementations* and *Implementation Reviews*

The SWG did not have time to discuss this Item at the meeting. Given this, the SWG **agreed** that the item would be referred to the intersessional workshop and the Chair agreed to circulate a draft proposal at least one month before the workshop.

7.2 Scientific aspects of an aboriginal whaling scheme
The SWG refers to the previous discussions of this matter and notes that the Commission is still considering the Committee's recommended text on this matter (IWC, 2002)

8. PLANNING FOR A BOWHEAD WHALE *IMPLEMENTATION REVIEW*

8.1 Summary of relevant BRG discussions
Kitakado reported that the BRG sub-committee had received some updates on genetic analyses and age determination of bowhead whales. It also welcomed information on dedicated ice-based abundance surveys (with visual and acoustic components) with independent observers in 2010 and 2011, and a concurrent 2011 aerial photo-identification survey. It noted that SC/63/BRG1 had presented a sophisticated method to estimate detection probabilities using the 2010 ice-based data. Work is continuing to develop a new abundance estimate but this is not expected to be completed before 2013.

8.2 Work plan
The purpose of an *Implementation Review* is to examine new information to see if the current situation is outside the parameter space tested in the existing trials. The SWG noted that no information had been presented at the present meeting to suggest that this was the case. It **agreed** that an *Implementation Review* should be scheduled for the 2012 Annual Meeting. In accordance with the Committee's DAA, the following deadlines apply:

Final dates for the 2012 meeting are not yet known but likely deadlines for the DAA process are:

Final datasets available (6 months): 30 November 2011.

Papers using novel methods (3 months): 28 February 2012.

Papers using standard methods (2 months): 31 March 2012.

Papers responding to those above (1 month): 30 April 2012.

The SWG recognised that it was unlikely that a new abundance estimate would be available for the *Review*. It noted that this is not a required component of an *Implementation Review*. Once an agreed abundance estimate is received it will be incorporated routinely into the *SLA* for the provision of management advice.

9. PROGRESS OF FOLLOW-UP WORK ON CONVERSION FACTORS FOR THE GREENLANDIC HUNT
For indigenous hunting of whales in West Greenland, need is expressed in terms of kg of edible product (across species), whereas for the development of *SLA*s the SWG approach is to express need in terms of numbers of strikes (per species). Based on the recommendations in the report of the Commission's Small Working Group on Conversion Factors for use in Greenland Hunts (Donovan *et al*., 2010), the Committee had requested Greenland to provide information on its sampling scheme and data validation protocols to the present meeting. The focus of the recommendations concerned the fin, humpback and bowhead whales for which provisional conversion factors ad been proposed; sufficient data had been available to develop a conversion factor for the common minke whale (Donovan *et al*., 2010).

The SWG received a response to this request (Appendix 4). It was informed that data had been obtained for a small number of humpback whales, fin whales and bowhead whales using a new protocol and with the assistance of wildlife officers. The Greenland Institute of Natural Resources is planning to continue its efforts this year, targeting humpback and bowhead whales, with the effort extending to fin and minke whales in later years. The Greenland Ministry of Fisheries indicated that data collection will have to run for 'quite some years before an appropriate sampling size is reached'.

The SWG welcomed the provision of a report and appreciated and encouraged this work, recognizing the logistical difficulty of collecting this kind of data. However, it noted that considerably more detail is needed for it to evaluate the proposed programme; it noted that the authors of the original report had offered to assist in the development of a programme and the SWG **urges** Greenland to take advantage of this offer and it **requests** that a detailed report be presented for consideration at the next meeting.

In particular, the report should provide:

(1) a description of the field protocols and sampling strategy, including effort and likely sample sizes;

(2) a description of analysis methods and models; and

(3) presentation from results thus far, including from preliminary analyses with the available data.

Such information will assist the SWG in addressing issues such as appropriate sample size.

10. WORK PLAN
Details of the work plan can be found under the relevant agenda items. The priority topics for next year will be:

(1) Continue work on the development of *SLA*s for the Greenlandic hunts with a focus on common minke whales and fin whales (Item 3).

(2) Complete the *Implementation Review* for eastern gray whales with a focus on the PCFG (Item 4).

(3) Complete an *Implementation Review* for BCB bowhead whales (Item 8).

(4) Develop guidelines for *Implementations* and *Implementation Reviews* (Item 7).

(5) Provide management advice for the appropriate subsistence hunts (Item 6).

(6) Review the Greenlandic programme to provide information on conversion factors (Item 9).

Essential components of achieving this work are:

(1) The holding of an intersessional Workshop, probably in March 2012 with a focus on:

(a) operating models for Greenland fin and minke *SLA* development based on RMP *Implementations* (if time is available, progress on humpback and bowhead whales will also be reviewed);

(b) gray whale *Implementation Review*; and

(c) draft of guidelines for *Implementation*.

(2) Continuation of the AWMP Developer's Fund.

11. ADOPTION OF REPORT

The report was adopted at 16:22 on 7 June 2011. The SWG thanked Donovan for his predictably excellent chairmanship. Donovan thanked the rapporteurs and particularly Punt for his unstinting dedication to undertaking the computing work and his almost superhuman ability to work without sleep.

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Table 1a

The *Evaluation Trials*. Values given in bold type show differences from the base case trial. The values under 'Immigration' only pertain to the 'E' trials. The trials indicated by a 'Y' in the 'Tested' column were considered in detail by the SWG during the meeting.

Trial	Tested	Description	$MSYR_{1+}$ North	$MSYR_{1+}$ PCFG	Final Need	Immigration%	Survey freq.	Survey Bias(North)	Future Survey CV
GE01	Y	Base case	4.5%	4.5%	340 / 7	20+0	10 / 1	1	Base
GE02	Y	$MSYR_{1+}$ = 1%	4.5%	1%	340 / 7	20+0	10 / 1	1	Base
GE03	Y	$MSYR_{1+}$ = 2%	**2%**	**2%**	340 / 7	20+0	10 / 1	**0.5→1**	Base
GE04		$MSYR_{1+}$ = 6%	**6%**	**6%**	340 / 7	20+0	10 / 1	1	Base
GE05		$MSYR_{1+}$ = 1%; Immigration = 2	4.5%	1%	340 / 7	**20+2**	10 / 1	1	Base
GE06	Y	$MSYR_{1+}$ = 2%; Immigration = 2	**2%**	**2%**	340 / 7	**20+2**	10 / 1	**0.5→1**	Base
GE07		$MSYR_{1+}$ = 1%; Immigration = 4	4.5%	1%	340 / 7	**20+4**	10 / 1	1	Base
GE08		$MSYR_{1+}$ = 2%; Immigration = 4	**2%**	**2%**	340 / 7	**20+4**	10 / 1	**0.5→1**	Base
GE09		$MSYR_{1+}$ = 1%; Immigration = 6	4.5%	1%	340 / 7	**20+6**	10 / 1	1	Base
GE10		$MSYR_{1+}$ = 2%; Immigration = 6	**2%**	**2%**	340 / 7	**20+6**	10 / 1	**0.5→1**	Base
GE11		$MSYR_{1+}$ = 2%; Difficult	**2%**	**2%**	340 / 7	20+0	10 / 1	**0.5→1**	**½ CV_{est}**
GE12		$MSYR_{1+}$ = 2%; Immigration = 2; Difficult	**2%**	**2%**	340 / 7	**20+2**	10 / 1	**0.5→1**	**½ CV_{est}**
GE13		High need	4.5%	4.5%	**530 / 7**	20+0	10 / 1	1	Base
GE14	Y	$MSYR_{1+}$ = 2%; High need	**2%**	**2%**	**530 / 7**	20+0	10 / 1	**0.5→1**	Base
GE15		$MSYR_{1+}$ = 2%; Immigration = 2; High need	**2%**	**2%**	**530 / 7**	**20+2**	10 / 1	**0.5→1**	Base
GE16	Y	GE01 + 3 episodic events$^{\&}$	4.5%	4.5%	340 / 7	20+0	10 / 1	1	Base
GE17		All PCFG whales; ϕ_{fut}=1.000	4.5%	4.5%	340 / 7	20+0	10 / 1	1	Base
GE18		ϕ_{fut}=0.600	4.5%	4.5%	340 / 7	20+0	10 / 1	1	Base
GE19	Y	Struck & Lost (0%)	4.5%	4.5%	340 / 7	20+0	10 / 1	1	Base
GE20		Struck & Lost (75%)	4.5%	4.5%	340 / 7	20+0	10 / 1	1	Base
GE21		All PCFG catches in May	4.5%	4.5%	340 / 7	20+0	10 / 1	1	Base
GE22		$MSYR_{1+}$ = 2%; Struck & Lost (0%)	**2%**	**2%**	340 / 7	20+0	10 / 1	**0.5→1***	Base
GE23		$MSYR_{1+}$ = 2%; Struck & Lost (75%)	**2%**	**2%**	340 / 7	20+0	10 / 1	**0.5→1***	Base
GE24		$MSYR_{1+}$ = 2%; All PCFG catches in May	**2%**	**2%**	340 / 7	20+0	10 / 1	**0.5→1***	Base
GE25		$MSYR_{1+}$ = 2%; Immigration = 2; Struck & Lost (0%)	**2%**	**2%**	340 / 7	**20+2**	10 / 1	**0.5→1***	Base
GE26		$MSYR_{1+}$ = 2%; Immigration = 2; Struck & Lost (75%)	**2%**	**2%**	340 / 7	**20+2**	10 / 1	**0.5→1***	Base
GE27		$MSYR_{1+}$ = 2%; Immigration = 2; All PCFG catches in May	**2%**	**2%**	340 / 7	**20+2**	10 / 1	**0.5→1***	Base
GE28		Higher 1999-2000 Immigration	4.5%	4.5%	340 / 7	**30+0**	10 / 1	1	Base
GE29		$MSYR_{1+}$ = 2%; Higher 1999-2000 Immigration	**2%**	**2%**	340 / 7	**30+0**	10 / 1	**0.5→1**	Base
GE30		Lower 1999-2000 Immigration	4.5%	4.5%	340 / 7	**10+0**	10 / 1	1	Base
GE31		$MSYR_{1+}$ = 2%; Lower 1999-2000 Immigration	**2%**	**2%**	340 / 7	**10+0**	10 / 1	**0.5→1**	Base
GE32		Stochastic events 10% every 5 years$^{\&}$	4.5%	4.5%	340 / 7	20+0	10 / 1	1	Base
GE33		$MSYR_{1+}$ = 2%; Stochastic events 10% every 5 years$^{\&}$	**2%**	**2%**	340 / 7	20+0	10 / 1	**0.5→1***	Base
GE34		$MSYR_{1+}$ = 1%; Immigration = 2; Stochastic events 10% every 5 years$^{\&}$	4.5%	**1%**	340 / 7	**20+2**	10 / 1	1	Base
GE35	Y	$MSYR_{1+}$ = 2%; Immigration = 2; Stochastic events 10% every 5 years$^{\&}$	**2%**	**2%**	340 / 7	**20+2**	10 / 1	**0.5→1***	Base
GE36		Base case + PCFG sex-ratio = 0.59	4.5%	4.5%	340 / 7	20+0	10 / 1	1	Base
GE37		$MSYR_{1+}$ = 1%; Immigration = 2; PCFG sex-ratio = 0.59	4.5%	**1%**	340 / 7	**20+2**	10 / 1	**1**	Base
GE38	Y	$MSYR_{1+}$ = 2%; Immigration = 2; PCFG sex-ratio = 0.59	**2%**	**2%**	340 / 7	**20+2**	10 / 1	**0.5→1***	Base
GE39		All PCFG whales; ϕ_{PCFG}=1.000; MSYR = 2%	2%	2%	340 / 7	20+0	10 / 1	**0.5→1**	Base

*To be adjusted based on initial analyses

& The average value for adult survival needs to be adjusted to ensure the population is table for these trials

+ The provided CV is half of the true value.

% First value is the 1999/2000 immigration and the other number is the non-1999/2000 immigration

Table 1b
The Robustness Trials.

Trial	**Description**	$MSYR_{1+}$ North	$MSYR_{1+}$ PCFG	Final Need	Survey freq.	Survey Bias(North)	Future Survey CV
GR01	5 year surveys	4.5%	4.5%	340 / 7	10 / 1	1	Base
GR02	Difficult 2%+5yr surveys	2%	2%	340 / 7	10 / 1	0.5→1	½ CV_{est}
GR03	Linear decrease in *K*	4.5%	4.5%	340 / 7	10 / 1	1	Base
GR04	Linear increase in PCFG *K* ; decrease for North K	4.5%	4.5%	340 / 7	10 / 1	1	Base
GR05	Linear decrease in PCFG *K* ; increase for North K	4.5%	4.5%	340 / 7	10 / 1	1	Base
GR07	Linear increase in *M*	4.5%	4.5%	340 / 7	10 / 1	1	Base
GR08	Linear increase in PCFG *M*	4.5%	4.5%	340 / 7	10 / 1	1	Base
GR09	Linear increase in north *M*	4.5%	4.5%	340 / 7	10 / 1	1	Base
GR10	No PCFG whales; ϕ_{PCFG}=0.000	2%	2%	340 / 7	10 / 1	0.5→1	Base
GR11	Perfect detection; $p_1 = 0$; $p_2 = 0$;	4.5%	4.5%	340 / 7	10 / 1	1	Base
GR12	Perfect detection; p_1 =0; p2=0.01-0.05	4.5%	4.5%	340 / 7	10 / 1	1	Base
GR13	Survey bias PCFG + $p_1 = 0.5$	4.5%	4.5%	340 / 7	10 / 1	1	Base
GR14	Survey bias PCFG + $p_1 = 0.5$	2%	2%	340 / 7	10 / 1	1	Base
GR15	Correlation (draw for N; same quantile in the range for PCFG)	4.5%	4.5%	340 / 7	10 / 1	1	Base
GR16	Correlation (draw for N; same quantile in the range for PCFG)	2%	2%	340 / 7	10 / 1	1	Base
GR17	3 PCFG unepisodic event of 75 years; MSYR = 2%	2%	2%	340 / 7	10 / 1	0.5→1	Base

DETAILS OF FACTORS

Factors	Other Levels (Reference levels shown bold and underlined)
$MSYR_{1+}$	2%, **4.5%**, 6%
Immigration rate (annual)	**0, 2**, 4, 6
Immigration rate (1999/2000)	10, **20**, 30
Proportion of PCFG whales in PCFG area, ϕ_{fut}	0, **0.203**, 1
Struck and lost are	0, **50%,** 100%
Northern need in final year (linear change from 150 in 2009)	**340**, 530
Historic survey bias	**None,** Increasing between 1967 to 2002 from 0.5→1 50% (PCFG only)
Survey CV	**BaseCase,** ½ CV_{est}
Future episodic events	**None**, 3 events occur between yrs 1-75 (with at least 2 in yrs 1-50) in which 20% of the animals die events occur every 5 years in 10% of the animals die
Time dependence in *K*	**Constant**, Halve linearly over 100yr
Time dependence in natural mortality, *M* *	**Constant,** Double linearly over 100yr
Timing of harvest	**April,** **May**
Parameter correlations	Yes, **No**
Probability of mismatching north whales, p_2	0, **0.01**, 0.01-0.05
Probability of mismatching PCFG whales, p_1	**0**, 0.5
Frequency of PCFG surveys	**Annual**, 5-year

Table 2
Most recent abundance estimates for minke whales in the Central North Atlantic.

Small Area(s)	Year(s)	Abundance and CV
CM	2005	26,739 (CV=0.39)
CIC	2007	10,680 (CV=0.29)
CG	2007	1,048 (CV=0.60)
CIP	2007	1,350 (CV=0.38)

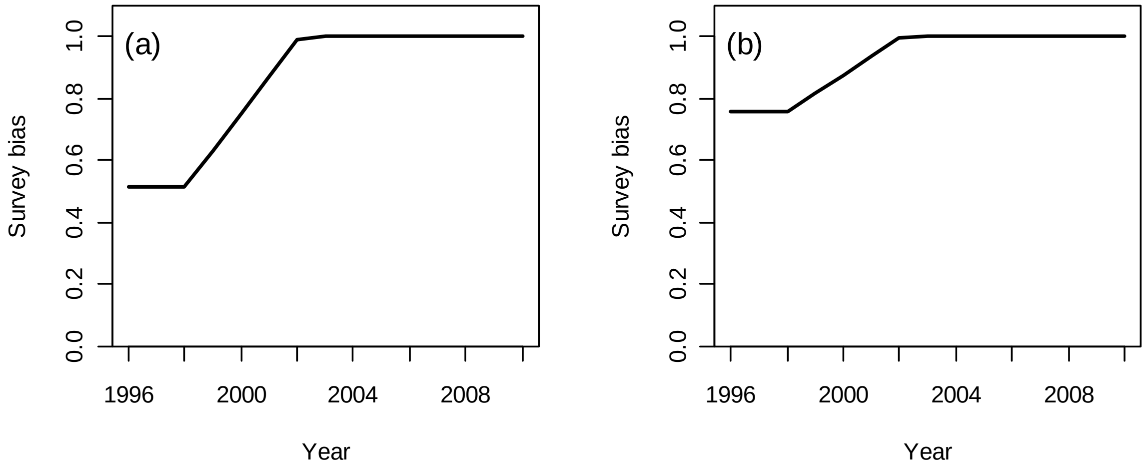

Fig. 1. Bias as a function of time for the 'A' trials (left panel) and the 'Y' trials (right panel).

Appendix 1

AGENDA

1. Introductory items
    - 1.1 Convenor's opening remarks
    - 1.2 Arrangements for the meeting
    - 1.3 Election of Chair
    - 1.4 Appointment of rapporteurs
    - 1.5 Adoption of agenda
    - 1.6 Documents available
2. Conclusion on the sex ratio method (SC/63/AWMP5)
3. Consideration of work required to develop *SLA*s for all Greenland Hunts before the end of the interim period
    - 3.1 Common minke whales
        - 3.1.1 Comments from the intersessional workshop (SC/63/Rep2)
        - 3.1.2 Discussion and work plan
    - 3.2 Fin whales
        - 3.2.1 Comments from the intersessional workshop (SC/63/Rep2)
        - 3.2.2 Discussion and work plan
    - 3.3 Humpback whales (SC/63/AWMP2)
        - 3.3.1 Comments from the intersessional workshop (SC/63/Rep2)
        - 3.3.2 Discussion and work plan
    - 3.4 Bowhead whales (SC/63/AWMP3)
        - 3.4.1 Comments from the intersessional workshop (SC/63/Rep2)
        - 3.4.2 Discussion and work plan

4. implementation review of gray whales with emphasis on the PCFG
    - 4.1 Summary of intersessional workshop (SC/63/Rep2)
    - 4.2 Review of information on the PCFG (SC/63/AWMP1)
    - 4.2 Progress with intersessional tasks (SC/63/Rep2; SC/63/AWMP4)
        - 4.2.1 Finalise the specifications for the trials
        - 4.2.2 Refine the estimates of PCFG/north mixing based on the 2009 photo-ID data
        - 4.2.3 Coding and validation
        - 4.2.4 Conditioning
    - 4.3 Review of results, conclusions and workplan (NB see Item 5)

5. Implications of new information on gray whale stock STRUCTURE (with BRG)
    - 5.1 Summary of relevant BRG discussions
    - 5.2 Conclusions with respect to *Implementation Review*

6. Annual review of management advice
    - 6.1 Common minke whales off West Greenland
        - 6.1.1 New information (incl. catch data and agreed abundance estimates)
        - 6.1.2 Management advice
    - 6.2 Common minke whales off East Greenland
        - 6.2.1 New information (incl. catch data and agreed abundance estimates)
        - 6.2.2 Management advice

6.3 Fin whales off West Greenland
        - 6.3.1 New information (incl. catch data and agreed abundance estimates)
        - 6.3.2 Management advice
    - 6.4 Humpback whales off West Greenland
        - 6.4.1 New information (incl. catch data and agreed abundance estimates)
        - 6.4.2 Management advice
    - 6.5 Humpback whales off St Vincent and The Grenadines
        - 6.5.1 New information (incl. catch data and agreed abundance estimates)
        - 6.5.2 Management advice

7. Aboriginal Whaling Management Scheme
    - 7.1 Draft guidelines for Implementations and Implementation Reviews
    - 7.2 Scientific aspects of an aboriginal whaling scheme

8. Planning for a bowhead whale *Implementation Review* (with BRG)
    - 8.1 Summary of relevant BRG discussions
    - 8.2 Work plan

9. Progress on follow-up work on conversion factors for the Greenlandic hunt

10. Work plan

11. Adoption of Report

Appendix 2

ASSESSING POTENTIAL FOR SURVEY BIAS IN THE PCFG TIME SERIES OF ABUNDANCE

Brandon, Lang, Scordino, Weller

In discussion of SC/63/AWMP4, the question was posed if the apparent pulse of external recruitment during 1999-2002 might have been due to survey bias. Survey bias could be generated by differences in effort over time or due to differences in the availability of whales over time.

Effort - Based on examination of SC/62/BRG32 and our understanding of survey effort included in that study, there seems to be no dramatic trends in effort over time, although some inter-annual variation has occurred. However, we did find a shift in effort through time in the sub-area of Northern California (NCA)[3]. This shift can be seen in Table 7 of SC/62/ BRG32 that shows whales seen annually by sub-area. The apparent pulse of early effort in NCA coincided with the Humboldt State (HSU) research group's survey effort during 1998-2002 (with a gap in HSU effort until 2008).

To better understand this issue, Jeff Laake was contacted via e-mail and asked the following question: 'What percentage of the 'Recruited' animals during 1998-2002 (and 2008) entered your updated abundance estimates via photos from NCA?' His response is as follows:

> '… there was effort in NCA and S. Oregon even though we hadn't contracted HSU because CRC[4] sampled in that area (John C[5] can verify that). Also, there is likely quite a bit of shifting in gray whale distribution between NCA and SOR[6]. Secondly, the pattern in the population estimates is the same even if you restrict the estimates to OR-SVI[7] region as shown in the plot I put together for the meeting (see Annex F, SC/63/Rep2). I also went ahead and ran the abundance estimates excluding NCA and you can see that the pattern is the same for it'
>
> 'There was certainly a reduction in effort in some years (I believe it was in 2006 where NMML had no funding to provide) and there have also been shifts in whale distribution like in 2007 where whales went off in Oregon and were largely absent from SVI that typically produces the most sightings. However, I don't think this will affect the overall pattern greatly. The 'increase' is certainly influenced by discovery of whales that have been around and not seen, but using the sample of those seen prior to 1998 and not in 1998, this tapered off quickly with most added in 1999 and very few added past 2000'

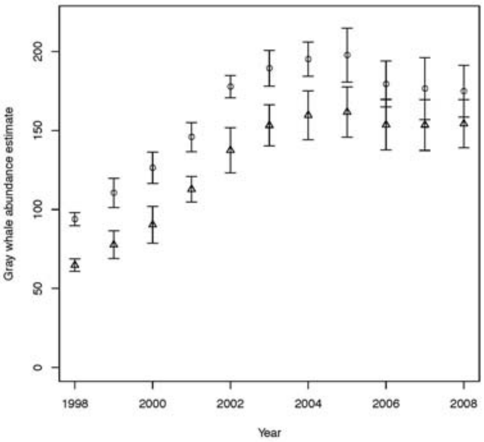

Fig. A, from Laake (*pers comm*). Plot of PCFG (41-52°)(circle) and OR-NBC[8] (triangle) abundance estimates from 1998-2008 with +/- 1 standard error bars. The OR-NBC abundance estimate excludes data from NCA.

Availability– If the availability of whales has shifted through time (for example, if many PCFG whales consistently fed offshore until 1999, then began to use inshore waters more consistently), this could lead to bias in the time series of abundance estimates. Given the data available, however, it is difficult to quantify this hypothesis, and thus to judge its plausibility.

Genetics - If survey bias is not present, the high number of new whales observed in some years of the study suggests external recruitment into the PCFG. Given the high haplotype diversity in the ENP gray whale population, it is likely that recruits would carry haplotypes not previously found in the PCFG. The addition of haplotypes found in single animals into the PCFG sample set would not have a large effect on frequency-based analyses, suggesting that some immigration into the PCFG could occur while maintaining genetic differentiation from the northern feeding group. As well, while photo-identification data may pick up a pulse of new recruits within a season, there would be some time lag

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[3] The geographic area (41-52N) for the proposed abundance estimates is slightly different than those for abundance estimates calculated in SC/62/BRG32, but does include NCA at its southern extent (See Figure 1 of SC/62/BRG32).

[4] Cascadia Research Collective

[5] John Calambokidis, Cascadia Research Collective

[6] Southern Oregon

[7] Oregon – Southern Vancouver Island

[8] Northern British Colombia, which is at the northern extent of the proposed abundance estimates (see SC/62/BRG32, Fig. 1).

before the signature of that pulse is picked up in the genetics. This suggests that a recent and discrete pulse of new animals into the PCFG may not yet have had a large impact on estimates of genetic differentiation. However, it does not seem plausible that we would observe genetic differentiation between the PCFG and northern feeding whales if ~20 animals per year were recruited into the PCFG on a consistent basis.

To better assess the plausibility of these and other scenarios, we suggest that simulations (built on the TOSSM model) could be used in the future to assess the extent of external recruitment into the PCFG that could occur while maintaining genetic differentiation between the PCFG and northern feeding strata.

Appendix 3

GRAY WHALE TRIALS SPECIFICATIONS

This document outlines a set of trials to evaluate the performance of *SLA*s for hunting in the Pacific Northwest, with a primary focus on the PCFG (Pacific Coast Feeding Group). The operating model assumes the two groups (the ‘north’ group and the PCFG) are separate stocks.

A. The population dynamics model

The underlying population dynamics model is deterministic, age- and sex-structured, and based on a two-stock version of the Baleen II model (Punt, 1999).

A.1 Basic dynamics

Equation A1.1 provides the underlying 1+ dynamics.

$$\begin{aligned}
R^{s,m/f}_{t+1,a+1} &= (R^{s,m/f}_{t,a} + I^{s,m/f}_{t,a} - C^{s,m/f}_{t,a})\,\tilde{S}^s_t\,S_a + U^{s,m/f}_{t,a}\,\tilde{S}^s_t\,S_a\,\delta_{a+1} && 0 \le a \le x-2 \\
R^{s,m/f}_{t+1,x} &= (R^{s,m/f}_{t,x} + I^{s,m/f}_{t,x} - C^{s,m/f}_{t,x})\,\tilde{S}^s_t\,S_x + (R^{s,m/f}_{t,x-1} + I^{s,m/f}_{t,x-1} - C^{s,m/f}_{t,x-1})\,\tilde{S}^s_t S_{x-1} && \\
U^{s,m/f}_{t+1,a+1} &= U^{s,m/f}_{t,a}\,\tilde{S}^s_t\,S_a\,(1-\delta_{a+1}) && 0 \le a \le x-2
\end{aligned} \qquad (A1.1)$$

$R^{s,m/f}_{t,a}$	is the number of recruited males/females of age *a* in stock *s* at the start of year *t*;
$U^{s,m/f}_{t,a}$	is the number of unrecruited males/females of age *a* in stock *s* at the start of year *t*;
$C^{s,m/f}_{t,a}$	is the catch of males/females of age *a* from stock *s* during year *t* (whaling is assumed to take place in a pulse at the start of each year);
δ_a	is the fraction of unrecruited animals of age *a*-1 which recruit at age *a* (assumed to be independent of sex and stock);
S_a	is the annual survival rate of animals of age *a* in the absence of catastrophic mortality events (assumed to be the same for males and females):

$$S_a = \begin{cases} S_0 & \text{if } a = 0 \\ S_{1+} & \text{if } 1 < a \end{cases} \qquad (A1.2)$$

S_0	is the calf survival rate;
S_{1+}	is the survival rate for animals aged 1 and older;
$\tilde{S}^s_t$	is the amount of catastrophic mortality (represented in the form of a survival rate) for stock *s* during year *t* (catastrophic events are assumed to occur at the start of the year before mortality due to whaling and natural causes; in general $\tilde{S}^s_t$=1, i.e. there is no catastrophic mortality);
$I^{s,m/f}_{t,a}$	is the net migration of female/male animals of age *a* into stock *s* during year *t*; and
x	is the maximum (lumped) age-class (all animals in this and the *x*-1 class are assumed to be recruited and to have reached the age of first parturition). *x* is taken to be 15 for these trials.

Catastrophic mortality is assumed to be zero (i.e., $\tilde{S}^s_t = 1$) except for the north stock for 1999 and 2000 when it is assumed to be equal to the parameter $\tilde{S}$. This assumption reflects the large number of dead ENP gray whales observed stranded along the coasts of Oregon and Washington during 1999 and 2000 relative to annual numbers stranding there historically (Gulland *et al.*, 2005; Brownell *et al.*, 2007). The mortality event is assumed to have only impact the north stock because the abundance estimates for the PCFG stock increased when the mortality event occurred in contrast to those for the north stock which declined substantially.

Immigration only occurs from the north stock to the PCFG stock and only animals aged 1+ immigrate. The annual number of animals immigrating is given by $I_t = \bar{I}\, N_t^{\text{north},1+}/20000$ where $\bar{I}$ is the hypothesized recent average number of individuals recruiting into the PCFG from the north stock (i.e., 2, 4 or 6). The annual number of immigrants by age and sex is given by:

$$I_{t,a}^{s,m/f} = I_t \frac{N_{t,a}^{\text{north},m/\text{f}}}{\sum_{a=1}^{x}(N_{t,a}^{\text{north,m}} + N_{t,a}^{\text{north,f}})} \qquad \text{(A1.3)}$$

A.2 Births

The number of births to stock *s* at the start of year *t*+1, B_{t+1}^s, is given by:

$$B_{t+1}^s = b_{t+1}^s\, N_{t+1}^{s,f} \qquad \text{(A2.1)}$$

$N_t^{s,f}$ is the number of mature females in stock *s* at the start of year *t*:

$$N_t^{s,f} = \sum_{a=a_m}^{x} (R_{t,a}^{s,f} + U_{t,a}^{s,f}) \qquad \text{(A2.2)}$$

a_{m} is the age-at-maturity (the convention of referring to the mature population is used here, although this actually refers to animals that have reached the age of first parturition);

b_{t+1}^s is the probability of birth/calf survival for mature females:

$$b_{t+1}^s = b_{-\infty}\{1 + A^s(1-(D_{t+1}^s / D_{-\infty}^s)^{z^s})\} \qquad \text{(A2.3)}$$

$b_{-\infty}$ is the average number of live births per year per mature female in the pristine (pre-exploitation) population;

A^s is the resilience parameter for stock *s*;

z^s is the degree of compensation for stock *s*;

D_t^s is the size of the component of stock *s* in year *t* upon which the density-dependence is assumed to act;

and

$D_{-\infty}^s$ is the pristine size of the component of stock *s* upon which the density-dependence is assumed to act.

The number of female births, $B_t^{s,f}$, is computed from the total number of the births during year *t* according to the equation:

$$B_t^{s,f} = 0.5\, B_t^s \qquad \text{(A2.4)}$$

The numbers of recruited/unrecruited calves is given by:

$$\begin{aligned} R_t^{s,f} &= \pi_0\, B_t^{s,f} & R_t^{s,m} &= \pi_0\,(B_t^s - B_t^{s,f}) \\ U_t^{s,f} &= (1-\pi_0)\, B_t^{s,f} & U_t^{s,m} &= (1-\pi_0)(B_t^s - B_t^{s,f}) \end{aligned} \qquad \text{(A2.5)}$$

π_0 is the proportion of animals of age 0 which are recruited (0 for these trials).

For the trials $D_t^s = N_t^{s,1+}$ and $D_{-\infty}^s = K^{s,1+}$ because density-dependence is assumed to act on the 1+ component of the population and affects fecundity and infant survival. $N_t^{s,1+}$ and $K^{s,1+}$ are defined according to the equations:

$$N_t^{s,1+} = \sum_{a=1}^{x}(R_{t,a}^{s,f} + U_{t,a}^{s,f} + R_{t,a}^{s,m} + U_{t,a}^{s,m}) \qquad K^{s,1+} = \sum_{a=1}^{x}(R_{-\infty,a}^{s,f} + U_{-\infty,a}^{s,f} + R_{-\infty,a}^{s,m} + U_{-\infty,a}^{s,m}) \qquad \text{(A2.6)}$$

A.3 Catches

The historical (t<2010) catches by stratum (north, south, PCFG December – May, and PCFG June – November) are taken to be equal to the reported catches (Table 1). The historical catches are allocated to stocks in fixed proportions as follows:

(1) North area catches: all north animals;

(2) PCFG area catches in December – May: PCFG animals with probability ϕPCFG (base-case value 0.203, as determined by the photo-ID data);

(3) PCFG area catches in June – November: all PCFG animals; and

(4) South area catches: PCFG animals with probability ϕsouth (base-case value 0.01, as determined by relative abundance).

The future catches by stratum are incidental catches and the catches arising from application of the *SLA*s. Subsistence catches are only assumed to occur in the north and the PCFG area from December – May. The sex-ratio of future catches is assumed to be 50:50. The catches are allocated to stock as outlined above, except that the subsistence catches from the PCFG area in June – November are modelled individually. Thus, the catch from the PCFG area is allocated to the PCFG stock based on a Bernoulli trial with probability:

$$\frac{\sum_{m/f}\sum_{a'} R_{y,a'}^{PCFG,m/f}}{\delta \sum_{m/f}\sum_{a''} R_{y,a''}^{north,m/f} + \sum_{a''} R_{y,a''}^{PCFG,m/f}} \qquad \text{(A3.1)}$$

where δ is the relative probability of harvesting a PCFG versus a north animal had the sizes of the two populations been the same. δ is calculated from ϕ under the assumption that the number of PCFG animals is 200 and north animals is 20000, i.e:

$$\delta = (200/\phi - 200)/20000 \qquad \text{(A3.2)}$$

The incidental catches by stratum for the historical period are computed using the equation:

$$C_y^{1/s} = \begin{cases} 0.5\left\{p^I - \frac{p^I - 1}{69}[y - 1999]\right\}\bar{C}^I & \text{if } y \le 1999 \\ \bar{C}^I & \text{otherwise} \end{cases} \qquad \text{(A3.3)}$$

$C_y^{1/s}$ is the incidental catch of animals of sex s during year y;

$\bar{C}^I$ is the mean catch in the stratum (see Table 2).

The catches from the PCFG and north stocks are then allocated to age and size using the formula:

$$C_{t,a}^{s,m} = C_t^{s,m} R_{y,a}^{s,m} / \sum_{a''} R_{y,a''}^{s,m}; \quad C_{t,a}^{s,f} = C_t^{s,f} R_{y,a}^{s,f} / \sum_{a''} R_{y,a''}^{s,f}; \qquad \text{(A3.4)}$$

The probability of not identifying a PCFG whale as such, is p_2, (base-case value 0) while the probability of incorrectly identifying a north whale as a PCFG whale is, p_1,(base-case 0.01). If the survey frequency is not annually, p_2 is defined as:

$$p_{2,t} = 1 - \frac{\sum_{a \ge SF} (R_{t,a}^{\text{PCFG,m}} + R_{t,a}^{\text{PCFG,f}} + U_{t,a}^{\text{PCFG,m}} + U_{t,a}^{\text{PCFG,f}})}{\sum_{a \ge 1} (R_{t,a}^{\text{PCFG,m}} + R_{t,a}^{\text{PCFG,f}} + U_{t,a}^{\text{PCFG,m}} + U_{t,a}^{\text{PCFG,f}})} \qquad \text{(A3.5)}$$

where SF is the survey frequency for the PCFG area.

A.4 Recruitment

The proportion of animals of age a that would be recruited if the population was pristine is a knife-edged function of age at age 0, i.e.:

$$\pi_a = \begin{cases} 0 & \text{if } \ a = 0 \\ 1 & \text{otherwise} \end{cases} \qquad \text{(A4.1)}$$

The (expected) number of unrecruited animals of age a that survive to age a+1 is $U_{t,a}^{s,m/f} S_a$. The fraction of these that then recruit is:

$$\delta_{a+1} = \begin{cases} [\pi_{a+1} - \pi_a]/[1-\pi_a] & \text{if } 0 \le \alpha_a < 1 \\ 1 & \text{otherwise} \end{cases} \tag{A4.2}$$

A.5 Maturity

Maturity is assumed to be a knife-edged function of age at age a_m.

A.6 Initialising the population vector

The numbers at age in the pristine population are given by:

$$\begin{aligned} R^{s,m/f}_{-\infty,a} &= 0.5 \;\; N^s_{-\infty,0} \;\; \pi_a \prod_{a'=0}^{a-1} S_{a'} & \text{if} \quad 0 \le a < x \\ U^{s,m/f}_{-\infty,a} &= 0.5 \;\; N^s_{-\infty,0} \;\; (1-\pi_a) \prod_{a'=0}^{a-1} S_{a'} & \text{if} \quad 0 \le a < x \\ R^{s,m/f}_{-\infty,x} &= 0.5 \;\; N^s_{-\infty,0} \prod_{a'=0}^{x-1} \frac{S_{a'}}{(1-S_x)} & \text{if} \quad a = x \end{aligned} \tag{A6.1}$$

$R^{s,m/f}_{-\infty,a}$ is the number of animals of age *a* that would be recruited in the pristine population;

$U^{s,m/f}_{-\infty,a}$ is the number of animals of age *a* that would be unrecruited in the pristine population; and

$N^s_{-\infty,0}$ is the total number of animals of age 0 in the pristine population.

The value for $N^s_{-\infty,0}$ is determined from the value for the pre-exploitation size of the 1+ component of the population using the equation:

$$N^s_{-\infty,0} = K^{s,1+} / \left(\sum_{a=1}^{x-1} \left(\prod_{a'=0}^{a-1} S_{a'} \right) + \frac{1}{1-S_x} \prod_{a'=0}^{x-1} S_{a'} \right) \tag{A6.2}$$

It is well-known that it is not possible to make a simple density-dependent population dynamics model consistent with the abundance estimates for the eastern north Pacific stock of gray whales (Reilly, 1981; 1984; Cooke, 1986; Lankester and Beddington, 1986; Butterworth *et al.*, 2002). This is why recent assessments of this stock (e.g. Punt and Wade, in press) have been based on starting population projections from a more recent year (denoted as τ) than that in which the first recorded catch occurred. The trials are therefore based on the assumption that the age-structure at the start of τ=1930 is stable rather than that the population was at its pre-exploitation equilibrium size at the start of 1600, the first year for which catch estimates are available. The choice of 1930 for the first year of the simulation is motivated by the fact that the key assessment results are not sensitive to a choice for this year from 1930-1968 (Punt and Butterworth, 2002; Punt and Wade, in press). Note that even though the operating model ignores the catch data for 1600-1929, these catches are nevertheless provided to the *SLA* for the north area.

The determination of the age-structure at the start of 1930 involves specifying the effective 'rate of increase', γ, that applies to each age-class. There are two components contributing to γ, one relating to the overall population rate of increase (γ^+) and the other to the exploitation rate. Under the assumption of knife-edge recruitment to the fishery at age 1, only the γ^+ component (assumed to be zero following Punt and Butterworth, 2002) applies to ages *a* of age 0. The number of animals of age *a* at the start of τ=1930 relative to the number of calves at that time, $N^{s,*}_{\tau,a}$, is therefore given by the equation:

$$N^{s,*}_{\tau,a} = \begin{cases} 1 & \text{if } a = 0 \\ N^{s,*}_{\tau,a-1} \, S_{a-1} (1-\gamma^+) & \text{if } a \le 1 \\ N^{s,*}_{\tau,a-1} \, S_{a-1} \, (1-\gamma^s) & \text{if } 1 < a < x \\ N^{s,*}_{\tau,x-1} \, S_{x-1} (1-\gamma^s) / (1 - S_x \, (1-\gamma^s)) & \text{if } a = x \end{cases} \tag{A6.3}$$

B^s_τ is the number of calves in year τ (=1930) and is derived directly from equations A2.1 and A2.3 (for further details see Punt, 1999):

$$B^s_\tau = \left(1 - \left[1/(N^{s,f}_\tau b_{-\infty}) - 1\right] / A^s \right)^{1/z^s} \frac{D^s_{-\infty}}{D^{s,*}_\tau} \tag{A6.4}$$

$D^{s,*}_\tau$ is the number of animals in the density dependent component of the population relative to the number of births at that time (see equation A2.6).

The effective rate of increase, γ, is selected so that if the population dynamics model is projected from 1930 to 1968, the size of the 1+ component of the population (both stocks) in 1968 equals a pre-specified value, P_{1968}.

A.7 z and A

A^s, z^s and S_0, are obtained by solving the system of equations that relate *MSYL*, *MSYR*, S_0, S_{1+}, $f_{\max}$ $a_{\rm m}$, A^s and z^s, where $f_{\max}$ is the maximum theoretical pregnancy rate (Punt, 1999).

A.8 Conditioning

The method for conditioning the trials (i.e. selecting the 100 sets of values for the parameters $a_{\rm m}$, S_0, S_{1+}, $\tilde{S}$, K_{1+}^{N} , K_{1+}^{PCFG} A^N , A^{PCFG} , z^N , and z^{PCFG}) is based on a Bayesian assessment of the eastern North Pacific stock of gray whales (Punt and Butterworth, 2002; Wade, 2002). The algorithm for conducting the Bayesian assessment is as follows:

(a) Draw values for the parameters S_{1+}, $f_{\max}$, $a_{\rm m}$, K_{1+}^{N}, K_{1+}^{PCFG} , P_{1968}^{N} , P_{1968}^{PCFG} , $\tilde{S}$, CV_{add}^{N} (the additional variance for the estimate of 1+ abundance Carmel, California in 1968), CV_{add}^{PCFG} (the additional variance for the estimate of 1+ abundance from North California to Southeast Alaska in 1968 – had such a survey taken place) from the priors in Table 3. It is not necessary to draw values for $MSYR_{1+}$ and $MSYL_{1+}$ because the values for these quantities are pre-specified rather than being determined during the conditioning process.

(b) Solve the system of equations that relate $MSYL^s$, $MSYR^s$, S_0, S_{1+}, $f_{\max}$, $a_{\rm m}$, A^s and z^s to find values for S_0, A^s and z^s.

(c) Calculate the likelihood of the projection for each area, given by

$$-\ell{\rm n}L = 0.5\ell{\rm n}\,|\,\mathbf{V}+\Omega\,| + 0.5\sum_i\sum_j(\ell{\rm n}N_i^{\rm obs} - \ell{\rm n}\hat{P}_i^{1+})[(\mathbf{V}+\Omega)^{-1}]_{i,j}(\ell{\rm n}N_j^{\rm obs} - \ell{\rm n}\hat{P}_j^{1+}) \tag{A8.1}$$

$N_i^{\rm obs}$ is the $i^{\rm th}$ estimate of abundance[9] (Tables 4a, 4b),

$\hat{P}_i$ is the model-estimate corresponding to $N_i^{\rm obs}$,

$\mathbf{V}$ is the variance-covariance matrix for the abundance estimates, and

Ω is a diagonal matrix with elements given by $E(CV_{add,t}^2)$:

$$E(CV_{add,t}^2) = \eta(0.1 + 0.013P^* / \hat{P}_t) = CV_{add}^2\,\frac{0.1 + 0.013P^* / \hat{P}_t}{0.1 + 0.013P^* / \hat{P}_{1968}} \tag{A8.2}$$

(a) Steps (a) – (c) are repeated a large number (typically 1,000,000) of times.

(b) 100 sets of parameters vectors are selected randomly from those generated using steps (a) – (c), assigning a probability of selecting a particular vector proportional to its likelihood. The number of times steps (a) – (c) are repeated is chosen to ensure that each of the 100 parameter vectors are unique.

The expected value for the estimate of abundance of the north area is taken to the total abundance (PCFG and north stocks combined) while the abundance estimates for the PCFG area are assumed to pertain to the PCFG stock.

B. Data generation

B.1 Absolute Abundance Estimates

The historic (t<2010) abundance estimates (and their CVs) are provided to the *SLA* and are taken to be those in Tables 4a, 4c. Future estimates of absolute abundance (and their estimated CVs) are generated and provided to the *SLA* once every *F* years during the management period (starting in year 2011 where *F*=10 for the northern area and *F*=1 for the PCFG area). The CV of the abundance estimate (CV_{true}) may be different from the CV provided to the *SLA* (further details are provided below).

The survey estimate, $\hat{S}$, may be written as:

$$\hat{S} = B_A P Y\, w / \mu = B_A\, P^*\, \beta^2\, Y\, w \tag{B1.1}$$

B_A is the bias (the bias for the bulk of the simulations for the north area is 1 while the bias for PCFG area is generated from $\ell{\rm n}B_A \sim N(-0.335, 0.112)$ – this bias reflects the difference between the abundance estimates on which the ABL is based [which pertain to Oregon to Southern Vancouver Island] and the abundance of the entire stock];

P is the current total 1+ population size ($= N_t^{1+}$); (B1.2)

Y is a lognormal random variable: $Y = e^{\phi}$ where: $\phi \sim N[0;\sigma_\phi^2]$ and $\sigma_\phi^2 = \ell{\rm n}(1+\alpha^2)$ (B1.3)

w is a Poisson random variable, independent of Y, with $E(w) = {\rm var}(w) = \mu = (P\ /\ P^*)/\beta^2$; and (B1.4)

P^* is the reference population level (the pristine 1+ population, $= K^{1+}$).

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[9] The shore-based abundance estimate for year *y*/*y*+1 is assumed to pertain to abundance at the start of year *y*+1.

Note that under the approximation $CV^2(ab) = CV^2(a) + CV^2(b)$,

$$E(\hat{S}) = B_A P_t \text{ and } CV^2_{true}(\hat{S}) = \alpha^2 + \beta^2 P^* / P \tag{B1.5}$$

[10]The steps used in the program to generate the abundance estimates and their CVs are given below.

The *SLA* is provided with estimates of CV_{est} (the estimation error associated with factors considered historically) for each future sightings estimate.

The estimate of $CV_{est,t}$ is given by:

$$\hat{C}V_{est,t} = \sqrt{\sigma_t^2 (\chi_n^2 / n)} \qquad \sigma_t^2 = \ell\text{n}(1 + E(CV^2_{est,t})) \tag{B1.6}$$

$E(CV^2_{est,t})$ is the sum of the squares of the actual CVs due to estimation error:

$$E(CV^2_{est,t}) = \theta^2 (a^2 + b^2 / w\beta^2) \tag{B1.7}$$

χ_n^2 is a random number from a χ^2 distribution with *n* (=19; the value assumed for the single stock trials for the RMP) degrees of freedom;

a^2, b^2 are constants and equal to 0.02 and 0.012 respectively;

The relationship between CV_{est} and CV_{true} is given by:

$$\eta = [E(CV^2_{true}) - E(CV^2_{est})] / (0.1 + 0.013 P^* / P) \tag{B1.8a}$$

where η is a constant known as the additional variance factor. The value of η is based on the population size and CVs for 1968 (for consistency with the way the CV for P_{1968} is generated in Table 3):

$$\eta = CV^2_{add} / (0.1 + 0.013 P^* / P_{1968}) \tag{B1.8b}$$

The values of α and β are then computed as:

$$\alpha^2 = \theta^2 a^2 + \eta\, 0.1\,, \qquad \beta^2 = \theta^2 b^2 + \eta\, 0.013 \tag{B1.9}$$

C. Need

The level of need in each year, Q_t, will be supplied to the *SLA*. The need is given by $Q_t = Q_{2010} + \frac{t - 2010}{100}(Q_{2110} - Q_{2010})$ where Q_{2010} (=150/7 for the north and PCFG areas respectively) is the need at the start of the first year in which the AWMP is applied and Q_{2110} is the value 100 years later. The level of need supplied.

D. Implementing the Makah harvest regime

Thus, the overall application of the Makah management regime is as follows:

(1) Compute the ABL (Allowable bycatch limit of PCFG whales)

(2) Strike an animal

(3) If the animal is struck-and lost in December-April[11]:

(a) If the total number of struck and lost animals is 3, stop the hunt.

(b) If the total number of struck animals equals the need of 7 stop the hunt.

(c) Go to step (2).

(4) If the animal is struck-and lost in May:

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10 The steps used to generate estimates of abundance and their CVs are as follows (steps i) – iii) are part of the conditioning process).

(i) Read in CV_{est} (basecase value= 0.075 = value used to generate the 1968 abundance). Generate values of CV^2_{add} for 1968.

(ii) Set η using equation B1.8b and the value of CV_{add} generated in step i).

(iii) Set θ 2 using equation B1.7a and the values for CV_{est} from step (i) and $w\beta^2 = P / P^* = P_{1968} / P^*$. Set α2 and β 2 using equation B1.9.

(iv) Generate w (Poisson random variable – see equation B1.4) and ϕ (lognormal random variable – see equation B1.3).

(v) Set abundance estimate $\hat{S}$ using equation B1.1.

(vi) Set $E(CV^2_{est,t})$ using eqn B1.7a.

(vii) Generate $\hat{C}V_{est,t}$ from a χ_n^2 distribution using equation B1.6a.

[11] Whether a whale is struck and lost is determined from a Bernoulli trial with probability 0.5 (base-case).

(a) Add one to the number of whales counted towards the ABL

(b) If the ABL is reached; stop the hunt

(c) If the total number of struck and lost animals is 3, stop the hunt.

(d) If the total number of struck animals equals the need of 7; stop the hunt.

(e) Go to step (2).

(5) If the animal is landed and is matched against the catalogue[12]:

(a) Add one to the number of whales counted towards the ABL

(b) If the ABL is reached; stop the hunt

(c) If the total number of landed whales equals 5; stop the hunt

(d) If the total number of struck animals equals the need of 7; stop the hunt.

(e) If the number of landed whales for the current five-year block equals 20; stop the hunt

(f) Go to step (2).

(6) If the animal is landed and does not match any whale in the catalogue:

(a) If the total number of landed whales equals 5; stop the hunt

(b) If the total number of struck animals equals the need of 7; stop the hunt.

(c) If the number of landed whales for the current five-year block equals 20; stop the hunt

(d) Go to step (2).

E. Statistics

The risk- and recovery-related performance statistics are computed for the mature female and for the total (1+) population sizes (i.e. P_t is either the size of the mature female component of the population, N_t^f , or the size of the total (1+) population, N_t^{1+}). P_t^* is the population size in year t under a scenario of zero strikes in the northern and PCFG area (but allowing for incidental catches) over the years t≥2010 (defined as t=0 below), P_t^{**} is the population size in year t under a scenario of zero strikes in the PCFG area (but allowing for incidental catches and strikes in the north area) over the years t≥2010 (defined as t=0 below), and K_t^* is the population size in year t if there had never been any harvest.

The trials are based on a 100-year time horizon, but a final decision regarding the time horizon will depend inter alia on interactions between the Committee and the Commission regarding need envelopes and on the period over which recovery might occur. To allow for this, results are calculated for T=20 and 100.

Statistics marked in bold face have previously been considered the more important. Note that the statistic identification numbers have not been altered for reasons of consistency. Hence, there are gaps in the numbers where some statistics have been deleted.

E.1 Risk

D1. Final depletion: P_T / K . In trials with varying *K* this statistic is defined as P_T / K_t^* .

D2. Lowest depletion: $\min(P_t / K) : t = 0,1,...,T$. In trials with varying *K* this statistic is defined as $\min(P_t / K_t^*):\ t = 0,1,...,T$.

D6. Plots for simulations 1-100 of $\{ P_t : t = 0,1,..,T\}$, $\{ P_t^* : t = 0,1,..,T\}$, $\{ P_t^{**} : t = 0,1,..,T\}$

D7. Plots of $\{ P_{t[x]} : t = 0,1,..,T\}$ $\{ P_{t[x]}^* : t = 0,1,..,T\}$ and $\{ P_{t[x]}^{**} : t = 0,1,..,T\}$ where $P_{t[x]}$ is the *x*th percentile of the distribution of P_t. Results are presented for *x* = 5 and *x* = 50.

D8. Rescaled final population: P_T / P_T^* and P_T / P_T^{**}

D9. Minimum population level in terms of mature females, $\min(P_t):\ t = 0,1,...,T$

D10. Relative increase P_T / P_0

E.2 Need (for PCFG, statistics N1- N12 will be computed for the total number of strikes as well as the number of landed animals)

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[12] PCFG whales are mismatched as north stock whales with probability p_1 while north stock whales are matched to the catalogue with probability p_2.

N1. Total need satisfaction: $\sum_{t=0}^{T-1} C_t / \sum_{t=0}^{T-1} Q_t$

N2. Length of shortfall = (negative of the greatest number of consecutive years in which $C_t < Q_t$) / T

N4. Fraction of years in which $C_t = Q_t$

N5. Proportion of block need satisfaction: $\Gamma/(T-h+1)$ where Γ is the number of blocks of h years in which the total catch equals the total need; h is 5 for these trials.

N7. Plot of $\{V_{t[x]} : t = 0, 1, T-1\}$ where $V_{t[x]}$ is the xth percentile of the distribution of $V_t = C_t / Q_t$ [catch for the PCFG area]

N8. Plots of V_t for simulations 1-100.

N9. Average need satisfaction: $\frac{1}{T} \sum_{t=0}^{T-1} \frac{C_t}{Q_t}$

N10. AAV (Average Annual Variation): $\sum_{t=-1}^{T-2} \left| C_{t+1} - C_t \right| / \sum_{t=-1}^{T-2} C_t$

N11. Anti-curvature: $\frac{1}{T-1} \sum_{t=0}^{T-2} \left| \frac{C_t - M_t}{\max(10, M_t)} \right|$ where $M_t = \left(C_{t+1} + C_{t-1}\right)/2$

N12. Mean downstep (or modified AAV): $\sum_{t=-1}^{T-2} \left| \min\left(C_{t+1} - C_t, 0\right) \right| / \sum_{t=-1}^{T-2} C_t$

N13. Average annual number of animals landed

N14. Average annual number of animals struck and lost.

N15. Ray Plot. For each simulation, make a line plot of cumulative absolute year-to-year quota changes versus time (x-axis). Superimpose all these rays.

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Table 1

Historical catches of eastern north Pacific gray whales

Year	South			PCFG Jun-Nov			PCFG Dec-May			North			Total		
	M	**F**	**Total**	**M**	**F**	**Total**	**M**	**F**	**Total**	**M**	**F**	**Total**	**M**	**F**	**Total**
1930	0	0	0	0	0	0	0	0	0	23	24	47	23	24	47
1931	0	0	0	0	0	0	0	0	0	5	5	10	5	5	10
1932	5	5	10	0	0	0	0	0	0	5	5	10	10	10	20
1933	30	30	60	0	0	0	0	0	0	8	7	15	38	37	75
1934	30	30	60	0	0	0	0	0	0	36	30	66	66	60	126
1935	55	55	110	0	0	0	0	0	0	16	28	44	71	83	154
1936	43	43	86	0	0	0	0	0	0	50	62	112	93	105	198
1937	0	0	0	0	0	0	0	0	0	12	12	24	12	12	24
1938	0	0	0	0	0	0	0	0	0	32	32	64	32	32	64
1939	0	0	0	0	0	0	0	0	0	19	20	39	19	20	39
1940	0	0	0	0	0	0	0	0	0	56	69	125	56	69	125
1941	0	0	0	0	0	0	0	0	0	38	39	77	38	39	77
1942	0	0	0	0	0	0	0	0	0	60	61	121	60	61	121
1943	0	0	0	0	0	0	0	0	0	59	60	119	59	60	119
1944	0	0	0	0	0	0	0	0	0	3	3	6	3	3	6
1945	0	0	0	0	0	0	0	0	0	25	33	58	25	33	58
1946	0	0	0	0	0	0	0	0	0	14	16	30	14	16	30
1947	0	0	0	0	0	0	0	0	0	11	20	31	11	20	31
1948	0	0	0	0	0	0	0	0	0	7	12	19	7	12	19
1949	0	0	0	0	0	0	0	0	0	10	16	26	10	16	26
1950	0	0	0	0	0	0	0	0	0	4	7	11	4	7	11
1951	0	0	0	0	0	0	1	0	1	5	8	13	6	8	14
1952	0	0	0	0	0	0	0	0	0	17	27	44	17	27	44
1953	0	0	0	0	0	0	6	4	10	15	23	38	21	27	48
1954	0	0	0	0	0	0	0	0	0	14	25	39	14	25	39
1955	0	0	0	0	0	0	0	0	0	22	37	59	22	37	59
1956	0	0	0	0	0	0	0	0	0	45	77	122	45	77	122
1957	0	0	0	0	0	0	0	0	0	36	60	96	36	60	96
1958	0	0	0	0	0	0	0	0	0	55	93	148	55	93	148
1959	1	1	2	0	0	0	0	0	0	73	121	194	74	122	196
1960	0	0	0	0	0	0	0	0	0	58	98	156	58	98	156
1961	0	0	0	0	0	0	0	0	0	77	131	208	77	131	208
1962	4	0	4	0	0	0	0	0	0	55	92	147	59	92	151
1963	0	0	0	0	0	0	0	0	0	68	112	180	68	112	180
1964	15	5	20	0	0	0	0	0	0	75	124	199	90	129	219
1965	0	0	0	0	0	0	0	0	0	71	110	181	71	110	181
1966	15	11	26	0	0	0	0	0	0	80	114	194	95	125	220
1967	52	73	125	0	0	0	0	0	0	109	140	249	161	213	374
1968	41	25	66	0	0	0	0	0	0	48	87	135	89	112	201
1969	39	35	74	0	0	0	0	0	0	50	90	140	89	125	214
1970	0	0	0	0	0	0	0	0	0	71	80	151	71	80	151
1971	0	0	0	0	0	0	0	0	0	57	96	153	57	96	153
1972	0	0	0	0	0	0	0	0	0	61	121	182	61	121	182
1973	0	0	0	0	0	0	0	0	0	97	81	178	97	81	178
1974	0	0	0	0	0	0	0	0	0	94	90	184	94	90	184
1975	0	0	0	0	0	0	0	0	0	58	113	171	58	113	171
1976	0	0	0	0	0	0	0	0	0	69	96	165	69	96	165
1977	0	0	0	0	0	0	0	0	0	87	100	187	87	100	187
1978	0	0	0	0	0	0	0	0	0	94	90	184	94	90	184
1979	0	0	0	0	0	0	0	0	0	58	125	183	58	125	183
1980	0	0	0	0	0	0	0	0	0	53	129	182	53	129	182
1981	0	0	0	0	0	0	0	0	0	36	100	136	36	100	136
1982	0	0	0	0	0	0	0	0	0	57	111	168	57	111	168
1983	0	0	0	0	0	0	0	0	0	46	125	171	46	125	171
1984	0	0	0	0	0	0	0	0	0	59	110	169	59	110	169
1985	0	0	0	0	0	0	0	0	0	54	116	170	54	116	170
1986	0	0	0	0	0	0	0	0	0	46	125	171	46	125	171
1987	0	0	0	0	0	0	0	0	0	48	111	159	48	111	159
1988	0	0	0	0	0	0	0	0	0	43	108	151	43	108	151
1989	0	0	0	0	0	0	0	0	0	61	119	180	61	119	180
1990	0	0	0	0	0	0	0	0	0	67	95	162	67	95	162
1991	0	0	0	0	0	0	0	0	0	67	102	169	67	102	169
1992	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1993	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1994	0	0	0	0	0	0	0	0	0	21	23	44	21	23	44
1995	0	0	0	0	0	0	0	0	0	48	44	92	48	44	92
1996	0	0	0	0	0	0	0	0	0	18	25	43	18	25	43
1997	0	0	0	0	0	0	0	0	0	48	31	79	48	31	79

Cont.

Year	South			PCFG Jun-Nov			PCFG Dec-May			North			Total		
	M	**F**	**Total**	**M**	**F**	**Total**	**M**	**F**	**Total**	**M**	**F**	**Total**	**M**	**F**	**Total**
1998	0	0	0	0	0	0	0	0	0	64	61	125	64	61	125
1999	0	0	0	0	0	0	0	1	1	69	54	123	69	55	124
2000	0	0	0	0	0	0	0	0	0	63	52	115	63	52	115
2001	0	0	0	0	0	0	0	0	0	62	50	112	62	50	112
2002	0	0	0	0	0	0	0	0	0	80	51	131	80	51	131
2003	0	0	0	0	0	0	0	0	0	71	57	128	71	57	128
2004	0	0	0	0	0	0	0	0	0	43	68	111	43	68	111
2005	0	0	0	0	0	0	0	0	0	49	75	124	49	75	124
2006	0	0	0	0	0	0	0	0	0	57	77	134	57	77	134
2007	0	0	0	0	1	1	0	0	0	50	81	131	50	82	132
2008	0	0	0	0	0	0	0	0	0	64	66	130	64	66	130
2009	0	0	0	0	0	0	0	0	0	59	57	116	59	57	116
Total	**330**	**313**	**643**	**0**	**1**	**1**	**7**	**5**	**12**	**3,715**	**5,345**	**9,060**	**4,052**	**5,664**	**9,716**

Table 2

Average historical incidental catches.

Stratum	Average incidental catch
North	0[1]
PCFG [Dec – May]	2
PCFG [Jun – Nov]	1.4[2]
South	3.4

[1] – obviously not actually zero, but will be small relative to population size

[2] – includes southern whales during June – November as these whales are almost certainly PCFG animals

Table 3

The prior distributions for the eastern north Pacific stock of gray whales.

Parameter	Prior distribution
Non-calf survival rate, S_{1+}	U[0.95, 0.999]
Age-at-maturity, a_m	U[6, 12]
K_{1+}^{N}	U[16,000, 70,000]
K_{1+}^{PCFG}	U[100, 500]
Maximum pregnancy rate, f_{max}	U[0.3, 0.6]
Additional variation (population estimates), CV_{add}, in 1968	U[0, 0.35]
1968 abundance, P_{1968}^{N}	U[8,000, 16,000]
1968 abundance, P_{1968}^{PCFG}	U[50, 300]
Catastrophic mortality	U[0.2,1.0]

Table 4a

Estimates of absolute abundance (with associated standard errors) for the eastern north Pacific stock of gray whales based on shore counts (source: Laake *et al*, 2010).

Year	Estimate	CV	Year	Estimate	CV
1967/68	13426	0.094	1979/80	19763	0.083
1968/69	14548	0.080	1984/85	23499	0.089
1969/70	14553	0.083	1985/86	22921	0.081
1970/71	12771	0.081	1987/88	26916	0.058
1971/72	11079	0.092	1992/93	15762	0.067
1972/73	17365	0.079	1993/94	20103	0.055
1973/74	17375	0.082	1995/96	20944	0.061
1974/75	15290	0.084	1997/98	21135	0.068
1975/76	17564	0.086	2000/01	16369	0.061
1976/77	18377	0.080	2001/02	16033	0.069
1977/78	19538	0.088	2006/07	19126	0.071
1978/79	15384	0.080			

Table 4b

Estimates of absolute abundance (with associated standard errors) for 41^0-52^0N (source: J. Laake, pers. commn).

Year	Estimate	CV	Year	Estimate	CV
1998	104	0.044	2004	206	0.058
1999	122	0.082	2005	205	0.087
2000	146	0.072	2006	188	0.083
2001	170	0.061	2007	186	0.106
2002	198	0.039	2008	194	0.087
2003	204	0.063			

Table 4c

Estimates of absolute abundance (with associated standard errors) for the Oregon to Southern Vancouver Island (source: J. Laake, pers. commn).

Year	Estimate	CV	Year	Estimate	CV
1998	65	0.061	2004	160	0.097
1999	78	0.113	2005	162	0.098
2000	90	0.130	2006	154	0.104
2001	113	0.071	2007	153	0.105
2002	137	0.104	2008	154	0.099
2003	153	0.085			

Appendix 4

GREENLANDIC RESPONSE TO ‘9.1 CONVERSION FACTORS FOR EDIBLE PRODUCTS FOR GREENLAND FISHERIES’ FROM THE IWC SCIENTIFIC COMMITTEE MEETING, 2010

Ministry of Fisheries, Hunting and Agriculture, Government of Greenland

The SWG requested Greenland to provide information on its sampling scheme and data validation protocols at the IWC SC meeting 2011 meeting.

Shortly after the 62nd Annual IWC meeting, a meeting between hunters, scientists, wildlife officers and managers concerning a revised sampling scheme resulted in a suggestion of using bins for the collection of the three types of edible products, weighing one and counting how many times it was filled with each product as a way of validating the total weight measurements.

This suggestion was implemented by including it in the executive order (nr. 11, 16 July 2010) regulating the hunt on large whales. Normally, it takes at least 3 months to prepare a new executive order due to the hearing process. Because of its importance, the Greenland Cabinet made a decision to implement the executive order with a shorter hearing process.

Furthermore an instruction on how to collect relevant data has been made to the wildlife officers following a hunt and a flensing situation on bowhead and humpback whales.

Focusing on the largest species, since the implementation of the extended sampling scheme 10 humpback whales (9 in 2010 and 1 in 2011), 2 fin whales (2010) and 1 bowhead whale (2011) have been caught in Greenland. Of these 13 catches, wildlife officers were able to follow the hunt of the bowhead whale and 2 humpback whale catches. During the last three hunting seasons all 7 bowhead whale caught in Greenland have been followed by wildlife officers and/or scientist/managers resulting in a working paper presented at IWC and a scientific paper under review. This covering has required a high level of effort and resources from the wildlife officers and the scientist/managers involved.

The Greenland Institute of Natural Resources are planning to have 2-3 persons collecting samples from this years hunt on humpback whales in Mid-Greenland (3 animals). During this field work an effort for estimating bin weight of the three types of edible products will also be prioritised. The plan is to extent this work to fin whales and minke whale.

The experience, especially on challenges of organising the practicalities so far shows that this revised data collection will have to run for quite some years before an appropriate sampling size is reached.

Assessment of stock structure among gray whales utilizing feeding grounds in the Eastern North Pacific

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ABSTRACT

Although the majority of Eastern North Pacific (ENP) gray whales spend their summers feeding in the Bering, Beaufort, and Chukchi Seas, a small number of individuals, referred to as the Pacific Coast Feeding Group (PCFG), feed in waters between northern California and southeastern Alaska during summer and fall. Many individuals identified within this southern feeding area demonstrate intra- and inter-seasonal fidelity to the region, suggesting that structure could be present among ENP gray whales utilizing different areas for feeding. Little is known, however, about patterns of site fidelity of individuals feeding in northern waters. We utilized samples collected from individual gray whales within both southern (n=100) and northern (n=106) feeding areas to assess possible stock structure using both mtDNA control region sequences and 8 microsatellite markers. Significant mtDNA differentiation was found when the subset of samples representing individuals (n=71) sighted over two or more years within the seasonal range of the PCFG were compared to the combined set of samples collected from the northern feeding area(s) (F_{ST}=0.01, p=0.005; Fisher's exact test, p=0.008) as well as when the PCFG samples were compared to only those samples which were collected off Chukotka, Russia (n=71, F_{ST}=0.01, p=0.012; Fisher's exact test, p=0.030). No significant differences were found for any of the comparisons utilizing microsatellites. These results indicate that structure is present among gray whales utilizing different feeding areas and suggest that matrilineal fidelity plays a role in creating such structure. The lack of differentiation detected using nuclear markers (χ^2 test, p=0.636, PCFG versus northern; p=0.753, PCFG versus Chukotka) suggests that individuals from different feeding areas may interbreed. These results are important in evaluating the management of the ENP gray whale population, especially in light of the Makah Tribe's proposal to resume whaling in an area of the Washington coast utilized by both feeding and migrating whales. Although the proposed hunt is designed to target whales migrating to/from the northern feeding grounds, the possibility of taking a PCFG whale cannot be eliminated. Increasing our understanding of recruitment into this group is needed to assess potential impacts of a hunt.

INTRODUCTION

The current distribution of gray whales is limited to the eastern and western margins of the North Pacific (Rice & Wolman, 1971), where a small western population (~130 individuals, Cooke *et al.,* 2008) and a much larger eastern population (~19,000 individuals based on surveys in 2006/2007, Laake *et al.,* 2009) are recognized. Much of what is known about the western population is derived from photo-identification and genetic studies of individuals on the population's primary feeding ground, which is located in the coastal waters of northeastern Sakhalin Island, Russia (Weller *et al.,* 1999; Weller *et al.,* 2008; LeDuc *et al.,* 2002; Lang *et al.,* 2010). Photo-identification studies have documented seasonal site fidelity and annual return of individuals to this feeding area (Weller *et al.,* 1999). Reproductive females are known to utilize the Sakhalin feeding ground in years when they are accompanied by calves as well as when they are pregnant or resting, and the return of many individuals first identified as calves accompanying their mothers has been documented (Weller *et al.,* 2009). Genetic comparisons of samples collected from gray whales feeding off Sakhalin with samples collected from whales in the eastern North Pacific (ENP) have supported recognition of the two populations as distinct, with differentiation in both mtDNA haplotype and microsatellite allele frequencies (LeDuc *et al.,* 2002; Lang *et al.,* 2010).

Gray whales in the ENP population feed in waters between California and the Bering, Beaufort, and Chukchi Seas during summer and fall. Most of the population then migrates south along the coast of North America to overwinter in the lagoons and coastal waters of Baja Mexico. Three primary calving lagoons are utilized, with some females known to make repeated returns to specific lagoons (Jones, 1990). Genetic studies have demonstrated small but significant mtDNA differentiation between females (mothers with calves) utilizing two of the primary calving lagoons and females sampled in other areas (Goerlitz *et al.,* 2003). An additional study, utilizing both mtDNA and microsatellites with samples collected from all three of the primary calving lagoons, also identified small but significant departure from panmixia between two of the lagoons using nuclear data, although no significant differences were identified using mtDNA (Alter *et al.,* 2009).

Sub-structuring within the feeding range of the eastern population could also be present. Although little is known about fidelity of gray whales feeding north of the Aleutians, a small number of individuals, referred to as the Pacific Coast Feeding Group (PCFG; IWC, 2010), are known to show fidelity to more southern feeding grounds located in the coastal waters between northern California and southeastern Alaska (Gilmore, 1960; Pike, 1962; Hatler & Darling 1974; Darling, 1984; Calambokidis *et al.,* 2002, 2010). Within these waters, photo-identification research, which commenced in the early 1970s, has identified some whales that demonstrate consistent return to specific areas within this larger region, although movements between areas within the region also occur regularly (Hatler & Darling, 1974; Darling, 1984; Calambokidis *et al.,* 2002, 2010). In addition, photographic evidence has shown that some whales considered part of the PCFG move at least as far north as Kodiak Island, Alaska (Calambokidis *et al.,* 2010, Gosho *et al*., 2011). Recent estimates of the annual abundance of the PCFG suggest that at most a few hundred individuals utilize this feeding area (Calambokidis *et al.,* 2010).

Satellite tagging studies of 18 whales off the coast of Oregon and California have provided additional information on the movements of individual whales considered part of the PCFG (Mate *et al.,* 2010). Although the duration of tag attachment differed between individuals, movement patterns of the tagged animals were variable, with some individuals remaining in a relatively small area within the larger PCFG seasonal range and others traveling more widely. Only two of the eighteen whales moved north of Washington while tagged; one of these animals traveled at least as far north as southeastern Alaska (Mate *et al.*, 2010). All six of the individuals whose tags continued to transmit through the southbound migration utilized the wintering area within and adjacent to Laguna Ojo de Liebre. Although this lagoon is by far the most heavily used of the three major wintering lagoons, these results raised the possibility that PCFG whales may demonstrate philopatry to this particular wintering area (Mate *et al.,* 2010).

Concern for the PCFG of gray whales has stemmed in part from recent interest in the resumption of whaling by the Makah Tribe in northwest Washington, an area used by migrating whales as well as by whales considered part of the PCFG. The current proposal by the Makah Tribe includes time/area restrictions which will limit the hunt to between 1 December and 31 May and will not allow hunting in the Strait of Juan de Fuca east of Cape Flattery. The Makah Tribe also proposes to compare photographs of any whales harvested in the hunt to a photo-identification catalogue of known PCFG whales and to suspend the hunt for the year if the number of known PCFG gray whales struck is equal to the annual allowable bycatch level calculated for the PCFG (Makah Tribal Council, 2011). These restrictions are designed to reduce the probability of killing a PCFG whale and to focus the hunt on whales migrating to/from feeding areas north of the PCFG. Nevertheless, it is impossible to ensure that no PCFG whales would be killed. Evaluating whether such kills would, over time, have the potential to deplete the PCFG requires an understanding of how individuals are recruited into the group. If recruitment into the area is exclusively driven by calves learning the location of feeding grounds from their mothers (i.e., internally), then a PCFG individual that is removed would not be replaced by immigration. However, if recruitment is largely external, such that some whales stop to feed during the migration and then return to the PCFG area as their primary feeding destination in subsequent years, then it is likely that any takes from the PCFG would be offset by immigration into the group by whales that in previous years fed in northern areas.

Understanding recruitment into the PCFG is relevant to management under the Marine Mammal Protection Act (MMPA). The goal of the MMPA is to maintain population stocks as functioning elements of their ecosystem. The National Marine Fisheries Service considers stocks to be demographically independent units, such that the population dynamics of the affected group is more a consequence of births and deaths within the group (internal dynamics) rather than of immigration or emigration (external dynamics). Thus, the exchange of individuals between population stocks is not great enough to prevent the depletion of one of the populations as a result of increased mortality or lower birth rates (NMFS, 2005).

Previous genetic studies of the PCFG whales have focused on evaluating patterns of recruitment. Initial work utilizing a simulation-based approach indicated that if the PCFG originated from a single recent colonization event in the past 40 to 100 years, with no subsequent external recruitment into the group, detectable mtDNA genetic differentiation would be generated (Ramakrishnan & Taylor, 2000). Subsequent empirical analysis, however, failed to detect such a signal when comparing 16 samples collected from known PCFG whales utilizing Clayoquot Sound, British Columbia, with samples (n=41) collected from individuals presumably feeding in more northern areas (Steeves *et al.,* 2001). Additional genetic analysis utilizing an extended set of samples (n=45) collected from whales within the range of the PCFG indicated that the level of genetic diversity and the number of mtDNA haplotypes identified were inconsistent with measures, based on simulations, which would be expected if recruitment into the group were exclusively internal (Ramakrishnan *et al.,* 2001). However, both simulation-based studies focused on evaluating only the hypothesis of founding by a single and recent colonization event and did not evaluate alternative scenarios, such as limited dispersal of whales from other areas into the PCFG, which could have implications for management (Ramakrishnan and Taylor 2000, Ramakrishnan *et al.,* 2001). More recently, Frasier *et al.* (In press) have shown significant levels of mtDNA differentiation when comparing samples collected from 40 individuals considered part of the PCFG with published data generated from 104 samples collected from ENP gray whales, most of which stranded along the migratory route (LeDuc *et al.,* 2002). These results suggest that matrilineally directed fidelity may play a role in use of this area and led the authors to support recognition of the PCFG as a distinct management unit.

The lack of available samples collected from gray whales feeding in northern areas has limited previous genetic studies from directly addressing the potential for demographic independence among whales utilizing different feeding regions within the ENP. Here we use samples collected from various locations north of the Aleutians as well as samples collected from within the seasonal range of the PCFG. A high proportion of the samples collected north of the Aleutians were collected from individuals harvested off Chukotka, Russia, where between 111 and 134 whales per year have been taken during aboriginal whaling over the last decade (IWC, 2010). We also increased the number of samples collected from whales within the seasonal PCFG range and, for those samples linked to photographed individuals, were able to further refine our representation of the PCFG by incorporating sighting histories of known individuals in some comparisons.

The primary goal of this study was to evaluate whether multiple demographically independent units of gray whales exist on feeding grounds, with a special focus on comparing PCFG whales with whales utilizing northern feeding areas. Although other scenarios are possible, here we test three hypotheses using data from both mitochondrial and nuclear markers (n=8 microsatellite loci):

1. No population structure (e.g., panmixia) is present among gray whales utilizing feeding areas in the ENP; individuals move between feeding areas and exhibit random mating. This hypothesis would be supported by a finding of no nuclear or mitochondrial differentiation between samples collected in northern versus southern feeding areas.
2. Utilization of feeding areas is influenced by internal recruitment, with calves following their mothers to feeding grounds and returning in subsequent years. Mating is random with respect to feeding ground affiliation. This hypothesis would be supported by a finding of significant differences in mtDNA haplotype frequencies when comparing samples collected on northern versus southern feeding grounds, but no significant differences are expected in microsatellite allele frequencies between groups of samples from specific geographic areas (i.e., “strata”).
3. Utilization of feeding areas is influenced by matrilineal fidelity and mating is not random with respect to feeding ground affiliation. This hypothesis would be supported by a finding of significant differences in both mtDNA haplotype and microsatellite allele frequencies.

Support for the second hypothesis would indicate that groups of individuals feeding in northern and southern areas are demographically independent but not reproductively isolated, while support for the third hypothesis would provide support for both demographic independence and reproductive isolation.

METHODS

Sample Collection

A total of 277 samples were processed for this study. The majority of samples (n=185, including all samples collected between Northern California and British Columbia, Canada) were collected as biopsies from free-ranging individuals, with the remainder collected from individuals taken as part of the subsistence whaling (n= 75 samples from Chukotka) or from stranded individuals (n=17). Collection locations ranged from northern California to Barrow, Alaska and Chukotka, Russia (Figure 1).

For each of the biopsy samples collected, efforts were made to obtain a photograph of the biopsied whale. For whales biopsied between northern California and British Columbia, Canada, photographs were compared to photo-identification catalogues maintained by Cascadia Research Collective. This approach allowed sighting histories of individual individuals to be linked to samples and utilized (as described below) in the stratification of samples for comparisons.

Figure 1 shows that most of the PCFG samples utilized in this study came from the southern portion of the PCFG range. Although the original design of the study was to have both a Russian and a Barrow, Alaska strata, the sample size for the latter (n=14) was insufficient to characterize genetic frequencies from that area. We were therefore unable to directly address hypotheses about whether there are multiple demographically independent feeding units to the north of the Aleutian Islands.

Laboratory Processing

DNA extraction, PCR Amplification and Sequencing – DNA was extracted from samples using standard protocols. The 5' end of the hyper-variable mtDNA control region was amplified from extracted genomic DNA, using the polymerase chain reaction (PCR) and then sequenced using standard techniques (Saiki *et al.,* 1988; Palumbi *et al.,* 1991). DNA was amplified using a 25 ul reaction of 1ul DNA, 18.25 ul of water, 2.5 ul of buffer [10 mM Tris-HCl (pH 8.3), 50 mM KCl, 1.5 µl of 10 mM dNTP], 0.75 µl of each 10 µM primer, and 0.25 ul of Taq DNA polymerase. The PCR cycling profile consisted of 90°C for 2 min, followed by 35 cycles of 94°C for 50 sec, an annealing temperature of 60°C for 50 sec, and 72°C for 1 min, then a final extension of 72°C for 5 min. A 523 base pair region of the 5' end of the mtDNA control region was amplified using primers B (5’-TACCAAATGTATGAAACCTCAG - 3’; Rosel *et al.,* 1995) and TRO (5′- CCTCCCTAAGACTCAAGG-3′; developed at SWFSC). Both strands of the amplified DNA product were sequenced independently as mutual controls on the Applied Biosystems Inc. (ABI) model 3730 sequencer. All sequences were aligned using Sequencher v4.8

software (Gene Codes Corp., 2000). If discrepancies were found within the replication the sample was re-sequenced from extracted DNA. If the discrepancy was still not resolved, DNA was re-extracted from tissue and the sample was resequenced until the haplotype was confirmed. For a small number of samples (n=4), the mtDNA sequence contained an ambiguous base call which could not be resolved; these samples were excluded from the mtDNA analysis. In addition, if a sample was identified as having a mtDNA haplotype that was not found among any of the other samples, mtDNA amplification and sequencing was replicated to confirm the haplotype identity.

Nuclear DNA processing – Eight microsatellite loci isolated from other cetacean species were used to genotype the samples (Table 1). Extracted DNA was amplified using a 25 µl reaction of 1 µl of DNA, 18 µl of MilliQ water (Millipore, Bedford, MA), 2.5 µl of 10x PCR buffer (500 mM KCl, 100 mM Tris-HCl, pH 8.3, and 15 mM $MgCl_2$), 1.5 µl of 10 mM dNTP, 0.75 µl of each 10 µM primer, and 0.5 units of Taq DNA polymerase. The PCR cycling profile included 90 °C for 2.5 min, followed by 35 cycles of 94 °C for 45 sec, 1 min at the optimal annealing temperature (Table 1), and 72 °C for 1.5 min, then a final extension of 72 °C for 5 min. PCR products were assessed electrophoretically. Genotype data was generated on ABI's 3730 genetic analyzer and analyzed with ABI's Genemapper (version 4.0) software.

Sex determination - Samples were genetically sexed by amplification and Real-Time PCR (MX3000p, Stratagene Inc) of the zinc finger (ZFX and ZFY) genes. Sex was determined by the amplification pattern: males had two products and females had one (Morin *et al.,* 2005).

Quality Control – Quality control and sample tracking procedures, as detailed in Morin *et al.* 2010, were implemented for all laboratory processing by incorporating control samples (negative and positive) into all amplifications. In addition, a set of samples were randomly chosen to act as replicates for error tracking and error rate estimation. For these samples ("random replicates"), which represented ≥10% of all samples processed, the mtDNA sequence, sex, and microsatellite genotype were re-generated from DNA for each sample.

Analysis

Stratification of Samples – Two stratification hypotheses were tested in the analysis. The "Northern versus Southern" hypothesis assumed that individuals utilize each of these general regions in a relatively uniform manner such that sampling location within each stratum does not matter. The stratification used for the Northern-versus-Southern hypothesis included all samples described above (Figure 1). Those samples which were collected north of the Aleutian Island Chain were included in the "North" stratum, while all samples collected between northern California and southeastern Alaska (i.e. from within the described range of the PCFG) were included in the "South" stratum (Figure 1).

The second hypothesis is referred to as the "Fine-scale Feeding Aggregation" hypothesis. This hypothesis considers that there may be multiple feeding aggregations north of the Aleutians and hence sampling location within each stratum does matter. The only fine-scale area that was sampled adequately to capture genetic frequencies in the "North" stratum included the individuals hunted off Chukotka (Figure 2). The "Fine-scale Feeding Aggregation" hypothesis also used more stringent criteria than location and season to define individuals assigned to the PCFG stratum. The rationale for more stringent criteria is that photo-identification studies have indicated that whales utilizing the PCFG's seasonal range fall into two categories: 1) whales that return frequently and account for the majority of sightings, and 2) apparent stragglers from the migration that are sighted in only one year (Calambokidis *et al.,* 2010). The criteria for assigning samples to the PCFG stratum were intended to make this stratum representative of the first category of whales. Inclusion in the PCFG stratum for the "Fine-scale Feeding Aggregation" hypothesis relied on two criteria: 1) the sample was linked to a photographed animal with high or medium confidence, and 2) the photographed animal had been sighted two or more years within the season (June – November) and area representative of the PCFG.

Data Review – To avoid including duplicate samples, the Excel Microsatellite Toolkit (Park, 2001) was used to identify samples with identical genotypes, indicating that they may have been collected from the same animal. These sample pairs were then checked to see if they also shared the same mtDNA haplotype and sex, and, when possible, photo-identification records were used to confirm the genetic match. For all samples which shared identical mtDNA haplotypes, sexes, and genotypes, one sample from each pair was removed.

Genotyping Error Rate – For all plates of samples used to generate microsatellite genotypes, a random subset of samples, representing >10% of the samples on each plate, were assigned as replicates. Replicate and original genotypes were compared, and a per-allele error rate was calculated by determining the number of discrepant allele calls divided by the total number of allele calls compared across all loci.

Genetic Diversity – For the mtDNA, haplotypic diversity (h) and nucleotide diversity (π) were calculated using Arlequin 3.5.1.2 (Excoffier *et al.,* 2005). For the microsatellite data, the number of alleles per locus and observed and expected heterozygosities were calculated using custom R-code (eiaGenetics, available upon request[1]). Fstat (Goudet 1995) was used to calculate allelic richness for each stratum. Deviations from Hardy-Weinberg equilibrium (HWE) were assessed for each microsatellite locus using Genepop (version 4.0.11, Rousset 2008). Both the probability test (Guo & Thompson, 1992) and the test for heterozygote deficiency (Rousset and Raymond 1995) were conducted using the program defaults for the Markov chain parameters (10,000 dememorization steps, 20 batches, 5000 iterations/batch). Genepop was also used to test for linkage disequilibrium (LD) for each pair of loci. All tests were run for the combined dataset as well as for each stratum, and a sequential Bonferroni correction was applied across all tests for each stratum.

Genetic Structure – Pairwise estimates of genetic divergence were calculated using both F_{ST} and and Φ_{ST} (based on pairwise differences between sequences as the measure of genetic distance) for the mtDNA data as implemented in Arlequin 3.5.1.2 (Excoffier *et al.,* 2005). Statistical significance was assessed using 20,000 permutations. Fisher's exact test (Raymond & Rousset, 1995) was also used to test for mtDNA differentiation between strata using 100,000 replications to test for significance.

For the microsatellite data, F_{ST} (Weir &Cockerham, 1984), Jost's D (Jost, 2008), and a χ^2 test were used to assess genetic differentiation. These tests were implemented using custom code (eiaGenetics[1]) written in the statistical program language R (R Core Development Team, 2009). Statistical significance was determined from 10,000 permutations of each data set.

RESULTS

Data Review - Fifteen samples (including n = 11 samples collected from stranded whales) amplified at ≤5 microsatellite loci and were removed from the analysis. The remaining samples were genotyped for at least seven of the eight microsatellite loci. Fifty-six samples had microsatellite genotypes, mtDNA haplotypes, and sexes which matched at least one other sample in the dataset; these samples were removed from further analysis. No movements of animals between regions representing different strata were identified based on genetic matches (i.e., all samples sharing identical genetic profiles were part of the same stratum).

Genotyping Error Rate – Based on the samples randomly chosen for replication, a per-allele error rate of 0.16% was detected for the microsatellite data.

Genetic Diversity – Thirty-nine mtDNA haplotypes defined by 37 variable sites were identified from the 202 gray whale samples representing unique individuals (Table 2). Haplotype diversity (h) was high in all four strata ("Northern v. Southern" and "Fine-scale Feeding Aggregations") defined for the analysis (0.945 - 0.953). Nucleotide diversity (π) was also similar among the four defined strata (1.4 – 1.6%).

The frequency of each haplotype in the defined strata (including Barrow) is shown in Table 3. For the "Fine-scale Feeding Aggregations" strata, eighteen haplotypes were shared between Chukotka and the PCFG, with nine haplotypes found only in Chukotka and five haplotypes found only in the PCFG. For both Chukotka and the PCFG, many haplotypes were found in only one individual (n=12 haplotypes in Chukotka, n = 8 haplotypes in the PCFG).

The median-joining network shows the relationship among mtDNA haplotypes and their frequency in each stratum (Figure 4). MtDNA haplotypes from both Chukotka and the PCFG are dispersed throughout the network, and no phylogeographic pattern is apparent.

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A summary of microsatellite diversity for each locus is shown in Table 4. None of the tests for HWE were significant after the correction for multiple tests was applied. Significant linkage disequilibrium was found for only one pair of loci (EV14t and Gt023t) in the PCFG strata. No significant LD was found for these two loci in any of the other strata or for the combined dataset, so these loci were retained for the analysis.

Measures of genetic diversity for each stratum after averaging across loci are shown in Table 5. As in the comparisons of mtDNA diversity, nuclear diversity was similar across all strata.

Sex Ratio – A female bias was present among the samples, ranging from 1.3 – 1.5 females per male in each stratum (Table 6). This female bias is similar to that (1.47 females per male) described in Frasier *et al.* (In press) but contrasts with earlier studies (Steeves *et al.,* 2001; Ramakrishnan *et al.,* 2001). The male bias (1.7 males per female) described in Steeves *et al.* 2001 was based on a small sample size (n=16 samples). When the gender determination method utilized here was applied to the sample set used in the Ramakrishnan *et al.* 2001 study, only a slight male bias was identified (1.25 males/female). These results contrast with those presented in Ramakrishnan *et al.* (1.8 males/female) and indicates that an issue with the gender determination assay used at that time was responsible for falsely identifying some samples as males.

Genetic Structure – The results of the mtDNA comparisons are shown in Table 7. Low but statistically significant differences were detected when the PCFG stratum was compared with the North stratum (Φ_{ST} = 0.030, p= 0.0118; F_{ST}= 0.010, p=0.0052; Fisher's exact test p=0.0080) and with the Chukotka stratum (Φ_{ST} = 0.020, p=; F_{ST}= 0.012, p=0.0295; Fisher's exact test p = 0.0304). The F_{ST} comparisons for mtDNA were also significant when the North and South strata were compared (F_{ST}=0.007, p = 0.0272), although none of the other mtDNA comparisons involving the South stratum demonstrated significant differences. None of the comparisons across strata utilizing the microsatellite data were significant (Table 8), providing no evidence of nuclear structure among feeding areas.

DISCUSSION

The results presented here are consistent with the second hypothesis that was evaluated, indicating that utilization of at least some feeding areas is influenced by internal recruitment (e.g., matrilineal fidelity), but that individuals from different feeding grounds interbreed. The extent of differentiation, while significant, was low and was detected only in the mtDNA comparisons. Diversity within the PCFG strata was high and similar to that found among strata in the north.

The low level of mtDNA differentiation between strata, as well as the high diversity found in the PCFG, could be a reflection of relatively recent colonization (or re-colonization following depletion of the population by commercial whaling) of the PCFG area. If recruitment into the PCFG is driven exclusively by the return of individuals which followed their mothers to the area as calves, then over time those mtDNA haplotypes originally found only in males or non-reproducing females would be removed via genetic drift, while haplotypes found in females and their returning offspring would build to higher frequencies. By this process, genetic differences would develop between the PCFG and other feeding aggregations, and, given its small size, the PCFG would be expected to maintain low haplotypic diversity. However, if colonization of the PCFG area occurred relatively recently, strong mtDNA differences between the PCFG and individuals feeding further north may not have had time to develop, and the number and distribution of haplotypes in the PCFG may not yet have been affected by genetic drift.

The low level of mtDNA differentiation and high diversity is also consistent with a scenario in which the population structuring is largely driven by matrilineal fidelity (perhaps over longer time scales) but in which some low-level external recruitment also occurs. Some degree of external recruitment would slow the accumulation of genetic differences between the PCFG and northern individuals. As well, external recruits would likely carry haplotypes not previously found among PCFG individuals and would increase the number and diversity of haplotypes found.

These two explanations are not exclusive, and it is plausible that some combination of these scenarios (recent colonization and/or low-level external recruitment) may be occurring. The origin of the PCFG is unknown, and use of the area may date back to the "Little Ice Age" [ca. 1450-1850] when access to the Bering Sea feeding areas would have been limited by heavy ice and some whales may have started to use the PCFG range. Gray whales have been recorded feeding in the southern portion of the PCFG range as early as 1926, when a single gray whale, which was reported to have been feeding with four other whales, was taken by the Trinidad whaling station off the entrance to the Crescent City Harbor in July (Howell & Huey, 1930). The repeated return of individual whales to the area was first documented starting in the 1970s (Hatler & Darling, 1974; Darling, 1984). Photo-identification studies have identified some individuals that have consistently returned to the PCFG seasonal range over time, including some known reproductive females and their calves (Calambokidis *et al.,* 2010). However, "new" whales continue to appear annually and many are resighted in subsequent years (Calambokidis *et al.,* 2010). These new individuals may be internal recruits that were not sighted as calves, but could also be external recruits that return to the area following a successful feeding season. Even if some low-level external recruitment to the area is occurring, however, the differences in mtDNA haplotype frequencies observed in our comparisons indicate that matrilineal fidelity to the area does occur and is important in influencing population structure on the feeding grounds utilized by ENP gray whales.

Conception in gray whales is thought to primarily occur during a three week period between late November and early December (Nov 27 – Dec 13), although if no conception occurs during this first period, a second estrus may occur about 40 days later when whales are on or near their wintering grounds (Rice & Wolman, 1971). Rugh *et al.* (2001) estimate that the median (peak) sighting dates for the southbound migration are 12 December for Unimak Pass, Alaska, suggesting that many gray whales would be north of the PCFG seasonal range during the first mating period. In addition, of the eight individuals which had retained their satellite tags when they started the southbound migration, four (two males and two females) remained on the PCFG feeding ground after mid-December, with two staying until mid-January or later (Mate *et al.,* 2010). These findings raise the possibility that some segregation in breeding could occur based on feeding ground affiliation. However, while the results of the mtDNA comparisons indicate that matrilineal fidelity is generating structure among feeding areas utilized by ENP gray whales, the lack of differentiation found in the nuclear comparisons supports mixing of individuals from different feeding areas while breeding.

The genetic signal of matrilineal fidelity in the PCFG is less marked than that seen among gray whales feeding off Sakhalin Island in the western North Pacific (WNP). Although significant differences in F_{ST} and Φ_{ST} were observed in the mtDNA comparisons between the PCFG and the northern strata, the magnitude of differentiation is lower than that seen in the WNP versus ENP comparisons (F_{ST}=0.068, p≤0.001; Lang *et al.,* 2010). In addition, a pattern of matrilineal fidelity to the area is also reflected in the distribution of haplotypes among individuals in the western population, such that two haplotypes are found in very high frequencies (representing 36% and 31% of all sampled individuals, Lang *et al.,* 2010). This pattern would be expected if utilization of this area was driven in large part by the continued return over time of a small number of females and their offspring (and eventually their offspring's offspring), and examination of the haplotypes carried by individuals revealed that 16 of the 23 known reproductive females (between 1995 and 2007, Weller *et al.,* 2008) share one of these two common haplotypes (Lang, 2010). In the PCFG stratum, however, the three highest frequency haplotypes are found in only 10 to 13% of sampled individuals, which is consistent with more recent colonization of the PCFG area by a relatively large number of founders. In addition, genetic differentiation based on microsatellite allele frequencies was observed between the Sakhalin and ENP strata (F_{ST} = 0.009, p≤0.001; Exact test, p≤0.001), indicating that, unlike what has been suggested in the PCFG, some degree of reproductive isolation also occurs between these groups.

The results presented here are consistent with those presented in Frasier *et al*. (In press), which also found evidence of maternally driven structure when comparing samples collected from PCFG whales with samples from LeDuc *et al*. 2002, which were collected primarily from animals which stranded along the migratory route. The samples utilized in the Frasier *et al*. (In press) study were all collected from Clayoquot Sound, British Columbia. In contrast, the majority of samples representing the PCFG in this study were collected from animals in the waters off northern California, Oregon, and Washington, with only 11 samples collected from waters off British Columbia. Although some whales are known to move throughout the range of the PCFG, sightings of most whales are concentrated within subareas of the range (Calambokidis *et al*. 2010). This pattern is illustrated in Figure 7 of Calambokidis *et al.* (2010), which shows the distribution of latitudes of sightings for whales with 6 or more sightings after 1 June from 1998-2008. The patterns evident in this figure reveal that individual gray whales do not utilize the range of the PCFG randomly and indicate that, while there is likely overlap among the individuals sampled in Frasier *et al*. (In press) and the current study, neither represents random sampling across the range of the PCFG. To date, the photographs and/or genetic identities of sampled whales in the Frasier *et al*. (In press) study have not been compared with those used in the current study. In the future, such comparisons, along with the collection of additional samples from whales in the northern portion of the PCFG range, would be valuable in allowing sampling effort to be more evenly distributed throughout the range of the PCFG.

As aforementioned, the results presented here are consistent with the hypothesis that utilization of at least some feeding areas by ENP gray whales is influenced by internal recruitment. Within the PCFG, these findings are concordant with photo-identification records demonstrating site fidelity of individuals, including some known reproductive females and their calves, to the seasonal range (Calambokidis *et al.,* 2010). However, interpretation of the results is complicated by our lack of understanding of the potential for structuring within the northern feeding ground(s). If there is no structure on the feeding grounds north of the Aleutians, then the northern strata (both "north" and "Chukotka") can be considered representative of the genetic diversity of whales feeding throughout the northern feeding area. As such, the mtDNA differences observed here would be driven by fidelity of individuals to the PCFG seasonal range. However, if structuring is present among northern feeding areas, then the differences demonstrated here may be influenced by fidelity of individuals in either or both areas (Chukotka and PCFG). The collection of additional samples from northern feeding areas would be valuable in further elucidating the mechanisms creating the observed differences and in evaluating whether structuring is present among whales utilizing the northern feeding grounds.

Although the lack of nuclear differentiation found in our study indicates that gray whales from different feeding regions may be interbreeding, the significant differences in mtDNA haplotype frequencies that were identified in the study suggest that groups of gray whales utilizing different (northern versus southern) feeding regions are demographically independent. A similar pattern has been observed among humpback whales in the North Atlantic, where four feeding regions are present (Katona & Beard, 1990; Stevick *et al*., 2006). Within feeding regions, individuals demonstrate intra- and inter-seasonal site fidelity, with only low levels of interchange between regions (Stevick *et al*., 2006). Although most of the whales from these four feeding regions share a common mating ground in the West Indies (Katona & Beard, 1990; Clapham *et al.,* 1993; Palsbøll *et al.,* 1997; Stevick *et al.,* 1998), individuals utilizing the Gulf of Maine have been classified as a separate feeding stock, based on matrilineally-derived fidelity of individuals to this area and the assumption that, should this subpopulation be extirpated, repopulation by whales using adjacent areas would not occur on a management timescale (Waring *et al.,* 2000). It has been suggested that the timeframe for management should be, at most, decadal in scope (i.e., <100 years; Clapham *et al*., 2008).

Future Work - The low level of differentiation identified, as well as the high diversity found in the PCFG strata, may indicate relatively recent colonization of the PCFG but is also consistent with a scenario in which some low-level external recruitment into the PCFG may occur. Relatedness analysis, in which microsatellite genotypes are used to identify putative parent-offspring pairs, would provide insight into the proportion of internal versus external recruitment that is occurring. Such analysis would require genotyping additional microsatellite loci for sampled individuals and would benefit from the collection of additional samples from individuals within the PCFG.

As part of previous work exploring genetic differentiation between gray whales in the eastern and western North Pacific (Lang *et al.,* 2010), the genetic profiles of samples collected from individuals on the Sakhalin feeding ground (n=142) were compared to those generated from samples collected in the eastern North Pacific (n=136). Two individuals that were sampled off Sakhalin had matching genders, genotypes (n=13 loci), and mtDNA haplotypes to two individuals sampled off central California in 1995 (Lang, 2010). Although subject to caveats, these genetic matches may have represented movements of gray whales between the eastern and western North Pacific. Given that additional gray whale samples from feeding grounds in the ENP have been processed as part of this study, an expanded genetic comparison of all processed samples is currently underway to look for additional matches between the eastern and western populations.

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Figure 1. Map of sample collection locations showing the “Northern versus Southern” stratification

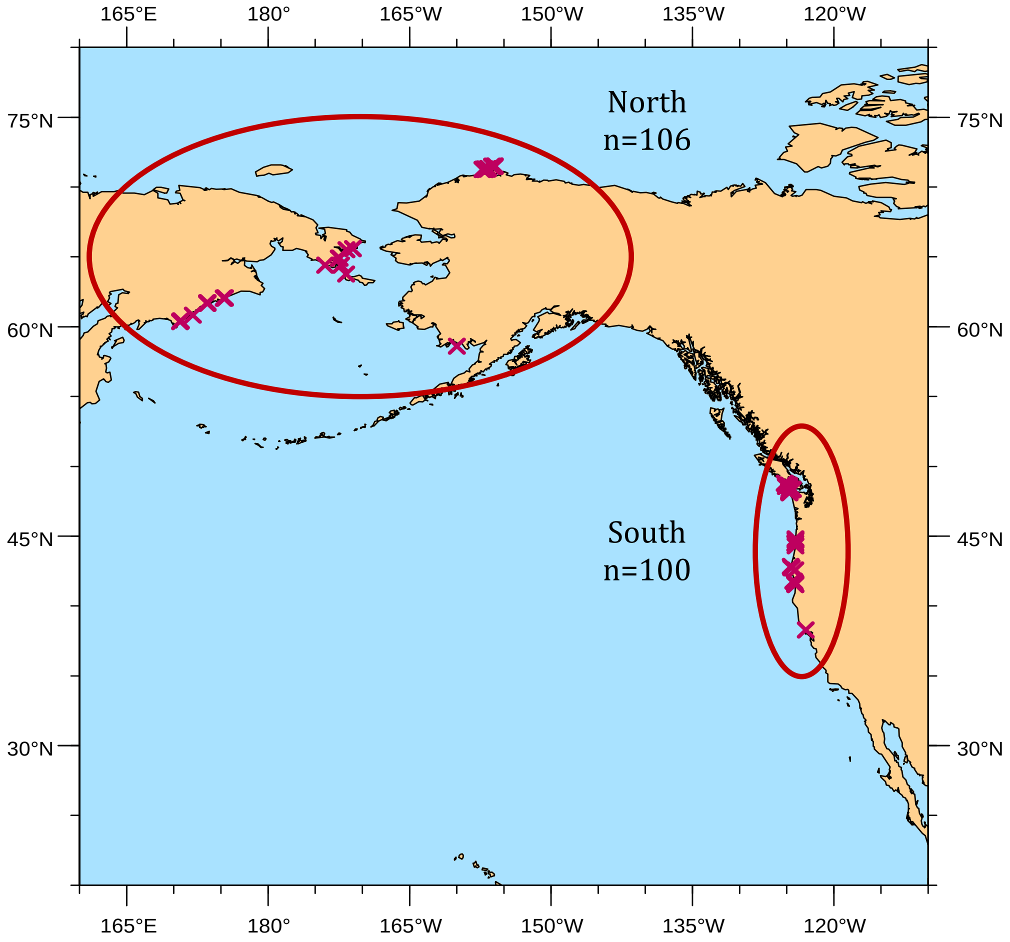

Figure 2. Map of sample collection locations showing the "Fine-scale Feeding Aggregations" stratification

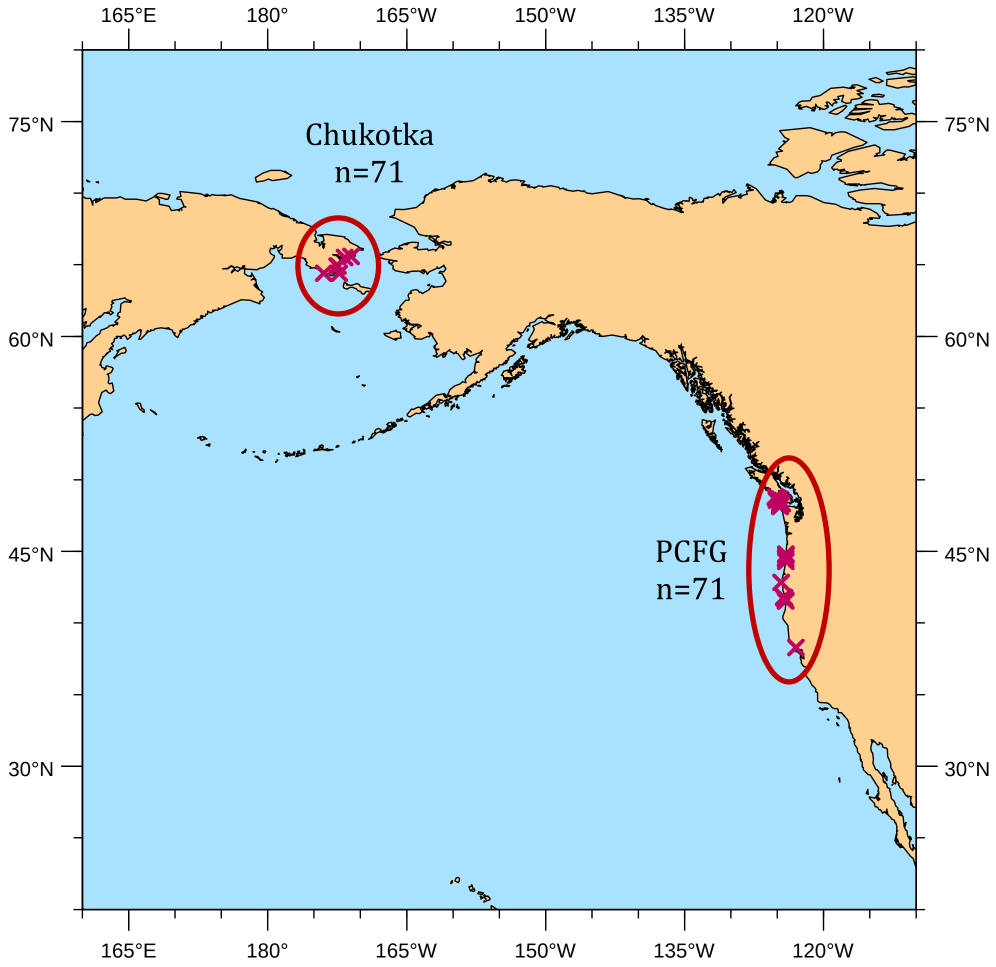

Table 1. Microsatellite loci used in the study. Includes the species for which primers were initially designed, size of repeats, annealing temperature (T_a), and reference listing primer sequences.[2]

Locus	Source Species	Repeat Size (bp)	T_a (°C)	Reference
EV14t	*Megaptera novaeangliae*	2	55	Valsecchi and Amos 1996
EV94t	*Megaptera novaeangliae*	2	52	Valsecchi and Amos 1996
Gata028t	*Megaptera novaeangliae*	4	54	Palsboll *et al.,* 1997
Gata417t	*Megaptera novaeangliae*	4	54	Palsboll *et al.,* 1997
Gt023t	*Megaptera novaeangliae*	2	54	Palsboll *et al.,* 1997
RW31t	*Eubalaena glacialis*	2	54	Waldick *et al.,* 1999
SW13t	*Physeter macrocephalus*	2	55	Richard *et al.,* 1996
SW19t	*Physeter macrocephalus*	2	55	Richard *et al.,* 1996

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[2] For all primers, the sequence has been modified from the original design by placing the sequence GTTTCTT on the 5' end of the reverse primer (Brownstein *et al.,* 1996)

Table 2. Sequence statistics for gray whale mitochondrial DNA control region sequences for the strata used in the population structure analysis

Strata		No. of Samples	No. of Haplotypes	Gene Diversity (h)	Nucleotide Diversity (π)
All		202	39	0.955 (±0.004)	0.0151 (± 0.008)
"Northern v. Southern"	North	103	32	0.952 (± 0.008)	0.0141 (± 0.007)
	South	99	29	0.953 (± 0.007)	0.0160 (± 0.008)
"Fine-scale Feeding Aggregations"	PCFG	71	23	0.945 (± 0.010)	0.0148 (± 0.008)
	Chukotka	69	27	0.953 (± 0.011)	0.0142 (± 0.007)

Table 3. The number of samples with each mtDNA haplotype for each stratum.

	"Northern v. Southern"		"Fine-scale Feeding Aggregations"		
MtDNA Haplotype ID	North (n=103)	South (n=99)	Chukotka (n=69)	PCFG 2 (n=71)	Barrow (n=14)
1	10	7	8	7	2
2	3	7	2	4	0
3	14	4	9	1	1
4	5	9	4	6	0
5	1	2	1	1	0
7	7	8	4	6	0
8	1	3	1	2	0
9	1	0	1	0	0
11	3	3	2	3	1
12	5	4	4	3	1
13	5	10	3	9	0
14	1	9	1	7	0
15	3	0	0	0	2
16	1	0	0	0	1
17	1	0	0	0	0
18	3	2	3	2	0
20	6	4	1	2	2
21	2	3	1	3	1
22	1	0	1	0	0
23	5	1	4	0	0
24	2	3	2	3	0
25	6	2	4	1	0
26	2	1	1	0	1
27	0	4	0	4	0
28	2	2	2	2	0
29	2	1	2	0	0
30	0	1	0	1	0
31	1	0	1	0	0
33	5	3	4	1	0
35	1	0	0	0	1
36	1	1	0	1	1
38	1	0	1	0	0
39	0	1	0	0	0
42	1	0	1	0	0
43	1	0	1	0	0
44	0	1	0	0	0
45	0	1	0	0	0
46	0	1	0	1	0
47	0	1	0	1	0

Figure 4. Median joining network

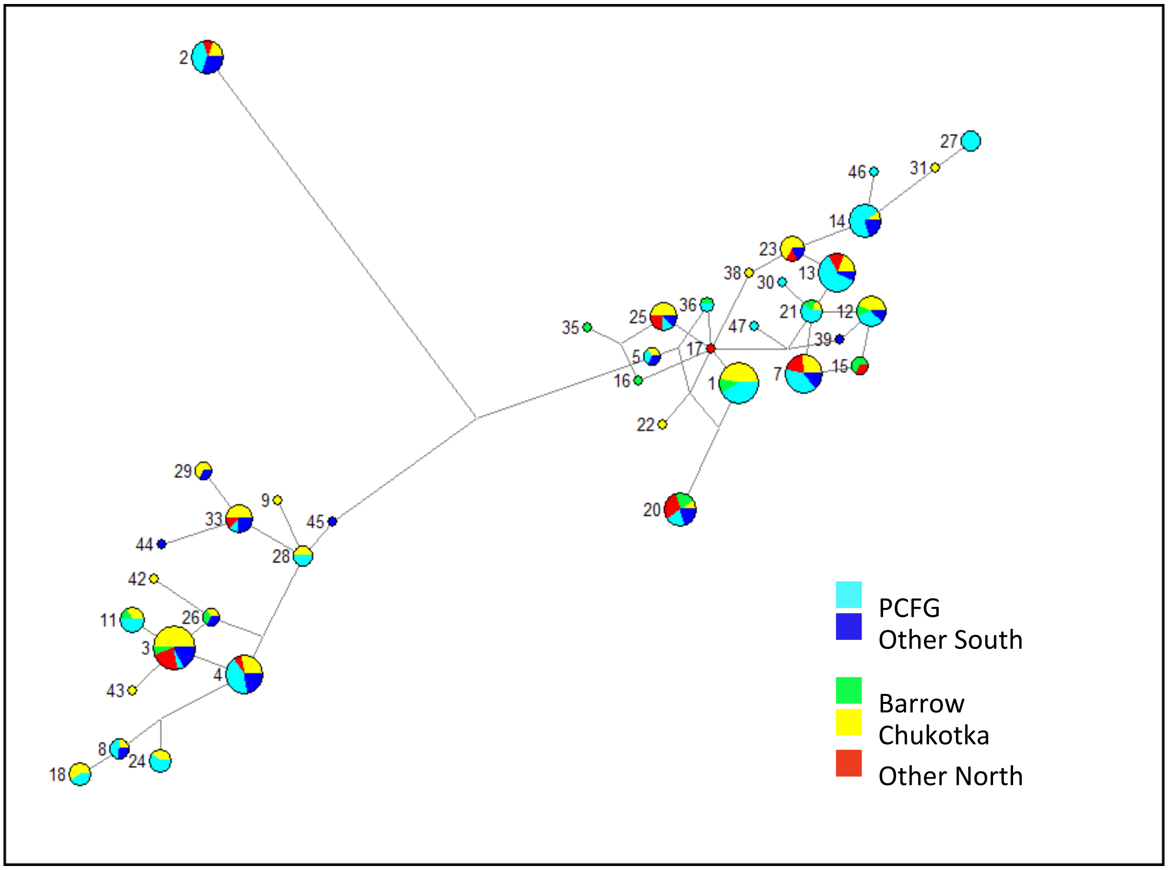

Table 4. Characteristics of the microsatellite loci utilized in the study.

Locus	Number of alleles	Number of missing genotypes	He	Ho	HWE (prob)
EV14t	10	0	0.829	0.850	0.533
EV94t	11	1	0.790	0.766	0.065
Gata028t	7	0	0.766	0.777	0.656
GATA417t	6	1	0.715	0.737	0.690
Gt023t	8	0	0.730	0.714	0.220
RW31t	10	0	0.830	0.782	0.017
SW13t	7	0	0.603	0.612	0.775
SW19t	10	1	0.709	0.707	0.213

Table 5. Gene diversity for the nuclear DNA data set, including the mean number of alleles, mean observed heterozygosity, and mean allelic richness.

Strata		No. of Samples	Mean number of alleles	Mean Ho	Mean allelic richness
"Northern v. Southern"	North	106	8.25	0.728 (±0.068)	8.18
	South	100	8.38	0.758 (±0.088)	8.36
"Fine-scale Feeding Aggregations"	PCFG	71	7.38	0.752 (±0.085)	7.37
	Chukotka	71	7.88	0.737 (±0.095)	7.86

Table 6. The sex ratio for each strata.

Strata		No. of Females	No. of Males	Ratio
Overall		117	85	1.4
"Northern v. Southern"	North	61	42	1.5
	South	56	43	1.3
"Fine-scale Feeding Aggregation"	PCFG	42	29	1.5
	Chukotka	41	28	1.5

Table 7. Results of MtDNA comparisons across strata. Significant p-values are shown in bold.

Pairwise Comparison	φst	p-value	F_{st}	p-value	Fisher exact test p-value
North (103) v. South (99)	0.006	0.1295	0.007	**0.0272**	0.0693
North (103) v. PCFG (71)	0.020	**0.0232**	0.012	**0.0052**	**0.0080**
Chukotka (69) v. South (99)	0.011	0.0872	0.005	0.0932	0.2234
Chukotka (69) v. PCFG (71)	0.030	**0.0118**	0.010	**0.0295**	**0.0304**

Table 8. Results of nuclear comparisons across strata

Pairwise Comparison	F_{st}	p-value	Jost's D	p-value	X^2 p-value
North (106) v. South (100)	-0.002	0.9740	-0.003	0.9491	0.9331
North (106) v. PCFG (71)	-0.002	0.8362	-0.001	0.8032	0.7532
Chukotka (71) v. South (100)	-0.002	0.9520	-0.003	0.9021	0.9021
Chukotka (71) v. PCFG (71)	-0.001	0.7303	0.000	0.6813	0.6364

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Assessment of population substructure in relation to summer feeding ground use in the eastern North Pacific gray whale

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ABSTRACT: The eastern North Pacific gray whale *Eschrichtius robustus* was removed from the US Endangered Species List in 1994, and since then aboriginal groups in Washington (USA) and British Columbia (Canada) have discussed the resumption of traditional whaling. In particular, the Makah are pursuing legal permission to resume their hunt. Although the majority of whales in this population migrate to summer feeding grounds in the Bering, Chukchi, and Beaufort Seas, a small number of individuals (~200) spend the summers feeding in the waters ranging from northern California to southeast Alaska. The relationship of these 'southern feeding group' whales to the rest of the population is unknown. This information is key to making appropriate management decisions, because these whales inhabit the waters directly adjacent to the aboriginal communities interested in resuming whaling. We compared mitochondrial sequence data from 40 southern feeding group individuals to sequences from 105 individuals representing the larger population. We found significant differences in haplotype frequencies between the 2 groups, with an estimated long-term rate of exchange between the groups being <<1 %. Moreover, estimates of Θ ($N_e\mu$ for mtDNA data, i.e. the probability of a mutation occurring within the population in each generation) were significantly different between the 2 groups, indicating that the maternal lineages of the southern feeding group represent a distinct seasonal subpopulation. Combined, these data show that the southern feeding group of gray whales qualifies as a separate management unit, which should be considered when making conservation decisions.

KEY WORDS: Gray whale · *Eschrichtius robustus* · Whaling · Population structure · mtDNA · Management unit

INTRODUCTION

The eastern North Pacific gray whale *Eschrichtius robustus* represents one of the few populations that have been removed from the US Endangered Species List, with the classification changing from 'endangered' to 'recovered' in 1994. Commercial whaling targeting gray whales in the eastern Pacific began in ~1845 (Henderson 1984) and reduced the population from an estimated 12 000–15 000 ind. to as low as 1500–1900 ind. by 1900 (Henderson 1984, Reilly 1992, Butterworth et al. 2002). International protection began in 1937, when the United States and Norway ended their gray whale hunts, but it was not until 1951 that all modern whaling countries agreed to stop hunting gray whales (Reeves 1984). Systematic surveys from 1967 to 1998 showed that the population increased at an annual rate of ~2.6 %, reaching as many as 30 000 ind. (Shelden & Laake 2002, Rugh et al. 2005). Current estimates hover around 20 000 ind., and

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there are even some suggestions that the population has reached carrying capacity (Moore et al. 2001, Wade 2002, Rugh et al. 2005, but see Alter et al. 2007 for an alternative perspective).

During the late fall and early winter, whales migrate to the lagoons of Baja California and the Gulf of California, which represent the winter calving grounds for this population (Swartz 1986, Findley & Vidal 2002, Swartz et al. 2006). During the spring, the majority of whales migrate to their northern feeding grounds in the Bering, Chukchi, and Beaufort Seas (Moore & Ljungblad 1984). However, a small subset of the population (~200 ind.) remains in more southerly feeding grounds ranging from northern California to southeast Alaska (Pike 1962, Hatler & Darling 1974, Darling 1984, Darling et al. 1998, Calambokidis et al. 2002, Swartz et al. 2006). These 2 subsets of the population will be referred to as the southern feeding group and the larger population, respectively.

Subdivision with respect to summer feeding ground use is common in baleen whales, and results from maternally directed site fidelity to different feeding grounds. For example, in humpback whales *Megaptera novaeangliae* and North Atlantic right whales *Eubalaena glacialis*, calves nurse for ~11 mo (and occasionally longer) and learn migration routes and the location of summer feeding grounds through cultural transmission from their mother (e.g. Baker et al. 1990, Malik et al. 1999). Thus, if there is differential use of feeding grounds by mothers, these preferences will be passed on to their offspring and result in substructuring with respect to summer feeding ground use. Gray whale calves nurse for a much shorter period of time (~6 mo; Swartz 1986). Although their length of lactation is still long enough to learn migratory routes and the location of summer feeding grounds, it is not yet clear whether gray whales show this maternally directed site fidelity. Because mitochondrial DNA (mtDNA) is maternally inherited, patterns of mtDNA diversity should reflect any maternally based patterns of movement and distribution. Therefore, analysis of mtDNA is ideal for testing hypotheses of maternally based site fidelity and subsequent population structure in baleen whales.

The relationship between the southern feeding group and the larger population is unknown. It is currently assumed that both of these groups use the same breeding ground, and therefore represent the same breeding population (e.g. Swartz et al. 2006). Given the known patterns in other baleen whale species, it seems likely that the southern feeding group and the larger population, and perhaps even smaller, as yet undefined subdivisions, result from maternally directed site fidelity to different feeding grounds by gray whale mothers. Photo-identification data are consistent with this hypothesis, showing that the majority of whales sighted in the southern feeding areas are re-sighted there in subsequent years, and therefore show the expected site fidelity (Darling 1984, Calambokidis et al. 2002, 2010). For example, Calambokidis et al. (2002) found that between 70 and 100% of the whales photo-identified off British Columbia had been sighted there in previous years. Moreover, the majority (63%) of calves first sighted in the southern feeding area with their mothers are resighted there in subsequent years, suggesting that this differential use of feeding grounds is indeed the result of maternally directed site fidelity (Calambokidis et al. 2010). This resighting rate is high, given the numerous factors that can reduce the resighting rates of calves, including: (1) mortality of individuals between their calf and subsequent year (as this age class has the highest mortality rate in many mammalian populations; Caughley 1966); and (2) changes in physical features that prevent re-identification (Calambokidis et al. 2010). However, preliminary genetic analyses of population structure based on mtDNA were inconclusive (Steeves et al. 2001).

Understanding the relationship between the southern feeding group and the rest of the population is of increasing importance due to the intention of some aboriginal communities to resume hunting gray whales. Several aboriginal groups traditionally hunted gray whales, but voluntarily stopped hunting as whale numbers decreased and/or were required to stop when the population received international protection (O'Leary 1984, Russell 2004). The exception was off Chukotka, Russia, where whaling was allowed to continue. In 1998, the Makah (in Washington, USA) resumed whaling and caught/killed a whale in 1999, but have been prevented from continuing since 2000 by litigation. Specifically, the Makah were given the right to hunt gray whales at traditional sites under the Treaty of Neah Bay in 1855. However, a final court ruling in 2004 determined that in order to resume their hunt, they must follow the necessary procedures for obtaining a waiver under the Marine Mammal Protection Act (MMPA). The Makah have applied for this waiver, and this request is still being processed. The outcome of the Makah application will have large implications for the resumption of whaling by other aboriginal communities in the area as well (Russell 2004).

The relationship of these 'southern feeding group' whales to the rest of the population is unknown. This information is key to making appropriate management decisions, because these whales inhabit the waters directly adjacent to the aboriginal communities interested in resuming whaling. The negative consequences of ignoring potential population structure when making management decisions, such as the extinction of unrecognized populations and/or species, are well known (e.g. Daugherty et al. 1990, Taylor 1997, Frankham et al. 2002). For the current gray whale situation, an understanding of population substructure in relation to known summer feeding ground use is required to infer how the whales in each feeding area, and the population as a whole, will respond to the removal of individuals through the proposed hunts. Therefore, if informed management decisions are to be made regarding resuming this hunt, it is first necessary to understand the relationship of this southern feeding group to the rest of the larger population. Here, we conducted analyses of the mitochondrial DNA of gray whales representing the southern feeding group, as well as the larger population, in order to better understand their relationship, and therefore inform management decisions.

MATERIALS AND METHODS

Sample collection. Skin samples were collected from whales representing the southern feeding group in Clayoquot Sound, British Columbia, from 1995 to 2006. Individuals of this group appear to move freely between specific feeding sites throughout this southern feeding range from northern California to southeast Alaska in summer (Calambokidis et al. 2002, 2010). Clayoquot Sound on central Vancouver Island is one such site (Darling 1984, Darling et al. 1998). Biopsy samples were collected using a crossbow and modified bolt (e.g. Lambertsen 1987, Palsbøll et al. 1991) or a pneumatic rifle biopsy system (Barrett-Lennard et al. 1996). The samples were collected in association with ongoing photo-identification research (e.g. Darling 1984), and the photo-identification data were used to ensure that individual whales were only represented once within the genetic data set. Moreover, the entire population migrates near this area on its northern and southern migrations. Therefore, samples were only used from whales sampled between 1 July and 15 November, i.e. the time period after which all northward migrants have passed and before which the first migrants start heading south (Darling 1984), to ensure that the sampled individuals actually represented the southern feeding group, as opposed to migratory animals. Tissue samples were stored in a 20% dimethyl sulfoxide (DMSO) solution (Seutin et al. 1991).

Genetic analysis. Approximately 40 mg from each sample was used for subsequent DNA extraction procedures. The skin was frozen in liquid nitrogen, ground to a fine powder, and transferred to a tube with 500 µl of lysis buffer (4 M urea, 0.2 M NaCl, 0.5% *n*-lauroylsarcosine, 10 mM 1,2-cyclohexanediaminetetraacetic acid, 100 mM Tris-HCl, pH 8.0). Samples were rotated in the lysis buffer at room temperature for ≥5 d, after which time they were subjected to 3 aliquots of Proteinase K, each at a concentration of 0.5 U mg^{-1} tissue. The addition of Proteinase K was as follows: after adding the first aliquot, samples were rotated at room temperature overnight; after adding the second aliquot, the samples were placed in a 65°C waterbath for 1 h, then transferred to a 37°C incubator for 1 h; after adding the third aliquot, the samples were rotated at room temperature overnight. Approximately 250 µl of the tissue/lysis buffer solution was subsequently extracted using Qiagen DNeasy Tissue Extraction Kits. DNA quantity was estimated using PicoGreen (Singer et al. 1997). Extracted samples included those previously analyzed by Steeves et al. (2001), which were re-extracted and analyzed here, along with the newly collected samples.

A 345 bp portion of the mitochondrial DNA control region was amplified using the primers t-PRO and Primer-2 from Yoshida et al. (2001). PCR cycling conditions consisted of: (1) an initial denaturation step of 5 min at 94°C; (2) 30 cycles of 94°C for 30 s, 57°C for 1 min, and 72°C for 1 min; and (3) a final extension step of 60°C for 45 min. Reactions were carried out in 20 µl volumes containing 1× PCR Buffer (20 mM Tris-HCl pH 8.0, 50 mM KCl), 0.05 U µl^{-1} *Taq* polymerase (Invitrogen), 1.5 mM $MgCl_2$, 0.2 mM each dNTP (Invitrogen), and 10 ng of DNA. After amplification, primers and unincorporated dNTPs were degraded using EXOSAP-IT (Dugan et al. 2002), and products were sequenced using the DYEnamic dye terminator kit (GE Healthcare). Products were size-separated and visualized on a MegaBACE 1000 (GE Healthcare). Sequences were edited using MEGA 4 (Kumar et al. 2008). Gender was determined for all individuals using the method described by Shaw et al. (2003).

Data analysis. To compare the data from southern feeding group whales to those of the larger population, we compared our mitochondrial sequence data to those reported by LeDuc et al. (2002). Their study reported mitochondrial sequences from 120 ind. representing eastern Pacific gray whales. The majority (>90%) of the samples were from stranded individuals found throughout their range, from southern California to the Chukotka Peninsula in Russia. The remaining samples were collected from subsistence takes, as biopsies of live whales, and from fisheries bycatch. Fifteen of the samples in LeDuc et al. (2002) were from southern feeding group whales. These were removed from the analyses, leaving 105 samples from the LeDuc et al. (2002) data set to compare with our data set of 40 ind. Because the vast majority of samples from the study by LeDuc et al. (2002) were from dead individuals (either stranded, as bycatch, or hunted), the chance of duplicate samples from the same individual being represented in their data is negligible. Given the number and geographic range of the sampled whales in the study by LeDuc et al. (2002), our rationale for choosing these for comparison was that these sequences would be a good representation of the larger population of eastern gray whales.

Sequences were aligned with CLUSTALX (Thompson et al. 1994). Alignments were conducted under a range of gap opening and extension penalties and compared by eye to establish the optimal alignment. The sequences were very similar, and all alignments were the same under the tested conditions. Haplotype and nucleotide diversity (π) (Nei 1987) were estimated using Arlequin ver. 3.5.1.2 (Excoffier et al. 2005). Variations between mtDNA sequences were recorded, and identical sequences were grouped into haplotypes. Final haplotype assignments were confirmed with FaBox ver. 1.35 (Villesen 2007). Population differentiation of the mtDNA sequences between the southern feeding group and the larger population was estimated using the analysis of molecular variance approach described by Excoffier et al. (1992) as implemented in the program Arlequin. The significance of the resulting estimates of F_{ST} and Φ_{ST} was tested using 1000 permutations. Relationships among haplotypes were visualized via a median-joining network using the program Network 4.5.1.6 (Fluxus Technology).

To gain insight into the nature of the observed population substructure, we estimated effective population sizes, migration rates, time since divergence, and growth rates for the 2 sample sets using the Isolation with Migration program (IM; Nielsen & Wakely 2001, Hey & Nielsen 2004, Hey et al. 2004). However, repeated trials with various parameter options suggested that there was not enough information in our data set to obtain accurate estimates for all of these values (data not shown). Instead, we focused on estimating just the effective population sizes and migration rates using the program MIGRATE (Beerli & Felsenstein 2001, Beerli 2006). The Bayesian inference approach was implemented, using a transition/transversion ratio of 11.22 and an α estimate of 0.09 for the gamma distribution of mutation rate heterogeneity among sites (both estimated using TREE-PUZZLE, Schmidt et al. 2002). We used the Metropolis-Hastings method of generating posterior distributions. The program was run with uniform prior distributions and 1 long chain. To ensure consistency between runs, MIGRATE was run 5 times with a burn-in of 100 000 steps, and a run length of 10 000 000 steps with data recorded every 500 steps. The likelihood ratio test option of MIGRATE was also used to test the hypothesis that the 2 sample sets have different effective population sizes. For the likelihood ratio test, 10 short chains and 1 long chain were run, with a burn-in of 50 000 steps. For the short and long chains, the run length was 10 000 000 steps with data recorded every 500 steps. Specifically, the hypothesis tested was $\Theta_{southern} = \Theta_{larger}$. Theta ($\Theta$) is a parameter that describes the genetic diversity within a population. The genetic variation existing within a single population is ultimately the result of mutations. The rate at which mutations are observed is a combination of the mutation rate (μ), which is how often mutations occur, and the effective population size (N_e), which represents how many 'opportunities' there are for mutations to occur in each generation. The product of these values represents the probability of a mutation occurring within the population in each generation, and this value is called Θ ($\Theta = N_e\mu$ for mitochondrial sequence data). With genetic data, we tend not to know the values of N_e and μ, but the data available are often the frequency of different DNA sequences and the number of mutations separating them. Thus, it is possible to estimate Θ from the data, and use that to make inferences of N_e and μ. Therefore, in this case we can assume that μ is the same for the southern feeding group and the larger population, and therefore comparisons of Θ estimates between the 2 groups directly correspond to comparisons of N_e.

RESULTS

DNA was extracted and mtDNA control regions sequenced from 40 gray whales representing the southern feeding group. Gender was determined for 37 of the 40 sampled whales, and resulted in 15 males and 22 females. This represents a slight female bias, which is contrary to previous studies, which obtained a slight male bias (Steeves et al. 2001). The sequencing protocol resulted in 336 bp of comparable sequence among individuals. Twenty-seven polymorphic sites were identified, which resulted in 18 haplotypes in the southern feeding group whales (Fig. 1). The sequences published in the study by LeDuc et al. (2002) (522 bp) were longer than those obtained here, and therefore all 336 bp from the southern feeding group sequences could be compared to those from the larger population. None of the variable sites or haplotypes identified in the southern feeding group were new; all were also represented by the sequences described by LeDuc et al. (2002) (Fig. 1). However, trimming the sequences of LeDuc et al. (2002) to the comparable 336 bp between the data sets did remove some variable sites that differentiated some of their haplotypes. Specifically, their haplotypes 'G' and 'O' were collapsed into 1 sequence (called 'G' in Fig. 1), haplotypes 'L', 'U,' and 'AD' were collapsed into sequence 'L,' and haplotypes 'AC' and 'AG' were collapsed into haplotype 'AC' (Fig. 1).

Although no haplotypes were found only in the southern feeding group samples, the distribution of

Haplotype	19	53	73	74	75	83	87	89	90	91	109	156	178	233	249	250	251	256	269	273	274	275	284	292	295	296	305	316	324	NFG	SFG	TOT
A	A	T	C	T	T	T	T	C	T	C	G	T	T	T	G	T	A	T	T	G	T	C	C	C	T	T	T	A	A	12	1	**13**
B	.	C	T	.	C	.	.	T	.	T	A	.	.	C	.	C	G	.	C	.	.	.	.	T	C	.	.	.	G	11	4	**15**
C	.	.	.	.	.	.	.	.	.	T	.	C	.	.	.	.	G	C	C	.	.	T	.	.	.	.	.	.	.	9	1	**10**
D	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	G	C	C	.	.	T	.	.	.	.	.	.	.	10	1	**11**
E	.	.	.	.	C	.	.	.	.	T	.	.	.	.	.	.	G	C	.	.	.	.	.	.	.	.	.	.	.	2	0	**2**
G	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	C	.	A	.	.	.	.	.	.	.	G	.	8	6	**14**
H	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	G	C	C	.	.	T	.	T	.	.	.	.	.	0	1	**1**
K	.	.	.	.	.	.	.	.	C	T	.	C	.	.	.	.	G	C	C	.	.	T	.	.	.	.	.	.	.	4	1	**5**
L	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	A	.	.	.	.	.	.	.	G	.	7	2	**9**
M	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	C	.	A	.	.	.	.	.	.	.	G	.	3	7	**10**
N	.	.	.	.	.	.	C	.	.	.	.	.	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	G	.	4	4	**8**
P	G	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	3	0	**3**
Q	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	1	0	**1**
R	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	G	C	C	.	.	.	.	T	.	.	.	.	.	3	1	**4**
S	.	.	.	.	.	C	.	.	.	T	.	.	C	.	.	.	G	C	C	.	.	T	.	T	.	.	.	.	.	1	0	**1**
T	.	.	.	C	.	.	.	.	.	T	.	.	.	.	.	.	.	.	.	.	.	.	T	.	C	.	.	.	.	6	3	**9**
V	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	.	.	C	.	.	C	.	.	.	.	.	.	.	.	2	0	**2**
W	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	G	.	1	1	**2**
X	.	.	.	.	.	C	.	.	.	T	.	.	.	.	.	.	G	C	C	.	.	T	.	T	.	.	.	.	.	1	0	**1**
Y	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	.	.	.	4	1	**5**
Z	.	.	.	.	.	.	.	.	.	T	.	C	.	.	.	.	G	.	C	.	.	T	.	.	.	.	.	.	.	2	1	**3**
AA	.	.	.	C	.	.	C	.	.	T	.	.	.	.	A	.	.	.	.	.	C	.	.	.	.	.	.	G	.	1	3	**4**
AB	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	C	G	.	C	.	.	T	.	.	.	.	.	.	.	2	0	**2**
AC	.	.	.	.	.	.	.	.	.	T	.	.	.	.	.	C	G	.	C	.	.	.	.	.	.	C	C	.	.	3	2	**5**
AE	.	.	.	C	.	.	C	.	.	.	.	.	.	.	A	.	.	.	.	.	C	.	.	.	.	.	.	G	.	1	0	**1**
AF	.	.	.	.	.	.	C	.	.	.	.	C	.	.	A	.	.	.	.	.	.	.	.	.	.	.	.	G	.	1	0	**1**
AH	.	.	.	.	C	.	.	.	.	T	.	.	.	.	.	.	G	C	C	.	.	T	.	.	.	.	.	.	.	1	0	**1**
AI	G	.	.	.	.	.	.	.	C	.	.	.	.	.	.	.	.	C	.	.	.	T	T	.	.	.	.	.	.	1	0	**1**
AJ	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	G	C	.	.	.	.	.	.	.	.	.	.	.	1	0	**1**
																										Total				**105**	**40**	**145**

Fig. 1. *Eschrichtius robustus.* Variable sites characterizing haplotypes from both sample sets of gray whales. NFG, SFG, and TOT (top right) indicate the number of individuals from the northern feeding group (i.e. the larger population), the southern feeding group, and the total number of individuals with each haplotype, respectively

haplotypes was significantly different between the 2 groups, with values of 0.0125 for F_{ST} ($p = 0.0303$) and 0.0311 for Φ_{ST} ($p = 0.0254$). The median-joining network shows that although there is some differentiation between the haplotypes from the 2 feeding groups, for the most part the haplotypes from each are scattered throughout the network (Fig. 2). Haplotype diversity and π were estimated at 0.928 and 0.0199, respectively, for the southern feeding group. These values are very similar to estimates obtained for samples representative of the larger population, which were 0.95 and 0.016, respectively (LeDuc et al. 2002).

The results from the MIGRATE analyses are shown in Table 1. Estimates for each value are very similar across iterations, suggesting that the program was run long enough to reach convergence on the estimates. The estimates of Θ for the southern feeding group and the larger population are clearly different. This observation was confirmed by the likelihood ratio test, which rejected the hypothesis of $\Theta_{southern} = \Theta_{larger}$ ($p < 0.001$). The 95% confidence intervals for the migration rate estimates are extremely large, making them uninformative. This result is not surprising, however, because the approach implemented by MIGRATE is known to recover precise and accurate estimates of Θ even in situations where there is not enough information in the data to recover meaningful migration rate estimates (Beerli 2006).

Because the sample of haplotypes found in the southern feeding group represents a subset of the haplotypes found in the larger population (albeit at different frequencies), we conducted further analyses to ensure that our results were not simply due to the effect of sampling. For this assessment, we generated a new set of 40 sequences (representing a simulated southern feeding group data set) by randomly sampling the sequences of LeDuc et al. (2002), using R (R Development Core Team 2009). Thus, this process generated a simulated data set for the southern feeding group under the hypothesis that it represents a random subset of the larger population. This process

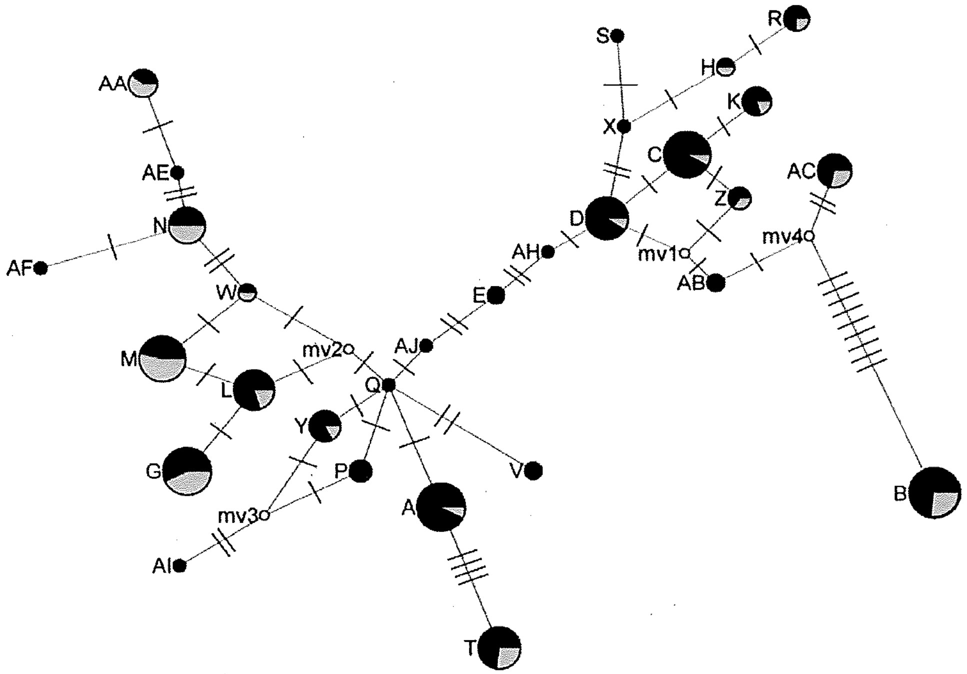

Fig. 2. *Eschrichtius robustus.* Median-joining network for the gray whale sequences. Transitional mutations are indicated with a line, with the number of lines showing the number of transitional mutations. Lengths of the lines connecting nodes are not proportional to the number of mutations. Sizes of the circles are proportional to the haplotype frequencies in the entire data set. Pie charts indicate the proportion of that haplotype found in the larger population (black) and southern feeding group (gray). 'mv' nodes represent inferred nodes that are missing from the data set

was repeated 10 times, generating 10 simulated data sets containing the data from LeDuc et al. (2002), as well as the simulated data for the southern feeding group. Analyses of F_{ST} and Φ_{ST} were conducted for each simulated data set using Arlequin, as were likelihood ratio tests for testing the hypothesis of $\Theta_{southern} = \Theta_{larger}$ using MIGRATE, under the same conditions as were used for the original data.

Table 1. *Eschrichtius robustus.* Results from the MIGRATE analysis. Included is the estimated mean for each parameter, as well as the 95% credibility intervals in parentheses (both obtained using the Bayesian approach in MIGRATE). M is the immigration rate m divided by the mutation rate μ. For mitochondrial DNA data, the number of immigrants per generation can be calculated by multiplying M by Θ. Included are the estimates for each of the 5 iterations of the program, as well as the average across all 5 iterations. Southern and larger indicate the southern feeding group of the eastern North Pacific gray whale population, and larger population, respectively

Iteration	Θ_{larger}	$\Theta_{southern}$	$M_{southern-larger}$	$M_{northern-southern}$
1	0.0430 (0.0220–0.0690)	0.0206 (0.00550–0.0380)	522 (205–860)	572 (250–920)
2	0.0462 (0.0235–0.0735)	0.0199 (0.00550–0.0385)	516 (190–865)	565 (245–960)
3	0.0437 (0.0205–0.0730)	0.0208 (0.00650–0.0385)	523 (195–870)	562 (210–920)
4	0.0421 (0.0165–0.0715)	0.0212 (0.00650–0.0425)	515 (190–865)	572 (240–950)
5	0.0430 (0.0200–0.0710)	0.0220 (0.00650–0.0445)	480 (175–810)	526 (195–875)
Avg	0.0436 (0.0205–0.0716)	0.0209 (0.00610–0.0404)	511 (191–854)	559 (228–925)

None of the simulated data sets showed significant signs of structuring based on F_{ST} or Φ_{ST}, and none showed significant differences in estimates of Θ (Table 2). Thus, the significant differentiation found for the real data set, based on all 3 of these analyses, suggests that the observed differentiation is indeed real, and not just an artifact of sampling.

DISCUSSION

The conservation and/or management of wildlife populations requires knowledge of how individuals are subdivided into separate entities that have relatively independent demographic processes, which are often referred to as 'management units' (MU). Such information is required to identify how each unit, and the popu-

Table 2. *Eschrichtius robustus*. Results from simulation tests under the hypothesis that the southern feeding group represents a random sample of the data set from LeDuc et al. (2002). Included are the F_{ST} and Φ_{ST} estimates, and associated p-values (in parentheses), from Arlequin, as well as p-values from likelihood ratio tests conducted in MIGRATE testing the hypothesis of $\Theta_{southern} = \Theta_{larger}$, where southern is the southern feeding group of the eastern North Pacific gray whale population, and larger is the larger population (not including the southern feeding group)

Iteration	F_{ST}	Φ_{ST}	$\Theta_{southern} = \Theta_{larger}$ p
1	−0.01136 (0.9991)	−0.01489 (1.000)	0.9882
2	−0.00180 (0.5699)	−0.00266 (0.5122)	0.7236
3	0.00019 (0.4018)	−0.00673 (0.7224)	0.1658
4	−0.00980 (0.9863)	−0.01235 (0.9717)	0.9421
5	−0.01047 (1.000)	−0.01156 (0.9609)	0.1167
6	−0.00578 (0.8651)	−0.00873 (0.8358)	0.9632
7	−0.00445 (0.7859)	−0.01000 (0.9042)	0.9805
8	0.00146 (0.3744)	−0.00448 (0.6090)	0.1023
9	−0.00419 (0.7468)	−0.00889 (0.8436)	0.7233
10	−0.00531 (0.82796)	0.00425 (0.2678)	0.2074

lation as a whole, will respond to exploitation and/or unintentional impacts. Moritz (1994) was the first to provide a working definition of MUs in a population genetics context, and defined them as

> ...populations with significant divergence of allele frequencies at nuclear or mitochondrial loci, regardless of the phylogenetic distinctiveness of the alleles. (p. 374)

While this definition has been widely applied in population genetics studies, it has recently been argued that MUs should be defined based on criteria demonstrating demographic isolation rather than simply rejecting the hypothesis of panmixia (Waples & Gaggiotti 2006, Palsbøll et al. 2007, Waples et al. 2008). This idea makes intuitive sense, because the true question for management is whether the units will respond differently to the pressures of concern (e.g. exploitation and/or unintentional mortality). However, there is a disconnect between inferring demographic independence and genetic estimates of differentiation because populations can be demographically independent even when long-term migration rates are high enough to result in relative genetic homogeneity (Waples & Gaggiotti 2006, Waples et al. 2008).

The data presented here show that the southern feeding group of gray whales represents a distinct MU under both of these criteria. The analysis showing statistically significant differentiation of mitochondrial haplotypes demonstrates qualification as an MU under the criteria of Moritz (1994). Moreover, the analysis showing that the effective sizes of both groups are different ($\Theta_{southern} \neq \Theta_{larger}$) shows that the maternal lineages of the southern feeding group represent a distinct seasonal subpopulation. Indeed, if they were not an independent unit but instead just represent different samples from the same mitochondrial 'population,' then estimates of Θ from the 2 data sets should converge on the same value. Thus, the southern feeding group qualifies as a separate MU under the criterion of Palsbøll et al. (2007). Combined, these data show that the southern feeding group requires separate management consideration with regards to resuming whaling.

Hastings (1993) showed that populations behave in a demographically independent manner when migration rates are less than ~10%. We have intentionally not converted Θ estimates to N_e estimates because this requires knowledge of the substitution rate (μ). Estimates of μ for the control region of baleen whale mtDNA vary by over an order of magnitude (e.g. Rooney et al. 2001). Moreover, μ, whatever its true value is, is undoubtedly the same for the southern feeding group and the larger population, and therefore comparing estimates of Θ is an appropriate and less controversial method for comparing N_e. Regardless, if we apply the μ estimate of 1.0×10^{-10} mutations $site^{-1}$ yr^{-1}, estimated by Alter & Palumbi (2009) for North Pacific gray whales, the resulting estimates of migration rates are << 1%. In this case, we are not dealing with migration rates between reproductive populations per se, but rather exchange rates between maternally based feeding groups. As with the haplotype frequency data, this result shows that the southern feeding group represents a distinct seasonal subpopulation.

Estimates of Θ represent long-term averages over the lifetime of the population; therefore, these genetic analyses provide information on an evolutionary time scale, whereas wildlife managers are generally more interested in the current state of a population (e.g. at the ecological time scale; Waples et al. 2008). To address this disconnect, we reiterate that photo-identification data of contemporary individuals also results in the same conclusion that the southern feeding group represents a distinct seasonal subpopulation based on maternally directed site fidelity. Photo-identification data show that the majority of whales sighted in the southern feeding areas are re-sighted there in subsequent years (Darling 1984, Calambokidis et al. 2002), and that the majority of calves first sighted in the southern feeding area with their mothers are re-sighted there as juveniles and adults (Calambokidis et al. 2010). Therefore, the combination of photo-identification and genetic data suggests distinct subdivision of the southern feeding group at both the evolutionary and contemporary (or ecological) time scales.

We reiterate that the southern feeding group likely mates with the rest of the population in the winter breeding grounds, and that the structuring we see is the result of maternally directed site fidelity to different feeding grounds. We used mtDNA (rather than nuclear markers) to test this hypothesis specifically for this reason, because such a pattern would be reflected in mtDNA and not nuclear DNA. This type of population substructure is common in whales (e.g. Hoelzel 1998), and has proven important for management. The rationale is that, because of this site fidelity, knowledge of specific feeding areas is only present within certain matrilines. Therefore, if whales are extirpated from a specific feeding ground, they will not be 'replaced' (or the area will not be re-populated) by others from the larger population because knowledge of that feeding area has been lost. Indeed, such localized extinctions and lack of subsequent re-population of areas (despite an increasing overall population size) is widely documented in whales (e.g. Northridge 2008). Thus, the combined genetic and photo-identification data showing that the southern feeding group represents a distinct maternally based seasonal subpopulation indicate that these whales require separate management consideration from the larger population.

Previous studies have suggested that the haplotype diversity in the southern feeding group is too high to have resulted from strict maternally directed site fidelity beginning with a few founders after the cessation of commercial whaling within the past century (Ramakrishnan et al. 2001). Under the hypothesis that this group was founded after the cessation of whaling, only a few closely related haplotypes should be represented within the southern feeding group, as opposed to the pattern seen in Fig. 2. In addition, the hypothesis of a founding event within the past century is not consistent with the known sighting information. Indeed, gray whales have been seen in the southern feeding grounds throughout their history, including in times of lowest abundance (Swartz et al. 2006, and references therein). Moreover, if a few individuals recently founded the southern feeding group, then the estimate of Θ_{southern} should be substantially smaller, as effective population size estimates are heavily influenced by bottlenecks.

Instead, what the sighting and genetic data suggest is that the southern feeding group of gray whales predates whaling. Under this hypothesis, the haplotype diversity is expected to be high, because those lineages that survived whaling would be a random sample from a much larger population. Substantial gaps would also be expected between existing haplotypes resulting from the removal of haplotypes by whaling. This pattern is exactly what is seen in Fig. 2. The similarity of haplotypes, and the degree of haplotype sharing between the southern feeding group and the larger population, both suggest some degree of migration between the 2 groups. However, although reliable estimates of migration rates could not be obtained here, the data clearly show that the rate of migration is low enough for the 2 groups to represent independent demographic entities. The southern feeding group therefore qualifies as a separate MU, and requires separate management consideration.

A larger sample set, and the analysis of more molecular markers (particularly nuclear markers), is obviously desirable for addressing topics such as this one. Moreover, it is possible that further structuring within each of these identified groups exists, but is as yet undetected. However, given the clarity of the results obtained and the implications that they have for the management of these whales, it seemed important to publish these data as soon as possible so that they could be available for informing management decisions. We are currently collecting more samples and collaborating with other scientists to increase the number and geographical representation of our sample set. Protocols for analyzing nuclear loci are also being developed. Combined, these efforts will allow for larger-scale analyses of this issue in the near future.

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Lack of nuclear differentiation suggests reproductive connectivity between the 'southern feeding group' and the larger population of eastern North Pacific gray whales, despite previous detection of mitochondrial differences

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ABSTRACT

During winter, eastern North Pacific gray whales migrate south to calving grounds in the lagoons of Baja California, and in spring they migrate north to their summer feeding grounds in the Chukchi and Beaufort Seas. Although the majority of the population makes this migration, a small subset of the population known as the 'southern feeding group' ends their northward migration early, spending summers feeding in waters ranging from northern California to southern Alaska. Previous analyses based on photo-ID and mtDNA data indicate that this seasonal substructuring results from maternally-directed site fidelity to different feeding grounds, and that this site fidelity and feeding ground preference is passed from mothers to their offspring. It is currently assumed, but not known, that the individuals of the southern feeding group mate with the rest of the population, and therefore that the eastern North Pacific gray whale represents one interbreeding population. Testing this assumption and understanding how these whales are related to the rest of the population, is key to making appropriate management decisions, which are particularly relevant given the recent increase in potential removals, or threats in the area such as the proposed resumption of aboriginal whaling, and increased oil pipeline development and subsequent vessel traffic. This paper analyses 15 nuclear microsatellite loci in 59 individuals from the southern feeding group and 40 individuals from the calving lagoons (representative of the larger population) to test the hypothesis that the eastern North Pacific gray whale represents one interbreeding population. No indication of population substructuring was found based on these nuclear loci, suggesting that all sampled whales do indeed represent one interbreeding population. Combined, these data from mitochondrial and nuclear markers therefore suggest one interbreeding population that is seasonally subdivided based on maternally-directed site fidelity to different feeding areas.

KEYWORDS: EASTERN NORTH PACIFIC; GRAY WHALE; REPRODUCTION; WHALING–ABORIGINAL; FEEDING GROUNDS; GENETICS; SITE FIDELITY; SEGREGATION

INTRODUCTION

The eastern North Pacific gray whale (*Eschrichtius robustus*) was extensively hunted from the mid-1800s through the early 1900s, reducing the population to just a fraction of its estimated pre-exploitation population size (Butterworth *et al.*, 2002; Henderson, 1984; Reilly, 1992). However, since gaining international protection, the population has steadily increased to roughly 20,000 individuals (Laake *et al.*, 2012; Rugh *et al.*, 2005; Sheldon and Laake, 2002). This recovery resulted in the removal of this population from the US Endangered Species List in 1994, and some data suggest it has recovered to its pre-exploitation population size (Alter *et al.*, 2007; Moore *et al.*, 2001; Rugh *et al.*, 2005; Wade, 2002). Despite this recovery, the population is still faced with numerous threats throughout its range, particularly in the area encompassing the Pacific northwest of the USA and the Pacific southwest of Canada (roughly Northern California through southeast Alaska). Here, there are several proposed activities where informed management will be critical. These include the proposed resumption of gray whale hunts by some aboriginal groups, the development of new oil pipelines off the British Columbia coast and the subsequent increase in tanker traffic for shipping oil to Asia.

One of the primary topics of relevance to management is population structure: how individuals are divided in space and/or time such that some groups may be differentially affected by direct hunting or by non-intentional threats. If such structuring exists, then the different groups often require separate management/conservation consideration because the detrimental effects will not be spread evenly throughout the population, but instead will disproportionally affect the different groups (e.g. Hoelzel, 1998; Taylor, 2005; Wang, 2009). Such localised impacts on structured populations, if not considered, can nullify otherwise well-planned management/conservation initiatives. Indeed, there are several case studies where the effectiveness of conservation actions has been compromised because population structure was not taken into consideration (e.g. Daugherty *et al.*, 1990; Frankham *et al.*, 2002).

Previous studies have detected seasonal population substructuring in the eastern North Pacific gray whale in relation to summer feeding ground use (Frasier *et al.*, 2011). As with many other baleen whales, gray whales show a seasonal migration from low-latitude calving grounds in the winter to high-latitude feeding grounds in the summer. The winter calving grounds for this population are located in the lagoons of Baja California (Findley and Vidal, 2002; Swartz, 1986; Swartz *et al.*, 2006), whereas during the summer the majority of the population feeds in the Bering and Chukchi Seas (Moore and Ljungblad, 1984). However, there is a small

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subset of the population—estimated at roughly 200 individuals (Calambokidis *et al.*, 2002) that spends the summer in lower-latitude feeding areas ranging from northern California to southeastern Alaska (Calambokidis *et al.*, 2002; Darling, 1984; Hatler and Darling, 1974; Pike, 1962; Swartz *et al.*, 2006). This group is often referred to as the 'southern feeding group', but is also referred to as the 'Pacific coastal feeding group' by the Scientific Committee of the International Whaling Commission (IWC, 2011; 2013a). Data from photo-ID and mitochondrial DNA (mtDNA) show that this seasonal population substructuring results from maternally-directed site fidelity to different feeding areas, and that this differential use of feeding areas is passed from mothers to offspring (Calambokidis *et al.*, 2002; Calambokidis *et al.*, 2010; Darling, 1984; Frasier *et al.*, 2011). This type of seasonal substructuring is common in baleen whales (e.g. Baker *et al.,* 1990; Malik *et al.,* 1999).

Despite this substructuring during the summer, it has always been assumed, but not known, that individuals from all feeding areas utilise the same mating area(s), and therefore represent one interbreeding population. Unfortunately, there is a lack of clarity regarding where fertilisation likely occurs, and hence where the mating grounds are. Sexual behaviour is frequently observed on the winter calving grounds (e.g. Swartz, 1986), and indeed these are often referred to as 'breeding grounds' (e.g. Alter *et al.*, 2009; Goerlitz *et al.*, 2003; Jones, 1990). However, the limited physiological data available actually suggest that fertilisation most often occurs during the southward migration, prior to arrival at the lagoons (Rice and Wolman, 1971). Thus, there is potential for differential feeding area use to also result in substructuring with respect to reproductive patterns.

There is also evidence that individuals show differential use of the calving grounds, with some females showing fidelity to particular lagoons (Jones, 1990; Goerlitz *et al.*, 2003; Alter *et al.*, 2009). Combined, there are enough questions regarding the timing and location of mating, as well as potential for differential habitat use of potential 'breeding' grounds, to warrant a full evaluation of the hypothesis of one interbreeding population. This paper uses data from nuclear microsatellite loci to compare genetic data from individuals of the southern feeding group to samples obtained from one of the calving lagoons (Laguna San Ignacio) used here as representatives of the larger population to test the hypothesis that individuals of the southern feeding group interbreed with individuals from the larger population. These data, in combination with previous information regarding structuring of mitochondrial haplotypes, can identify the degree of substructuring of the southern feeding group.

METHODS

Sample collection

Samples used for these analyses were collected over many years as part of other long-term research programmes on eastern North Pacific gray whales: off Vancouver Island, Canada by one of the authors (JDD); and off San Ignacio Bay, Mexico by another (JUR). Specifically, 86 samples from Vancouver Island (representing the southern feeding group, collected from 1996–2010) and 51 samples from San Ignacio Bay (representing the larger population, collected from 1996–1997) were analysed. All samples were collected using a crossbow and a modified bolt, as is common for collecting small skin samples from free-ranging large whales (Lambertsen, 1987; Palsbøll *et al.*, 1991). This method of sample collection has been extensively scrutinised, has proven to be safe, and does not have any short- or long-term impacts on the whales, other than an immediate startle response (Best *et al.*, 2005; Brown *et al.*, 1991). All sample collection procedures were conducted under permits obtained from the relevant governmental agencies. The timing of sample collection overlaps between the two sample sets, as is appropriate for comparison. The longer time for sample collection off Vancouver Island should not bias the results because the long life span and generation time of gray whales suggest that substantial genetic change within this putative population would take longer than the time interval sampled here. Thus, both sample sets should represent comparable genetic pools for analysis.

Genetic analyses

DNA was extracted from ~40mg of tissue from all samples using standard phenol:chloroform procedures as commonly used for whale skin (e.g. Wang *et al.*, 2008). The quantity of DNA obtained from each sample was estimated based on spectrophotometry using a NanoDrop 2000 (Thermo Scientific Inc.). The quality of DNA obtained (i.e. the amount of DNA degradation) was assessed based on electrophoresis through 2.0% agarose gels stained with SYBR Green I (Invitrogen). Sex was determined for each sample based on PCR amplification of a region on the X and Y chromosomes using the primers described in Gilson *et al.* (1998).

To identify useful microsatellite markers for this study, 23 loci were screened for amplification and variability in gray whales (Table 1). These loci were chosen because previous experience showed that they amplify well, and are highly variable, across a wide range of whale species. Specifically, loci were initially tested based on the amplification of two gray whale samples (one from the southern feeding group and one from the larger population) using annealing temperatures of 50, 55 and 60°C. The reactions contained 10ng of template DNA, 1X PCR Buffer (20 mM Tris pH 8.4, 50 mM KCl), 1.5 mM $MgCl_2$, 0.05 U/µl *Taq* DNA polymerase (Invitrogen), 0.2 mM each dNTP (Invitrogen), 0.3 µM each primer, and 0.1 mg/ml of bovine serum albumin (BSA) (Invitrogen). The cycling conditions were as follows: an initial denaturing step of 94°C for 5 minutes; 30 cycles of 94°C for 30 seconds, annealing temperature for 1 minute, and 72°C for 1 minute; followed by a final extension step of 60°C for 45 minutes. All PCR was conducted on Veriti® 96-well thermal cyclers (Applied Biosystems). PCR products were then size-separated and visualised via electrophoresis through 1.5% agarose gels stained with ethidium bromide. Loci that showed a clean PCR product (without amplification of multiple regions) were selected for further development.

For primer pairs that amplified well, the forward primer was re-ordered with one of four fluorescent tags (6FAM-Blue, VIC-Green, PET-Red, or NED-Yellow). Each locus was then screened for variation by amplifying 10 samples using the optimal conditions that had previously been

Table 1

Name, and reference for each of the 23 microsatellite loci tested for amplification and variability in gray whales.

Locus	Reference
EV1*Pm*	Valsecchi and Amos (1996)
EV5*Pm*	Valsecchi and Amos (1996)
EV14*Pm*	Valsecchi and Amos (1996)
EV37*Mn*	Valsecchi and Amos (1996)
EV94*Mn*	Valsecchi and Amos (1996)
EV104*Mn*	Valsecchi and Amos (1996)
FCB1	Buchanan *et al*. (1996)
FCB4	Buchanan *et al*. (1996)
FCB5	Buchanan *et al*. (1996)
FCB14	Buchanan *et al*. (1996)
FCB17	Buchanan *et al*. (1996)
GATA028	Palsbøll *et al.* (1997)
GATA098	Palsbøll *et al.* (1997)
GATA417	Palsbøll *et al.* (1997)
GT023	Bérubé *et al*. (2000)
IGF1	Barendse *et al.* (1994)
RW31	Waldick *et al*. (1999)
RW34	Waldick *et al*. (1999)
RW48	Waldick *et al*. (1999)
SW10	Richard *et al*. (1996)
SW13	Richard *et al*. (1996)
SW19	Richard *et al*. (1996)
TexVet5	Rooney *et al*. (1999)

determined. PCR amplification was carried out using the same conditions as described for testing annealing temperatures. PCR products were de-salted via ethanol precipitation (Irwin *et al.*, 2003), and size-separated and visualised on an ABI 3500xl capillary-based genetic analyser (Applied Biosystems).

Based on these amplification data (i.e. peak height and allele ranges) multiplex reactions where multiple loci are amplified simultaneously in the same PCR were developed through testing the amplification of different combinations of loci. These tests resulted in combinations of loci that minimised the number of reactions that were needed to amplify the variable loci. These protocols were then used to genotype all individuals. Alleles were scored using the GeneMarker software (SoftGenetics). Each 96-well plate of samples contained 2 individuals as ‘standards’, meaning that these same two individuals were present on all plates, to ensure consistency in genotyping across plates. All samples were scored by two individuals in a double-blind fashion to identify any potential scoring errors (Morin *et al.*, 2010).

Statistical analyses

Once genotypes for each sample had been obtained, the program CERVUS (Marshall *et al.*, 1998) was used to identify any duplicate genotypes (i.e. individuals that had unknowingly been sampled more than once). Based on these data, duplicate individuals were removed. CERVUS was also used to obtain estimates of allele frequencies and to estimate the frequency of null alleles for each locus. Loci were tested for deviations from linkage and Hardy-Weinberg Equilibrium (HWE) using exact tests as implemented in the program GENEPOP (Rousset, 2008).

Population structure was assessed using ‘classical’ approaches based on estimating differentiation of allele frequencies between pre-defined groups of individuals and Bayesian techniques. Classical methods have the benefit of being far more powerful than available Bayesian methods but have the detriment of requiring pre-defined groups of individuals, which may or may not represent the real biological patterns (e.g. Waples and Gaggiotti, 2006). On the other hand, Bayesian methods allow for simultaneous assessment of the number of groups represented by the sampled individuals and the assignment of individuals to those groups (and therefore do not requiring pre-defined groupings) but suffer from lower power.

The classical assessment of population differentiation was conducted using the program GENEPOP. Here, individuals were categorised as representing either the southern feeding group or the larger population, based on sampling location. Specifically, samples collected off Vancouver Island were classified as the southern feeding group, while samples collected on the calving grounds off Baja California were classified as representing the larger population. Based on this division, estimates of F_{ST} were obtained and exact tests of population differentiation were conducted.

To assess the power to detect population structure using the methods implemented in GENEPOP (exact tests), the simulation program POWSIM (Ryman and Palm, 2006) was used. Specifically, conditions were simulated that would result in differing levels of differentiation (F_{ST} = 0.001, 0.0025, 0.005, 0.01, 0.025, and 0.05), given the characteristics of the loci. There are two biologically realistic scenarios that can result in the same F_{ST} value. First, two populations that are not completely isolated will eventually reach an equilibrium F_{ST} value dependent upon the migration rate between populations (N_m). Second, if two populations have recently become reproductively isolated, they will drift apart, with F_{ST} values increasing with increasing time since divergence. POWSIM obtains desired F_{ST} values under the latter scenario by generating a single simulated population and then splitting it into equally sized populations with complete isolation once the split occurs. In this way, different F_{ST} values are obtained based on the number of generations that have passed since the split. Thus, users obtain estimates of the power to detect different degrees of differentiation by selecting combinations of N_e and t that result in the desired F_{ST} value, where $F_{ST} = 1 - (1 - 1/2N_e)^t$ (e.g. Nei, 1987, p.359). Due to uncertainty regarding N_e for the two putative gray whale populations, power to detect the different F_{ST} values (0.001, 0.0025, 0.005 0.01, 0.02, 0.025, and 0.05) was estimated using N_e values spanning three orders of magnitude (500, 5,000, and 50,000) and using t values for each that would result in the appropriate F_{ST} value. Simulations for each scenario (N_e and F_{ST} value) were conducted 100 times and the proportion of iterations where significant differentiation was detected (using a critical α value of 0.05) was recorded.

Population structure was also assessed without making *a priori* assumptions about the nature of population structure (e.g. how many groups there are, and which individuals represent each group). These analyses were conducted in two different ways: using the programs STRUCTURE (Hubisz *et al.*, 2009; Pritchard *et al.*, 2000), and STRUCTURAMA (Huelsenbeck and Andolfatto, 2007). For the analyses in STRUCTURE, the number of groups, and the membership of individuals within those groups, were estimated based a run length of 1,000,000 Markov Chain Monte Carlo

(MCMC) steps, with 50,000 steps as the burn-in period. The program was run assuming that allele frequencies were correlated between groups, and allowing for admixture (i.e. allowing for individuals to have ancestry in more than one group). The program was run 16 times, testing for 1–4 populations (*K* = 1–4), with four iterations of each *K*. The average likelihood over the four iterations for each *K* was taken as the likelihood for that *K*.

The program STRUCTURAMA works in a similar manner as STRUCTURE but differs in how the user specifies the number of populations to be tested. With STRUCTURE, the user must explicitly specify the number of populations considered and then run the program independently for each hypothesised number, and subsequently compare the probabilities associated with each. With STRUCTURAMA the number of populations considered can be a random variable within the model (Pella and Masuda, 2006) and therefore the posterior probabilities associated with a range of values for the number of putative populations can be obtained within a single run, without requiring *a priori* specification by the user (Huelsenbeck and Andolfatto, 2007). STRUCTURAMA was run allowing the number of populations to be a random variable with a Dirichlet process prior. The alpha value (which determines the shape of Dirichlet prior, where smaller values result in individuals being distributed across fewer populations and larger values result in individuals being dispersed across more populations) was also treated as a random variable, following a gamma distribution. A shape parameter of 1.0001 and a scale parameter of 0.0001 were initially used, which result in a relatively flat distribution. However, to test the robustness of the subsequent posterior probabilities to the choice of shape and scale values, STRUCTURAMA was also run with the shape and scale values both set to 1, which results in an L-shaped distribution. Each scenario was run three times, to ensure consistency between runs under the same conditions. All analyses were run for 1,000,000 MCMC steps, with 10,000 steps used as the burn-in.

Finally, it has been argued that estimating migration rates between putative populations is more biologically meaningful than simply rejecting panmixia when trying to identify biologically independent 'units' for conservation (e.g. Palsbøll *et al.*, 2006). Estimating migration rates from genetic data is challenging, however, particularly when migration rates are high. This is because demographic independence can occur at migration rates that are high enough to genetically homogenise allele frequencies (e.g. Waples and Gaggiotti, 2006). Regardless, great progress has recently been made in the development of analytical techniques designed to address this issue and better infer biological processes from genetic data. For management, the parameter of interest is estimated contemporary migration rates. BayesAss has become the software commonly used for this purpose (Wilson and Rannala, 2003). However, the approach implemented therein is known to perform poorly when genetic differentiation is low (Faubet *et al.*, 2007). Our results suggest extremely low differentiation between the putative groups and perhaps none (see Results), therefore BayesAss was not appropriate for estimating migration rates for our data. Instead, the programs IMa and MIGRATE were used to jointly estimate migration rates in both directions, as well as effective population sizes of each putative population (Beerli, 2006; Beerli and Felsenstein, 1999; 2001; Hey and Nielsen, 2004).

RESULTS

The average yield of DNA from the extraction process was 2.80 nanograms (ng) of DNA per milligram (mg) of tissue for the samples from Vancouver Island, and 0.42 ng/mg for the samples from San Ignacio Bay. This lower yield from the San Ignacio Bay samples likely results from the fact that these samples were stored in ethanol rather than DMSO, and DNA degradation is known to occur at a higher rate in ethanol than DMSO (e.g. Michaud and Foran, 2011).

The tests of microsatellite amplification and variability resulted in the identification of 15 loci that amplify well in gray whales, and are also variable. Multiplex reaction development resulted in all 15 loci being amplified in 5 reactions (Table 2), which were subsequently used for genotyping all samples.

No genotypes differed between the duplicate scoring personnel, indicating that allele calls were consistent across scorers. Genotypes were considered to be 'full' if individuals were missing data from 3 or fewer loci (i.e. they had data for at least 12 of the 15 loci). Full microsatellite profiles were not obtained for 14 samples, resulting in 123 genotyped samples that were used for subsequent analyses. Analysis of the genotypes identified 24 duplicate sampling events (23 off Vancouver Island, 1 from Laguna San Ignacio). All re-sampling events were from the same location (i.e. there were no cases where one individual was sampled in one location and re-sampled at the other). These duplicates were removed from the data set, resulting in genotype data for 99 individuals (59 from off Vancouver Island, 40 from Laguna San Ignacio). The genotypes did not show any significant deviations from Hardy-Weinberg Equilibrium expectations when analysed independently for each putative population, or when the data were combined into one 'population' (Table 3). Out of the 105 pairwise comparisons for assessing linkage between loci (considering all individuals together), six (5.7%) had p-values <0.05. However, none of these were significant after Bonferroni correction (Hochberg, 1988).

Table 2

Amplification information. Included is the locus name, fluorescent label, and reaction number for all loci. The annealing temperature for all reactions is 55°C.

Locus	Label	Reaction
EV14*Pm*	6FAM	1
EV37*Mn*	VIC	1
FCB14	VIC	1
GATA028	NED	1
FCB5	NED	1
GT023	VIC	2
FCB4	PET	2
EV1*Pm*	NED	2
TexVet5	NED	2
FCB17	6FAM	3
GATA417	PET	3
SW10	NED	3
SW13	6FAM	4
EV94*Mn*	6FAM	5
RW31	VIC	5

Table 3

Characteristics of each locus in each putative population for: (a) the southern feeding group; and (b) the larger population. Included is the locus name, the number of alleles, observed heterozygosity (H_O), expected heterozygosity (H_E, Nei, 1987), the polymorphic information content (*PIC*, Botstein *et al*., 1980), and the p-value for deviation from HWE. No p-values were statistically significant after Bonferroni correction (correction conducted independently for each putative population).

Locus	Alleles	H_O	HE	PIC	P-Value
(a) Southern feeding group					
EV14*Pm*	10	0.828	0.852	0.826	0.688
EV37*Mn*	17	0.845	0.886	0.867	0.204
FCB14	7	0.741	0.808	0.773	0.273
FCB5	4	0.500	0.438	0.402	0.765
GATA028	5	0.780	0.753	0.704	0.437
GT023	6	0.741	0.741	0.688	0.642
EV1*Pm*	3	0.603	0.508	0.385	0.184
TexVet5	5	0.741	0.730	0.678	0.678
FCB4	3	0.143	0.250	0.221	0.008
FCB17	13	0.930	0.907	0.890	0.984
SW10	7	0.776	0.776	0.733	0.832
GATA417	7	0.707	0.723	0.676	0.161
SW13	8	0.706	0.630	0.552	0.062
EV94*Mn*	9	0.831	0.816	0.783	0.458
RW31	9	0.828	0.822	0.790	0.216
(b) Larger population					
EV14*Pm*	10	0.769	0.840	0.809	0.132
EV37*Mn*	15	0.914	0.873	0.848	0.644
FCB14	7	0.759	0.836	0.798	0.033
FCB5	4	0.500	0.489	0.451	0.745
GATA028	5	0.769	0.764	0.715	0.185
GT023	7	0.650	0.685	0.627	0.276
EV1*Pm*	2	0.564	0.498	0.371	0.517
TexVet5	5	0.725	0.683	0.621	0.857
FCB4	2	0.105	0.191	0.171	0.036
FCB17	14	0.972	0.903	0.881	0.996
SW10	7	0.750	0.805	0.766	0.295
GATA417	6	0.700	0.717	0.676	0.182
SW13	5	0.629	0.611	0.530	0.738
EV94*Mn*	9	0.806	0.810	0.770	0.757
RW31	9	0.825	0.815	0.777	0.301

No loci had estimates of null allele frequencies greater than 0.05.

Sex could be determined for 86 of the 99 individuals, with 38 males and 48 females. The DNA was too degraded from the remaining 13 individuals to obtain reliable sex information. Within each region, the sex ratios were 33 females: 24 males and 15 females: 14 males for Vancouver Island and Laguna San Ignacio, respectively.

The 'classic' tests (based on hypothesis testing of pre-defined groupings) did not show any significant signs of genetic differentiation between the genotypes of the southern feeding group and the larger population. Specifically, the F_{ST} estimate was –0.0010, with a *P*-value estimate of 0.489. Simulation analysis showed that the power to detect structure, if it exists, was quite high. Specifically, given the sample sizes and the characteristics of the loci, we would expect to detect population structure over 70% of the time with an F_{ST} value as low as 0.005 (Fig. 1). The STRUCTURE analyses also did not detect any significant genetic differentiation within the data set, with one population (K = 1) having the highest probability (Table 4). Similar results were also obtained with STRUCTURAMA, with the scenario of the data representing one single population having a higher probability than scenarios with any other putative number of populations (Table 5).

Table 4

Results from STRUCTURE analysis. Shown is the estimated natural logarithm (*ln*) of the probability of the data with the number of populations (*K*) ranging from one to four, and performing four iterations of each *K*. The bold value indicates the average *K* with the highest probability.

	K			
Iteration	1	2	3	4
1	–4,219.9	–4,243.6	–4,273.9	–4,276.9
2	–4,220.9	–4,243.6	–4,268.5	–4,272.6
3	–4,220.3	–4,238.9	–4,266.2	–4,257.1
4	–4,220.6	–4,228.6	–4,248.7	–4,263.9
Average	–4,220.4	–4,238.7	–4,264.3	–4,267.6

Table 5

Results from STRUCTURAMA analysis. Shown are the estimated posterior probabilities of the data representing 1–3 populations. The top panel shows these probabilities calculated with the alpha value for the Dirichlet process being a random variable following a gamma distribution with a shape parameter of 1.0001, and a scale parameter of 0.0001. The second panel shows these probabilities calculated when the shape and scale value parameters were both set to 1.

	Number of populations		
Iteration	1	2	3
gamma(1.0001,0.0001)			
1	0.96	0.04	0
2	0.96	0.04	0
3	0.96	0.04	0
gamma(1,1)			
1	0.97	0.03	0
2	0.97	0.03	0
3	0.97	0.03	0

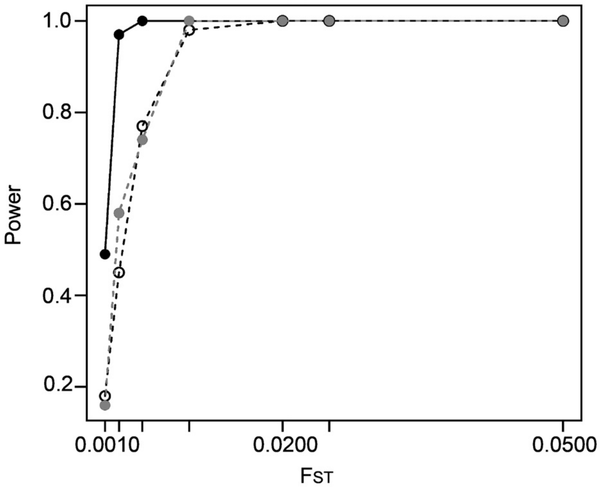

Fig. 1. Results from the POWSIM analyses. Shown is the power of the data (the proportion of simulations where population structure was detected (using a critical α value of 0.05)) under the different scenarios. The F_{ST} values tested were 0.05, 0.025, 0.02, 0.01, 0.005, 0.0025, and 0.001. These F_{ST} values were generated under three scenarios, N_e = 500, 5,000, and 50,000, with the time since divergence (t) varying to result in the desired F_{ST} values.

Despite testing a wide range of options with both IMa and MIGRATE, we were unable to get either program to converge on consistent estimates of migration rates. Our interpretation is that this inability is due to the lack of genetic differentiation of nuclear markers between the putative groups. This interpretation, as opposed to a lack of information in the data, seems appropriate particularly because we have previously obtained consistent estimates from these same programs and the same individuals but based on mitochondrial data, which showed significant structuring and limited migration consistent with maternally-directed site fidelity (Frasier *et al.*, 2011).

DISCUSSION

The differential recovery of DNA from tissue stored in different solutions merits consideration for future sample storage. Several studies have compared the ability of different solutions (primarily ethanol and DMSO) to preserve DNA over long periods of time (e.g. Michaud and Foran, 2011; Seutin *et al.*, 1991). All such studies indicate that DMSO solutions preserve DNA at a higher quality, and over a longer period of time. However, many researchers and museum staff still use ethanol for the long-term preservation of tissue. The differential yields of DNA obtained here add to the growing amount of data suggesting that DMSO is the desirable storage solution for long-term storage of tissue that may be used as a source of DNA.

The results of all analyses of population structure lead to the same conclusion: a lack of differentiation of nuclear genotypes. The 'classical' tests did not detect significant differences in allele frequencies between whales of the southern feeding group and those sampled in Laguna San Ignacio, and both Bayesian approaches indicated that the probability that all samples originated from one single population was substantially higher than any other alternatives. These data suggest that the whales of the southern feeding group do indeed freely interbreed with whales that utilise other summer feeding grounds. Thus, from these data, it appears that the eastern North Pacific gray whale represents one interbreeding population.

One caveat of our study is that samples representing the larger population were all collected from whales in one of the lagoons Laguna San Ignacio (but spanning several years). Gray whales are not evenly distributed throughout the three known lagoons in winter. Instead, photo-ID data suggest that females show some site fidelity to different lagoons (e.g. Jones, 1990) and genetic data also suggest some structuring (Goerlitz *et al.*, 2003; Alter *et al.*, 2009). However, the patterns and degree of structuring between lagoons remains unclear. For example, Alter *et al.* (2009) did not find significant structuring of mitochondrial haplotypes between the lagoons, but found slight but statistically significant differentiation of microsatellite alleles between Laguna San Ignacio and Bahia Magdalena. The authors attribute this pattern to either a high contemporary migration rate, or perhaps to stronger patterns of structuring being erased by whaling and only beginning to accumulate and leave a detectible genetic signature today.

Our justification for using samples from Laguna San Ignacio as representative of the larger population, are three-fold. First, based on numbers of single individuals and mother-calf pairs, Laguna San Ignacio represents the second most populated lagoon, with numbers of whales that are vastly larger than the estimated size of the southern feeding group (Jones and Swartz, 1984; Urban R *et al.*, 2003). Thus, Laguna San Ignacio is clearly used by a larger subset of the population than the southern feeding group. Second, although there are data suggesting that some females show fidelity to specific lagoons, there is also an abundance of data showing that some individuals move freely between lagoons, and that average residence times within the lagoon (for non-mother-calf pairs) are less than a week (Jones and Swartz, 1984; Urbán R *et al.*, 2003), suggesting that at least single whales move readily between lagoons. Moreover, some mothers are known to utilise different lagoons in different years (Swartz, 1986). Lastly, even if mothers do show fidelity to specific lagoons, this should not result in corresponding structuring of nuclear gene flow because fertilisation is thought to take place during the southward migration, prior to arrival at the lagoons (Rice and Wolman, 1971). Thus, although it would be ideal to have representative samples from all known lagoons, the available data provide no reason to doubt that the samples from Laguna San Ignacio are representative of the larger population.

These data based on nuclear markers add to previous photo-ID and mtDNA data to provide a more complete picture of the relationship between seasonal habitat use patterns and gene flow throughout the population. The photo-ID and mtDNA data indicate that, during the summer, whales of the southern feeding group represent a seasonal subpopulation, where this differential habitat use is driven by maternally-directed site fidelity to this feeding area that is then passed on to their offspring (Frasier *et al.*, 2011). However, the nuclear DNA data suggest that these whales breed with whales that show fidelity to other feeding grounds, and therefore are part of one interbreeding population. Thus, the combined picture is one of seasonal subdivision on summer feeding grounds, but with no such substructuring during the mating season, where all individuals in the eastern North Pacific represent one gene pool.

This result and interpretation is consistent with other data relating to known migration patterns and the timing of fertilisation. Briefly, it is thought that conceptions may occur in December, during the southern migration (Rice and Wolman, 1971). Whales that use the northern feeding grounds migrate through the areas occupied by the southern feeding group suggesting that whales from both known feeding grounds may migrate together the remainder of the way to the winter calving grounds (Darling, 1984). The peak time of migrants passing through the southern feeding area is mid-December to mid-January (Darling, 1984). Thus, the timing of fertilisation coincides with when whales from different feeding grounds become intermingled during their southern migration. This pattern indicates the strong potential for interbreeding regardless of any substructuring that may exist during the summer, or on the winter calving grounds.

Despite the presence of nuclear gene flow between whales from the southern feeding group and the rest of the population, this group still represents a separate management unit that warrants separate consideration with respect to the impacts of proposed threats, such as the resumption of traditional whaling and the impacts of oil distribution. This is the approach being used by the IWC Scientific Committee in examining the potential impacts of hunting (e.g. see IWC, 2013b). The presence of long-term site fidelity to this area that is passed on from mothers to offspring, indicates that these whales represent a seasonal subpopulation. Thus, detrimental impacts (e.g. 'takes') to these whales will not have a 'random' impact on the population at large, but will instead primarily impact these matrilines specifically. The resulting effect on this local subpopulation could be far greater than would be expected under the assumption of a single, unstructured population. Potential impacts could include the loss of knowledge of these feeding areas from this population, and localised extirpation. For example, if the whales that currently show this site fidelity are removed, then this information will be lost, and thus these whales will not likely be replaced by others from the larger population, resulting in localised extirpation. Indeed, the recognition of such seasonal subpopulations as separate management units is recommended, and common, for baleen whales (e.g. Dizon *et al.*, 1997).

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SC/67B/REP/07 Rev1

Fifth Rangewide Workshop on the Status of North Pacific Gray Whales

IWC

INTERNATIONAL
WHALING COMMISSION

Fifth Rangewide Workshop on the Status of North Pacific Gray Whales[1]

1. INTRODUCTORY ITEMS

1.1 Convenors' opening remarks

The Workshop was held at the Granite Canyon Laboratory (Big Sur, California) of the Southwest Fisheries Science Center from 28-31 March 2018. The list of participants is given as Annex A. Brownell welcomed the participants and explained the history of the facility, which has been used for almost five decades to census gray whales during their southbound migration. Donovan and Punt (co-convenors) noted that the primary tasks of the workshop were to review the results of the modelling work identified at the Fourth Workshop and SC67a, to examine the new proposed Makah Management Plan (submitted by the USA on gray whaling off Washington state and to update as possible (and develop a workplan for) updating the scientific components of the Conservation Management Plan (CMP) for western gray whales.

1.2 Election of Chair

Donovan and Punt were elected Chairs (Donovan chaired from the 28-30 March and Punt on 31 March).

1.3 Appointment of rapporteurs

Calambokidis, Cooke, Lang, Punt, Reeves, Scordino and Weller served as rapporteurs.

1.4 Adoption of Agenda

The Adopted agenda is given as Annex B.

1.5 Documents and data available

The documents available to the meeting are listed in Annex C. Annex D summarizes the terminology used to designate breeding stocks and feeding aggregations.

2. PROGRESS ON 'NON-MODELLING' RECOMMENDATIONS AND NEW DATA

2.1 Updated information from co-operative genetics studies

Bickham presented the results of a multi-authored study of SNPs using samples from approximately 50 whales feeding off Sakhalin Island ('western' gray whales) and approximately 100 whales from the Mexican wintering grounds (assumed 'eastern' gray whales); the full study was to be presented at SC67a. The methods used are described in DeWoody *et al.* (2017). Bickham stated that a finished version of the paper will be presented at the 2018 IWC SC meeting. The authors believe that the results will have implications for prioritising the various stock structure hypotheses being modelled in the Rangewide Review (see below).

Multiple duplicate biopsies were found within both the Sakhalin and Mexico sample sets, but none were shared between the two localities. SNP genotypes were also presented for two mitochondrial and two sex-linked loci (Zfx and Zfy). One of the sex-linked SNPs (ZFY_342) had an apparent fixed heterozygosity in the Mexican whales and thus only the second locus could be used for determining the sex of the whales. The Workshop noted that whilst there is no single explanation of this, one possibility is that there was a translocation (duplication) of the Y-linked SNP to the X or to an autosome.

Bickham also presented the results of the STRUCTURE analyses for the SNPs. In the cases with locality as a prior and without locality as a prior, $K = 2$ genomes (or populations) was the best solution; the plot with geography as a prior showed better differentiation with one predominating in the east (Mexico) and the other predominated in the west (Sakhalin). All eastern samples showed admixed ancestry (including some with predominantly the "western" genome) but the western samples showed a much higher proportion of admixture including individuals of nearly 'pure' eastern and western genomes. He also presented results for an analytical approach called Landscape and Ecological Associations (LEA)[2]. The LEA analysis also identified K = 2 genomes but with greater separation. In the Sakhalin sample set the western genome still predominated but there were both individuals with pure western and others with pure eastern genomes as well as admixed individuals. The more equal proportions

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[1] Not all attendees have had a chance to comment on this final version although much of the report was agreed at the Workshop itself.

[2] http://membres-timc.imag.fr/Olivier.Francois/LEA/tutorial.htm

of western and eastern genomes in the Sakhalin samples was consistent with an Mxy estimate of genetic similarity (the Sakhalin sample set had a notably higher variance for genetic relatedness between paired samples than was observed in the Mexican sample set).

The authors of the working paper concluded that the Sakhalin population might be comprised of two types of individuals representing two breeding stocks (i.e., two different genomes), along with individuals of mixed ancestry (admixture). The proportions of the two genomes are vastly different in the two sample sets.

The Workshop **agreed** that incorporating photo-id data into the genetic results will greatly improve interpretation of stock structure and movements and **recommended** that the genetic dataset should be examined comparing whales seen only once off Sakhalin with those whales seen in multiple years.

Lang gave a brief update of her work on SNPs, using the next-generation sequencing approach ddRAD. She is analysing approximately 200 gray whales representing approximately equal sample sizes of PCFG (Pacific Coast Feeding Group), western gray whales, and Northern Feeding Group whales. She expects to present the results of at the 2019 gray whale *Implementation Review.*

The Workshop **welcomed** news from Bickham that a request to the government of Japan to obtain gray whale samples for genetics studies (including of the possible extant western breeding stock).

It was noted that the extent of mixing of gray whales in the past had probably fluctuated in response to changes in sea ice (glacial versus interglacial periods). Bickham responded that additional genome sequencing was planned and that the reconstruction of the historical demography of western and eastern gray whales is one goal of that study. Analyses may reveal associations with the climate cycles of the Pleistocene.

2.2 Updated information from photo-identification studies including consolidation of WGW catalogues

SC/MP/CMP/02 reviewed the results of long-term photo-identification studies conducted between 2002-2017 off northeast Sakhalin Island by the Joint Monitoring Program of two oil and gas companies[3]. The photo-identification catalogue resulting from this work contains 283 identified individual gray whales, including: (a) 175 whales that use the Sakhalin Island feeding area on a regular annual, (b) 27 occasionally-sighted whales (recorded at intervals greater than 3 years), and (c) 71 individuals that have been recorded only once. Forty-eight of the one-time visitors were recorded as calves, excluding the nine calves first identified in 2017. There are 29 identified mothers and 127 whales first identified as calves in the catalogue. Six mother-calf pairs were identified in 2017, along with three unpaired calves. Whale no. KOGW127 (aka “Agent”), was identified as a calf in 2005 and was first recorded as a mother in 2017 at the age of 12 years. Agent was satellite tagged in 2011 and her winter migration was tracked to the Gulf of Alaska before the transponder stopped working (Mate et al., 2015).

Drone-based photography was incorporated into the joint-programme field program in 2017. In most cases, the drone was used at an average distance of about 800 m from shore with a standard altitude of 8 meters. The range of the drone presently in use is 2.5 km from the shore. With the collection of aerial photographs from drones, a new body aspect (“back”) was added to the photo-identification catalogue. Also, a new supplemental catalogue of drone-collected video was created for 35 individuals.

The catalogues of the ENL-SEIC joint programme and the Russian Gray Whale Programme (previously the Russia-US programme) were last cross-matched using data available through 2011. At that time, the two Sakhalin photo-identification catalogues contained a total of 222 whales, of which 186 were common to both. Seventeen whales were found only in the Russian Gray Whale Programme catalogue and 19 only in the ENL-SEIC catalogue (IUCN, 2013). An updated catalogue comparison, under the auspices of the IWC, is being discussed as is the concept of a common shared catalogue and database.

In discussion, the Workshop **agreed** on the importance of the long-term nature of the research programmes being conducted off Sakhalin. The concept of a common catalogue and database was welcomed and several measures to ensure data compatibility were mentioned, including the important step to standardize reporting of effort and protocols used to designate calves versus yearlings. It was further mentioned that sighting histories of whales photo-identified off Kamchatka should be evaluated to determine patterns of annual occurrence. Finally, the availability of a shared catalogue and regular updating of such was highlighted with respect to the research component of the hunt management plan proposed for the Makah hunt.

2.3 Gray whales off Korea

SC/M18/CMP/04 reported the possible occurrence of a gray whale off Korea in 2015. Video footage of what appears to be a gray whale was uploaded on YouTube in 2015[4]. The whale was swimming near a port facility in

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[3] Exxon Neftegas Limited (ENL) and Sakhalin Energy Investment Company (SEIC)

[4] https://www.youtube.com/watch?v=dJ4J7luGgcE

Samcheok, on the east coast of Korea. While the poor quality of the video prevented positive identification to species, some features of the whale suggest that it was a gray whale. Additional information is being sought to confirm the species identification. If this sighting was indeed of a gray whale, it would be the first record from Korea since 1977. The Workshop thanked D. Yasutaka Imai for alerting Kim to the existence of this video.

3. UPDATING SCIENTIFIC ASPECTS OF THE CMP

Donovan reported recent progress on the "Rangewide Review of the Status of North Pacific Gray Whales" and the 'Western Gray Whale Conservation Management Plan' (CMP). Since 2004, the IUCN and IWC have emphasized the need for a comprehensive international CMP to mitigate anthropogenic threats facing gray whales throughout their range in the western North Pacific. This CMP was initiated at an IUCN-convened international workshop in Tokyo in summer 2008 (IUCN 2009). A draft of the CMP was completed in 2010 (Brownell *et al.* 2010) and this was endorsed by both the IWC and IUCN. The first successes of the CMP included completion of a telemetry project conducted off Sakhalin and a Pacific-wide photo-identification catalogue comparison. The results of these projects showed that some of the whales sighted off Sakhalin in the summer migrate east, across the Pacific, reaching portions of the North American coast between British Columbia, Canada and the wintering lagoons off Baja California, Mexico. In light of this new information, the IWC has been engaged in the present rangewide review.

In support of the CMP initiative, in 2014 a 'Memorandum of Cooperation Concerning Conservation Measures for the Western Gray Whale Population' (the MoC), was signed by Japan, Russian Federation and the USA. In 2016, the memorandum was signed by Mexico and the Republic of Korea and Prof. Hidehiro Kato of the Tokyo University of Marine Science and Technology was appointed as coordinator of the memorandum. It is hoped that in time the other remaining range states will also sign the memorandum.

3.1 Review of existing sections

The Workshop noted that the work to complete the computing specifications, especially taking into account the new Makah Management Plan, meant that there was insufficient time to update the CMP sections, also recognising that this could best be completed after the modelling results became available, ideally at SC67b. Attention was drawn to the updated seasonal maps[5] and participants were asked to send any comments or suggestion for modification to Donovan and Reeves.

The Workshop **recommended** that the Scientific Committee considers establishing a small drafting group comprised of at least the national co-ordinators of the MoC, Reeves (IUCN) and Donovan be convened to meet intersessionally (e.g. at IUCN headquarters) to provide an updated version of the plan after SC67b.

3.2 Consideration of future stakeholder workshop

An important component of the CMP effort is the need for a stakeholder workshop (tentatively forecast to occur in 2019) that helps to finalize the CMP and develops a strategy for its implementation (IWC, 2017b). The workshop, which would be co-sponsored by IWC, IUCN and the signatories to the Memorandum of Cooperation, should be broad-based and include representatives of national and local governments, industry (e.g. oil and gas, fishing, shipping and tourism), IGOs and NGOs. Objectives of this meeting should include: (1) review and updating of the CMP taking into account any new scientific results from the rangewide workshops, (2) establish a stakeholder Steering Group to monitor CMP implementation, (3) arrange for a coordinator of the CMP and (4) establish a work plan and consider funding mechanisms to implement the actions of the plan. The IWC has a Voluntary Fund for Conservation, to which donations can be specifically directed towards the gray whale CMP and related work. It is expected, however, that after the first year of CMP implementation, range states will contribute the necessary funds to advance the conservation actions listed in the plan. The Workshop welcomed the support offered by IUCN with respect to organising the stakeholder workshop.

4 UPDATE ON MODELLING FRAMEWORK AND RUNS

4.1 Progress of modelling since SC67a including validation

4.1.1 General progress, including validation

Punt informed the Workshop that code implementing the specifications agreed at the 4th Rangewide Workshop and modified during SC67a had been written and used to condition the reference trials based on stock hypotheses 3a, 3e and 5a, along with the sensitivity tests that implement stock hypotheses 3b and 6b.

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[5] https://iwc.int/western-gray-whale-cmp

Brandon summarized progress on validating the code implementing the operating model and the conditioning process. SC/M18/CMP/03 provides an update on code validation, including a brief overview of the code and input files, and a list of verification steps taken to date. The main focus of the validation process has been on the FORTRAN procedures necessary for the conditioning phase. Conditioning the operating model is the first and most computationally expensive phase of the Rangewide modelling effort because this code involves the bulk of calls to numerical methods to estimate parameters given model fits to the data. To this end, the conditioning code has been checked against the mathematical and statistical model specifications, to ensure that the procedures as implemented are consistent with the specifications (see Annex D for the specifications of the Rangewide model). Likewise, diagnostic output from the code has been checked against expected values. No errors in the coding were identified.

4.1.2 Modelling related to the proposed Makah management plan

Punt informed the Workshop that code implementing the Makah Management Plan (Annex X) had been developed and initial results presented to the March 2018 AWMP meeting. However, Brandon has yet to validate this code. The code implementing the Makah Management Plan needs to be validated prior to SC67b.

During the Workshop, the Makah Management Plan was clarified/updated as shown below.

(1) It was clarified that the hunt will be stopped if the PCFG 10-yr strike limit less number of PCFG-designated animals drops below 1 or if the PCFG 10-yr female strike limit less number of PCFG-designated females drops below 1. The initial implementation only stopped the hunt only when these differences were less or equal to zero.
(2) It was agreed to incorporate an ‘unknown identity’ component for landed whales because it may not be possible to obtain a useable photograph of landed as well as struck and lost whales (although at a lower probability).
(3) It was agreed to allowing for the fact that the amount that unidentified whales count towards the PCFG 10-year strike limit will be updated based on available data rather than always being assumed to be 0.4. The error associated with the estimate of the proportion of PCFG whales in even-year hunts needs to be accounted for (see Item 4.4.1).

4.2 Review of stock hypotheses

The Workshop reviewed how the three baseline stock hypotheses (3a, 3e and 5a) and the two stock hypotheses considered as tests of sensitivity (3b and 6b) had been implemented, noting that some of the ‘limited’ movements (light arrows in Annex E) had been omitted from the baseline hypotheses, but would be considered in tests of sensitivity (e.g. the PCFG in sub-area BSCS). The omission of the associated links was due to lack of mixing data to allow the links to be modelled. It was also noted that that there are no data (abundance estimates, mixing proportions, catches) for some of the sub-area (e.g. the OS sub-area), which implies that the results will be identical no matter how such regions are treated in the modelling.

The Workshop noted that the current implementation of hypothesis 5a did not include the WBS in the SKNK sub-area. This is because there was currently no basis to specify a mixing proportion for WBS vs WFG animals in the sub-area. Cooke provided abundance estimates by breeding stock / feeding group (see Item 4.3.1), which means that it is no longer necessary to specify mixing proportions for the SKNK sub-area.

The Workshop **agreed** that stock hypotheses 3a and 5a would form the references for the analyses as they appear to be most plausible, while trials would also be conducted for stock hypotheses 3b, 3c, 3e and 6b. Annex E shows the final stock hypotheses considered in the trials graphically, while Annex D, Table 2 shows the resulting mixing matrices. The γ values in Annex D, Table 2 indicate parameters that are estimated during the model fitting process.

4.2.1 Plausibility of stock hypothesis 6b

SC/M18/CMP/01 aimed to reopen discussion on the plausibility of the stock hypotheses previously considered as high priority for modelling, with special emphasis on stock hypothesis 6b. Stock hypothesis 6b assumes that the WBS has no fidelity to wintering ground and uses both wintering grounds in both Asia and Mexico. SC/M18/CMP/01 argued that this hypothesis was elevated to high priority due to discussions regarding the movements of humpback whales and the social aggregating hypothesis of Clapham and Zerbini (2015). This hypothesis involves humpback whales learning of new wintering grounds, likely through hearing other humpback whales, and temporarily immigrating. SC/M18/CMP/01 argued that this hypothesis does not apply well to gray whales because they are much quieter than humpback whales and there is a large distance between the distribution of WBS and eastern breeding stock whales (as portrayed by hypothesis 6b) preventing communication between whales. Furthermore, humpback whales and gray whales have very different breeding behaviour, with humpback whales aggregating on modified leks (Clapham and Zerbini 2015). There does not appear to be a functional benefit for WGW to justify shifting their migration to go to wintering grounds in Mexico instead of Asia given the extra 4,000 km of travel required (Villegas-Amtmann *et al*., 2015). Furthermore, it does not appear likely that the WBS used both wintering grounds without fidelity prior to commercial whaling given that whaling occurred off Japan and Korea during a period when the whales using the Mexican wintering grounds were depleted. Bickham et al. (2013) has also presented arguments based on genetics on why hypothesis 6b has low plausibility. SC/M18/CMP/01 also suggested that hypothesis 3e has low plausibility because it assumes that WBS whales occur in their historical feeding range but do not use the Piltun Lagoon area of Sakhalin Island, which has proved to be an important feeding area since the mid-1980s. It is more likely that if the WBS exists, that this breeding stock would spend at least some time feeding near Piltun Lagoon. SC/M18/CMP/01 concluded the trials based on stock hypotheses other than 3a and 5a should be sensitivity tests.

In discussion, it was noted that gray whales that feed off Sakhalin and traditionally used wintering grounds in the western North Pacific could be driven to occasionally use migratory routes and wintering areas in the Eastern North Pacific. While the Rangewide model does not explicitly account for breeding so does not incorporate information on when or where whales breed, this hypothesis could provide an explanation for the observations of Sakhalin whales in the eastern North Pacific. There is evidence showing that whales from the same feeding groups migrate together; both Sakhalin and PCFG whales have been photographically identified in the same groups and in localized areas while on migratory routes (Weller et al. 2012, Calambokidis and Perez 2017). This could provide a mechanism by which whales that feed together, but have traditionally used different wintering areas, could learn new migratory routes.

Although the possibility that gray whales use multiple wintering grounds could not be ruled out, the Workshop **agreed** that stock hypotheses 6b would be considered as a sensitivity test. It was also **agreed** that stock hypothesis 3e would be considered a sensitivity test.

4.3 Confirm final data sets

4.3.1 Removals (direct and incidental)

IWC (2018) referenced records of gray whale deaths from entanglement/entrapment, ship strike, and unknown causes in Japan from 1982 until the present (Nakamura *et al.*, 2017). A small group (Scordino, Reeves, Brownell) met to confirm and update what had been stated previously on removals in Japan (and elsewhere), recalling that the adult that ‘died off Hokkaido in 1996’ was killed deliberately (Brownell, 1999).

The Workshop **endorsed** the conclusions of the small group as summarised below.

(1) Of the six gray whales reported as beached in Japan between 1990 and 2016 but with cause of death undetermined, some proportion should be assumed to have died from either entanglement/entrapment or ship strike. The under-reporting factor (usually x4 but with sensitivities of x10 and x20; Annex D, tables 8 and 9) used in the model to convert observed mortality to true mortality in the case of bycatch and ship strike would account for this.

(2) There was no reason to believe there had been any change in fishing effort (e.g. set net fishing) in Japan between 1930 and 1982. Therefore, the removal rate from 1982 to the present should be extended back to 1930 for modelling purposes.

(3) Finally, with respect to commercial set gillnet fishing in California prior to 1981, as noted last year (IWC, 2018), a seabass fishery operated in northern Mexico and southern California prior to the 1980s (e.g. landing 412,000 pounds of black seabass and 873,000 pounds of white seabass in 1953; Marine Fisheries Branch, 1956). In fact, this fishery was active and overall fishing effort ‘fairly constant’ from before 1930 until the early 1980s (Vojkovich and Reed, 1983). There was no observer effort in this fishery before 1981, nor was an official stranding record of cetaceans maintained in California before that time. However, a coordinated reporting system for stranding was established in the early 1960s under the auspices of the American Society of Mammalogists, and stranded gray whales were regularly reported. For example, 24 dead gray whales were reported as stranded in California between 1960 and 1968, of which seven were confirmed or suspected of having been either entangled in fishing gear or struck by a ship; Brownell, 1971). A gray whale that stranded at Ocean Beach, California, on 19 February 1953 was missing its flukes and bore ‘several gashes’ on the body – all suggestive of an entanglement death (Robert Orr, pers. comm. to R. Brownell, April 1964).

At last year’s workshop, it was assumed that set gillnet fishing effort for halibut in California declined linearly from 1982 to no effort in 1975. To model the effect of this assumption, it was decided to assign all records of gray whales recorded as injured or killed in halibut or other set gillnet fisheries to a single fishery and modelled separately from all other California fisheries. It was also decided to examine both a low case that assigned no deaths to set gillnet fisheries and a high case that considered all bycatch reports related to gillnet, set gillnet, net, and halibut fisheries in California as if they came from a single fishery (IWC, 2018). A recently found publication (Bureau of Commercial Fisheries, 1936) reported that both set gillnets and trammel nets were used in the 1930s in California for halibut and white seabass fishing. Based on this new information, the Workshop **agreed** to drop the assumption that fishing effort declined linearly to zero from 1982 to 1975 and therefore there was no reason to evaluate high and low scenarios as a way of accounting for bycatch in California prior to 1975.

Set gillnetting effort off California changed markedly in 1991 due to regulations passed in November 1990 intended to eliminate gillnet fishing within 3 n.miles of the mainland and within 1 n.mile of any offshore island in southern California by 1994 (Barlow *et al.*, 1994). To address this, a second set gillnet fishery was added to the model starting in 1991 and the set gillnet fishery described in the preceding paragraph was modelled as having ended in 1990.

Table 1

Abundance estimates (1+) for the WFG feeding aggregation and the western breeding stock

Year	Group	Hypothesis	Estimate	SD	CV
1995	WFG	3a/3c/3e/6b	75.1	3.8	0.051
1995	WBS	3b	25.8	7.3	0.282
1995	WFG	3b	75.5	3.3	0.043
1995	WBS	3e	30.0*	15.0	0.500
1995	WBS	5a	26.6	6.9	0.259
1995	WFG	5a	47.8	7.7	0.160
1995	WBS+WFG	5a	74.4	3.9	0.052
1995	WBS/(WBS+WFG)	5a	0.358	0.093	0.259
2015	WFG	3a/3c/3e/6b	199.8	5.4	0.027
2015	WBS	3b	63.8	15.8	0.248
2015	WFG	3b	198.9	5.7	0.029
2015	WBS	3e	30.0*	15.0	0.500
2015	WBS	5a	64.4	14.0	0.218
2015	WFG	5a	135.6	14.1	0.104
2015	WBS+WFG	5a	200.0	5.7	0.029
2015	WBS/(WBS+WFG)	5a	0.322	0.069	0.200

* Guestimate because the WBS cannot be distinguished given the available information.

4.3.2 Abundance estimates

There were no updates to the estimates of abundance for the PCFG or the ENP stock. New abundance estimates for western gray whales had been presented to the last WGWAP meeting (Cooke *et al*., 2017), which will also be presented to the SC67b. Estimates for the WFG were extracted at the Workshop that would correspond to the stock structure hypotheses listed in Annex E (table 1). The larger estimates for the WFG correspond to the hypothesis that all whales visiting SE Kamchatka and/or Sakhalin belong to the WFG, while the smaller ones correspond with the hypothesis that only whales that visit Sakhalin belong to the WFG (regardless of whether these individuals also visit Kamchatka).

For the hypotheses where a proportion of the WFG belongs to the western breeding stock (WBS), this proportion is highly uncertain (and could be zero) even though the estimate for the total WFG is reasonably precise. The estimates of the numbers of WFG animals in each of the two breeding stocks are, therefore, highly negatively correlated. In these cases, the multi-stock model uses as inputs the estimate of the total WFG and the estimated proportion of this that belongs to the WBS.

Table 2

Mixing proportions for use in the trials

Sub-area	Season	Stock / Feeding aggregation	Mixing proportion
EJPJ	All	WBS/NFG	0.33
SEA	Feeding	PCFG	0.57[1]
SEA	Migration	PCFG	0.1[2]
SEA	Migration	WGW	0.002[3]
BCNC	Feeding	PCFG	0.93
BCNC	Feeding	WGW	0
BCNC	Migration	PCFG	0.28
BCNC	Migration	WGW	0.002
CA	Feeding	PCFG	0.60
CA	Feeding	WGW	0
CA	Migration	PCFG	0.1
CA	Migration	WGW	0.002[3]

1: Not used in the conditioning as no bycatch is recorded for the SEA sub-area during the feeding season.

2: Assumed value owing to lack of data to estimate mixing proportions.

3: Set to the value calculated for BCNC by Moore and Weller 2013)

4.3.3 Mixing proportions

Table 2 lists the updated mixing proportions. The mixing proportion for the EJPJ sub-area is unchanged from that specified at the 4th Rangewide Workshop because none of whales encountered recently in this sub-area had adequate photographs to allow for matching (Table 3).

Table 3

Updated information on matches between whales encountered off Japan and those photographed off Sakhalin (D. Weller, SWFSC).

Date	Location and source	Conclusion
April 2016	Shizuoka, beached	no useable photos/no match
February 2017	Kanagawa, sighting	poor quality video only/no match
April 2017	Chiba, sighting	poor quality video only/no match
March 2017	Aogashima, sighting	no useable photos/no match
February 2018	Aogashima, sighting	no useable photos/no match

New mixing proportions were calculated for PCFG whales by sub-area for the winter/spring (migrating) and summer/fall (feeding) seasons (Table 4). The sub-regions of the BCNC region used for the analysis were northern Oregon, southern Washington, and northern Washington because they were thought to have the least chance of bias in calculated mixing proportions. Updated data through 2015 based on matches to the PCFG catalogue were used. There was considerable discussion about how to calculate the mixing rate for the Oregon-Washington outer coast area due to a dramatic change in proportion of PCFG whales in northern Washington from surveys in early April 2015. Those surveys identified a large number of whales in a previously poorly sampled area that had very few PCFG whales. Identifications in spring 2015 (heavily influenced by these April surveys) reduced the overall proportion of PCFG whales based on pooled proportions through 2015 to 24% (it had been 36% based on data through 2014). To provide a value less influenced by these two days of surveys, the proportions of PCFG whales were averaged over sub-region and month to compute an overall average of 28% (an average of the eight values presented in Table 4.

Table 4

Proportion of PCFG whales by region and month for cells with >10 IDs; complete through 2015 for OR-WA Jan to May (no Dec data)

Region	Jan	Feb	Mar	April	May
NWA	0.09		0.09	0.10	0.41
SWA			0.38	0.21	0.33
NOR					0.63

Mean of above cells for OR to WA: **Unweighted = 28%**, Pooled = 24%
Mean of above for just N WA: Unweighted = 17%, Pooled = 20%

The Workshop **agreed to** adopt 28% for the proportion of PCFG whales in the BCNC sub-area during the migrating season for the bulk of the trials, and that sensitivity would be evaluated to 17%. This value is obtained by restricting the analysis of mixing rates of PCFG whales during the winter/spring to just northern Washington where the hunt would occur (based on the unweighted average of the 4 months where there were at least 10 photo-IDs, table 4). Pooling all 622 photo-IDs for December to May would result in a rate of 20%, although this approach weights values towards periods with more photo-IDs.

Considering some of the uncertainty around the estimate for the portion of PCFG whales present in the spring off the Washington-Oregon coast and the variation by location, month, and year, the Workshop **agreed** the current best estimate of 28% to be +-20% (8-48%) for the true PCFG mixing rate. The rationale for the choice is that very different results would be obtained in different areas such as 1) the recently sampled zone north of Tatoosh Island in the early spring where migrating whales appear to gather in some years where recent efforts revealed almost no PCFG whales, compared to 2) areas along the Northern Washington Coast or for example in Barkley Sound that are feeding areas for PCFG whales and where their proportion compared to migrating whales would be highest.

4.4. Confirm final trial structure and conditioning

4.4.1 Changes to the trials specifications, including stock structure

Annex D lists the specifications for the model that will form the basis for drawing final conclusions regarding the implications of alternative stock structure hypotheses and of the implementation of the Makah management plan. The specifications (see also Annex D and Table 5 and 6) reflect changes to how the stock hypotheses are implemented as well as how the abundance estimates for the western Pacific are used in conditioning. The Workshop also agreed that the following additional changes will be made the trials specifications:

(1) the base-case survival rate for animals aged 1 and older would be assumed to be 0.98, which reflects the estimates obtained by Cooke (ref) and Punt and Wade (2012); the values used in previous trials was 0.95;

(2) the SET1 and SET2 fleets (set gillnets off California in the feeding and migration seasons) would be split between 1990 and 1991 given the changes in regulations in the associated fisheries that appear to have changed bycatch rates;
(3) the survey plan for the California counts were updated to reflect the current plan (two surveys in every five-year block); and
(4) the periods used to calculate average bycatch rates to infer bycatch prior to the establish of monitoring networks into the future as generally but the earliest and most recent five years, but a longer period is specification for sub-areas (e.g. EJPJ and SI) with limited data (Annex D, table 3)

Evaluation of the Makah Management Plan requires specification of the probability of photographing a landed or struck and lost whale, as well as the probability of correctly deciding that such a whale is from the PCFG or the WFG. In addition, it is necessary to specify the probability of striking and losing a whale and assigning a sex to an animal for which a match has been made. These probabilities are specified as follows:

(1) *Probability of obtaining a photograph of sufficient quality to allow it to be matched to the catalogue*. For struck and lost whales, this probability is estimated to be a 0.6 for winter/spring and 0.8 for summer/fall (due less favourable light and weather in winter/spring compared to summer/fall). For landed whales, it is estimated to be 0.9 for all seasons.
(2) *Probability of struck and lost*. The review of the Makah whale *SLA* concluded in 2013 was based on a value for this probability of 0.5, which was informed by two strikes that occurred during the Makah 1999 hunt in which one strike resulted in a landing and the other contacted the whale but did not penetrate the skin. The Workshop agreed to retain the assumption of a 50% struck and lost rate for hunts during the winter and spring. It was decided that hunts occurring during the summer and fall were much less likely to have struck and lost due to better weather conditions and more predictive movement behaviours of whales in the normal feeding depths of PCFG whales. The Workshop therefore agreed that the struck and lost rate for summer and fall hunts would be 0.1 and that sensitivity would be explored to a value of 0.5.
(3) *False positive rate for PCFG (i.e. probability of a non-PCFG being identified as from the PCFG given a good quality photograph*). The probability that a non-PCFG whale might be falsely identified as a PCFG whale is estimated to be 0.05. Normally, there is a near 100% confidence for matches that are identified to Cascadia's PCFG catalogue because these are double checked and photographs of poorer quality where there is some ambiguity are treated as Poor Quality and not used. The value of 0.05 is based on the assumption that a slightly different set of circumstances would exist for comparison of a whale struck or landed because there would be pressure to try to match regardless of the quality of the photograph and it would be hard to justify not reporting as a match something where there was a relatively high degree of confidence (i.e. 95% confident of the match to a PCFG whale).
(4) *False negative rate for PCFG* (i.e. *i.e. probability of a PCFG whale not being identified as such given a good quality photograph*). This probability is estimated to be 0.25 for a hunt in the winter/spring, and zero for a hunt in summer since all struck whales are assumed to be of the PCFG. This value of 0.25 accounts for several factors, including whales only seen in fewer in two years in the PCFG because of a combination of being young, not being photographed, and the one year lag in available catalogue. In addition, there could be a matcher error in missing a match due to things like changed markings.
(5) *False positive rate for WFG (i.e. probability of a non-WFG being identified as from the WFG given a good quality photograph*). This probability is estimated to be 0.01 based on the WFG catalogue being smaller and more well-known. Also, it is suspected that the matcher would likely only declare a match when there was a high level of confidence given the infrequent rate of these matches.
(6) *False negative rate for WFG* (i.e. *i.e. probability of a WFG whale not being identified as such given a good quality photograph*). On the assumption that calves and lactating mothers will not be hunted, the proportion of huntable WFG whales that would not be known as WFG whales if taken during the spring northward migration was estimated using the population model fit to the Sakhalin and Kamchatka photo-id data. An animal that has been seen off Sakhalin is assumed to be a WFG animal if seen or taken in the eastern North Pacific. An animal seen off eastern Kamchatka but not Sakhalin is not assumed to be a WFG animal, because it might be an NFG animal. The estimated proportion, averaged across the posterior distribution of the population trajectory, was 4-5% depending on the hypothesis. These estimates used data through 2011 only, that being the last season for which the catalogues were cross-matched. If only a single catalogue were used, the rate would be higher. The values used in the trials are: stock hypotheses 3a, 3c, 3e, and 6b: 0.041; stock hypothesis 3b: 0.040; stock hypothesis 5a: 0.049.
(7) *Probability of not assigning a sex to a struck and lost animal that has been identified to the PCFG.*
    a. This probability is estimated at 19% for the feeding season based on 81% of encounters of PCFG whales from June-Nov through 2015 for the Oregon and Washington outer coast having known sex. For those with known sex in this sample 58% were female and 42% male, but this could be

biased by some directed sampling toward females so the sex ratio should be treated as 50:50 in the management plan.

b. This probability is estimated at 27% for the migrating season based on 73% of encounters of PCFG whales from Dec-May through 2015 for the Oregon and Washington outer coast having known sex. For those with known sex in this sample 46% were female and 54% were male. This male-biased sex ratio is in the opposite direction of the bias from intentionally sampling females, which suggests males are actually more abundant and available in the spring off the Oregon and Washington outer coast likely as a result of females with calves migrating later and being less available in spring. Given the bias for trying to sample known females, it is likely that the sex ratio in spring is likely closer to 60:40 male:female. If hunters avoid taking mothers with calves it would further reduce the chances of taking a female.

Estimates of the proportion of PCFG whales used in the Makah management plan for assigning a struck unidentified whale in the winter/spring hunt are subject to uncertainty due to for example shifting proportions based on sampling differences and these should be considered subject to a bias (which depends on trials) that ranges from -0.1 to 0.1.

Table 5

Factors considered in the model scenarios. The bold values are the base-levels and the values in standard font form the basis for sensitivity analyses.

Factor	Levels
Model fitting related	
Stock hypothesis	**3a,** 3b, 3c, 3e, **5a,** 6b
MSYR_{1+} (western)	As for WFG
MSYR_{1+} (north)	**4.5%**, 5.5%, Estimated (common); estimate (separately)
MSYR_{1+} (WFG)	**4.5%** Estimated (common); estimate (separately)
MSYR_{1+} (PCFG)	2%, **4.5%**, 5.5%, Estimated (common); estimate (separately)
Mixing rate (migration season in BCBC	**0.28**, 0.17, 1.00
Immigration into the PCFG	0, 1, **2**, 4
Bycatches and ship strikes	Numbers dead + M/SI, **dead x 4**; dead x 10; dead x 20
Pulse migrations into the PCFG	10, **20**, 30
Projection-related	
Additional catch off Sakhalin (mature female)	0, 1
Catastrophic events	**None**, once in years 0 – 49, and once in years 50-99
Northern need in final year (from 150 in 2014)	**340**
Struck and lost rate	**(0.1; odd-years; 0.5 even years),** 0.5 all years
Future effort	**Constant**, Increase by 100% over 100 years
Probability of a photo (struck and lost whales)	**0.8; odd-years; 0.6 even years**
Probability of a photo (landed whales)	**0.9**
Probability of false positive rate PCFG	**0.05**, 0.1
Probability of false negative rate PCFG	**0.25**
Probability of false positive rate WFG	**0.01**
Probability of false negative rate WFG	**0.041 (stock hypotheses 3a, 3c, 3e, 6b);** 0.040 (stock hypothesis 3b); **0.049 (stock hypothesis 5a)**
Probability of a sex assignment given a PCFG match	**0.81**

4.4.2 Base-case trials and sensitivity tests

The 4th Rangewide workshop specified a series of trials. However, it had not been possible to implement all of these trials during the intersessional period. The Workshop reviewed the set of trials and made the following changes (trial numbers relate to revised numbering system):

(1) stock hypothesis 3e is now treated as a sensitivity test as it is a variant of stock hypothesis 5a (with no WBS animals in the SI sub-area);

(2) a new sensitivity test (18C) based on stock hypothesis 3c has been added as agreed at the 4th Rangewide workshop (IWC, 2018);

(3) the sensitivity test exploring a higher proportion of WBS whales in sub-area SI (3B) involves increasing the estimates of abundance for the WBS by 50% and correspondingly reducing the estimates of abundance for the WFG;

(4) the trials involving PCFG whales in the BSCS sub-area (12A/B) are based on assuming that all PCFG whales are in the BSCS sub-area. The assumption will be conservative given that most PCFG whales are located elsewhere when the aboriginal hunt off Chukotka occurs;

(5) the trials involving WFG whales in the BSCS sub-area (13A/B) are based on assuming that all WFG whales are in the BSCS sub-area. The assumption will be conservative given that most WFG whales are located elsewhere when the aboriginal hunt off Chukotka occurs;

(6) the trials exploring the sensitivity of how the California set gillnet catches were modelled (trials 14 and 15 in Table 8 of IWC (2018)) were dropped as the approach for modelling the SET1 and SET2 fleets was modified (see Item 4.3.1);

(7) the trials with MSYR estimated and a higher pulse were dropped as these trials are unlikely to be informative (trials 14A/B and 8A/B examine these factors individually);

(8) variants of trials 5A/B and 16A/B (trials 18A/B and 19A/B) that have net immigration of 1 to the PCFG were added because the assumption of zero immigration into the PCFG is unlikely given the results of Lang and Martien (2012);

(9) trials 7A/B and 16A/B exclude the PCFG abundance estimates for 1998-2002 as a low pulse would not allow the model to mimic these data – this change in model specifications mimics the adoption in the trials used to evaluate the *SLA* for a Makah hunt by IWC (2013) of a time-varying survey bias;

(10) trials 22A/B have been added to examine the future consequences of a catastrophic events in the NFG – these events occurs randomly once in the first 50 years and randomly once in the second 50 years, with a magnitude equivalent to that of the mortality event in 1999/2000; and

(11) trials 23A/B and 24A/B have been added to explore sensitivity to the struck and lost rate for a Makah hunt in the feeding season, and the false negative rate for a Makah hunt in summer.

Table 6

Final trial specifications

Trial	Description/stock hypothesis	PCFG or WFG in BSCS	MSYR$_{1+}$			PCFG		Bycatch	Condition?
			North	PCFG	WFG	Imm.	Pulse		
Base-case trials									
0A	Reference 3a	No	4.50%	4.50%	4.50%	2	20	D x 4	Yes
0B	Reference 5a	No	4.50%	4.50%	4.50%	2	20	D x 4	Yes
Sensitivity tests									
1A	Lower MSYR PCFG 3a	No	**4.50%**	**2%**	**4.50%**	2	20	D x 4	Yes
1B	Lower MSYR PCFG 5a	No	**4.50%**	**2%**	**4.50%**	2	20	D x 4	Yes
2A	Higher MSYR PCFG and North 3a	No	**5.50%**	**5.50%**	**4.50%**	2	20	D x 4	Yes
2B	Higher MSYR PCFG and North 5a	No	**5.50%**	**5.50%**	**4.50%**	2	20	D x 4	Yes
3A	Lower WBS in Sakhalin 5a (Hyp 3e)	No	4.50%	4.50%	4.50%	2	20	D x 4	Yes
3B	Higher WBS in Sakhalin 5a	No	4.50%	4.50%	4.50%	2	20	D x 4	Yes
4A	PCFG mixing based on Northern WA only 3a	No	4.50%	4.50%	4.50%	2	20	D x 4	Yes
4B	PCFG mixing based on Northern WA only 5a	No	4.50%	4.50%	4.50%	2	20	D x 4	Yes
5A	No PCFG Immigration 3a	No	4.50%	4.50%	4.50%	**0**	20	D x 4	Yes
5B	No PCFG Immigration 5a	No	4.50%	4.50%	4.50%	**0**	20	D x 4	Yes
6A	Higher PCFG Immigration 3a	No	4.50%	4.50%	4.50%	**4**	20	D x 4	Yes
6B	Higher PCFG Immigration 5a	No	4.50%	4.50%	4.50%	**4**	20	D x 4	Yes
7A	Lower Pulse into PCFG 3a (and no 1998-2002 PCFG data)	No	4.50%	4.50%	4.50%	2	**10**	D x 4	Yes
7B	Lower Pulse into PCFG 5a (and no 1998-2002 PCFG data)	No	4.50%	4.50%	4.50%	2	**10**	D x 4	Yes
8A	Higher pulse into PCFG 3a	No	4.50%	4.50%	4.50%	2	**30**	D x 4	Yes
8B	Higher pulse into PCFG 5a	No	4.50%	4.50%	4.50%	2	**30**	D x 4	Yes
9A	Bycatch=Dead + MSI 3a	No	4.50%	4.50%	4.50%	2	20	**D + MSI**	Yes
9B	Bycatch=Dead + MSI 5a	No	4.50%	4.50%	4.50%	2	20	**D + MSI**	Yes
10A	Bycatch x 10 3a	No	4.50%	4.50%	4.50%	2	20	**D x 10**	Yes
10B	Bycatch x 10 5a	No	4.50%	4.50%	4.50%	2	20	**D x 10**	Yes
11A	Bycatch x 20 3a	No	4.50%	4.50%	4.50%	2	20	**D x 20**	Yes
11B	Bycatch x 20 3e	No	4.50%	4.50%	4.50%	2	20	**D x 20**	Yes
12A	PCFG in BSCS 3a	**PCFG**	4.50%	4.50%	4.50%	2	20	D x 4	Yes
12B	PCFG in BSCS 5a	**PCFG**	4.50%	4.50%	4.50%	2	20	D x 4	Yes
13A	WFG in BSCS 3a	**WFG**	4.50%	4.50%	4.50%	2	20	D x 4	Yes
13B	WFG in BSCS 5a	**WFG**	4.50%	4.50%	4.50%	2	20	D x 4	Yes
14A	MSYR1+ estimated (common) 3a	No		**Estimated**		2	20	D x 4	Yes
14A	MSYR1+ estimated (common) 5a	No		**Estimated**		2	20	D x 4	Yes
15A	MSYR1+ estimated (by FA) 3a	No	**Est**	**Est**	**Est**	2	20	D x 4	Yes
15B	MSYR1+ estimated (by FA) 5a	No	**Est**	**Est**	**Est**	2	20	D x 4	Yes
16A	Lower PCFG immigration and higher bycatch 3a (and no 1998-2002 PCFG data)	No	4.50%	4.50%	4.50%	**0**	20	**D x 10**	Yes

Trial	Description/stock hypothesis	PCFG or WFG in BSCS	MSYR_{1+}			PCFG		Bycatch	Condition?
			North	PCFG	WFG	Imm.	Pulse		
16B	Lower PCFG immigration and higher bycatch 5a (and no 1998-2002 PCFG data)	No	4.50%	4.50%	4.50%	**0**	20	**D x 10**	Yes
17A	MSYR estimated and lower pulse 3a	No	**Est**	**Est**	**Est**	2	**10**	D x 4	Yes
17B	MSYR estimated and lower pulse 5a	No	**Est**	**Est**	**Est**	2	**10**	D x 4	Yes
18A	Stock hypothesis 3b	No	4.50%	4.50%	4.50%	2	20	D x 4	Yes
18B	Stock hypothesis 6b	No	4.50%	4.50%	4.50%	2	20	D x 4	Yes
18C	Stock hypothesis 3c	No	4.50%	4.50%	4.50%	2	20	D x 4	Yes
19A	Lower PCFG Immigration 3a	No	4.50%	4.50%	4.50%	**1**	20	D x 4	Yes
19B	Lower PCFG Immigration 5a	No	4.50%	4.50%	4.50%	**1**	20	D x 4	Yes
20A	Lower PCFG immigration and higher bycatch 3a	No	4.50%	4.50%	4.50%	**1**	20	**D x 10**	Yes
20B	Lower PCFG immigration and higher bycatch 5a	No	4.50%	4.50%	4.50%	**1**	20	**D x 10**	Yes
21A	Survival = 0.95; 3a	No	4.50%	4.50%	4.50%	2	20	D x 4	Yes
21B	Survival = 0.95; 3a	No	4.50%	4.50%	4.50%	2	20	D x 4	Yes
22A	Future catastrophic events (once in each of yrs 1-50 & 51-99) - 3a	No	4.50%	4.50%	4.50%	2	20	D x 4	No, 3a
22B	Future catastrophic events (once in each of yrs 1-50 & 51-99) - 5a	No	4.50%	4.50%	4.50%	2	20	D x 4	No, 5a
23A	Summer S&L rate = 0.5 - 3a	No	4.50%	4.50%	4.50%	2	20	D x 4	No, 3a
23B	Summer S&L rate = 0.5 - 5a	No	4.50%	4.50%	4.50%	2	20	D x 4	No, 5a
24A	PCFG false negative rate = 0.1 - 3a	No	4.50%	4.50%	4.50%	2	20	D x 4	No, 3a
24B	PCFG false negative rate = 0.1 - 5a	No	4.50%	4.50%	4.50%	2	20	D x 4	No, 5a
25A	PCFG mixing based on Northern WA is 100%	No	4.50%	4.50%	4.50%	2	20	D x 4	Yes
25B	PCFG mixing based on Northern WA is 100%	No	4.50%	4.50%	4.50%	2	20	D x 4	Yes

4.4.3 Conditioning statistics

The Workshop reviewed the diagnostic plots for evaluating the conditioning developed for the trials specified at the 4th Rangewide Workshop. The Workshop **agreed** that the following plots should be produced for each trial and provided to the Intersessional Steering Group for review:

(1) The estimates of absolute abundance (with 90% sampling intervals) and the median, 50% and 90% intervals for the time-trajectory of the model estimates of 1+ population size.
(2) The time-trajectory of the model estimates of the number of mature females.
(3) The distributions (median, 50% and 90% intervals) for the generated mixing proportions and those for the model-predicted mixing proportions.
(4) The distribution for the net immigration rate from the NFG to the PCFG and the target value (black vertical bar).
(5) The estimates of average bycatch over the period for which reporting is considered adequate [Annex D, table 3] (with 90% sampling intervals) and the median, 50% and 90% intervals for the model-estimate of the average bycatch over the period.
(6) The distributions (median, 50% and 90% intervals) for the generated survival rates for PCFG whales and those for the model-predicted survival rates for PCFG whales.
(7) The time-trajectories of removals, including the recorded removals (adjusted for under-reporting) and the bycatch inferred for the years for which reporting is not considered adequate.

4.4.4 Projection scenarios

Previous projections for the Sakhalin population (J. Cooke in Reeves *et al.*, 2005) considered a scenario in which there is future bycatch of 1.5 mature females off Japan based on inferences from bycatch at that time. The Workshop noted that observed bycatch off Japan has declined since then. The Workshop **agreed** that a projection scenario with 1 mature female taken each year in the EJPJ sub-area should to be conducted.

In addition, the Workshop **agreed** that, if possible, projections should be conducted for the current Makah *SLA*, although it was recognised this may not be feasible to achieve before 67b.

The Workshop noted that care needs to be taken to compare the results from the previous *Implementation Review* with those based on the Rangewide review because the population structure hypotheses have changed and the Rangewide review has more fully accounted for bycatch and its uncertainty.

4.4.5 Performance statistics

4.4.5.1 TIME-TRAJECTORIES OF POPULATIONS

The results of the model fits and the projections will be summarized by time-trajectories of 1+ numbers of breeding stock / feeding group and by sub-area

4.4.5.2 MAKAH MANAGEMENT PLAN

The results of the projections to evaluate the performance of the Makah management plan will be based on the standard statistics used by the Committee to evaluate the performance of Strike Limit Algorithms

(1) D1. Final depletion of 1+ and mature female numbers by breeding stock / feeding group (median, lower 5th and upper 5th percentiles)
(2) D8. Rescaled final depletion: P_T/P_0 (1+ and mature female numbers by breeding stock / feeding group; median, lower 5th and upper 5th percentiles) where P_0 is number of 1+ / mature female animals had there been no future Makah hunts.
(3) D10. Relative increase. The ratio of the 1+ and mature population size after 10 and 100 years to that at the start of the projection period by breeding stock / feeding group (median, lower 5th and upper 5th percentiles)
(4) N9. Need satisfaction. The proportion of the total number of requested strikes that were taken over the first 10 years and the entire 100-year period (median, lower 5th and upper 5th percentiles).

Results are provided for both 10 and 100 years for the D10 and N9 statistics because (a) the Makah management plan current only operates for 10 years, and (b) previous evaluations of the performance of management procedures (RMP and AWMP) have considered performance over 100 years. Population-related statistics should be also be provided for the case there is no future Makah hunt (only bycatch and hunting off Chukotka).

5. WORKPLAN

Before / during 67b

(1) Update the code for the operating model (Punt)
(2) Validate any changes to the historical (conditioning) component of the operating model (Brandon)
(3) Conduct conditioning and distribution of conditioning diagnostics to the Steering Group (Punt)
(4) Review of the conditioning results (Steering Group)
(5) Code the revised Makah management plan and the associated testing code (Punt)
(6) Validate the revised Makah management plan and the associated testing code (Brandon)
(7) Conduct the projections and assemble the projection results (Punt)

After 67b

(1) Complete drafting of the CMP.

6. ADOPTION OF REPORT

The co-chairs thanked Brownell and his colleagues for the excellent and historic facilities provided at the laboratory in the beautiful setting of Granite Canyon (complete with gray whales migrating by). The report was adopted by email.

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Annex A

List of Participants

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Annex B

Agenda

1. Introductory items
    - 1.1 Convenor's opening remarks
    - 1.2 Election of Chair
    - 1.3 Appointment of rapporteurs
    - 1.4 Adoption of Agenda
    - 1.5 Documents and data available
2. Progress on 'non-modelling' recommendations and new data
    - 2.1 Updated information from the co-operative genetics studies
    - 2.2 Updated information from photo-identification studies including consolidation of WGW catalogues
    - 2.3 Gray whales off Korea
3. Updating scientific aspects of the CMP
    - 3.1 Review of existing sections
    - 3.2 Consideration of future stakeholder workshop
    - 3.3
4. Update on modelling framework and runs
    - 4.1 Progress on modelling since SC/66b, including validation
        - 4.1.1 General progress, including validation
        - 4.1.2 Modelling related to the proposal Mkah management plan
    - 4.2 Review of stock hypothesis
    - 4.3 Confirm final data sets
        - 4.3.1 Removals (direct and incidental)
        - 4.3.2 Abundance estimates
        - 4.3.3 Mixing proportions
    - 4.4 Confirm final trial structure and conditioning
        - 4.4.1 Changes to the trial specifications, including stock structure
        - 4.4.2 Base-case trials and sensitivity tests
        - 4.4.3 Conditioning statistics
        - 4.4.4 Projection scenarios
        - 4.4.5 Performance statistics
5. Work plan
6. Adoption of Report

Annex C
List of Documents

SC/M18/CMP

1. Scordino, J. and Bickham, J. Plausibility of stock structure hypothesis 6b
2. Tyurneva, O.Y., Takovlev, Y.M., Vertyankin, V.V. van der Wolf, P. and Scott, M.J. Lomg-term photo-identification studies of gray whales (*Eschrichtius robustus*) offshore northeast Salhalin Island, Russia, 2002-2017.
3. Brandon, J. IWC Gray Whale Rangewide Model: Code Validation for the 2018 Workshop.
4. Kim, H.W. and Sohn, H. Possible occurrence of gray whale off Korea in 2015.

Annex D

Terminology Used with Respect to Stock Structure Hypotheses

Breeding stocks. There are up to two extant breeding stocks: Western (WBS) and Eastern (EBS).

*Feeding groups or aggregations**. There are up to three feeding groups or aggregations. There is dispersal between the PCFG and North Feeding Group (NFG), but the Western Feeding Group (WFG) is demographically independent of the other two feeding groups (i.e. there is no permanent movement of animals from the NFG or PCFG to the WFG).

	Feeding groups or aggregations	Abbreviation	Definition (may vary with hypothesis)
1	Western Feeding Group	WFG	Animals that feed regularly (define?) off Sakhalin Island* according to photo-identification data
2	Pacific Coast Feeding Group	PCFG	Animals that feed regularly (define?) in the PCFG area according to photo-identification data
3	North Feeding Group	NFG	Animals found in other feeding areas (and for which there is relatively little information including photo-ID)

* May need revising with regard to Southern Kamchatka animals given Justin's paper.

Sub-areas. The model includes 11 geographical sub-areas that are used to explain the movements of gray whales (breeding stocks and feeding groups) in the North Pacific and two 'latent sub-areas' used to link model predictions to observed indices of abundance.

	Sub-area	Abbreviation
1	Vietnam-South China Sea	VSC
2	Korea and western side of the Sea of Japan	KWJ
3	Eastern side of the Sea of Japan and the Pacific coast of Japan	EJPJ
4	Northeastern Sakhalin Island	SI
5	Southern Kamchatka and Northern Kuril Islands*	SKNK
6	Areas of the Okhotsk Sea not otherwise specified	OS
7	Northern Bering and Chukchi Sea	BSCS
8	Southeast Alaska	SEA
9	British Columbia to Northern California	BCNC
10	California	CA
11	Mexico	M
12	Latent sub-area	Calif-3
13	Latent sub-area	BC-BCA-3

* New at this workshop – replaces the old East Kamchatka and Kuril Islands to recognise the information from telemetry and photo-ID.

Annex E

Specifications of the rangewide model

A. Basic concepts and stock structure

The aim of the projections is to explore the population consequences of various scenarios regarding anthropogenic removals of gray whales, with a view to informing future conservation and management. The model distinguishes 'breeding stocks' and 'feeding aggregations'. Breeding stocks are demographically and genetically independent whereas feeding aggregations may be linked through dispersal of individuals[6], though perhaps at very low rates for some combinations of feeding aggregations. Each breeding stock / feeding aggregation is found in a set of sub-areas, each of which may have catches (commercial, aboriginal or incidental), proportions of breeding stock / feeding aggregation mixing[7] in those sub-areas, observed bycatch rates[8], estimates of survival rates, and indices of relative or absolute abundance. Removals may be specified to sets of months during the year for some sub-areas if the various feeding aggregations are not equally vulnerable to catches throughout the year for those sub-areas. The trials capture uncertainty regarding stock structure and MSYR, as well as uncertainty regarding bycatch and immigration.

The region concerned, the North Pacific, is divided into 11 sub-areas (Fig. 1). The model also includes several 'latent' sub-areas used to link model predictions to observed indices of abundance. These are denoted, WFG, WBS, WST, CA-3 and BCNC-3. There are up to two extant *breeding stocks* (Western and Eastern). The Eastern breeding stock consists of up to three *feeding aggregations* depending on the stock structure hypothesis: Western Feeding Group (WFG), Pacific Coast Feeding Group (PCFG) and North Feeding Group (NFG). There is dispersal between the PCFG and the NFG, but the WFG is demographically independent of the other two feeding aggregations (i.e. there is no *permanent* movement of animals from the NFG or PCFG to the WFG or vice-versa).

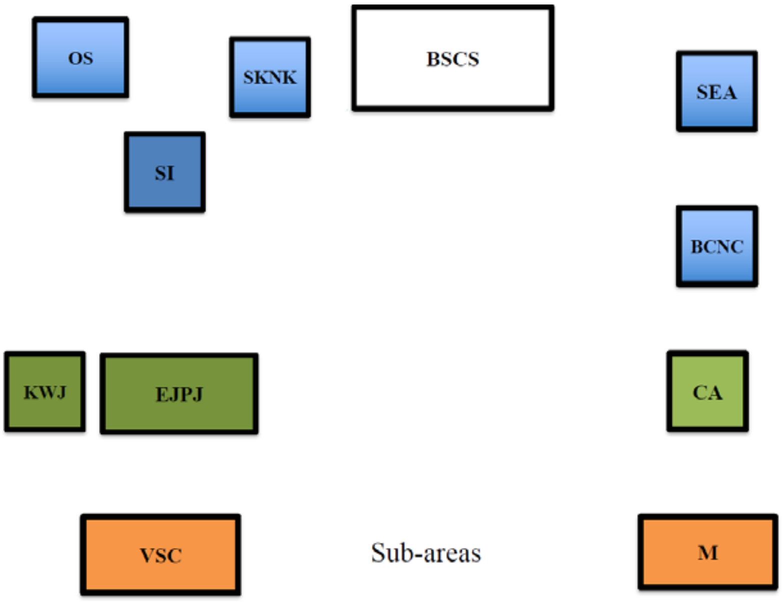

Fig. 1. The sub-areas in the model.

The trials consider five stock structure hypotheses

(1) *Hypothesis 3a.* Although two breeding stocks (Western and Eastern) may once have existed, the Western breeding stock is assumed to have been extirpated. Whales show matrilineal fidelity to feeding grounds, and the Eastern breeding stock includes three feeding aggregations: PCFG, NFG, and WFG.

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[6] The term 'dispersal' is used here in the sense of 'effective dispersal', and refers to permanent movement of individuals among feeding aggregations. Such individuals become part of the feeding aggregation to which they move and contribute to future reproduction.

[7] Mixing is defined here as two feeding aggregations that overlap at some time on the feeding grounds, but do not exchange individuals.

[8] Bycatch is understood to include mortality or 'serious' injury from entanglement or entrapment in fishing gear (or debris) and ship strikes.

(2) *Hypothesis 3b*. Identical to hypothesis 3a, except that NFG whales do not feed off SKNK. In addition, a Western breeding stock exists that overwinters in VSC and feeds in the OS (but not SI) and SKNK. Thus, SKNK is used by both the WFG whales and the whales of the Western breeding stock.

(3) *Hypothesis 3c*. Identical to 3a, except that on occasion whales migrating between the Sakhalin feeding region and Mexico travel through the BSCS sub-area

(4) *Hypothesis 3e*. Identical to hypothesis 3a, except that the Western breeding stock is extant and feeds off both coasts of Japan and Korea and in the northern Okhotsk Sea west of the Kamchatka Peninsula. All of the whales feeding off Sakhalin overwinter in the eastern North Pacific

(5) *Hypothesis 5a*. Identical to hypothesis 3e except that the whales feeding off Sakhalin include both whales that are part of the extant Western breeding stock and remain in the western North Pacific year-round, and whales that are part of the Eastern breeding stock and migrate between Sakhalin and the eastern North Pacific

(6) *Hypothesis 6b*. This hypothesis assumes that the WFG does not exist, but that whales feeding in the SI sub-area represent an extant Western breeding stock that utilizes two wintering grounds (VSC and M). This hypothesis differs from hypothesis 5a, in that 1) all removals off China and Japan are assumed to be Western breeding stock animals, and 2) the abundance estimates for Sakhalin are assumed to relate only to the Western breeding stock.

B. Basic dynamics

The population dynamics are based on the standard age- and sex-structured model, which has formed the basis for the evaluation of *Strike Limit Algorithms* for eastern North Pacific gray whales, i.e.:

$$\begin{aligned}
N^{m/f,i,j}_{t+1,0} &= 0.5B^{i,j}_{t+1} && a=0 \\
N^{m/f,i,j}_{t+1,a} &= (N^{m/f,i,j}_{t,a-1} + I^{m/f,i,j}_{t,a-1} - C^{m/f,i,j}_{t,a-1})\,S_{a-1}\,\tilde{S}^{i,j}_{t} && 1 \le a \le x-1 \\
N^{m/f,i,j}_{t+1,x} &= ((N^{m/f,i,j}_{t,x} + I^{m/f,i,j}_{t,\mathrm{x}} - C^{m/f,i,j}_{t,x})S_x + (N^{m/f,i,j}_{t,x-1} + I^{m/f,i,j}_{t,\mathrm{x}-1} - C^{m/f,i,j}_{t,x-1})\,S_{x-1})\,\tilde{S}^{i,j}_{t} && a=x
\end{aligned} \tag{B.1}$$

where $N^{m/f,i,f}_{t,a}$ is the number of males / females of age *a* in feeding aggregation *j* of breeding stock *i* at the start of year *t*; $C^{m/f,i,f}_{t,a}$ is the number of anthropogenic removals of males / females of age *a* in feeding aggregation *j* of breeding stock *i* during year *t* (whaling/incidental catches are assumed to take place in a pulse at the start of each year); S_a is the annual survival rate of animals of age *a* in the absence of catastrophic mortality events (assumed to be the same for males and females):

$$S_a = \begin{cases} S_0 & \text{if } a=0 \\ S_{1+} & \text{if } 1<a \end{cases} \tag{B.2}$$

S_0 is the calf survival rate; S_{1+} is the survival rate for animals aged 1 and older; $\tilde{S}^{i,j}_t$ is the amount of catastrophic mortality (represented in the form of a survival rate) for feeding aggregation *j* of breeding stock *i* during year *t* (catastrophic events are assumed to occur at the end of the year after mortality due to anthropogenic removals, whaling and non-catastrophic natural causes and dispersal; in general $\tilde{S}^{i,j}_t=1$, i.e. there is no catastrophic mortality); $B^{i,j}_{t+1}$ is the number of births to feeding aggregation *j* of breeding stock *i* during year *t*; $I^{s,m/f}_{t,a}$ is the net dispersal of female/male animals of age *a* into feeding aggregation *j* of breeding stock *i* during year *t*; and *x* is the maximum (lumped) age-class (all animals in this and the *x*-1 class are assumed to be recruited and to have reached the age of first parturition). *x* is taken to be 15.

C. Births and density-dependence

Density-dependence is assumed to be a function of numbers of animals aged 1 and older by feeding ground relative to the carrying capacity by feeding ground. The density-dependence component for feeding aggregation *j* of breeding stock *i* is the sum of the density-dependence components by feeding aggregation weighted by the proportion of animals from feeding aggregation *j* of breeding stock *i* that are found on each feeding ground, i.e.:

$$F(i,j,t) = \sum_A \psi^{A,i,j}\left(X^{A,i,j}(N^{1+,A}_t / K^{1+,A})^z\right) / \sum_A \psi^{A,i,j} X^{A,i,j} \tag{C.1}$$

where z is the degree of compensation; $\psi^{A,i,j}$ indicates whether sub-area A impacts density-dependence for feeding aggregation j of breeding stock i, N_t^{1+A} is the number of 1+ animals on feeding ground A at the start of year t:

$$N_t^{1+,A} = \sum_i \sum_j X^{A,i,j} \sum_{a=1}^{x} (N_{t,a}^{m,i,j} + N_{t,a}^{f,i,j}) \tag{C.2}$$

K^{1+A} is the carrying capacity for feeding ground A:

$$K^{1+,A} = \sum_i \sum_j X^{A,i,j} \sum_{a=1}^{x} (N_{-\infty,a}^{m,i,j} + N_{-\infty,a}^{f,i,j}) \tag{C.3}$$

$X^{A,i,j}$ is the proportion of animals of feeding aggregation j of breeding stock i that are found in feeding ground A[9] (Tables 1 and 2).

The number of births at the start of year t for feeding aggregation j of breeding stock i, $B_t^{i,j}$, is given by:

$$B_t^{i,j} = b_t^{i,j}\, N_t^{f,i,j} \tag{C.4}$$

where $N_t^{f,i,j}$ is the number of mature females in feeding aggregation j of breeding stock i at the start of year t:

$$N_t^{f,i,j} = \sum_{a=a_m}^{x} N_{t,a}^{f} \tag{C.5}$$

a_m is the age-at-maturity (the convention of referring to the mature population is used here, although this actually refers to females that have reached the age of first parturition); $b_t^{i,j}$ is the probability of birth/calf survival for mature females:

$$b_t^{i,j} = \max(0, b_K\{1 + A^{i,j}(1 - F(I, j, t))\}) \tag{C.6}$$

b_K is the average number of live births per year per mature female at carrying capacity; and $A^{i,j}$ is the resilience parameter for feeding aggregation j of breeding stock i.

D. **Immigration (dispersal)**

The numbers dispersing into feeding aggregation j of breeding stock i, include contributions from pulse migration as well as diffusive dispersal:

$$I_{t,a}^{s,j,i} = I_{t,a}^{1,s,j,a} - I_{t,a}^{2,s,j,a} \tag{D.1a}$$

$$I_{t,a}^{1,s,j,i} = \sum_{k \neq j} \delta^{k,j,i} N_{t,a}^{s,i,k} \left(\frac{N_t^{f,i,k}}{N_{-\infty}^{f,i,k}}\right)^{\tilde{\lambda}} + \sum_{k \neq j} \Omega_y^{k,j,i} \frac{N_{t,a}^{s,i,k}}{\sum_{a=1}^{x} (N_{t,a}^{m,i,k} + N_{t,a}^{f,i,k})} \tag{D.1b}$$

$$I_{t,a}^{2,s,j,i} = \sum_{k \neq j} \delta^{j,k,i} N_{t,a}^{s,i,j} \left(\frac{N_t^{f,i,j}}{N_{-\infty}^{f,i,j}}\right)^{\tilde{\lambda}} + \sum_{k \neq j} \Omega_y^{j,k,i} \frac{N_{t,a}^{s,i,j}}{\sum_{a=1}^{x} (N_{t,a}^{m,i,j} + N_{t,a}^{f,i,j})} \tag{D.1c}$$

---

[9] It is usually the case that $\sum X^{A,i,j} = 1$. However, for gray whales, this is not necessarily the case because removals can take place in the various sub-areas at different times. What is then important is the relative values of the $X^{A,i,j}$ among feeding aggregations for a given feeding ground.

where $\delta^{k,j,i}$ is the rate of dispersal from feeding aggregation *k* to feeding aggregation *j* of breeding stock *i*; λ is a factor to allow for density-dependence in the dispersal rate (set to 2); and $\Omega_y^{k,j,i}$ is the number of animals that disperse in year *y* from feeding aggregation *k* to feeding aggregation *j* of breeding stock *i* in a pulse.

E. **Anthropogenic removals**

The catch by feeding aggregation, sex and age is the sum of the catch over fleet (see Table 3 for fleet definitions), i.e.:

$$C_{t,a}^{m/f,i,j} = \sum_k C_t^{m/f,k} \frac{\alpha_a^k X^{A_k,i,j} N_{t,a}^{m/f,i,j}}{\sum_{i,j,a} \alpha_a^k X^{A_k,i,j} N_{t,a}^{m/f,i,j}} \qquad \text{(E.1)}$$

where $C_t^{m/f,k}$ is the catch of males/females by fleet *k* during year *t*; A_k is the sub-area in which fleet *k* operates; and α_a^k is the relative vulnerability of animals of age *a* to harvest by fleet *k*. The values for the catches by fleet and sex are either pre-specified (Table 4[10]) or computed using Equation E.2. for the years for which actual estimates are not available:

$$C_{t,a}^{m/f,k} = \lambda^k E_t^k \sum_{i,j,a,m/f} \alpha_a^k X^{A,i,j} N_{t,a}^{m/f,i,j} \qquad \text{(E.2)}$$

where E_t^k is a measure of the effort by fleet *k* during year *t* (Table 5) and λ^k is the catchability coefficient for fleet *k*.

F. **Initializing the parameter vector**

The numbers at age in the pristine population are given by:

$$\begin{aligned} N_{-\infty,a}^{m/f,i,j} &= 0.5\, N_{-\infty,0}^{i,j} \prod_{a'=0}^{a-1} S_{a'} && \text{if } a < x \\ N_{-\infty,x}^{m/f,i,j} &= 0.5\, N_{-\infty,0}^{i,j} \prod_{a'=0}^{x-1} S_{a'} / (1 - S_x) && \text{if } a = x \end{aligned} \qquad \text{(F.1)}$$

The value for $N_{-\infty,0}^{i,j}$ is determined from the value for the pre-exploitation size of the 1+ component of feeding aggregation *j* of breeding stock *i* using the equation:

$$N_{-\infty,0}^{m,i,j} = K^{1+,i,j} / \left(\sum_{a=1}^{x-1} \left(\prod_{a'=0}^{a-1} S_{a'} \right) + \frac{1}{1-S_x} \prod_{a'=0}^{x-1} S_{a'} \right) \qquad \text{(F.2)}$$

where $K^{1+,i,j}$ is the carrying capacity (in terms of the 1+ population size size) for feeding aggregation *j* of breeding stock *i*:

$$K_t^{1+,i,j} = \sum_{a=1}^{x} (N_{-\infty,a}^{m,i,j} + N_{-\infty,a}^{f,i,j}) \qquad \text{(F.3)}$$

$N_{-\infty,a}^{m/f,i,j}$ is the number of animals of age *a* that would be in feeding aggregation *j* of breeding stock *i* in the pristine population.

The model is based on the assumption that the age-structure at the start of year τ is stable rather than that the population was at its pre-exploitation equilibrium size at some much earlier year. The determination of the age-structure at the start of year τ involves specifying the effective 'rate of increase', γ, that applies to each age-class. There are two components contributing to γ, one relating to the overall population rate of increase (γ^+) and the other to the exploitation rate due to all forms of anthropogenic removal. Under the assumption of knife-edge recruitment to the fishery at age a_r, only the γ^+ component (assumed to be zero following Punt and Butterworth

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[10] The bycatches for 2016 are set equal to those for 2015 as data on bycatch for 2016 are not finalized at present.

[2002]) applies to ages *a* of a_r or less. The number of animals of age *a* at the start of year τ relative to the number of calves at that time, $N^*_{\tau,a}$, is therefore given by the equation:

$$N^*_{\tau,a} = \begin{cases} 1 & \text{if } a = 0 \\ N^*_{\tau,a-1}\, S_{a-1} & \text{if } a \le a_r \\ N^*_{\tau,a-1}\, S_{a-1}\,(1-\gamma) & \text{if } a_r < a < x \\ N^*_{\tau,x-1}\, S_{x-1}(1-\gamma)\,/\,(1-S_x\,(1-\gamma)) & \text{if } a = x \end{cases} \tag{F.4}$$

where B_τ is the number of calves in year τ and is derived directly from equations C.1 and C.6.

$$B_\tau = \left(1-\left[1/(N^f_\tau b_K)-1\right]/A\right)^{1/z} \frac{K^{1+}}{N^{1+,*}_\tau} \tag{F.5}$$

The effective rate of increase, γ, is selected so that if the population dynamics model is projected from year τ to a year Ψ, the size of the 1+ component of the population in a reference year Ψ equals a value, P_Ψ.

G. **Conditioning**

The parameters of the model are: (a) the carrying capacity of each stock, (b) the population size for each stock at the start of 1930 (expressed relative to carrying capacity), (c) MSYR by stock, (d) annual survival under 'normal' conditions, (e) maturity as a function of age, (f) the impact of the mortality event in the eastern Pacific in 1999 and 2000, (g) selectivity, (h) the rate of dispersal between the NFG and the PCFG, (i) the parameters of the mixing matrices, (j) the catchability coefficients that determine bycatch by fleet (Eqn E.2), and (k) the extent of additional variation for each abundance index. Some of these parameters are pre-specified:

(1) MSYR (except for trials 14, 15, and 17);
(2) Annual survival under 'normal' conditions (base-case 0.98);
(3) Maturity as a function of age (a logistic function of age, with an age-at-50%-first-parturition of 8 years and a minimum age-age-at-first parturition of 3 years); and
(4) Selectivity (Table 3).

Under the assumption that the estimates of abundance for a sub-area (Table 6) are log-normally distributed, the negative of the logarithm of the likelihood function is given by:

$$-\ell nL = \ell n\sqrt{\text{Det}[V]} + 0.5\sum_k (\ell\,\text{n}\,\underline{N}^{A,obs} - \ell\,\text{n}\,\underline{N}^{A})[V^{-1}](\ell\,\text{n}\,\underline{N}^{A,obs} - \ell\,\text{n}\,\underline{N}^{A})^T \tag{G.1}$$

where $N^{A,\text{obs}}_t$ is the survey estimate of abundance for sub-area *A* during year *t*; and V is the sum of the variance-covariance matrix for the abundance estimates plus an additional variance term (assumed to be independent of year). Note that the abundance estimates for the western areas (Table 6a) depend on the stock hypothesis under consideration.

The data on the proportion of each stock (Tables 6a and 7) in each sub-area are modelled under the assumption that the proportions are normally distributed, i.e.:

$$-\ell nL = \sum_i \sum_A \sum_t \tfrac{1}{2(\tau^{i,A}_t)^2}(p^{i,A}_t - p^{i,A,\text{obs}}_t)^2 \tag{G.2}$$

where $p^{i,A}_t$ is the model-estimate of the proportion of the animals in sub-area *A* that are from feeding aggregation *i* of the Eastern breeding stock*;* $p^{i,A,\text{obs}}_t$ is the observed proportion of animals in in sub-area *A* that are from feeding aggregation *i* of the Eastern breeding stock; and $\tau^{i,A}_t$ is the standard error of $p^{i,A,\text{obs}}_t$.

The (non-zero) bycatches by sub-area for the first five years for which data are available are assumed to be log-normally distributed, and the model is fitted to the average bycatch by sub-area over a pre-specified set of years (the years for which detection and reporting of entanglements, ship strikes, and strandings in general was relatively good; Table 3), i.e.:

$$-\ell\text{n}L = \sum_A \tfrac{1}{2\sigma_{BC}^2}\left(\ell\text{n}C^{I,A,\text{obs}} - \ell\text{n}\hat{\bar{C}}^{I,A}\right)^2 \tag{G.3}$$

where $C^{I,A,\text{obs}}$ is the observed average annual bycatch from sub-area *A* over the pre-specified period, $\hat{\bar{C}}^{I,A}$ is the average over this period of the model-estimate of the bycatch from sub-area *A*, and σ_{BC} is the standard error of the logarithms of the observed bycatches.

A penalty is imposed on the average number of animals moving permanently from the NFG into the PCFG between 2001 and 2008, i.e.:

$$-\ell nL = \tfrac{1}{2\sigma_I^2}\left(\tilde{I} - \frac{\delta^{\text{m/f,north,}West\text{st}}}{8}\sum_{t=2001}^{2008}\sum_{s=m/f}\sum_{a=1}^{x} I_{t,a}^{s,\text{East,north}}\right)^2 \tag{G.4}$$

where $\tilde{I}$ is the pre-specified average number of immigrants into the PCFG from the NFG, and σ_I is a weighting factor.

The estimates of survival for PCFG whales (Calambokidis *et al.*, 2017) are assumed to be normally distributed, i.e.:

$$-\ell\text{n}L = \tfrac{1}{2\sigma_{S,1}^2}(S^{\text{obs},1} - \hat{S}^1)^2 + \tfrac{1}{2\sigma_{S,2}^2}(S^{\text{obs},2} - \hat{S}^2)^2 \tag{G.5}$$

where $S^{\text{obs},1} = 0.917$, $\sigma_{L,1} = 0.0142$, $S^{\text{obs},2} = 0.967$, $\sigma_{L,2} = 0.0066$, $\hat{S}_1$ is the estimate of post-first-year survival for whales that entered in 1998 or earlier, and $\hat{S}_2$ is the estimate of post-first-year survival for whales that entered in 1999 or later.

H. **Quantifying uncertainty using bootstrap**

A bootstrap procedure is used to quantify uncertainty for a given model specification. Each bootstrap replicate involves:

(1) Generating pseudo time-series of abundance estimates based on the assumption that the abundance estimates are log-normally distributed with means and variance-covariance matrices given by the observed abundance estimates and the reported variance-covariance matrices.
(2) Generating pseudo mixing proportions from beta distributions with means and CVs given by the observed means and CVs.
(3) Generating pseudo bycatch rates by sub-area from log-normal distributions with means of $C^{I,A,\text{obs}}$ and a log standard error of σ_{BC}.
(4) Generating a pseudo immigration rate from the NFG into the PCFG based on a normal distribution (truncated at zero) with mean $\tilde{I}$ and standard error σ_I.
(5) Generating pseudo survival rates from normal distributions.

I. Generation of Data

The actual historical estimates of absolute abundance (and their associated CVs) provided to the *Strike Limit Algorithms* are listed in Table 6. The future estimates of abundance for sub-areas WFG, WST, BCNC-3 and CA-3 (say sub-area *K*) are generated using the formula:

$$\hat{P} = PYw / P^{*}\beta^2 Yw \tag{I.1}$$

where *Y* is a lognormal random variable Y=e$^{\varepsilon}$ where $\varepsilon \sim N(0;\sigma_\varepsilon^2)$ and $\sigma_\varepsilon^2 = \ell n(1+\alpha^2)$; *w* is a Poisson random variable with $E(w) = \text{var}(w) = \mu = (P/P^{*})/\beta^2$, *Y* and *w* are independent; *P* is the current total (1+) population size in survey area *K*:

$$P = P_t^K = \sum_i\sum_j\sum_g\sum_{a\geq 1} N_{t,a}^{g,i,j} \tag{I.2}$$

P^* is the reference population level, and is equal to the total (1+) population size in the survey area prior to the commencement of exploitation in the sub-area for which an abundance estimate is to be generated. For consistency with the first-stage screening trials for a single stock (IWC, 1991, 1994), the ratio $\alpha^2 : \beta^2 = 0.12 : 0.025$, so that $CV^2(\hat{P}) = \tau(0.12 + 0.025P^* / P)$. If $\overline{CV}$ is the target CV then $\tau = \overline{CV}^2 / (0.12 + 0.025P_{\text{ref}} / P^*)$ where P_{ref} is the population size in a reference year.

An estimate of the *CV* is generated for each estimate of abundance:

$$CV(\hat{P})^2_{\text{est}} = \sigma^2 \chi^2 / n \tag{I.3}$$

where $\sigma^2 = \ell n(1 + \alpha^2 + \beta^2 P^* / \hat{P})$, and χ is a random number from a Chi-square distribution with *n* degrees of freedom (where *n*=10 as used for NP minke trials; IWC, 2004).

J. Trials

The factors included in the trials are listed in Table 8 and the trials in Table 9.

K. Management options

The strike limits for the BSCS sub-area are based on the Gray Whale *SLA* (IWC, 2005). The strike limits for the BCNC sub-area based on the Makah Management Plan (Appendix 1) although sensitivity is explored using variant 1 agreed to in 2012 (IWC, 2013; Appendix 2).

Removals due to bycatch are based on the scenarios regarding future trends in effort. Table 8 lists the factors considered in the projections.

L. Output Statistics

The population-size statistics are produced for each breeding stock / feeding aggregation, while the removal-related statistics are for each sub-area.

I.1 Risk

D1. Final depletion: P_T/K (1+ and mature female numbers by breeding stock / feeding group (median, lower 5th and upper 5th percentiles)).

D2. Lowest depletion: $\min(P_t / K) : t = 0,1,...,T$.

D3. Plots of $\{P_{t[x]} : t = 0,1,..,T\}$ where $P_{t[x]}$ is the *x*th percentile of the distribution of P_i . Results are presented for x = 5, 50, and 95.

D8. Rescaled final depletion: P_T/P_0 (1+ and mature female numbers by breeding stock / feeding group; median, lower 5th and upper 5th percentiles) where P_0 is number of 1+ / mature female animals had there been no future Makah hunts.

D10. Relative increase. The ratio of the 1+ and mature population size after 10 and 100 years to that at the start of the projection period by breeding stock / feeding group (median, lower 5th and upper 5th percentiles)

I.2 Removal-related

N9. Need satisfaction. The proportion of the total number of requested strikes that were taken over the first 10 years and the entire 100-year period (median, lower 5th and upper 5th percentiles).

R1. Plots of strikes by year for simulations 1-100.

R2. Plots of landed whales by year for simulations 1-100.

R3. Plots of incidental catches by year for simulations 1-100 (median, lower 5th and upper 5th percentiles by year).

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Table 1
The presence matrices for stock structure hypotheses 3a, 3b, 3c, 3e, 5a and 6b.

[a] Hypothesis 3a (no extant Western breeding stock)

Breeding stock/ Feeding Aggregation	Sub-area													
	VSC	KWJ	EJPJ	OS	SI	SKNK	BSCS	SEA (J-N)	SEA (D-M)	BCNC (J-N)	BCNC (D-M)	CA (J-N)	CA (D-M)	M
Eastern														
WFG			1	1	1	1			1		1		1	1
North			1			1	1	1	1	1	1	1	1	1
PCFG							1[A]	1	1	1	1	1	1	1

A: Sensitivity test (12) only

[b] Hypothesis 3b (extant Western breeding stock)

Breeding stock/ Feeding Aggregation	Sub-area													
	VSC	KWJ	EJPJ	OS	SI	SKNK	BSCS	SEA (J-N)	SEA (D-M)	BCNC (J-N)	BCNC (D-M)	CA (J-N)	CA (D-M)	M
Western	1	1	1	1		1								
Eastern														
WFG				1	1	1			1		1		1	1
North			1				1	1	1	1	1	1	1	1
PCFG								1	1	1	1	1	1	1

[c] Hypothesis 3c (no extant Western breeding stock; WFG in BSCS)

Breeding stock/ Feeding Aggregation	Sub-area													
	VSC	KWJ	EJPJ	OS	SI	SKNK	BSCS	SEA (J-N)	SEA (D-M)	BCNC (J-N)	BCNC (D-M)	CA (J-N)	CA (D-M)	M
Eastern														
WFG			1	1	1	1	1		1		1		1	1
North			1			1	1	1	1	1	1	1	1	1
PCFG								1	1	1	1	1	1	1

[d] Hypothesis 3e (extant Western breeding stock; WFG in EJPJ)

Breeding stock/ Feeding Aggregation	Sub-area													
	VSC	KWJ	EJPJ	OS	SI	SKNK	BSCS	SEA (J-N)	SEA (D-M)	BCNC (J-N)	BCNC (D-M)	CA (J-N)	CA (D-M)	M
Western	1	1	1	1		1								
Eastern														
WFG			1	1	1	1			1		1		1	1
North						1	1	1	1	1	1	1	1	1
PCFG								1	1	1	1	1	1	1

[e] Hypothesis 5a (Western breeding stock in SI)

Breeding stock/ Feeding Aggregation	Sub-area													
	VSC	KWJ	EJPJ	OS	SI	SKNK	BSCS	SEA (J-N)	SEA (D-M)	BCNC (J-N)	BCNC (D-M)	CA (J-N)	CA (D-M)	M
Western	1	1	1	1	1	1								
Eastern														
WFG			1	1	1	1			1		1		1	1
North						1	1	1	1	1	1	1	1	1
PCFG							1[A]	1	1	1	1	1	1	1

A: Sensitivity test (12) only

[f] Hypothesis 6b (no Western feeding group)

Breeding stock/ Feeding Aggregation	Sub-area													
	VSC	KWJ	EJPJ	OS	SI	SKNK	BSCS	SEA (J-N)	SEA (D-M)	BCNC (J-N)	BCNC (D-M)	CA (J-N)	CA (D-M)	M
Western	1	1	1	1	1	1			1		1		1	1
Eastern														
North						1	1	1	1	1	1	1	1	1
PCFG								1	1	1	1	1	1	1

Table 2

The mixing matrices for stock structure hypotheses 3a, 3b, 3e, 5a and 6b. The γs denote the estimable parameters of the catch mixing matrix and the χs denote values that are varied in the tests of sensitivity.

[a] Hypothesis 3a (no extant Western breeding stock)

Breeding stock/ Feeding Aggregation	Sub-area													
	VSC	KWJ	EJPJ	OS	SI	SKNK	BSCS	SEA (J-N)	SEA (D-M)	BCNC (J-N)	BCNC (D-M)	CA (J-N)	CA (D-M)	M
Eastern														
WFG			1	1	1	1			γ_6		γ_3		γ_6	1
North			γ_1			1	1	1	1	1	1	1	1	1
PCFG							1^A	γ_8^B	γ_7	γ_2	γ_4	γ_5	γ_7	1

A: Sensitivity test (12) only
B: Sensitivity test (9) only

[b] Hypothesis 3b (extant Western breeding stock)

Breeding stock/ Feeding Aggregation	Sub-area													
	VSC	KWJ	EJPJ	OS	SI	SKNK	BSCS	SEA (J-N)	SEA (D-M)	BCNC (J-N)	BCNC (D-M)	CA (J-N)	CA (D-M)	M
Western	1	1	γ_1	1										
Eastern														
WFG				1	1	1			γ_6		γ_3		γ_6	1
North			1			1	1	1	1	1	1	1	1	1
PCFG								1	γ_7	γ_2	γ_4	γ_5	γ_7	1

[c] Hypothesis 3c (extant Western breeding stock; WFG in BSCS)

Breeding stock/ Feeding Aggregation	Sub-area													
	VSC	KWJ	EJPJ	OS	SI	SKNK	BSCS	SEA (J-N)	SEA (D-M)	BCNC (J-N)	BCNC (D-M)	CA (J-N)	CA (D-M)	M
Western	1	1												
Eastern														
			1	1	1	1	1		γ_6		γ_3		γ_6	1
North			γ_1			1	1	1	1	1	1	1	1	1
PCFG								1	γ_7	γ_2	γ_4	γ_5	γ_7	1

[d] Hypothesis 3e (extant Western breeding stock; WFG in EJPJ)

Breeding stock/ Feeding Aggregation	Sub-area													
	VSC	KWJ	EJPJ	OS	SI	SKNK	BSCS	SEA (J-N)	SEA (D-M)	BCNC (J-N)	BCNC (D-M)	CA (J-N)	CA (D-M)	M
Western	1	1	γ_1	1		1								
Eastern														
WFG			1	1	1	1			γ_6		γ_3		γ_6	1
North						1	1	1	1	1	1	1	1	1
PCFG								1	γ_7	γ_2	γ_4	γ_5	γ_7	1

[e] Hypothesis 5a (Western breeding stock in SI)

Breeding stock/ Feeding Aggregation	Sub-area													
	VSC	KWJ	EJPJ	OS	SI	SKNK	BSCS	SEA (J-N)	SEA (D-M)	BCNC (J-N)	BCNC (D-M)	CA (J-N)	CA (D-M)	M
Western	1	1	γ_1	1	1	1								
Eastern														
WFG			1	1	1	1			γ_6		γ_3		γ_6	1
North						1	1	1	1	1	1	1	1	1
PCFG							1^A	γ_8^B	γ_7	γ_2	γ_4	γ_5	γ_7	1

A: Sensitivity test (12) only
B: Sensitivity test (9) only

[f] Hypothesis 6b (no Western feeding group)

Breeding stock/ Feeding Aggregation	Sub-area													
	VSC	KWJ	EJPJ	OS	SI	SKNK	BSCS	SEA (J-N)	SEA (D-M)	BCNC (J-N)	BCNC (D-M)	CA (J-N)	CA (D-M)	M
Western	1	1	1	1	1	1			γ_6		γ_3		γ_6	1
Eastern														
North						1	1	1	1	1	1	1	1	1
PCFG								1	γ_7	γ_2	γ_4	γ_5	γ_7	1

Table 3

Fleets included in the population dynamics model, the associated selectivity patterns, and the years for which detection and reporting of entanglements, ship strikes, and strandings in general was relatively good. The columns “Years (hindcast)” and “Years (forecast)” denote the ranges of years used to infer bycatch rates respectively before and after the first year for which detection and reporting of entanglements, ship strikes, and strandings in general was relatively good

Fleet	Season	Type	Years	Years (hindcast)	Years (forecast)	Selectivity
Northern Bering and Chukchi Sea (BSCSA)	All	Subsistence	N/A			Uniform 1+
WA U&A (feeding) (WAUAF)	June-Nov	Subsistence	N/A			Uniform 1+
WA U&A (migration) (WAUAM)	Dec-May	Subsistence	N/A			Uniform 1+
CA-scientific (migration)	Dec-May	Scientific	N/A			Uniform 1+
Vietnam-South China Sea (VSC)	All	All removals	No removals			
Korea and western side of the Sea of Japan (KWJ)	All	All removals	No removals			
Eastern side of the Sea of Japan and the Pacific coast of Japan (EJPJ)	All	All removals	1982 – 2015	1982 – 2015	1982 – 2015	Uniform 0-5
Northeastern Sakhalin Island (SI)	All	All removals	1982 – 2015	1982 – 2015	1982 – 2015	Uniform 0-5
Southern Kamchatka and Northern Kuril Islands (SKNK)	All	All removals	No removals			
Areas of the Okhotsk Sea not otherwise specified (OS)	All	All removals	No removals			
Northern Bering and Chukchi Sea (BSCSE)	All	Entanglements	1987 – 2015	1987 – 1991	2011 – 2015	Uniform 0-5
Southeast Alaska (SEA1E)	June-Nov	Entanglements	M/SI only	1987 – 1991	2011 – 2015	Uniform 0-5
Southeast Alaska (SEA2E)	Dec-May	Entanglements	1987 – 2015	1987 – 1991	2011 – 2015	Uniform 0-5
British Columbia to Northern California (BCNC1E)	June-Nov	Entanglements	1990 – 2015	1990 – 1994	2011 – 2015	Uniform 0-5
British Columbia to Northern California (BCNC2E)	Dec-May	Entanglements	1990 – 2015	1990 – 1994	2011 – 2015	Uniform 0-5
California (CA1E)	June-Nov	Entanglements	1982 – 2015	1982 – 1986	2011 – 2015	Uniform 0-5
California (CA2E)	Dec-May	Entanglements	1982 – 2015	1982 – 1986	2011 – 2015	Uniform 0-5
Mexico (MEXE)	All	Entanglements	MS/I only	1982 – 1986	2011 – 2015	Uniform 0-5
Northern Bering and Chukchi Sea (BSCSS)	All	Ship strikes	No ship strikes			
Southeast Alaska (SEA1S)	June-Nov	Ship strikes	No ship strikes			
Southeast Alaska (SEA2S)	Dec-May	Ship strikes	1987 – 2015	1987 - 2015	1987 - 2015	Uniform 0+
British Columbia to Northern California (BCNC1S)	June-Nov	Ship strikes	1990 – 2015	1990 – 2015	1990 – 2015	Uniform 0+
British Columbia to Northern California (BCNC1S)	Dec-May	Ship strikes	1990 – 2015	1990 – 2015	1990 – 2015	Uniform 0+
California (CA1S)	June-Nov	Ship strikes	1982 – 2015	1982 – 2015	1982 – 2015	Uniform 0+
California (CA2S)	Dec-May	Ship strikes	1982 – 2015	1982 – 2015	1982 – 2015	Uniform 0+
Mexico (MEXS)	All	Ship strikes	MS/I only	1982 – 2015	1982 – 2015	Uniform 0+
California (SET1)	June-Nov	Set Gillnet	1982 – 1990	1982 – 1990	None	Uniform 0-5
California (SET2)	Dec-May	Set Gillnet	1982 – 1990	1982 – 1990	None	Uniform 0-5
California (SET3)	June-Nov	Set Gillnet	1991 – 2015	None	1991 – 2015	Uniform 0-5
California (SET4)	Dec-May	Set Gillnet	1991 – 2015	None	1991 – 2015	Uniform 0-5

Table 4a

Non-bycatch removals. The BSCS ‘fleet’ represents the aboriginal catches, the two WAUA ‘fleets’ represent Makah hunting in the Makah usual and accustomed area, and the CA migration ‘fleet’ is the scientific catches off California.

Year	Fleet			
	BSCS	WAUA Feeding	WAUA Migration	CA Migration
1930	47	0	0	0
1931	10	0	0	0
1932	10	0	0	10
1933	15	0	0	60
1934	66	0	0	60
1935	44	0	0	110
1936	112	0	0	86
1937	24	0	0	0
1938	64	0	0	0
1939	39	0	0	0
1940	125	0	0	0
1941	77	0	0	0
1942	121	0	0	0
1943	119	0	0	0
1944	6	0	0	0
1945	58	0	0	0
1946	30	0	0	0
1947	31	0	0	0
1948	19	0	0	0
1949	26	0	0	0
1950	11	0	0	0
1951	13	0	1	0
1952	44	0	0	0
1953	38	0	10	0
1954	39	0	0	0
1955	59	0	0	0
1956	122	0	0	0
1957	96	0	0	0
1958	148	0	0	0
1959	194	0	0	2
1960	156	0	0	0
1961	208	0	0	0
1962	147	0	0	4
1963	180	0	0	0
1964	199	0	0	20
1965	181	0	0	0
1966	194	0	0	26
1967	249	0	0	125
1968	135	0	0	66
1969	140	0	0	74
1970	151	0	0	0
1971	153	0	0	0
1972	182	0	0	0
1973	178	0	0	0
1974	184	0	0	0
1975	171	0	0	0
1976	165	0	0	0
1977	187	0	0	0
1978	184	0	0	0
1979	183	0	0	0
1980	182	0	0	0
1981	136	0	0	0
1982	168	0	0	0
1983	171	0	0	0
1984	169	0	0	0
1985	170	0	0	0
1986	171	0	0	0
1987	159	0	0	0
1988	151	0	0	0
1989	180	0	0	0
1990	162	0	0	0
1991	169	0	0	0
1992	0	0	0	0
1993	0	0	0	0
1994	44	0	0	0
1995	92	0	0	0
1996	43	0	0	0
1997	79	0	0	0
1998	125	0	0	0
1999	123	0	1	0
2000	115	0	0	0
2001	112	0	0	0
2002	131	0	0	0
2003	128	0	0	0
2004	111	0	0	0
2005	124	0	0	0
2006	134	0	0	0
2007	131	1	0	0
2008	130	0	0	0
2009	116	0	0	0
2010	118	0	0	0
2011	130	0	0	0
2012	143	0	0	0
2013	127	0	0	0
2014	124	0	0	0
2015	125	0	0	0
2016	120	0	0	0

Table 4b.
Bycatches. The bycatches in the remaining areas are: VSC (2 in 2011), EJPJ (1 in 1995; 1 in 1970; 1 in 1996; 5 in 2005; 1 in 2007); and SI (2 in 2014)). Values replaced by the predictions of Eqn E.2 are indicated by dashes.

(a) Deaths

Year	Entanglements								Ship strikes								Entanglements	
	BSCS	SEA	SEA	BCN	BCN	CA	CA	MEX	BSCS	SEA	SEA	BCN	BCN	CA	CA	MEX	SET	SET
		Feeding	Migration	Feeding	Migration	Feeding	Migration			Feeding	Migration	Feeding	Migration	Feeding	Migration		Feeding	Migration
1982	-	-	-	-	-	0	1	0	-	-	-	-	-	0	0	0	0	0
1983	-	--	-	-	-	1	2	0	-	--	-	-	-	0	0	0	0	0
1984	-	-	-	-	-	0	3	0	-	-	-	-	-	0	1	0	0	0
1985	-	-	-	-	-	0	6	0	-	-	-	-	-	0	0	0	1	2
1986	-	-	-	-	-	0	1	0	-	-	-	-	-	0	0	0	0	0
1987	1	0	0	-	-	0	2	0	0	0	0	-	-	0	4	0	0	1
1988	0	0	1	-	-	0	1	0	0	0	0	-	-	0	3	0	0.75	0
1989	0	0	0	-	-	0	1	0	0	0	0	-	-	0	0	0	0	2
1990	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	2
1991	0	0	0	0	0	0	2	0	0	0	0	0	0	0	3	0	0	0
1992	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
1993	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
1994	0	0	0	0	2	1	1	0	0	0	0	0	0	0	1	0	0	0
1995	0	0	0	1	1	0	1	0	0	0	0	1	0	0	1	0	0	0
1996	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0
1997	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1
1998	1	0	1	1	0	0	1	0	0	0	0	0	1	0	2	0	0	0
1999	2	0	0	1	0	1	1	0	0	0	0	0	0	0	1	0	0	0
2000	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
2001	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2002	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2003	0	0	0	1	1	0	1	0	0	0	0	0	0	0	1	0	0	0
2004	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0.75	0
2005	0	0	0	1	1	0	0	0	0	0	0	0	0	0	2	0	0	0
2006	0	0	0	0	1	0	1	0	0	0	0	0	0	0	2	0	0	0
2007	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
2008	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0
2009	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	0	0
2010	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0
2011	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
2012	0	0	0	1	1	1	2	0	0	0	0	0	0	0	0	0	0	0
2013	0	0	0	1	0	4	0	0	0	0	0	1	0	0	0	0	0	0
2014	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2015	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0.75	0

(b) Serious Injuries

Year	Entanglements								Ship strikes								Entanglements	
	BSCS	SEA	SEA	BCN	BCN	CA1	CA2	MEX	BSCS	SEA	SEA	BCN	BCN	CA	CA	MEX	SET	SET
		Feeding	Migration	Feeding	Migration	Feeding	Migration			Feeding	Migration	Feeding	Migration	Feeding	Migration		Feeding	Migration
1982	-	-	-	-	-	0	1	0	-	-	-	-	-	0	0	0	0	0
1983	-	--	-	-	-	1	2	0	-	--	-	-	-	0	0	0	0	0
1984	-	-	-	-	-	0	3	0	-	-	-	-	-	0	1	0	0	0.75
1985	-	-	-	-	-	0	10.75	0.75	-	-	-	-	-	0	0.14	0	1	4.5
1986	-	-	-	-	-	0	10.25	0	-	-	-	-	-	0	0	0	0	4.5
1987	1.75	0	0	-	-	1.5	5	0	0	0	0	-	-	0	4	0	0	3.5
1988	0	0	1	-	-	0	6	0	0	0	0	-	-	0	4	0	0.75	0
1989	0	0	0	0	0	0	3.5	0	0	0	0	-	-	0	0	0	0	2.75
1990	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0.52	0	0	3.75
1991	0	0	0	0	0	0.75	2.75	0	0	0	0	0	0	0	3	0	0	0
1992	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	1
1993	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
1994	0	0	0	0	0	1	2.75	0	0	0	0	0	0	0	1	0	0	0
1995	0	0	0.75	1	0	0	2.75	0.75	0	0	0	1	0	0	1.72	0	0	0
1996	0	0	0	0	0	0	3.75	0	0	0	0	0	0	0	0	0	0	0
1997	0	0	0	0	0	0.75	0.75	0.75	0	0	1	0	1	0	0	0	0	1.75
1998	1.75	0	1	1	0	0.75	2.5	0	0	0	0	0	2	0	3.56	0	0	0
1999	2	0	0	1.375	0	1	2.5	0	0	0	0	0	0.2	0	1.36	0	0	0
2000	0	0	0	0	0	0.75	3.25	0.75	0	0	0	0	0	0	0	0	0	1
2001	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0
2002	0	0	0	1	0	0	1.5	0	0	0	0	0	0	0	0	0	0	0
2003	0	0	0	1	0	0	1.75	0.75	0	0	0	0	0	0	1	0	0	0
2004	1	0.75	0	0	0	0	1.5	0	0	0	0	0	0	0	0	0	0.75	0
2005	0	0	0	1	0	0	1.5	0	0	0	0	0	0	0	2	0	0	0
2006	0	0	0	0	0	0	1.75	0.75	0	0	0	0	0	0	2.56	0	0	0
2007	1	0	0	0	0	1.5	0	0	0	0	0	0	0	1	0	0	0	0
2008	0	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0
2009	0	0	0.75	0.75	0	0	1.5	0	0	0	0	0.52	1	0	3	0	0	0
2010	0	0	0	0	0	1	2.5	0	0	0	0	0	0	0	1.52	0	0	0
2011	0	1	0	0	0	2	0	0	0	0	0	0	0	1	1.28	0	0	0
2012	2.5	0	0	1.75	0	2	7.75	0	0	0	0	0	0	0	0	0	0	0
2013	0	0	0	1	0	4	2.5	0	0	0	0	1	0	0	0	0	0	0
2014	0	0	0	0	0	2.5	1.5	0	0	0	0	0	0	0	0	0	0	0
2015	1	0	0	0	0	1.5	6	0	0	0	0	0	0	0	1	0	0.75	0

Table 5
Relative effort for the set gillnet fishery off California (J. Carrette, SWFSC, pers commn. Effort is constant at 1 prior to 1981

Year	Effort	Year	Effort	Year	Effort
1981	1.000	1993	1.438	2005	0.428
1982	1.819	1994	0.571	2006	0.365
1983	1.940	1995	0.460	2007	0.401
1984	2.459	1996	0.519	2008	0.384
1985	2.598	1997	0.690	2009	0.304
1986	2.048	1998	0.554	2010	0.358
1987	1.883	1999	0.737	2011	0.370
1988	1.560	2000	0.754	2012	0.324
1989	1.376	2001	0.624	2013	0.278
1990	1.444	2002	0.668	2014	0.265
1991	1.395	2003	0.607	2015	0.419
1992	1.197	2004	0.626		

Table 6a
Abundance estimates (1+) for the WFG feeding aggregation and the western breeding stock (J.G. Cooke, pers. commn)

Year	Group	Stock hypothesis	Estimate	SD	CV
1995	WFG	3a/3c/3e/6b	75.1	3.8	0.051
1995	WBS	3b	25.8	7.3	0.282
1995	WFG	3b	75.5	3.3	0.043
1995	WBS	3e	30.0*	15.0	0.500
1995	WBS	5a	26.6	6.9	0.259
1995	WFG	5a	47.8	7.7	0.160
1995	WBS+WFG	5a	74.4	3.9	0.052
1995	WBS/(WBS+WFG)	5a	0.358	0.093	0.259
2015	WFG	3a/3c/3e/6b	199.8	5.4	0.027
2015	WBS	3b	63.8	15.8	0.248
2015	WFG	3b	198.9	5.7	0.029
2015	WBS	3e	30.0*	15.0	0.500
2015	WBS	5a	64.4	14.0	0.218
2015	WFG	5a	135.6	14.1	0.104
2015	WBS+WFG	5a	200.0	5.7	0.029
2015	WBS/(WBS+WFG)	5a	0.322	0.069	0.200

* Guestimate because the WBS cannot be distinguished given the available information.

Table 6b
Estimates of absolute abundance (with associated standard errors) for the eastern North Pacific stock of gray whales based on shore counts (source: 1967/78-2006/07: Laake *et al*, 2012; 2006/07-2015/16: Durban *et al*, 2013, 2017). These estimates are assumed to pertain to the total number of gray whales.

Year	**Estimate**	**CV**	**Year**	**Estimate**	**CV**
1967/68	13426	0.094	1987/88	26916	0.058
1968/69	14548	0.080	1992/93	15762	0.067
1969/70	14553	0.083	1993/94	20103	0.055
1970/71	12771	0.081	1995/96	20944	0.061
1971/72	11079	0.092	1997/98	21135	0.068
1972/73	17365	0.079	2000/01	16369	0.061
1973/74	17375	0.082	2001/02	16033	0.069
1974/75	15290	0.084	2006/07	19126	0.071
1975/76	17564	0.086	2006/07	20750	0.060
1976/77	18377	0.080	2007/08	17820	0.054
1977/78	19538	0.088	2009/10	21210	0.046
1978/79	15384	0.080	2010/11	20990	0.044
1979/80	19763	0.083	2014/15	28790	0.130
1984/85	23499	0.089	2015/16	26960	0.050
1985/86	22921	0.081			

Table 6c

Estimates of absolute abundance (with associated CVs) for the PCFG feeding aggregation based on mark-recapture analysis (source: Calambokidis et al., 2017).

Year	Estimate	CV	Year	Estimate	CV
1998	126	0.087	2009	208	0.101
1999	145	0.101	2010	200	0.095
2000	146	0.098	2011	205	0.078
2001	178	0.076	2012	217	0.052
2002	197	0.069	2013	235	0.059
2003	207	0.084	2014	238	0.080
2004	216	0.077	2015	243	0.078
2005	215	0.125			
2006	197	0.108			
2007	192	0.136			
2008	210	0.089			

Table 7

Data on mixing proportions (definite and likely matches / non-matches only) to be used when conditioning the models.

Sub-area	Season	Stock / Feeding aggregation	Mixing proportion (assumed SD)
EJPJ	All	WBS/NFG	0.33 (0.1)
SEA	Feeding	PCFG	0.57[1] (0.1)
SEA	Feeding	WFG	0
SEA	Migration	PCFG	0.1[2] (0.1)
SEA	Migration	WFG	0.002[3] (0.05)
BCNC	Feeding	PCFG	0.93 (0.1)
BCNC	Feeding	WFG	0
BCNC	Migration	PCFG	0.28 (0.1)
BCNC	Migration	WFG	0.002 (0.05)
CA	Feeding	PCFG	0.60 (0.1)
CA	Feeding	WFG	0
CA	Migration	PCFG	0.1 (0.05)
CA	Migration	WFG	0.002[3] (0.05)

1: Not used in the conditioning except for the sensitivity test based when the bycatch is based on M/SI as no dead bycatch is recorded for the SEA sub-area during the feeding season.

2: Assumed value owing to lack of data to estimate mixing proportions.

3: Set to the value calculated for BCNC by Moore and Weller (2013)

Table 8

Factors considered in the model scenarios. The bold values are the base-levels and the values in standard font form the basis for sensitivity analyses.

Factor	Levels
Model fitting related	
Stock hypothesis	**3a,** 3b, 3c, 3e, **5a,** 6b
$MSYR_{1+}$ (western)	As for WFG
$MSYR_{1+}$ (north)	**4.5%**, 5.5%, Estimated (common); estimate (separately)
$MSYR_{1+}$ (WFG)	**4.5%** Estimated (common); estimate (separately)
$MSYR_{1+}$ (PCFG)	2%, **4.5%**, 5.5%¸ Estimated (common); estimate (separately)
Mixing rate (migration season in BCBC	**0.28**, 0.17, 1.00
Immigration into the PCFG	0, 1, **2**, 4
Bycatches and ship strikes	Numbers dead + M/SI, **dead x 4**; dead x 10; dead x 20
Pulse migrations into the PCFG	10, **20**, 30
Projection-related	
Additional catch off Sakhalin (mature female)	0, 1
Catastrophic events	**None**, once in years 0 – 49, and once in years 50-99
Northern need in final year (from 150 in 2014)	**340**
Struck and lost rate	**(0.1; odd-years; 0.5 even years),** 0.5 all years
Future effort	**Constant**, Increase by 100% over 100 years
Probability of a photo (struck and lost whales)	**0.8; odd-years; 0.6 even years**
Probability of a photo (landed whales)	**0.9**
Probability of false positive rate PCFG	**0.05**, 0.1
Probability of false negative rate PCFG	**0.25**
Probability of false positive rate WFG	**0.01**
Probability of false negative rate WFG	**0.041 (stock hypotheses 3a, 3c, 3e, 6b);** 0.040 (stock hypothesis 3b); **0.049 (stock hypothesis 5a)**
Probability of a sex assignment given a PCFG match	**0.81**

Table 9

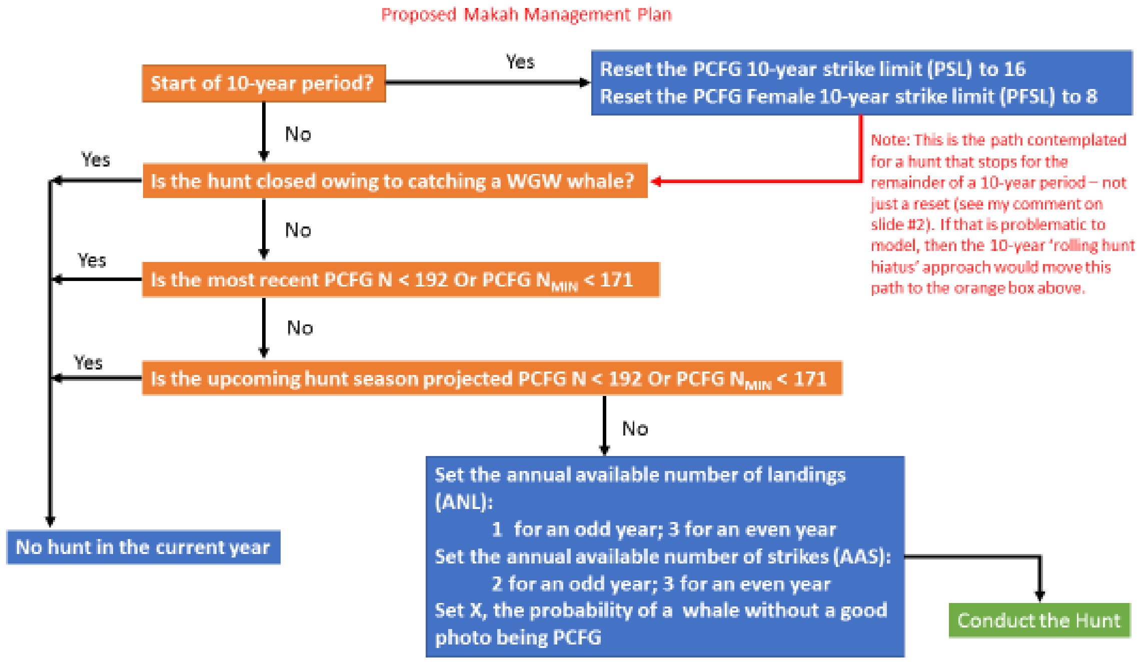
Final trial specifications

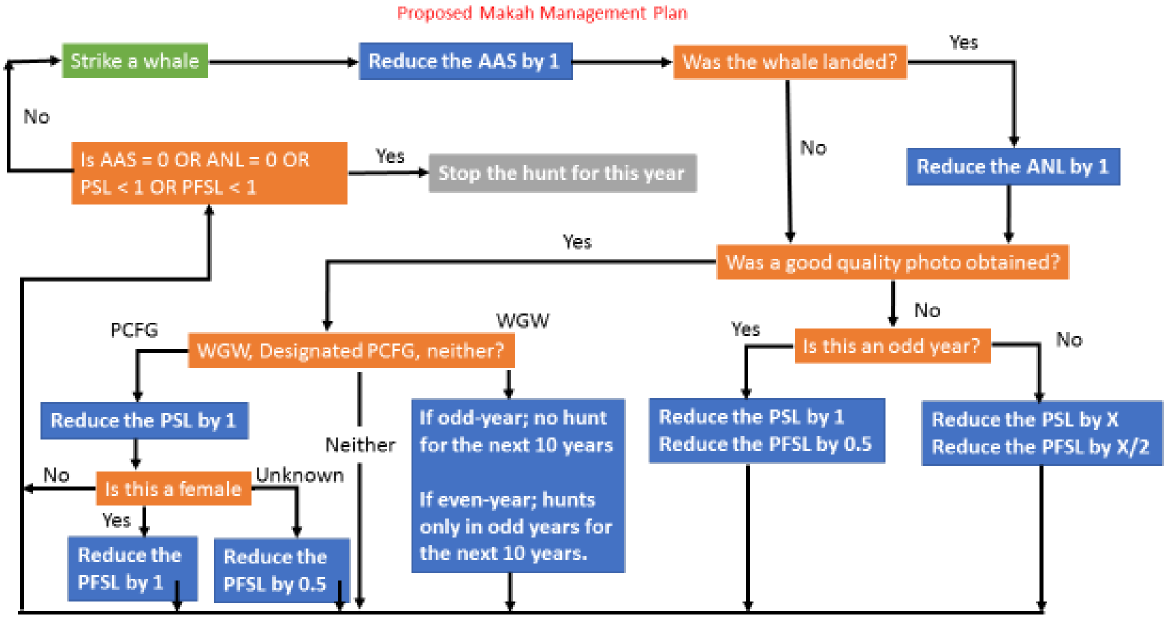
Trial	Description/stock hypothesis	PCFG or WFG in BSCS	MSYR$_{1+}$			PCFG		Bycatch	Conditioning
			North	PCFG	WFG	Imm.	Pulse		
Base-case trials									
0A	Reference 3a	No	4.50%	4.50%	4.50%	2	20	D x 4	Yes
0B	Reference 5a	No	4.50%	4.50%	4.50%	2	20	D x 4	Yes
Sensitivity tests									
1A	Lower MSYR PCFG 3a	No	**4.50%**	**2%**	**4.50%**	2	20	D x 4	Yes
1B	Lower MSYR PCFG 5a	No	**4.50%**	**2%**	**4.50%**	2	20	D x 4	Yes
2A	Higher MSYR PCFG and North 3a	No	**5.50%**	**5.50%**	**4.50%**	2	20	D x 4	Yes
2B	Higher MSYR PCFG and North 5a	No	**5.50%**	**5.50%**	**4.50%**	2	20	D x 4	Yes
3A	Lower WBS in Sakhalin 5a (Hyp 3e)	No	4.50%	4.50%	4.50%	2	20	D x 4	Yes
3B	Higher WBS in Sakhalin 5a	No	4.50%	4.50%	4.50%	2	20	D x 4	Yes
4A	PCFG mixing based on Northern WA only 3a	No	4.50%	4.50%	4.50%	2	20	D x 4	Yes
4B	PCFG mixing based on Northern WA only 5a	No	4.50%	4.50%	4.50%	2	20	D x 4	Yes
5A	No PCFG Immigration 3a	No	4.50%	4.50%	4.50%	**0**	20	D x 4	Yes
5B	No PCFG Immigration 5a	No	4.50%	4.50%	4.50%	**0**	20	D x 4	Yes
6A	Higher PCFG Immigration 3a	No	4.50%	4.50%	4.50%	**4**	20	D x 4	Yes
6B	Higher PCFG Immigration 5a	No	4.50%	4.50%	4.50%	**4**	20	D x 4	Yes
7A	Lower Pulse into PCFG 3a (and no 1998-2002 PCFG data)	No	4.50%	4.50%	4.50%	2	**10**	D x 4	Yes
7B	Lower Pulse into PCFG 5a (and no 1998-2002 PCFG data)	No	4.50%	4.50%	4.50%	2	**10**	D x 4	Yes
8A	Higher pulse into PCFG 3a	No	4.50%	4.50%	4.50%	2	**30**	D x 4	Yes
8B	Higher pulse into PCFG 5a	No	4.50%	4.50%	4.50%	2	**30**	D x 4	Yes
9A	Bycatch=Dead + MSI 3a	No	4.50%	4.50%	4.50%	2	20	**D + MSI**	Yes
9B	Bycatch=Dead + MSI 5a	No	4.50%	4.50%	4.50%	2	20	**D + MSI**	Yes
10A	Bycatch x 10 3a	No	4.50%	4.50%	4.50%	2	20	**D x 10**	Yes
10B	Bycatch x 10 5a	No	4.50%	4.50%	4.50%	2	20	**D x 10**	Yes
11A	Bycatch x 20 3a	No	4.50%	4.50%	4.50%	2	20	**D x 20**	Yes
11B	Bycatch x 20 3e	No	4.50%	4.50%	4.50%	2	20	**D x 20**	Yes
12A	PCFG in BSCS 3a	**PCFG**	4.50%	4.50%	4.50%	2	20	D x 4	Yes
12B	PCFG in BSCS 5a	**PCFG**	4.50%	4.50%	4.50%	2	20	D x 4	Yes
13A	WFG in BSCS 3a	**WFG**	4.50%	4.50%	4.50%	2	20	D x 4	Yes
13B	WFG in BSCS 5a	**WFG**	4.50%	4.50%	4.50%	2	20	D x 4	Yes
14A	MSYR1+ estimated (common) 3a	No		**Estimated**		2	20	D x 4	Yes
14A	MSYR1+ estimated (common) 5a	No		**Estimated**		2	20	D x 4	Yes
15A	MSYR1+ estimated (by FA) 3a	No	**Est**	**Est**	**Est**	2	20	D x 4	Yes
15B	MSYR1+ estimated (by FA) 5a	No	**Est**	**Est**	**Est**	2	20	D x 4	Yes
16A	Lower PCFG immigration and higher bycatch 3a (and no 1998-2002 PCFG data)	No	4.50%	4.50%	4.50%	**0**	20	**D x 10**	Yes
16B	Lower PCFG immigration and higher bycatch 5a (and no 1998-2002 PCFG data)	No	4.50%	4.50%	4.50%	**0**	20	**D x 10**	Yes
17A	MSYR estimated and lower pulse 3a	No	**Est**	**Est**	**Est**	2	**10**	D x 4	Yes
17B	MSYR estimated and lower pulse 5a	No	**Est**	**Est**	**Est**	2	**10**	D x 4	Yes

Trial	Description/stock hypothesis	PCFG or WFG in BSCS	MSYR$_{1+}$			PCFG		Bycatch	Conditioning
			North	PCFG	WFG	Imm.	Pulse		
18A	Stock hypothesis 3b	No	4.50%	4.50%	4.50%	2	20	D x 4	Yes
18B	Stock hypothesis 6b	No	4.50%	4.50%	4.50%	2	20	D x 4	Yes
18C	Stock hypothesis 3c	No	4.50%	4.50%	4.50%	2	20	D x 4	Yes
19A	Lower PCFG Immigration 3a	No	4.50%	4.50%	4.50%	**1**	20	D x 4	Yes
19B	Lower PCFG Immigration 5a	No	4.50%	4.50%	4.50%	**1**	20	D x 4	Yes
20A	Lower PCFG immigration and higher bycatch 3a	No	4.50%	4.50%	4.50%	**1**	20	**D x 10**	Yes
20B	Lower PCFG immigration and higher bycatch 5a	No	4.50%	4.50%	4.50%	**1**	20	**D x 10**	Yes
21A	Survival = 0.95; 3a	No	4.50%	4.50%	4.50%	2	20	D x 4	Yes
21B	Survival = 0.95; 3a	No	4.50%	4.50%	4.50%	2	20	D x 4	Yes
22A	Future catastrophic events (once in each of yrs 1-50 & 51-99) - 3a	No	4.50%	4.50%	4.50%	2	20	D x 4	No, 3a
22B	Future catastrophic events (once in each of yrs 1-50 & 51-99) - 5a	No	4.50%	4.50%	4.50%	2	20	D x 4	No, 5a
23A	Summer S&L rate = 0.5 - 3a	No	4.50%	4.50%	4.50%	2	20	D x 4	No, 3a
23B	Summer S&L rate = 0.5 - 5a	No	4.50%	4.50%	4.50%	2	20	D x 4	No, 5a
24A	PCFG false negative rate = 0.1 - 3a	No	4.50%	4.50%	4.50%	2	20	D x 4	No, 3a
24B	PCFG false negative rate = 0.1 - 5a	No	4.50%	4.50%	4.50%	2	20	D x 4	No, 5a
25A	PCFG mixing based on Northern WA is 100%	No	4.50%	4.50%	4.50%	2	20	D x 4	Yes
25B	PCFG mixing based on Northern WA is 100%	No	4.50%	4.50%	4.50%	2	20	D x 4	Yes

Appendix 1

OUTLINE OF THE MAKAH MANAGEMENT PLAN AND ITS IMPLEMENTATION IN TRIALS





Appendix 2
THE ‘RESEARCH WITH VARIANT’ (SLA VARIANT 1) OPTION (IWC, 2013).

This option operates as follows:

(1) Update the ABL (Allowable Bycatch Limit of PCFG whales) if this is the start of a new 6-year block as:

$$ABL = N_{MIN} * 0.5 * R_{MAX} * F_R$$

Where:

N_{MIN} is the log-normal 20th percentile of the most recent abundance estimate for the Oregon to Southern Vancouver (OR-SVI) sub-area of the PCFG. The abundance estimates for use in the ABL formula are generated as specified in Section I, except for allowance is made for a bias which differs among simulations but is constant over time between the estimates for OR-V and those for the PCFG, i.e. $\ell n B_A \sim N(-0.335, 0.112^2)$ (IWC, 2012).

R_{MAX} is equal to 0.04;

F_R is equal to 1.0.

(2) Strike an animal
(3) If the total number of struck animals equals the need of 7 stop the hunt.
(4) If the animal is struck-and lost:
  a. if the total number of struck and lost animals is 3, stop the hunt.
  b. go to step (2).
(5) If the animal is landed and is matched against the PCFG catalogue:
  a. add one to the number of whales counted towards the ABL
  b. if the ABL is reached; stop the hunt
  c. if the total number of landed whales equals 5; stop the hunt
  d. if the number of landed whales for the current six-year block equals 24; stop the hunt
  e. go to step (2).
(6) If the animal is landed and does not match any whale in the PCFG catalogue:
  a. if the total number of landed whales equals 5; stop the hunt
  b. if the number of landed whales for the current six-year block equals 24; stop the hunt
  c. go to step (2).

References

IWC. 2012. Report of the Standing Working Group in the Aboriginal Whaling Management Procedure. J. Cetacean Res. Manage. 13 (Suppl.) 130-53.

Geographic areas utilized by gray whales are illustrated with colored boxes:

🟦 Feeding region

🟩 Migratory region

🟧 Wintering region

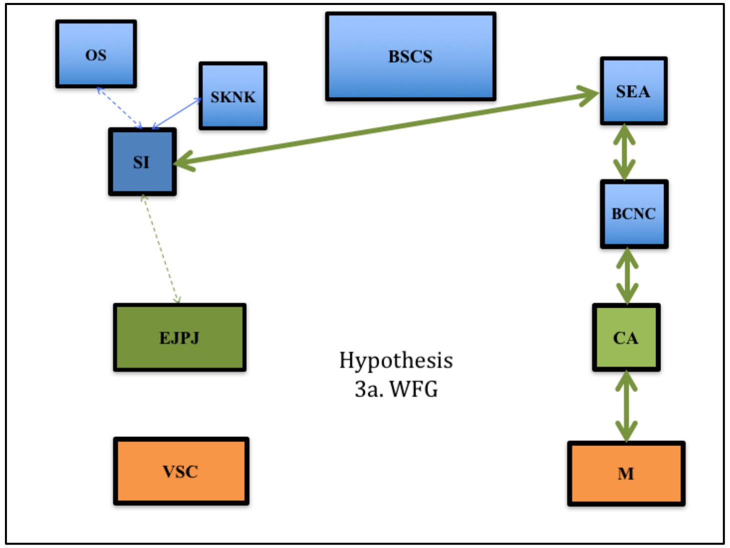
Arrows represent movements between geographic areas, with blue representing movements between feeding regions and green representing migratory movements:

⟺ Solid thick lines with arrows denote movements between regions of a significant proportion of individuals using the area

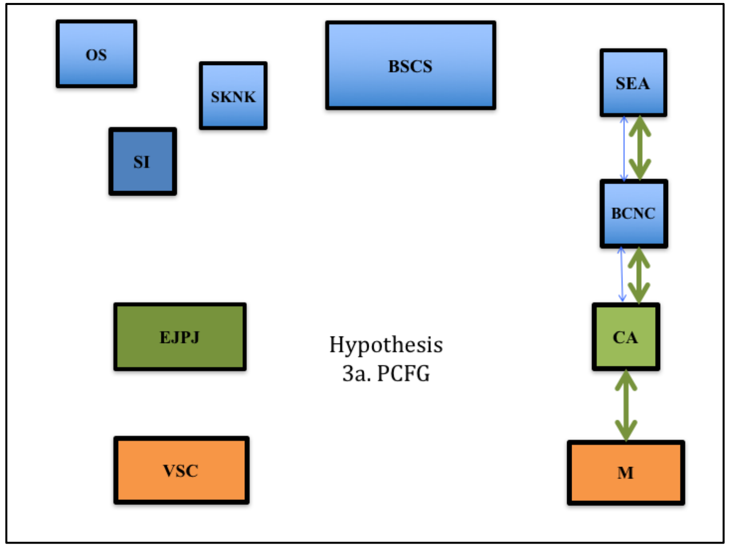
↔ Solid thin lines with arrows denote limited movements between regions

⇠⇢ Dashed thin lines with denote occasional movement between regions of small number of individuals

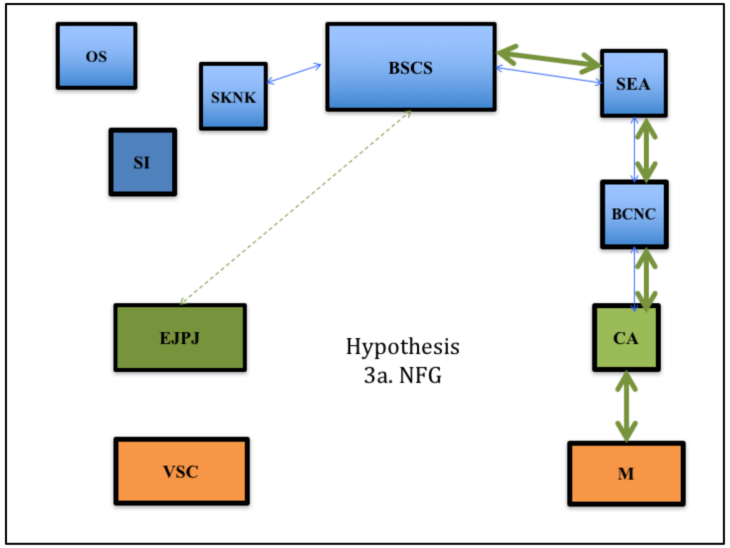
Hypothesis 3a:



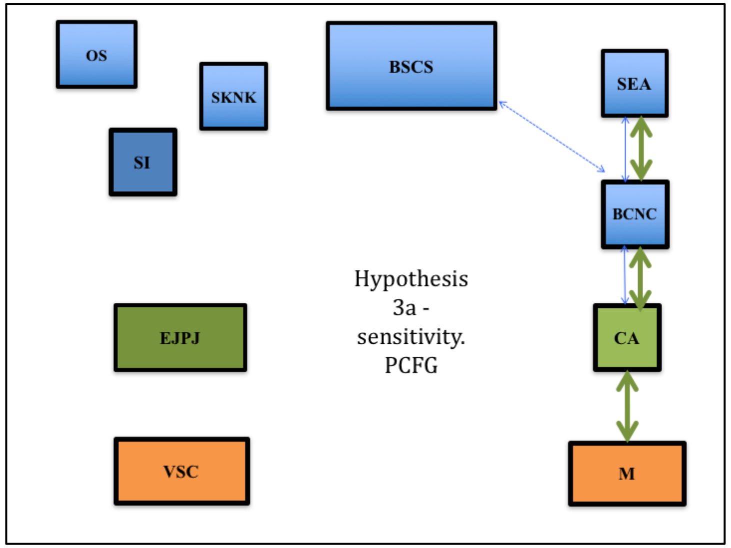
Hypothesis
3a. WFG



Hypothesis
3a. PCFG

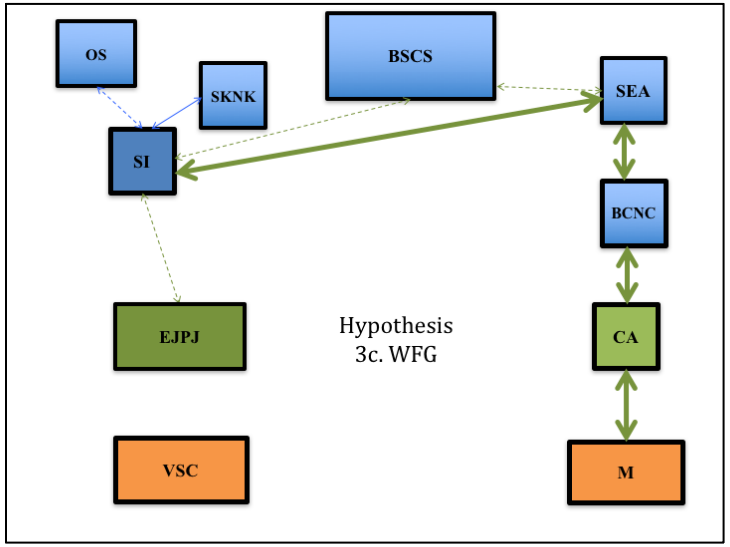


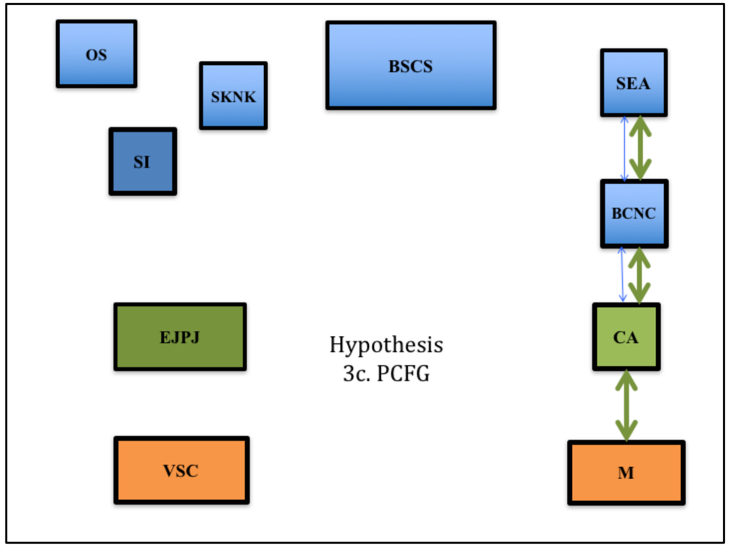
Hypothesis
3a. NFG

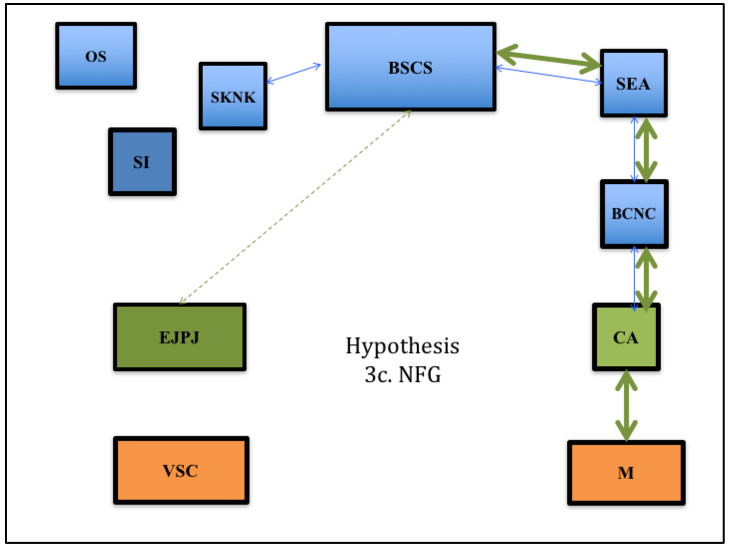


Hypothesis
3a -
sensitivity.
PCFG

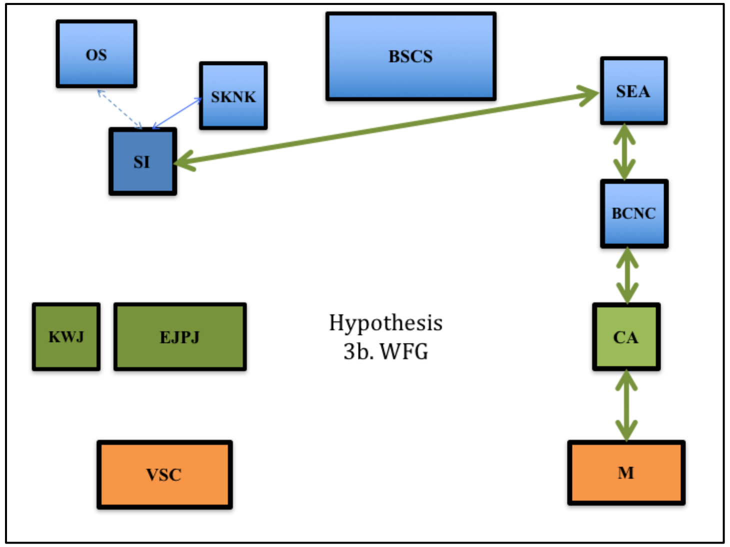
Hypothesis 3c:

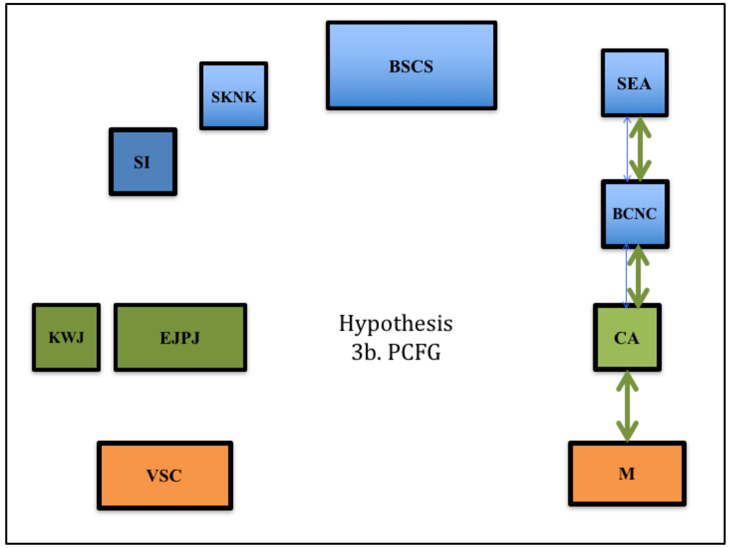


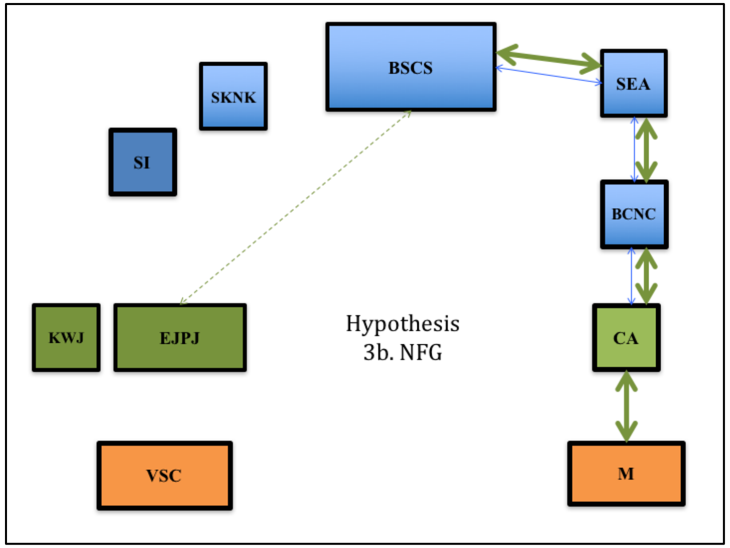


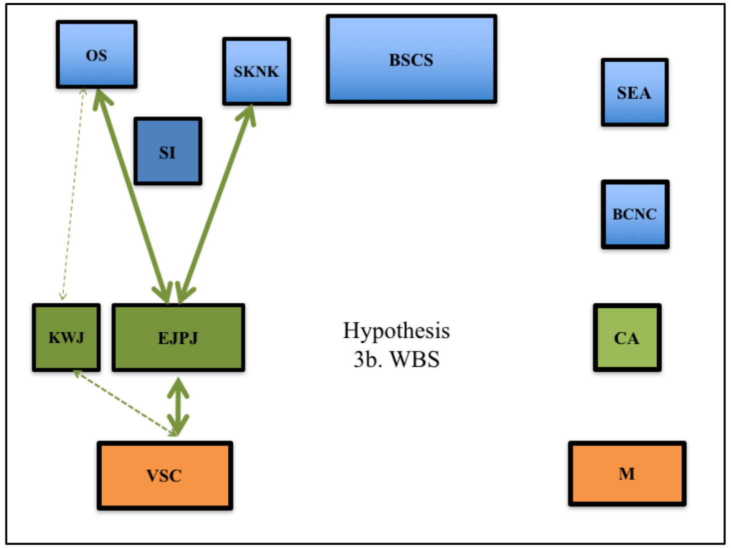


Hypothesis 3b:









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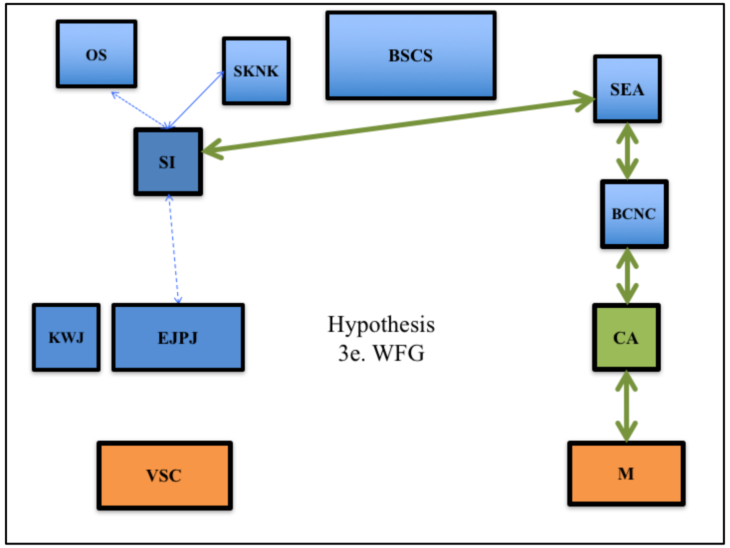

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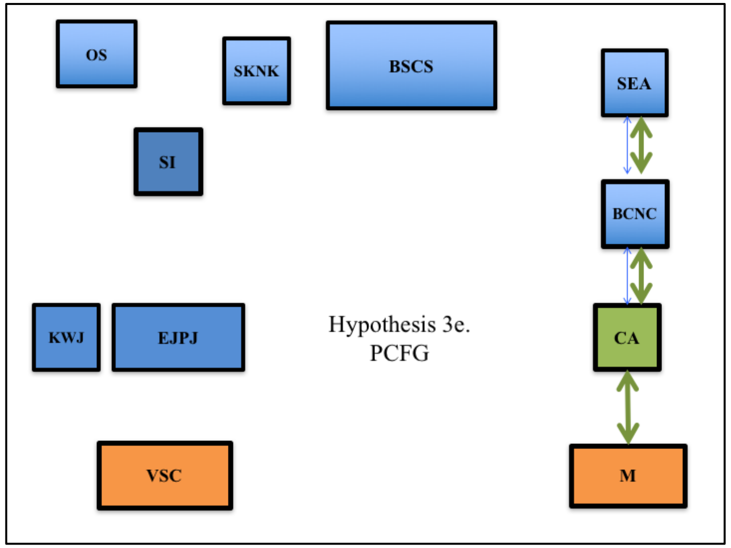
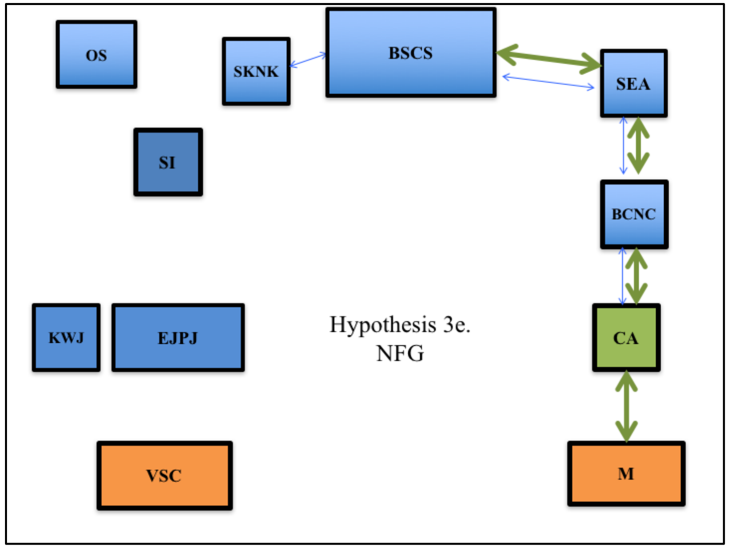
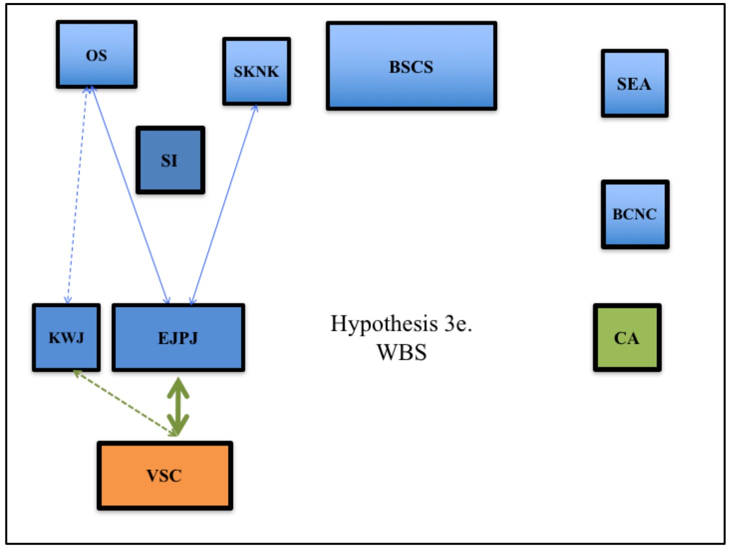


Hypothesis 3e. PCFG

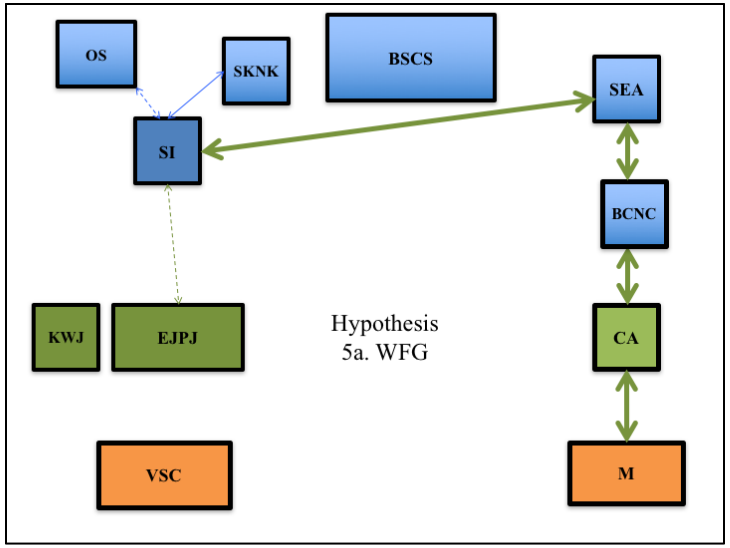


Hypothesis 3e. NFG

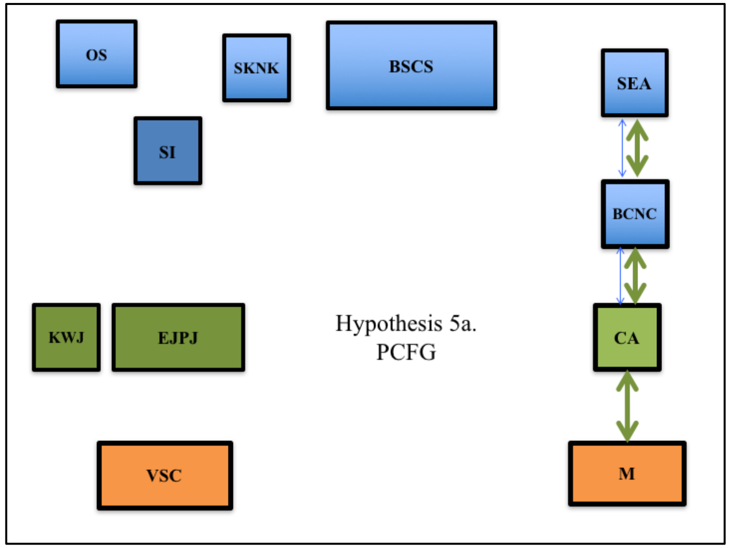


Hypothesis 3e. WBS

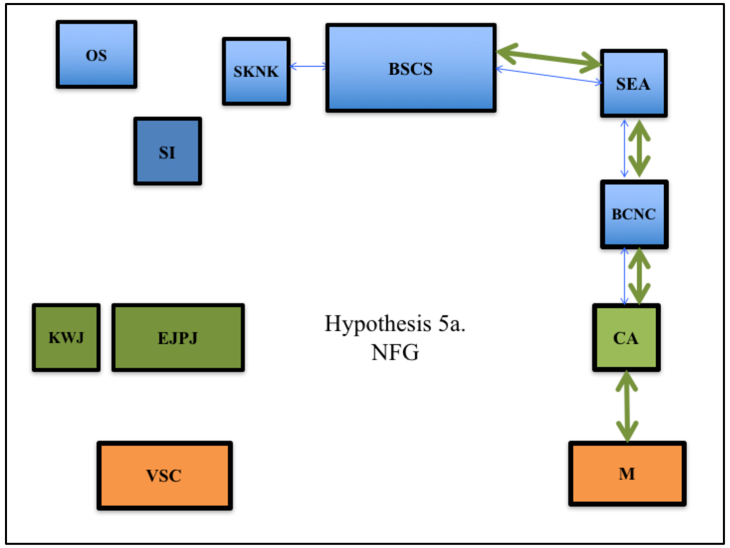
Hypothesis 5a:



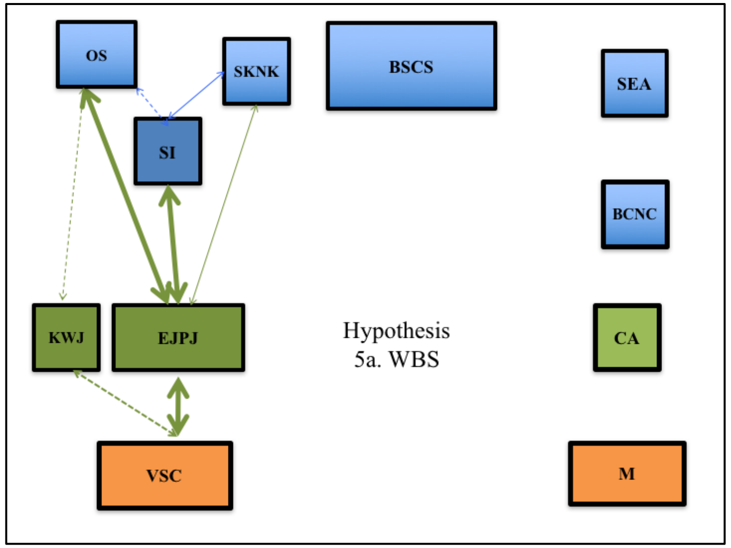
Hypothesis 5a. WFG



Hypothesis 5a. PCFG

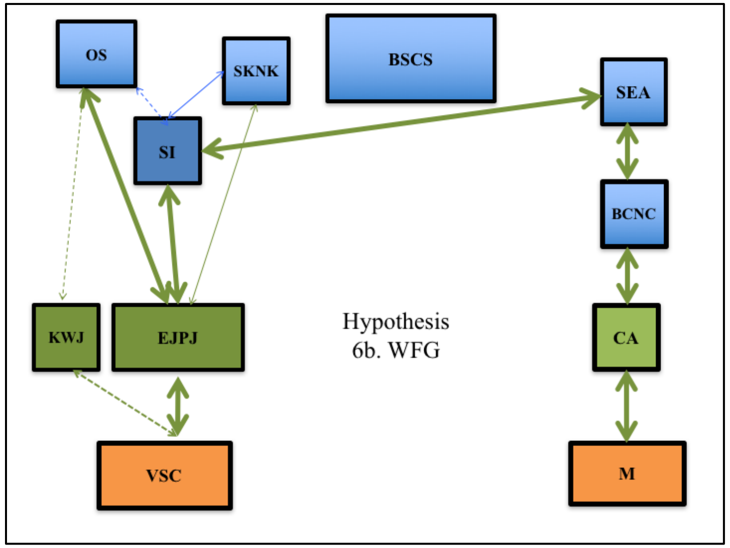


Hypothesis 5a. NFG

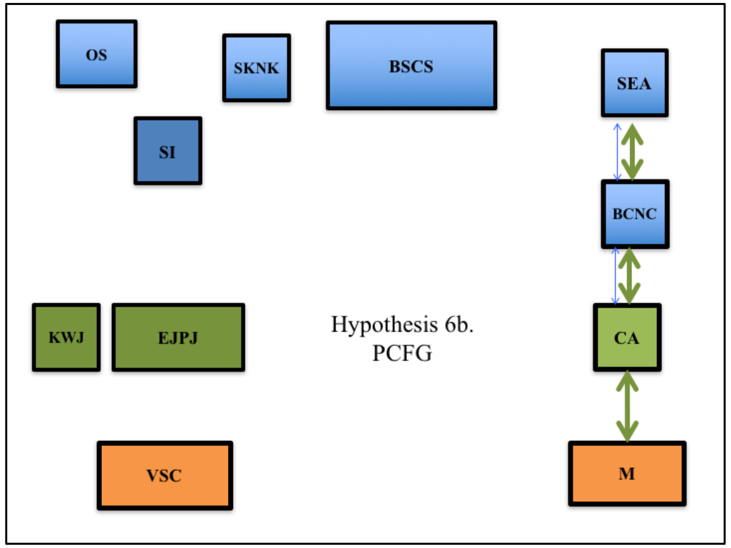


Hypothesis 5a. WBS

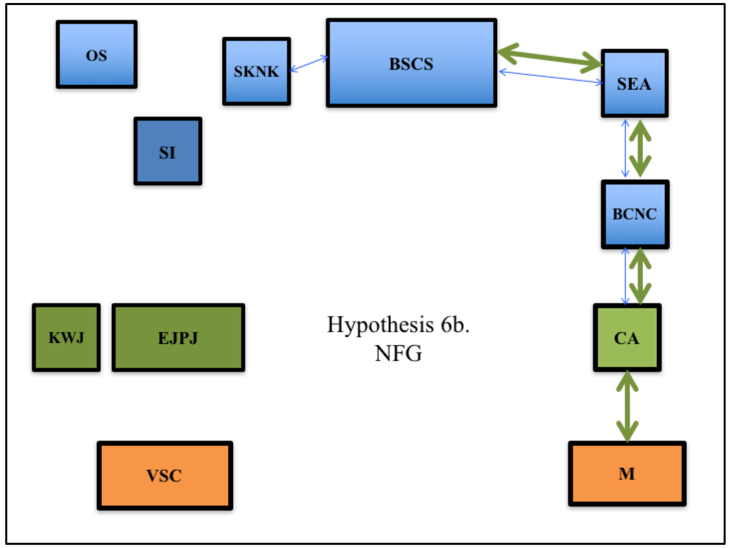
Hypothesis 6b:



Hypothesis 6b. WFG



Hypothesis 6b. PCFG



Hypothesis 6b. NFG

Estimating gray whale abundance from shore-based counts using a multilevel Bayesian model

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ABSTRACT

Counts of southbound migrating whales off California form the basis of abundance estimation for the eastern North Pacific stock of gray whales (*Eschrichtius robustus*). Previous assessments (1967–2007) have estimated detection probability (p) from the detection-non detection of pods by two independent observers. However, tracking distinct pods in the field can be difficult for single observers; resulting in biased estimates of pod sizes that needed correcting, and matching observations of the same pod by both observers involved key assumptions. Due to these limitations, a new observation approach has been adopted wherein a paired team of observers work together and use a computerised mapping application to better track and enumerate distinct pods and tally the number of whales passing during watch periods. This approach has produced consistent counts over four recently monitored migrations (2006/7, 2007/8, 2009/10 and 2010/11), with an apparent increase in p compared to the previous method. To evaluate p and estimate abundance in these four years, counts from two independent stations of paired observers operating simultaneously were compared using a hierarchical Bayesian '*N*-mixture' model to jointly estimate p and abundance without the challenge of matching pods between stations. The baseline detectability p_o was estimated as 0.80 (95% Highest Posterior Density Interval [HPDI] = 0.75–0.85), which varied with observation conditions, observer effects and changes in whale abundance during the migration. Abundance changes were described using Bayesian model selection between a parametric model for a normally distributed common migration trend and a semi-parametric model that estimated the time trends independently for each year; the resultant migration curve was a weighted compromise between models, allowing for key departures from the common trend. The summed estimates of migration abundance ranged from 17,820 (95% HPDI = 16,150–19,920) in 2007/08 to 21,210 (95% HPDI = 19,420–23,230) in 2009/10, consistent with previous estimates and indicative of a stable population.

KEYWORDS: ABUNDANCE ESTIMATE; MIGRATION; MODELLING; GRAY WHALE; SURVEY – SHORE BASED; PACIFIC OCEAN; NORTHERN HEMISPHERE

INTRODUCTION

The eastern North Pacific stock of gray whales migrates annually along the west coast of North America from high latitude feeding grounds to winter breeding grounds in the lagoons and adjacent ocean areas off Baja California, Mexico (Rugh *et al.*, 2001). This nearshore migration pattern has enabled repeated abundance estimates from shore-based counts off Granite Canyon, central California. In 23 years, between 1967 and 2007, counts of the number of observed pods travelling southbound have been rescaled using estimates of pods undetected during watch periods, pods passing outside watch periods, and night travel rate (Buckland and Breiwick, 2002; Buckland *et al.*, 1993; Hobbs *et al.*, 2004; Laake *et al.*, 2012; Laake *et al.*, 1994; Rugh *et al.*, 2005). Population models based on these estimates indicate that gray whales have increased substantially in population size, recovering from whaling operations in the 19th and 20th centuries, and are now close to carrying capacity and likely pre-exploitation levels (Punt and Wade, 2012). The most recent population estimate from abundance counts in 2006/07 was approximately 19,000 whales (Laake *et al.*, 2012).

To facilitate continued population monitoring, the abundance estimation approach has seen continual evolution throughout this time series to more realistically estimate detection probability (p) to link observed counts to true abundance; this paper describes the latest modification. Notably, previous assessments have estimated p from the detection and non-detection of pods by independent observers using an analytical mark-recapture approach. However, tracking distinct pods in the field is difficult (Rugh *et al*. 2008), particularly for a single observer using just hand-recorded entries onto a paper data form. As a result, matching observations of the same pod by both observers involved key (and untestable) assumptions and limited observations of a given pod required corrections for bias in pod size estimation (Rugh *et al*. 2008; Laake *et al*., 2012). Due to these limitations, a new observation approach has been developed wherein a paired team of observers work together and use a computerised mapping application to help better track distinct pods and tally the number of whales passing during watch periods (Durban *et al.*, 2010). This approach has a number of advantages, including open communication between observers, enabling observers to search for whales continually without the distraction of looking down to record data, and easier separation and tracking of distinct pods due to the precise computerised data recording and visualisation. As a result, this approach enables more repeated observations of each pod, leading to larger (and presumably less biased) estimates of pod size (Durban *et al*., 2010) and has produced consistent counts over four recently monitored migrations (2006/07, 2007/08, 2009/10 and 2010/11), with an apparent increase in p compared to the previous method (Durban *et al*., 2011).

To evaluate p for this new approach, watch period counts from two independent stations of paired observers operating simultaneously were compared during two of the four years (2009/10 and 2010/11), using a hierarchical Bayesian '*N*-mixture' model (Royle, 2004) to jointly estimate the probability of detection and abundance in all four years, without the challenge of matching pods between stations.

This ‘*N*-mixture’ approach has been successfully used to estimate abundance and detectability from replicate count data for a range of wildlife species where it has not been possible to match repeat sightings of individuals (e.g. Chelgren *et al.*, 2011; Joseph *et al.*, 2009; Kery *et al.*, 2005). The untility of this approach to extend the time series of abundance estimates for eastern North Pacific gray whales is demonstrated in this paper.

METHODS

Data samples

Counts of gray whales were conducted from shore-based watch stations at Granite Canyon, California, during the 2006/07, 2007/08, 2009/10 and 2010/11 southbound migrations (see Table 1). Counts were made by rotating teams of observer pairs using naked eye aided by 7×50 binoculars; the primary observer in the pair kept continual visual watch while the secondary observer served as a data recorder but also kept watch and assisted with tracking already identified pods whenever possible. Each observer had one 90 minute shift as primary observer, followed by a second 90 minute shift as secondary observer and then a 90 minute break. Sightings were entered into a real-time data logging PC program, which had a mapping screen to help track repeated sightings of the same pod. The map projected the likely movement tracks (and error ellipses) of the pods using predicted swimming speeds (1.44–1.95 ms^{-1}), allowing re-sightings and new sightings to be queried. Up to six lots of 1.5 hour watch periods were used to cover daylight hours from 07:30 to 16:30 local time, during which the observers recorded passing whales and environmental conditions, specifically visibility (subjectively categorised from 1–6 for excellent to unusable) and sea state (Beaufort scale). To control for weather conditions and for consistency with previous abundance estimations, only counts during watch periods with acceptable weather conditions throughout their entire duration were used, specifically visibility code <5 (excellent to fair) and Beaufort Scale <5.

Estimating detection probability

The ‘*N*-mixture’ approach was used (Royle, 2004) to simultaneously estimate detection probability p_{ijt} and abundance N_{jt} for each watch period *j* in each year *t*, based on the total aggregated counts n_{ijt} of passing whales recorded by each of $i = 1{:}2$ watch stations in each period. The observed counts n_{ijt} were modelled as a binomial outcome conditional on the unknown true number of whales passing N_{jt} and the detection probability p_{ijt} with hierarchical models assumed to describe variability in both *N* and *p* (e.g. Chelgren *et al.*, 2011). The power to estimate detectability was achieved by comparing gray whale counts from two independent stations of paired observers operating simultaneously during two years (2009/10 and 2010/11) from watch stations that were positioned 35m apart at the same elevation (22.5m) above sea level. In 2009/10 counts were compared from the two watch stations operating simultaneously during 70 lots of 1.5 hour watch periods with acceptable weather conditions, covering 20 different days of the migration; in 2010/11 simultaneous counts were available from 94 watch periods over 24 different days (see Table 1). However, detectability was extrapolated for all monitored watch periods in each of the four years based on the fitted model for detectability. In order to accomplish this, the counts for the south watch station were treated as zero-inflated binomial outcomes, with the binomial probability specified as a function $u_{ijt}\, p_{ijt}$ where $u = 1$ or 0 to indicate whether or not count data were actually collected from that station, thus ensuring that structural zero counts from periods without a second watch did not contribute to the likelihood for estimation of *p* or *N*.

Consistent with Laake *et al.* (2012), the model for detectability incorporated fixed effects β for visibility (VS) and Beaufort Scale (BF), as well as random effects associated with each observer *o* in 1:OB observers. These were modelled as additive effects on a general intercept so that the direction and magnitude of the estimated effects away from zero (no effect) could be assessed. The selection for the inclusion of these effects using Bayesian model selection with stochastic binary indicator variables *g* to switch each of the three possible effects either in or out of the model depending on their relevance to the observed data (Kuo and Mallick, 1998):

$$\text{logit}\,(p_{ijt}) = \text{logit}(p_{\text{o}}) + g^{bf}\beta^{bf}\,\text{BF}_{jt} + g^{vs}\beta^{vs}\,\text{VS}_{\text{jt}} + g^{ob}\boldsymbol{\beta}^{\boldsymbol{ob}}_{\boldsymbol{ijt=o}}$$

where the intercept p_{o} was the base detection probability in the absence of covariate effects, assigned a Uniform(0,1) prior distribution, and $\text{logit}(p_{\text{o}}) = \ln(p_{\text{o}}/1–p_{\text{o}})$. Centred around this base detectability, each of the fixed effects β^{bf} and β^{vs} was assigned a Normal prior distribution with mean zero and large standard deviation of 10; this prior value was smaller than the corresponding posterior estimates of standard deviation, and as such this was vague prior distribution that allowed any non-zero effects to emerge if supported. The random effect for each observer was drawn from a Normal distribution with mean zero and standard deviation σ^{ob}~Uniform(0,10). Each of the binary indicator variables, *g*, was assigned a Bernoulli(0.5) distribution to specify equal probability of inclusion or not of the effect in the model.

Table 1

The number of whales recorded during the southbound gray whale surveys from 2006/07 to 2010/11. Data are the total counts, hours and distinct days for watches during acceptable observation conditions.

	North Station			South Station		
Migration	Dates	Whales	Hours (days)	Dates	Whales	Hours (days)
2006/07	02/01–03/02	2,691	204 (34)	–	–	–
2007/08	02/01–09/02	2,079	202.5 (34)	–	–	–
2009/10	30/12–19/02	2,034	246 (43)	11/01–06/02	1,551	105 (20)
2010/11	03/01–18/02	2,885	265 (45)	10/01–04/02	1,754	141 (24)

Fitting migration curves

The *N*-mixture approach also accounted for variation in *p* relative to changes in *N* (latent watch period abundances) during the migration. So, some power to estimate detectability was achieved by assuming a model for changes in watch period abundance over the course of the migration. A Poisson distribution $N_{jt} \sim \text{Poisson}(\lambda_{jt})$ was adopted as a hierarchical prior for the distribution of abundances, and a model was specified for the Poisson mean λ in terms of the number of whales passing each day (*d*), with an offset for the effort duration of each watch period, E_{jt} in decimal days (e.g. Laake *et al.*, 2012):

$$\log(\lambda_{jt}) = \log(E_{jt}) + \text{model}_{d(j)t}$$

$$\text{model}_{dt} = z_{dt}\text{Common}_{dt} + (1\text{–}z_{dt})\ \text{Specific}_{dt}$$

Days were specified as $d = 0$ to D_t. In all four years *t* we used $D_t = 90$, where days were counted from 12:00am on 1 December, and we added an abundance of 0 whales passing for day 0 and D_t to anchor the fitted model when we assumed whales did not pass (following Buckland *et al.,* 1993). Estimates from the remaining days were derived from a mixture (or compromise) of two competing models (‘Common’ and ‘Specific’, e.g. Li *et al*., 2012) describing changes in abundance across each annual migration. The model contributing each daily estimate was indicated using stochastic binary indicator variables z_{dt}, each assigned a non-informative Bernoulli(0.5) prior distribution. As such, each z_{dt} indicated the probability of a daily estimate conforming to the common trend, allowing flexibility for departures from this trend that may only exist on certain days in certain years to be identified and modelled (rather than assuming all counts from an entire year conform to or depart from a common trend, which would be represented by z_t). The total number of whales passing during each migration was then estimated by summing the expected value from the model-averaged number of whales passing each day from time 0 to D_t (e.g. Laake *et al*., 2012). These estimates were then rescaled to account for the differential passage rate at night (Perryman *et al*., 1999), based on the nine hour day multiplicative correction factor of Rugh *et al.* (2005). Specifically, we applied a constant night time correction factor that was assumed to be a Normally distributed fixed effect with mean of 1.0875 and standard deviation of 0.037.

For the ‘Common model’, we assumed a typical trend in abundance throughout each annual migration (e.g. Buckland *et al.*, 1993), with abundance changes assumed Normally distributed around a migration mid-point, with a Normal distribution specified as a quadratic function of days, on the log scale:

$$\text{Common}_{dt} = a_t + b_t d_t + c_t d_t^2$$

where the mid-point of the migration curve for each year *t* was derived by $-b_t/2a_t$. This assumed common migration curve allowed information to be ‘borrowed’ across years when needed, specifying association across years to strengthen inference about migration curves in years with relatively sparse counts. However, we specified each of the curve parameters a_t, b_t and c_t to be drawn from hierarchical Normal distributions with means μ^a, μ^b, $\mu^c \sim$ N(0, 10) and standard deviations σ^a, σ^b, σ^c ~Uniform(0,10); hyper-parameters that were common across years, rather than assuming that the parameters themselves were constant. This random effects formulation allowed the timing, level and extent of the Normal migration curve to vary annually around the general pattern, if supported by the data.

Although it is likely that there is a typical pattern to the migration, it was acknowledged that abrupt departures may occur at any time in any particular year. To incorporate unusual patterns, the selection of an alternative ‘Specific’ migration model was allowed; a semi-parametric model that estimated the time trends independently for each year (e.g. Laake *et al.*, 2012). A method in which the shape of the relationship of abundance across days was determined by the data was adopted without making any prior assumptions about its form, by using penalised splines (Ruppert, 2002). Following Crainiceanu *et al.* (2005) a linear (on the log scale) penalised spline was used to describe this relationship:

$$\text{Specific}_{dt} = S_{0t} + S_{1t}d_t + \Sigma_{k=1}^{m}\ \lambda_{kt}\ (d_t - \kappa_{kt})$$

Where S_{0t}, S_{1t}, ${}_{1t}, \ldots, {}_{kt}$ were regression coefficients to be estimated separately for each year and $\kappa_{1t} < \kappa_{2t} < \ldots < \kappa_{kt}$ were fixed knots. We used $m = 15$ knots, a relatively large number to ensure the desired flexibility, and let κ_{kt} be the sample quantile of ’s corresponding to probability $k/(m + 1)$. To avoid overfitting, the λ’s were penalised by assuming that these coefficients were Normally distributed random variables with mean 0 and standard deviation ~Uniform(0,10). The parameters S_{0t}, S_{1t} were modeled as fixed effects with Normal(0, 10) prior distributions.

Bayesian inference using MCMC

The multi-level model was fit using Markov Chain Monte Carlo (MCMC) sampling using the WinBUGS software (Lunn *et al.*, 2000). Inference was based on 15,000 repeated draws from the posterior distribution of each model parameter conditional on the observed data, following 5,000 iterations that were discarded as burn-in. Convergence of parameters within these initial 5,000 iterations was determined based on Gelman-Rubin statistics below 1.05 (Brooks and Gelman, 1998) calculated from three independent chains begun from over-dispersed starting values. To gauge the adequacy of the model for each annual set of count data, Bayesian P-values were computed (Gelman *et al.*, 1996) by using the same MCMC sampler to predict a distribution for each watch-period count from the posterior estimates of model parameters and comparing the total predicted and observed counts. For each year, there was good agreement between the model predictions and observed counts, with Bayesian P-values ranging from 0.45 to 0.53; values close to 0.5 would indicate that the data was consistent with replications under the model, with the distribution of the predicted count symmetrically overlapping the observed count (Gelman *et al.*, 1996).

The MCMC sampling approach allowed uncertainty to be propagated across levels of the model. Notably, estimates of parameter values across MCMC iterations were used to estimate the probability of inclusion of covariate effects in the model for detectability, given by the posterior probability $p(g = 1)$ of each indicator variable *g*. Fitting and selection of the two competing migration models was achieved within the same MCMC run using the ‘cut’ function in WinBUGS to ensure that estimation of the two models was not affected by the selection of the model indicator (e.g. Li *et al.*, 2012). The posterior probability of conforming to the common trend model was then calculated by the relative frequency that each model was selected by the indicator z_{dt} in the overarching mixture model, and inference about abundance on each day was based on a weighted compromise between the competing models by sampling across the posterior distribution of z_{dt}.

RESULTS

The base detectability was estimated as $p_o = 0.80$ (95% Highest Posterior Density Interval [HPDI] = 0.75–0.85), which was modified by observation conditions and observer effects (see Table 2). The posterior distribution for the effect of sea state β^{bf}, measured using the Beaufort scale, largely overlapped with zero and there was therefore low support for including this effect in the model with $p(g^{bf} = 1) = 0.004$. In contrast, there was a relatively strong negative effect of visibility on detectability (higher visibility code = lower visibility = lower detectability), with the entire distribution for β^{vs} falling below zero [$p(g^{vs} = 1) = 1$]. There was also support for inclusion of observer effects [$p(g^{bs} = 1) = 1$], with both positive and negative effects reflecting relatively high and low counts by different observers. A total of 35 different observers were used over 4 years between North and South stations; 15/35 counted in multiple years (2 years = 7, 3 years = 4, 4 years = 4). The Posterior medians for observers' effects ranged from –0.59 to 0.80, but only five observer effects (all positive) had posterior distributions that did not include zero.

Detectability also varied with changes in whale abundance during the migration, as shown by the extent of extrapolation from the daily summed counts (effort adjusted) to the estimated daily abundances (Fig. 1). Detectability declined with increasing abundance, with a greater proportion of whales estimated to be missed as more whales passed during busy watch periods. In general, changes in abundance during the migrations were adequately described by a Normal curve over time, but there was greater uncertainty in the tails of the distribution resulting from generally sparse coverage. The Normal trend was useful for comparing migration timing: the median of the curve midpoints was 53.5 days since December 01 (23–24 January), ranging between 49–57 days. However, there were some notable deviations from the Normal trend, with estimates from the year-specific non-parametric trend model being favoured for some days in each of the four years. In particular, there was a high probability in favour of the Specific model [$p(z = 0) > 0.75$] on 9 days in 2006/07, 9 days in 2007/08, 16 days in 2009/10 and 11 days in 2010/11, representing key departures from the Normal migration trend. The summed (model-averaged) estimates of migration abundance ranged from a posterior median of 17,820 (95% HPD = 16,150–19,920) in 2007/08 to 21,210 (95% HPDI = 19,420–23,230) in 2009/10, consistent with previous estimates (Fig. 2). These new estimates were also relatively precise with coefficients of variation (CV = Posterior Standard Deviation/Posterior Median) ranging from 0.04 to 0.06 (median = 0.05), but nonetheless the 95% HDPI's of all four estimates overlapped.

DISCUSSION

The new counting method adopted here was intended to reduce reliance on the ability of single observers acting independently to record and track distinct whale groups. By adopting teams of paired observers working together, with the benefit of a real-time computerised tracking and

Table 2

Parameters of models for detectability, *p*. All estimates are presented as the 2.5%, 50%, 97.5% highest density posterior probability intervals, plus the probability of inclusion in a model (if tested), given by the posterior probability $p(g = 1)$ of each indicator variable *g*. Observers are arbitrarily numbered, differently for each year.

Detection model	2006/07	2007/08	2009/10	2010/11
p_o	0.75, **0.80**, 0.85	0.75, **0.80**,0.85	0.75, **0.80**,0.85	0.75, **0.80**,0.85
β^{bf} [$p(g^{bf} = 1)$]	–19.34, **–0.003**, 19.98 [0.004]	–19.34, **–0.003**, 19.98 [0.004]	–19.34, **–0.003**, 19.98 [0.004]	–19.34, **–0.003**, 19.98 [0.004]
β^{vs} [$p(g^{vs} = 1)$]	–0.38, **–0.30**, –0.20 [1]	–0.38, **–0.30**, –0.20 [1]	–0.38, **–0.30**, –0.20 [1]	–0.38, **–0.30**, –0.20 [1]
σ^{ob} [$p(g^{bs} = 1)$]	0.26, **0.37**, 0.54 [1]	0.26, **0.37**, 0.54 [1]	0.26, **0.37**, 0.54 [1]	0.26, **0.37**, 0.54 [1]
Observer 1	–0.36, **0.02**, 0.49	0.03, **0.37**, 0.81	–0.42,**–0.24**, 0.06	–0.13, **0.08**, 0.30
Observer 2	0.03, **0.37**, 0.81	–0.78, **–0.03**, 0.70	–0.09, **0.30**, 0.81	–0.36, **0.02**, 0.46
Observer 3	–0.24, **–0.07**, 0.11	–0.24, **–0.07**, 0.11	0.03, **0.37**, 0.81	–0.42, **–0.24**, 0.06
Observer 4	–0.42, **–0.01**, 0.49	–0.42, **–0.24**, 0.06	–0.13, **0.08**, 0.30	–0.25, **0.01**, 0.29
Observer 5	–0.04, **0.14**, 0.35	–0.13, **0.08**, 0.30	–0.24, **–0.07**, 0.11	0.16, **0.43**, 0.73
Observer 6	0.06, **0.42**, 0.83	–0.04, **0.14**, 0.35	–0.27, **–0.06**, 0.18	–0.04, **0.14**, 0.35
Observer 7	–0.17, **0.11**, 0.46	–0.18, **0.19**, 0.61	–0.04, **0.14**, 0.35	–0.50, **–0.13**, 0.26
Observer 8	–0.39, **–0.16**, 0.07	–0.17, **0.11**, 0.46	0.12, **0.33**, 0.59	–0.39, **–0.16**, 0.07
Observer 9	0.12, **0.33**, 0.59	0.12, **0.33**, 0.59	–0.25, **0.01**, 0.29	–0.09, **0.23**, 0.60
Observer 10	–	–0.39, **–0.16**, 0.07	–0.08, 0.26, 0.64	–0.27, **–0.06**, 0.18
Observer 11	–	–	–0.71, **–0.43**, 0.13	0.31, **0.80**, 1.46
Observer 12	–	–	–0.66, **–0.37**, 0.07	–0.54, **–0.29**, 0.04
Observer 13	–	–	–0.42, **0.00**, 0.49	–0.75, **–0.22**, 0.33
Observer 14	–	–	–0.63, **–0.13**, 0.40	0.12, **0.33**, 0.59
Observer 15	–	–	0.31, **0.80**, 1.46	–0.73, **–0.29**, 0.14
Observer 16	–	–	–0.18, 0.19, 0.61	–0.18, **0.19**, 0.61
Observer 17	–	–	0.16, **0.43**,0.72	–0.70, **0.02**, 0.76
Observer 18	–	–	–0.39, **–0.16**, 0.07	–0.63, **–0.13**, 0.40
Observer 19	–	–	–0.22, **0.22**, 0.72	–0.83, **–0.59**, 0.36
Observer 20	–	–	–0.28, **0.14**, 0.59	–0.24, **–0.07**, 0.11
Observer 21	–	–	–0.18, **0.28**, 0.83	–0.21, **0.11**, 0.47
Observer 22	–	–	–	–1.05, **–0.49**, 0.06

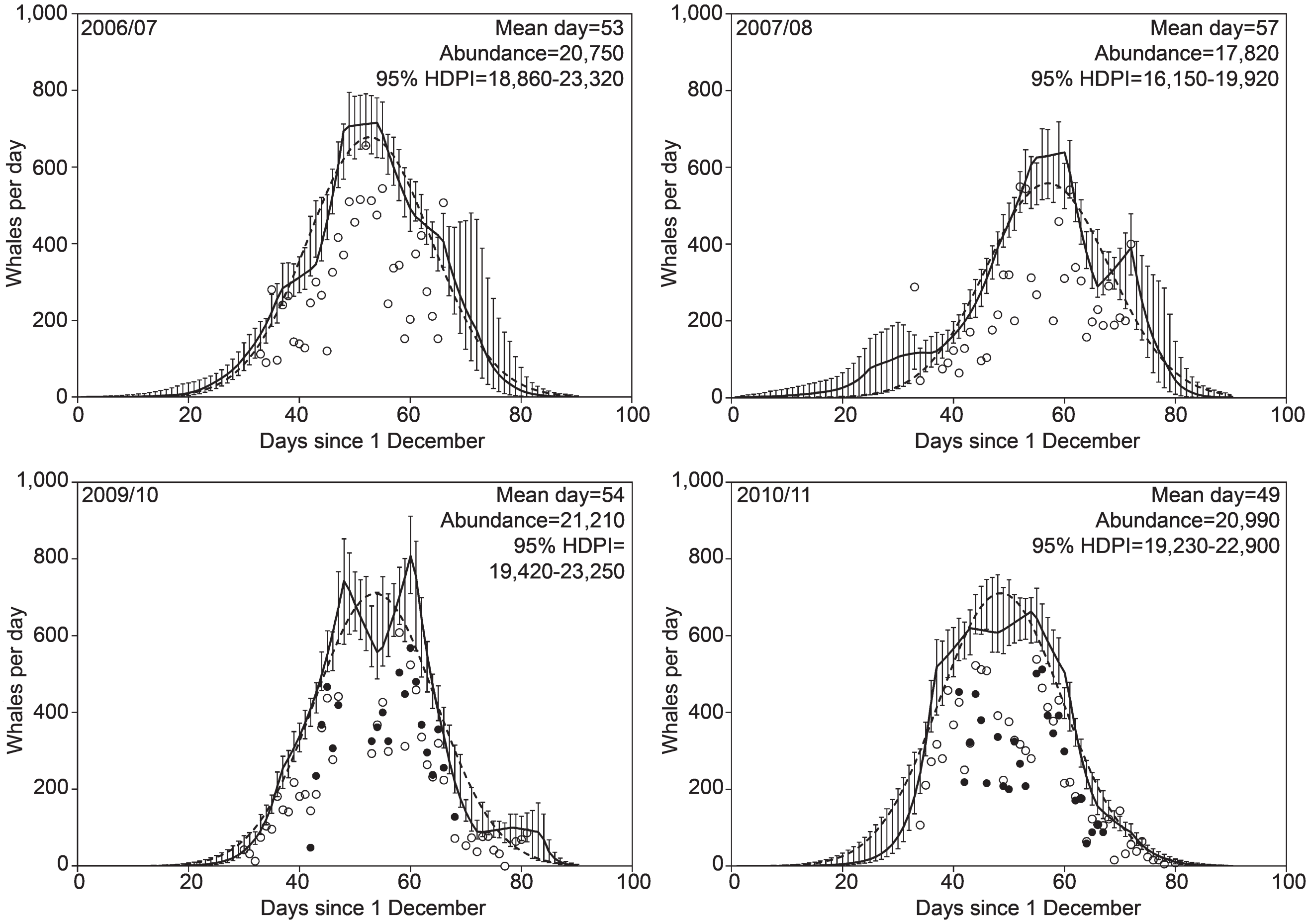

Fig. 1. Observed whale passage rates expressed as total counts per day/ proportion of day observed (circles) and fitted migrations models (lines) for the four southbound gray whale migration counts from 2006/07 to 2010/11. Solid circles represent counts from a second watch station, when operating. The broken line represents the median estimates from a hierarchical Normal model for migration and the solid line represents a semi-parametric model of penalised splines; the abundance estimate for each day (95% highest posterior density interval shown by vertical lines) is a model averaged compromise between the migration models, and these were summed to estimate the overall abundance for the migrations.

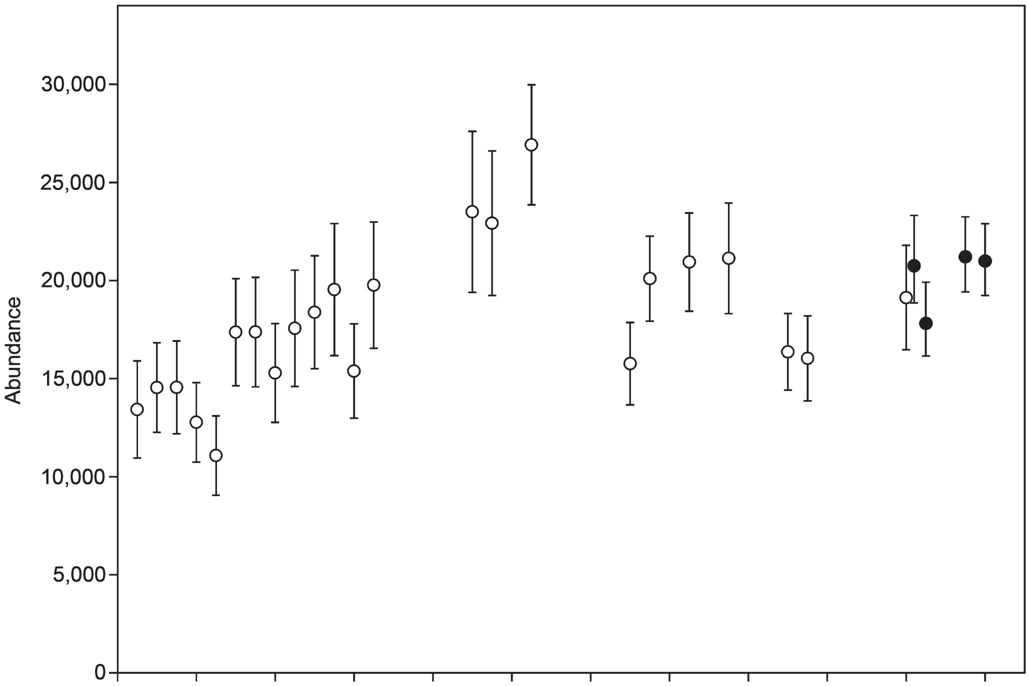

Fig. 2. Gray whale abundance estimates for each of 23 southbound migrations with an end year between 1967 and 2007 (open circles, with 95% confidence intervals; from Laake *et al.,* 2012) together with the four recent migrations reported here (closed circles show posterior medians, lines are 95% highest posterior density intervals).

visualisation tool, this approach has proved successful in increasing detection probability (Durban *et al.*, 2011) and also reducing variability in detections due to observer effects. Although still present, the magnitude of observer effects estimated from the new counts (see Table 2) was generally not as great as those apparent with the traditional counting approach (see Laake *et al.*, 2012, table 7).

Furthermore, our method for estimating detectability departed from the mark-recapture approach of matching detections and non-detections of specific pods by independent observers. Instead, inference was based on total watch period counts that were not sensitive to differential lumping and splitting of pods by observers, and avoided the assumptions required to match observed pods between pairs of observers. As an alternative to the mark-recapture analytic approach, we have shown how tallied watch period counts from two observer pairs counting simultaneously can lead to similar inference when analysed using with the *N*-mixture approach (Royle, 2004).

The *N*-mixture approach is conceptually simple: multiple observations of watch period counts, *n*, from the different observer teams represented different samples from an unknown binomial distribution with total population size *N* and detection probability *p*. A binomial likelihood function could then be easily used to estimate *N* and *p* from the sample of *n*'s. Although there were only a maximum of two samples of *N* during any specific watch period, a large sample of *n*'s was built up across many watch periods, allowing the estimation of the parameters. Layered on top of this core estimation process were both a trend model for true daily abundance through time based on the migration pattern and a model for how detection varied according to environmental conditions and different observers. Specifically, a hierarchical model fit to the replicate count samples allowed us to link detectability to key covariates, as in previous gray whale assessments (e.g. Laake *et al.*, 2012), and also extrapolate detectability based on these covariate relationships for watch periods without replicate counts. Similarly, by assuming a common underlying model for the migration pattern, this approach notably accounted for variation in *p* relative to changes in abundance *N* during the migration. Furthermore, this joint modelling of data from multiple years allowed the borrowing of strength across years to better parameterise the migration during years with sparse data.

Previously, two contrasting approaches have been used to model changes in abundance over the course of the annual gray whale migration: either by assuming a parametric model to determine the shape of the migration curve (Buckland *et al.*, 1993) or by fitting a non-parametric smoother to allow the data to determine the trend in abundance over time (Laake *et al.*, 2012). Here we drew on elements of both these approaches in a flexible framework using Bayesian model selection between a parametric model for a common migration trend and a semi-parametric model that estimated the time trends independently for each year; the resultant migration curve was a weighted compromise between models, allowing for key departures from the common trend.

The abundance estimates produced for 2006/07, 2007/08, 2009/10 and 2010/11 were internally consistent, consistent with previous estimates and indicative of a stable population (Fig. 2). The 95% HDPI's of all four estimates overlapped, and there was substantial overlap between the 95% HDPI from the 2006/7 estimate with the 95% confidence intervals of the estimate for the same migration produced using the previous counting and estimation approach (Laake *et al.* 2012). Further, our estimates are very similar to the predictions of Punt and Wade (2012) based on assessment models for the full time series; their baseline model prediction for 2009/10 had 90% posterior density intervals ranging from 17,726 to 23,247; the posterior distribution for our 2009/10 estimate was centered within these intervals at 21,210 (95% HPDI = 19,420–23,250). It is noteworthy that the estimates produced using our approach were relatively precise with CVs ranging from 0.04 to 0.06 (median = 0.05) in contrast to CVs ranging from 0.06 to 0.09 (median = 0.08) for the 23 previous estimates.

This consistency provides a level of confidence in our approach and resultant estimates, but nonetheless there are limitations to address. Our approach makes a number of important modelling assumptions, both in terms of distributional forms and model structure. It was assumed that the detectability relationships described by modelling repeated counts during two years were also applicable in the remaining two years with no replicate counts. We also assumed observer effects remained constant, although in reality this may change with experience. Additionally, the definition of what constituted the common migration trend was dependent on the joint modelling of just four years of data, and precise inference about the shape of the migration curve relies on count data being collected from throughout the migration time span. During at least 3/4 of the years reported here, count data were sparse (or non-existent) during the tails of the migration, resulting in uncertainty over the shape of the abundance curve. While this uncertainty was propagated into inference about overall abundance in our Bayesian inference using MCMC sampling, the resulting imprecision will ultimately constrain power to detect between-year changes in migration patterns and abundance. Data collected during further migrations will be incorporated into this hierarchical model and therefore used to refine parameter estimates; this will benefit from replicate counting experiments, repeated when possible. As the time series grows, specific goodness-of-fit tests should be adopted to investigate aspects of model structure and suggested changes as necessary.

There are also practical considerations as well as modelling assumptions. Previous work has shown that the new counting approach produces estimates of pod size that are typically larger (and presumably less biased) than the traditional counting approach (Durban *et al.*, 2010), likely because the computerised tracking software facilitates more repeated observations of the same groups. In fact, it has been assumed that estimates of pod size using this observation approach are effectively unbiased and have not been rescaled to tally watch period counts. This is an assumption that remains to be tested, but suitable calibration experiments are difficult to design and implement, particularly due to the inherently subjective differences between observers in lumping and splitting whales to define groups. Similarly, although observer effects have been accommodated in the model for detectability, it is clear that too many observers

(35 in total) counted too infrequently to allow precise parameterisation of their relative effects on detectability in many cases. This will have resulted in further imprecision.

Although there may be field protocols that could be adapted to address these limitations within the current approach, further modernisation of the observation process is recommended. Specifically, more accurate information could be gleaned from observations recorded with high-definition video files to allow subsequent review and re-review, rather than relying on instantaneous assessment by visual observers. The use of infra-red sensors would further allow for 24 hour monitoring (e.g. Perryman *et al*., 1999) and provide greater coverage of the entire migration during acceptable weather conditions; automated blow detectors (e.g. Santhaseelan *et al*., 2012) can be developed to eliminate observer effects and standardise detectability to provide counts with minimal (and quantifiable) bias. These extensions would further serve to build a more robust and automated observation model to combine with the flexible abundance model for the migration process described in this paper.

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REGIONAL VARIABILITY IN FOOD AVAILABILITY FOR ARCTIC MARINE MAMMALS

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Abstract. This review provides an overview of prey preferences of seven core Arctic marine mammal species (AMM) and four non-core species on a pan-Arctic scale with regional examples. Arctic marine mammal species exploit prey resources close to the sea ice, in the water column, and at the sea floor, including lipid-rich pelagic and benthic crustaceans and pelagic and ice-associated schooling fishes such as capelin and Arctic cod. Prey preferred by individual species range from cephalopods and benthic bivalves to Greenland halibut. A few AMM are very prey-, habitat-, and/or depth-specific (e.g., walrus, polar bear), while others are rather opportunistic and, therefore, likely less vulnerable to change (e.g., beluga, bearded seal). In the second section, we review prey distribution patterns and current biomass hotspots in the three major physical realms (sea ice, water column, and seafloor), highlighting relations to environmental parameters such as advection patterns and the sea ice regime. The third part of the contribution presents examples of documented changes in AMM prey distribution and biomass and, subsequently, suggests three potential scenarios of large-scale biotic change, based on published observations and predictions of environmental change. These scenarios discuss (1) increased pelagic primary and, hence, secondary production, particularly in the central Arctic, during open-water conditions in the summer (based on surplus nutrients currently unutilized); (2) reduced benthic and pelagic biomass in coastal/shelf areas (due to increased river runoff and, hence, changed salinity and turbidity conditions); and (3) increased pelagic grazing and recycling in open-water conditions at the expense of the current tight benthic–pelagic coupling in part of the ice-covered shelf regions (due to increased pelagic consumption vs. vertical flux). Should those scenarios hold true, pelagic-feeding and generalist AMM might be advantaged, while the range for benthic shelf-feeding, ice-dependent AMM such as walrus would decrease. New pelagic feeding grounds may open up to AMM and subarctic marine mammal species in the High Arctic basins while nearshore waters might provide less abundant food in the future.

Key words: Arctic; benthos; climate change; food availability; marine mammal; plankton; prey; sea ice; seal; whale.

Introduction

The physical and chemical settings of Arctic seas provide the framework for the structure of marine food webs, which support Arctic marine mammals (AMM) as top consumers. Unique features specific to the Arctic influencing habitat suitability and prey availability include the seasonal and permanent sea ice cover, the extreme seasonal variability of light and primary production and their consequences, the interannual and decadal climate variations, and the polar amplification of recent climate change (Walsh 2008). The focus area of this paper includes the deep central Arctic Basin, consisting of two major sub-basins (the Eurasian Basin and the Amerasian Basin) and the surrounding shallow continental shelves, occupying approximately 53% of the Arctic Ocean. The shelves vary in width, with narrow extents along part of the Beaufort Sea and Canadian Archipelago coastlines and wide shelves everywhere else. The shelves are the locations at which currently most of the annual ice formation and melt occurs and where AMM spend most of their time. Freshwater runoff from major river systems influences the Arctic hydrography and chemistry, contributing sediment, organic material, and inorganic nutrients to the shelves. Annual sea ice dominates on the shelves while unique multiyear sea ice covers the Arctic deep-sea basins (Wadhams 2000). The complex bathymetric and hydrographic structure of the Arctic basins and shelves influence their use by AMM as summarized by Laidre et al. (2008).

Large parts of the Arctic, in particular the shelves, are inhabited by AMM for at least part of the year (Laidre et al. 2008, Moore and Huntington 2008). During their feeding periods, AMM require energy hot spots to forage efficiently (e.g., Piatt and Methven 1992) and to build up reserves to sustain their metabolism and potentially produce a calf or pup during fasting periods. Caloric density at AMM feeding sites, therefore, appears

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to be at least as important as prey species choice per se (Darling et al. 1998). Some migratory AMM specifically select subarctic or Arctic latitudes for their foraging period (Laidre et al. 2008). Feeding can occur throughout the year (e.g., male polar bear), primarily in the summer (e.g., gray whale; Nerini 1984), or primarily outside the summer (e.g., narwhal; Laidre and Heide-Jørgensen 2005). Whatever the selected site or time period, AMM foraging areas are selected because of certain, typically high, levels of primary and/or secondary production at the trophic levels of phytoplankton through fishes (e.g., Bradstreet and Cross 1982, Piatt and Mathven 1992).

This review aims at providing an overview of AMM prey preferences and prey distribution patterns and current biomass hotspots, organized by the three major physical realms: sea ice, water column, and seafloor. Examples of observed changes in AMM prey distribution and biomass are presented and potential biotic change scenarios suggested, based on published observations and predictions of environmental change. We propose these scenarios to provide insights into possible linkages between environmental changes and effects and caution the reader that settings on local or regional scales might have different effects than those described. This paper tightly links to Walsh (2008), which describes the climatic conditions by which AMM prey species are framed, and Laidre et al. (2008), which reviews habitat utilization of AMM species and quantifies their sensitivity to climate-induced habitat change.

Prey Preferences

Here we summarize the main prey items at different Arctic foraging sites for seven Arctic core and four subarctic (non-core) AMMs (Moore and Huntington 2008), while acknowledging bias introduced by differences in digestion rates of different prey. The information is presented, albeit admittedly incomplete, in short paragraphs organized by core and non-core AMM species and in the form of two tables, one on major prey by species (Table 1) and one on energy content of major prey items (Table 2). We will use the term Arctic cod for *Boreogadus saida* (see Plate 1) and polar cod for *Arctogadus glacialis*, according to the fish name list used by the American Fisheries Society.

Core Arctic marine mammals

Bowhead whale (Balaena mysticetus).—Most information on bowhead whale feeding ecology comes from the Alaskan and Canadian Arctic. Bowhead whales primarily feed on zooplankton, mostly crustaceans such as copepods, euphausids, and hyperiid amphipods (Lowry et al. 2004), all of which have especially high lipid and therefore caloric content (Percy and Fife 1980; Table 2). Feeding behavior may be consistent within size cohorts and diving abilities of age classes (Finley 2000). Juvenile bowheads tend to feed on large swarming zooplankton such as mysids or euphausids or on the very small copepods *Pseudocalanus* and *Limnocalanus*, while adults prefer large *Calanus glacialis* and *C. hyperboreus* in offshore areas (Lowry et al. 2004). Less common food items such as mysids, fish, and isopods were more frequent in smaller whales in the Alaskan Beaufort Sea, although this difference was not statistically significant compared to bigger whales ($n = 32$). No differences between size classes or sexes were found in a large sample of bowhead whale stomachs in the Alaskan Beaufort Sea ($n = 242$; Lowry et al. 2004). On occasion, bowheads may feed on benthic prey, as indicated by mud plumes and stomach contents. Epibenthic prey includes mysids and cumaceans.

In the Alaskan Beaufort Sea, a large fraction of whales feed throughout the fall with regional differences regarding the major prey, such as a higher fraction of copepods in fall-hunted animals from Kaktovik, whereas fall-hunted whales from Barrow consumed more euphausids and hyperiid amphipods (Lowry et al. 2004). A substantial sample size covering 1969–2000 indicates that feeding during the spring migration is opportunistic, but may be more common than previously appreciated. Major feeding areas are known from the western and eastern Beaufort and Chukchi Seas (Lowry et al. 2004) and off Baffin Island (Finley 1990), where whales primarily fed on copepods. Stable isotope studies suggest that the Chukchi-Beaufort Sea stock may also be feeding in the Bering Sea and that habitat selection patterns were consistent over a three-year period (Hoekstra et al. 2002). Little is known about the foraging grounds of the Svalbard and Okhotsk bowhead stocks (Shelden and Rugh 1995).

Beluga (Delphinapterus leucas).—The North Atlantic Marine Mammal Commission (NAMMCO 2004) recently summarized beluga prey spectrum findings from various foraging grounds. *Boreogadus saida* dominated beluga whale diet in Greenland, the Canadian High Arctic, Russian waters, and waters around Svalbard. *Arctogadus glacialis* and whitefish (Coregonidae) were similarly common in the Upernavik area in Greenland and in Russian waters, respectively. Other items found in stomachs in Greenland-caught belugas included squid beaks, redfish (*Sebastes marinus*), Greenland halibut (*Reinhardtius hippoglossoides*), and the decapod *Pandalus borealis*. Belugas preyed largely upon salmon in the Okhotsk Sea (Sobolevskii 1983) and on saffron cod and other fishes as well as shrimps and octopus in Norton and Kotzebue Sounds (Seaman et al. 1982). In the St. Lawrence River and Hudson Bay, stomach contents were dominated by capelin, but also included sand lance, Atlantic cod, tomcod, and benthic invertebrates such as crustaceans and polychaetes (NAMMCO 2004).

Ice type and distribution may influence beluga feeding patterns (Seaman et al. 1982), but prey species distribution also appears to affect seasonal movement patterns. Spring prey in migrating belugas in the Chukchi Sea was dominated by Arctic cod, shrimps, and octopus, while summer foods in the coastal northern Bering and southern Chukchi Seas included saffron cod, sculpins, herring, smelt, capelin, salmon, and char (Seaman et al. 1982). However, foraging occurred to a large extent in the wintering grounds rather than at the shallow estuarine summer sites in belugas off west Greenland (NAMMCO 2004). Shallow murky areas with relatively warm temperatures and mollusk, crustacean, and fish bottom fauna are generally often occupied by females and their young.

Narwhal (Monodon monoceros).—Studies of narwhal stomach contents in the Canadian Arctic, off west Greenland, and in Russian waters revealed that Arctic and polar cod, squid, in particular *Gonatus fabricii*, and Greenland halibut were the primary prey items of narwhals during the summer (e.g., Finley and Gibb 1982, $n = 73$; Laidre and Heide-Jørgensen 2005, $n = 121$). Less prevalent were redfish, snail fish, and crustaceans (Baffin Island; Finley and Gibb 1982). Fall and winter prey were dominated by Greenland halibut and squid (Laidre and Heide-Jørgensen 2005). The deep-water fishes indicate the deep-diving capability of narwhals. Laidre and Heide-Jørgensen (2005) reported that stomachs taken off west Greenland contained considerably more and fresher food during the winter than stomachs sampled in the summer. Similarly, Finley and Gibb (1982) observed little feeding during later summer in the Canadian Arctic fjords and suggest that summering areas may not primarily be inhabited based on their prey availability.

Walrus (Odobenus rosmarus).—Walrus primarily feed on benthic bivalves, but stomachs of some walrus also included a variety of other benthic invertebrates from all major phyla and over 60 genera (e.g., Fay et al. 1984). Food items other than clams were suggested to only be consumed opportunistically while clams were preferred, although later digestion experiments indicated that differential digestion probably exaggerates the importance of bivalves in walrus' diet to some extent (Sheffield et al. 2001). In the Bering Sea, the clams *Mya truncata*, *Serripes groenlandicus* (see Plate 1), and *Macoma* spp. dominated stomach contents as well as benthic communities in which feeding pits and furrows of walrus were studied (Oliver et al. 1983). In the Foxe Basin, Northwest Territories, stomach contents were also dominated by the clam *Mya truncata*, and the same species was dominant in Atlantic walrus feces around Svalbard (e.g., Fisher and Steward 1997). *Mya truncata*, *Hiatella arctica*, and *Serripes groenlandicus* were dominant prey in Young Sound, east Greenland (Born et al. 2003). Other bivalves, holothurians, and polychaetes contributed most of the remaining share in the Canadian study (Fisher and Steward 1997). Occasionally, ringed seals, bearded seals, seabirds, and squid have been reported from walrus stomachs.

For east Greenland waters, a male 1200-kg walrus consumed on average 2576 kJ per dive (53.2 bivalves), and consumption in Alaskan waters was estimated at 6 bivalves/minute (Oliver et al. 1983). Some authors found that probably all soft parts of the bivalves were consumed, while others suggested that primarily the exposed tissue parts such as foot and siphon are taken (Sheffield et al. 2001).

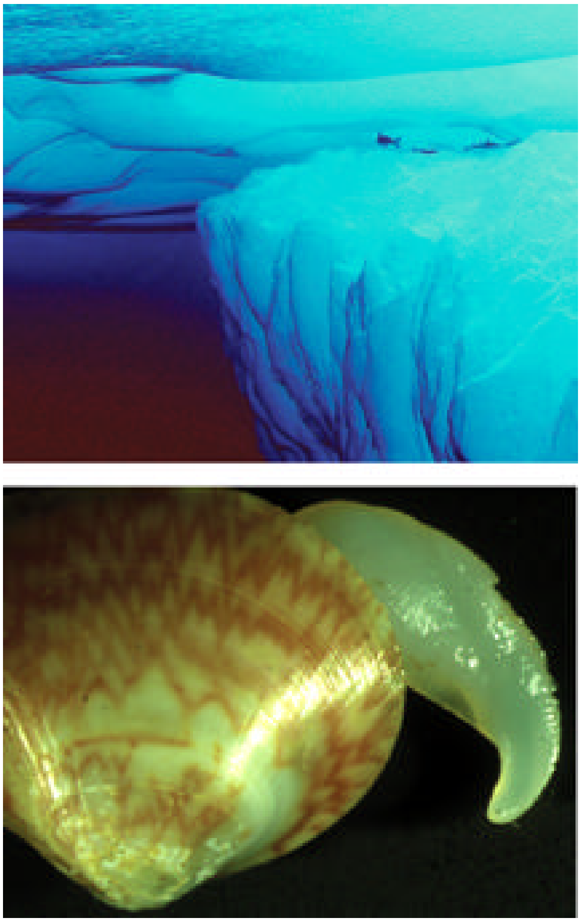

PLATE 1. Common prey organisms of Arctic marine mammals: (top) Arctic cod, *Boreogadus saida*, and (bottom) an example of benthic clam species, *Serripes groenlandicus*. Photo credits: cod, Katrin Iken; clam, B. Bluhm.

Bearded seal (Erignathus barbatus).—Bearded seals have been characterized as foraging generalists that prey on pelagic and demersal fishes as well as a wide range of infaunal and epifaunal invertebrates. The relative contribution of prey species varied between and within geographic areas and seasons (Antonelis et al. 1994). In a Bering Sea study, bearded seals primarily fed at the seafloor, where they consumed bivalves, crabs, and shimps, but few fishes, similar to findings from a southern Chukchi Sea study (Lowry et al. 1980*b*). Other invertebrates from seals taken around Svalbard include shrimps and whelks (Hjelset et al. 1999). In contrast, near St. Matthew Island, in the Bering Sea, 78 bearded seal stomachs were dominated by fishes, especially capelin, cod species, and eelpouts (Antonelis et al. 1994); snow crab, clams, snails, and amphipods were prevalent among the invertebrates in that study. Fish

TABLE 1. Primary prey and feeding areas of Arctic marine mammals.

Species and major feeding area	Feeding habits	Primary prey items	Trophic level	Reference
Core Arctic marine mammals				
Bowhead whale				
Chukchi and Beaufort Seas	shallow, pelagic, (hyperbenthic)	copepods, euphausids, mysids	3.2†	Lowry et al. (2004)
West Greenland, Baffin Bay	shallow, pelagic, (hyperbenthic)	copepods, euphausids, mysids	3.2†	Finley (2000)
Beluga whale				
Greenland, Russia	shallow, deep, pelagic, benthic	Arctic and polar cod, whitefish	4.0†	NAMMCO (2004)
Arctic Canada, Svalbard	shallow, deep, pelagic	Arctic cod	4.0†	NAMMCO (2004), Seaman et al. (1982)
Bering and Chukchi Seas	shallow, pelagic, benthic	saffron cod, shrimps	4.0†	NAMMCO (2004)
Hudson Bay, St. Lawrence Island	shallow, deep, pelagic, benthic	capelin, sand-lance, benthic invertebrates	4.0†	NAMMCO (2004)
Narwhal				
Baffin Bay, Canadian Archipelago, Russian waters	shallow, deep, pelagic, benthic	Arctic and polar cod, *Gonatus* sp. (su), Greenland halibut, squid (fall–wi)	4.2†	Finley and Gibb (1982), Laidre and Heide-Jørgensen (2005)
Walrus				
Bering and Chucki Seas	shallow, benthic	*Mya truncata, Macoma* spp., *Serripes groenlandicus*	3.4†	Fay et al. (1984)
Northwest Territories, Svalbard, Franz Josef Land	shallow, benthic	*Mya* spp.	3.4†	Gjertz and Wiig (1992), Fisher and Steward (1997)
Northeast Greenland	shallow, benthic	*Mya truncata, Hiatella arctica, Serripes groenlandicus*	3.4†	Born et al. (2003)
Bearded seal				
Bering and Chukchi Seas	shallow, benthic, pelagic	bivalves, crabs, shrimps	3.4†	Lowry et al. (1980*a*)
St. Matthew Island	shallow, benthic, pelagic	capelin, gadids, eelpouts, crustaceans	3.4†	Antonelis et al. (1994)
Canadian Arctic, Kara and Barents Seas, Svalbard	shallow, benthic, pelagic	various fishes, crustaceans	3.4†	Hjelset et al. (1999)
Ringed seal				
White, Barents, and Kara Seas, Greenland, Baffin Bay	shallow, pelagic, (hyperbenthic)	Arctic cod, mysids, shrimps, euphausids, amphipods	3.8,† 4.5‡	Siegstad et al. (1998)
Northern Bering	shallow, pelagic, hyperbenthic	saffron cod (su), Arctic cod (wi)	3.8,† 4.5‡	Lowry et al. (1980*b*)
Southern Chukchi Seas	shallow, pelagic	shrimps (su), Arctic cod (wi)	3.8,† 4.5‡	Lowry et al. (1980*b*)
Beaufort Sea	shallow, pelagic	hyperiid amphipods, euphausids (su), Arctic cod (wi)	3.8,† 4.5‡	Lowry et al. (1980*b*)
Polar bear				
Canada, Barents Sea	shallow, deep, pelagic, hyperbenthic	ringed seal, bearded seal, harp seal	5.5‡	Derocher et al. (2002)
Non-core Arctic marine mammals				
Gray whale				
Northern Bering, Chukchi Sea	shallow, benthic, (pelagic?)	Ampeliscid amphipods, other invertebrates	3.3†	Nerini (1984)
Kodiak Island	hyperbenthic	cumaceans	3.3†	Moore et al. (2007)
Vancouver Island	shallow, benthic, pelagic	mysids, crab larvae, herring eggs, polychaetes	3.3†	Darling et al. (1998)
Spotted seal				
Bering Sea	shallow, pelagic, (hyperbenthic)	pollock, capelin, Arctic and saffron cod, herring, zoarcids, octopus (spring); salmon (fall)	4.0†	Lowry et al. (2000)
Chukchi Sea	shallow, pelagic, (hyperbenthic)	herring, saffron cod, smelt, Arctic cod	4.0†	Lowry et al. (1980*a*)
Ribbon seal				
Bering Sea	shallow, pelagic	pollock, Arctic cod	3.8†	Frost and Lowry (1980, 1986)
Harp seal				
Norwegian coast	shallow, pelagic, hyperbenthic	gadoid, Atlantic herring, capelin	3.8†	Haug et al. (1991)

TABLE 1. Continued.

Species and major feeding area	Feeding habits	Primary prey items	Trophic level	Reference
Barents Sea	shallow, pelagic	*Parathemisto libellula*, shrimps, euphausids	3.8†	Nilssen et al. (1991)
Gulf of St. Lawrence	shallow, pelagic, hyperbenthic	capelin, Atlantic cod	3.8†	Stenson et al. (1997)
Newfoundland	shallow, pelagic	Arctic cod, capelin	3.8†	Stenson et al. (1997)
Greenland Sea	shallow, pelagic	*Parathemisto, Gonatus fabricii*, Arctic cod, capelin	3.8†	Haug et al. (2004)

Notes: Information in parentheses in the "Feeding habits" column indicates less common feeding habits. Information without parentheses indicates common feeding habits. Trophic level values are taken from Pauly et al. (1998) (indicated by a dagger) and Hobson et al. (2002) (indicated by a double dagger). Abbreviations are: su, summer; wi, winter.

were also major prey items for bearded seals in the Kara and Barents Seas, in the Canadian High Arctic, and in the Svalbard area (Hjelset et al. 1999). Like other researchers, these investigators expressed uncertainty about the degree of selective feeding because of sampling biases.

Diets were similar between genders in two Bering Sea studies (Lowry et al. 1980*b*, Antonelis et al. 1994). Contradictory results were published about age class-specific prey selection: Lowry et al. (1980*b*) found that young bearded seals preyed upon shrimps, crabs, and fish while adults preferred clams; no age-specific differences were found in the mainly fish-eating bearded seals near St. Matthew Island (Antonelis et al. 1994).

Ringed seal (Phoca hispida).—Studies from various Arctic areas showed considerable regional and seasonal variability in ringed seal primary prey. In Northwest and East Greenland *Boreogadus saida* and *Arctogadus glacialis* were the most dominant prey items, while seals in central West Greenland mainly preyed upon pelagic amphipods (*Parathemisto* spp.), capelin, redfish, and squid, while capelin was the most important prey item in southwest Greenland (Siegstad et al. 1998). In the northern Bering and southern Chucki Seas (U.S. sector),

TABLE 2. Energy value of major Arctic marine mammal prey items.

Species	Phylum or order	Energy content	Realm	Area	Reference
Aglantha digitale†	Cnidaria	4.7–5.0 kcal/mg AFDM	pelagic	Frobisher Bay, Canada	Percy and Fife (1980)
Autolytus spp.	Polychaeta	5.4–5.9 kcal/mg AFDM	benthic	Frobisher Bay, Canada	Percy and Fife (1980)
Clione limacina	Gastropoda	5.6–6.5 kcal/mg AFDM	pelagic	Frobisher Bay, Canada	Percy and Fife (1980)
Calanus glacialis/ hyperboreus	Copepoda	7.2–7.9 kcal/mg AFDM	pelagic	Frobisher Bay, Canada	Percy and Fife (1980)
Macoma calcarea	Bivalvia	4.3–6.3 kJ/g DM	benthic	Bering Sea (with shell)	Lovvorn et al. (2003)
Gonatus sp.	Cephalopoda	6.9 kJ/g WM	pelagic	Newfoundland and Labrador	Lawson et al. (1998)
Mesidotea sabini†	Isopoda	4.6 kcal/mg AFDM	benthic	Frobisher Bay, Canada	Percy and Fife (1980)
Parathemisto libellula	Amphipoda	5.2–6.6 kcal/mg AFDM	pelagic	Frobisher Bay, Canada	Percy and Fife (1980)
Anonyx nugax	Amphipoda	5.9–6.4 kcal/mg AFDM	benthic	Frobisher Bay, Canada	Percy and Fife (1980)
Thysanoessa inermis	Euphausiacea	5.3–6.6 kcal/mg AFDM	pelagic	Frobisher Bay, Canada	Percy and Fife (1980)
Pandalus borealis	Decapoda	4.8 kJ/g WM	pelagic	Newfoundland and Labrador	Lawson et al. (1998)
Boreogadus saida	Pisces	4.4 kJ/g WM	all realms	Newfoundland and Labrador	Lawson et al. (1998)
Gadus morhua	Pisces	4.2 kJ/g WM	demersal	Newfoundland and Labrador	Lawson et al. (1998)
Theragra chalcogramma (age 0)	Pisces	5.8 kcal/g AFDM	pelagic (to demersal)	Bering Sea	Perez (1994)
Clupea harengus	Pisces	9.4 kJ/g WM	pelagic	Newfoundland and Labrador	Lawson et al. (1998)
Mallotus villosus	Pisces	8.4 kJ/g WM	pelagic	Newfoundland and Labrador	Lawson et al. (1998)
Reinhardtius hippoglossoides	Pisces	5.5 kJ/g WM	demersal	Newfoundland and Labrador	Lawson et al. (1998)

Notes: The Frobisher Bay samples were collected from late July to mid-September. Abbreviations are: AFDM, ash-free dry mass; DM, dry mass; WM, wet mass.

† Other abundant species rarely preyed upon, given for comparison.

saffron cod dominated stomach contents in spring/summer, while the shrimps *Pandalus* spp., *Eualus* spp., *Lebbeus polaris*, and *Crangon septemspinosa* dominated in the north-central Bering, the hyperiid amphipod *Parathemisto libellula* in the central Beaufort Sea, and the euphausid *Thysanoessa* spp. in the Barrow area (Lowry et al. 1980*a*; total number of stomachs = 299). Similar prey taxa were preferred in Svalbard: Arctic cod, shrimps (*Pandalus borealis*), euphausids (*Thysanoessa inermis*), and amphipods (*Themisto libellula*) (Weslawski et al. 1994). A seasonal shift towards a dominance of Arctic cod was observed in the northern Bering, Chukchi, and Beaufort Seas in the winter, similar to findings from the Kara Sea and Novaya Zemlya (Lowry et al. 1980*a*). In other areas, saffron cod, smelt, and herring dominated the winter diet (Sea of Okhotsk), whereas no seasonality was found in yet other areas, where euphausids, amphipods, shrimps, mysids, Arctic cod, and other fishes were consumed throughout the year (e.g., northern Labrador and southwest Baffin). Age-specific differences in diet were found in some areas and included a smaller fraction of cod in pups than in adults in the northeast Bering and southeast Chukchi Seas and a decline of crustacean consumption with age in the Canadian Arctic. Based on energetic value and amounts consumed, Lowry et al. (1980*a*) concluded that species occurring in high densities or swarms were of particular importance for ringed seals.

Polar bear (Ursus maritimus).—Polar bears prey primarily on ringed seals, bearded seals, and harp seals (e.g., Derocher et al. [2002]). Based on 135 observations in Svalbard and the western Barents Sea, ringed seals were the dominant prey numerically (63%), while bearded seals contributed the highest biomass (55%). Prey composition was suggested to depend on the area a bear roamed for prey, with more ringed seals taken by near-shore bears on land-fast ice and more bearded and harp seals taken by off-shore bears (Mauritzen et al. 2003). Occasional opportunistic prey items include other marine mammals such as beluga whales, walrus, and narwhals as well as marine birds and even reindeer (references in Derocher et al. [2002]). Polar bears also opportunistically scavenge, for example in Barrow Alaska, where bears take advantage of subsistence-harvested bowhead whale carcasses (C. George, *personal communication*).

Non-core species

Gray whale (Eschrichtius robustus).—Throughout their feeding grounds in the northern Bering and Chukchi Seas and offshore Kodiak and Vancouver Islands, eastern North Pacific gray whales prey on a variety of invertebrates, ranging from benthic amphipods, polychaetes, cumaceans, and bivalves to pelagic mysids, herring eggs, and crab larvae (e.g., Nerini 1984, Darling et al. 1998). Dietary analysis indicated that ampeliscid amphipods, tube-building benthic crustaceans, are, or were, the primary prey item of gray whales in some northern feeding grounds, in particular the Chirikov Basin in the northern Bering Sea. Pelagic feeding has so far been reported less frequently from the northern feeding areas than from Vancouver Island (Darling et al. 1998), although some evidence for pelagic feeding is emerging. Overall, the taxonomic composition of the available prey per se may be less relevant than the energy density in gray whale feeding sites (Darling et al. 1998). Some authors attributed recent mortality events of gray whales to limited food supply in the northern feeding grounds, but other factors such as disease may also have played a role.

Spotted or Largha seal (Phoca largha).—The prey spectrum of spotted seals in the Bering Sea is dominated by pelagic fishes, but also includes invertebrates such as shrimp, crabs, and octopus (Sobolevskii 1996, Lowry et al. 2000). Spring foods included walleye pollock and zoarcids in the central Bering Sea and capelin, pollock, and herring in the southeast Bering Sea; Arctic cod was important prey in the northern Bering Sea, while octopus played an important role in the Gulf of Anadyr and Karaginsky Bay. In the fall, herring, saffron cod, and salmon were dominant prey (Lowry et al. 2000). In the Chukchi Sea, 41 spotted seals stomachs primarily contained herring (Lowry et al. 1980*b*), but saffron cod, smelt, Arctic cod, and capelin were also found in seals from the Chukchi Sea (Sobolevskii 1996). Spotted seals mostly utilized small to medium sized fishes as prey (Lowry et al. 1980*b*), e.g., two Bering Sea spotted seals primarily ate pollock with a mean fork length of 10.9 cm. In the Russian sector of the Bering Sea, young seals heavily depended upon crustaceans and octopus in the summer (Sobolevskii 1996).

Ribbon seal (Phoca fasciata).—Little has been published on the feeding ecology of ribbon seals. Walleye pollock and Arctic cod otoliths dominated digestive tracts of 61 ribbon seals from the south-central and northern Bering Sea, respectively (Frost and Lowry 1980). From concurrent trawls, these authors concluded that ribbon seals selected against sculpins and capelin in the central and northern Bering and preferred large Arctic cod to small ones. While pollock of all sizes were preyed upon in this study, ribbon seals primarily ate small pollock (mean 11.2 cm fork length) in a later study from the Bering Sea (Frost and Lowry 1986).

Harp seal (Phoca groenlandica).—The North Atlantic-wide-distributed harp seal preys on both pelagic and demersal fishes and pelagic invertebrates. Stomach contents of 369 harp seals in coastal waters of northern Norway were dominated by a variety of near-bottom fishes such as gadoids and energy-rich pelagic shoaling fish such as Atlantic herring and capelin (Haug et al. 1991). Shrimps and squid were present in stomachs, but less prevalent. Dominant prey species varied between years, areas, and age classes; for example, saithe was eaten by older seals off northern Norway, while Norway pout was consumed by younger seals. In the Barents Sea, the pelagic amphipod *Parathemisto libellula* dominated the diets of 22 harp seals by abundance and mass, and the shrimp *Pandalus borealis*, euphausids *Thysanoessa* spp., and fishes contributed the remaining 25% (Nilssen et al. 1991). In the Greenland Sea, pelagic amphipods (*Parathemisto*), the squid *Gonatus fabricii*, Arctic cod, and capelin combined constituted 63–99% of the observed diet biomass with the amphipod dominating in the summer (Haug et al. 2004). Arctic cod and capelin were the major prey species off eastern Newfoundland, while capelin and Atlantic cod were most important in the Gulf of St. Lawrence (Stenson et al. 1997).

Conclusion

In summary, AMM exploit a wide range of pelagic and benthic invertebrate and vertebrate food resources, ranging from small copepods to large fishes and other mammals. Some AMM or at least some populations are very prey-, habitat-, and/or depth-specific (e.g., walrus, polar bear) while others are more opportunistic (e.g., beluga, bearded seal). It is apparent that prey occurring in high densities and/or with high caloric values are preferred. The distribution and biomass of the various prey items is ultimately linked to the productivity of the Arctic marine food webs, which varies on temporal and regional scales.

Arctic Marine Food Webs

The occurrence of marine mammals in the Arctic is patchy due to variations in both physical and biological (prey) characteristics. The differences in water depth, ice cover, and hydrography (Walsh 2008) cause considerable differences in the rate of primary production and food web structure between different Arctic shelves and in particular between the shelves and the Arctic deep sea. Consequently, prey availability and use of that prey will largely depend on the physical settings of the habitat of any given AMM species (Laidre et al. 2008, Walsh 2008). Below we outline the general biological characteristics of the three major physical realms (sea ice, pelagic, and benthic) in the Arctic Seas and discuss their current relevance for the nutrition of Arctic marine mammals. This information will also be used as a platform to discuss the impacts of ongoing and future environmental changes in the Arctic marine environment on AMM.

Sea ice communities and food web

Sea ice, formed by freezing of seawater, is a key component in structuring polar environments in general (Gradinger 2002, Sakshaug 2004). In addition to its important role as a platform for marine mammals (Laidre et al. 2008) and birds, sea ice serves as a habitat for a unique, highly specialized community of bacteria, algae, protozoans, and metazoans, which contribute to the biogeochemical cycles of polar seas (Horner 1985, Gradinger 2002).

Two major types of Arctic sea ice can be distinguished, depending on location and ice age (Wadhams 2000). Fast ice is attached to land and forms ice sheets in coastal areas, where it may grow either annually or for several years. Pack ice consists of separate ice floes of varying sizes (ranging from a centimeter to a kilometer in scale), drifting on the surface of the ocean with wind and currents. The sea ice cover in the Arctic shows distinct seasonal patterns driven by the yearly melt and ice formation cycle, with maximum ice extent in March (average 15.7×10^6 km^2) and minimum extent in September (average 9.3×10^6 km^2; period 1979–1987) (Wadhams 2000). Most of the annual sea ice formation occurs on the shelves, while the central Arctic Ocean remains ice-covered by multiyear pack ice even in summer. The accumulation of snow is not well studied but a thickness of ~40 cm may accumulate over winter and starts to melt (depending on latitude) in May/June (Gradinger 2002).

On average, ice thickness increases from areas with mainly first-year ice (e.g., Russian Arctic: thickness <2 m) to areas with multiyear ice cover (central Arctic) to a maximum north of Greenland (thickness 7–8 m) (Wadhams 2000). Recent observations indicate a substantial reduction in the ice thickness by 0.5–1.5 m in various parts of the Arctic, parallel to a loss of ice extent by ~2–3% per decade (ACIA 2004).

The biology related to sea ice is largely controlled by its physical and chemical properties (e.g., Gradinger 2002), mainly light availability and nutrient supplies. The biota is found inside the sea ice in pockets and channels of brine between the ice crystals or is attached to the underside of the fast and pack ice. So far, more than 200 diatom species (mainly pennate taxa) and more than 70 species of flagellates are described from Arctic sea ice (Horner 1985). Ice algae contribute 4–26% to total primary production in seasonally ice-covered waters and more than 50% in the permanently ice-covered central Arctic (Gosselin et al. 1997, Sakshaug 2004; Fig. 1). Overall, absolute production rates of organic carbon were below 10 g C/yr. The organic matter produced within the sea ice serves as the base for the sympagic (ice-associated) food web including protozoans and metazoans, e.g., ciliates, rotifers, copepods, copepod nauplii, nematodes, turbellarians, and, in fast ice, larvae of benthic polychaetes and gastropods (Horner 1985). Meiofauna abundances decrease from the nearshore fast ice (up to 350 000 animals/m^2) to the deep-sea basin by about three orders of magnitude (Gradinger and Bluhm 2005, Gradinger et al. 2005). Although a variety of ice meiofauna and meroplanktic larvae consume ice algae, only a minor fraction (<10%) of the ice algal production is consumed by sea ice metazoans (Gradinger et al. 2005).

Gammaridean amphipods, the dominant macrofaunal taxon in the Arctic under-ice habitat, are the best-studied consumers of ice algal production in all parts of the Arctic (e.g., Gradinger and Bluhm 2004). Several

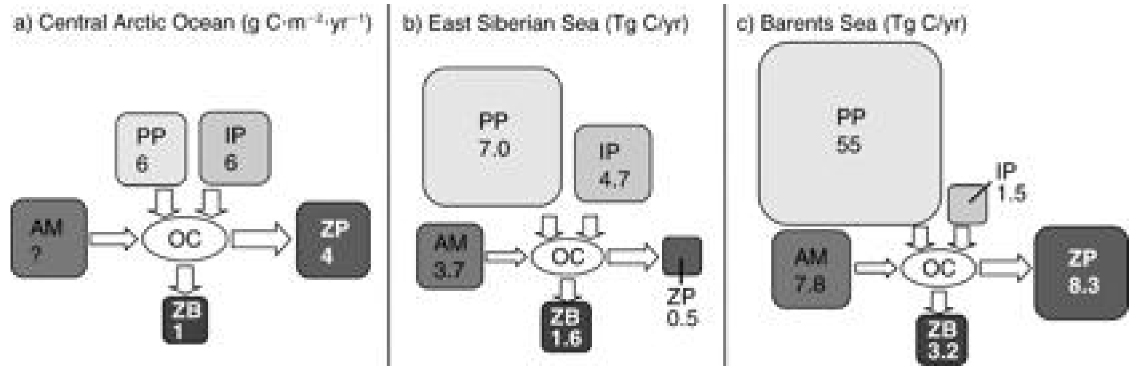

FIG. 1. Yearly production estimates for phytoplankton (PP), ice algae (IP), allochthonous material (AM), zooplankton (ZP), and zoobenthos (ZB) contributing to the organic-carbon pool (OC) for three different Arctic regions: (a) central Arctic Ocean (from Gosselin et al. 1997 [PP, IP], Klages et al. 2004 [ZB], and Mumm et al. 1998 [ZP]), (b) East Siberian Sea (Petrova et al. 2004), and (c) Barents Sea (Vetrov and Romankevich 2004). Units used correspond to those in the original data sources. This schematic depicts only rough estimates to emphasize the different sizes of the boxes in each region.

species of amphipods (e.g., *Gammarus wilkiztkii*, *Apherusa glacialis*, *Onisimus* spp.) are endemic to the multiyear sea ice cover and exploit the ice cover year-round, while benthic species such as *Onisimus litoralis* are common in nearshore seasonal ice regimes (Bradstreet and Cross 1982). Under-ice amphipods occur in abundances of 1–1000 individuals/m^2 in coastal areas and with, on average, 1–40 individuals/m^2 in offshore pack ice (Gradinger and Bluhm 2004). These under-ice amphipods are an important food source for Arctic diving birds and Arctic cod (*Boreogadus saida*) (Bradstreet and Cross 1982) and thereby provide the link from the food web within the sea ice to the more accessible open water below.

Arctic cod are frequently observed in close association with fast ice and pack ice year-round, and use the ice both for protection against potential predators and as a feeding habitat, ingesting under-amphipods and zooplankton (Gradinger and Bluhm 2004). In ice-free areas or conditions, Arctic cod is a pelagic species, but may also be found near the bottom in shallow shelves. Arctic cod can occur in small groups in protected seawater wedges within the offshore pack ice or form dense swarms of several million fish. This northernmost distributed gadid is the crucial link between the sea ice food web and AMM, in particular ringed seals, ribbon seals, and narwhals (e.g., Siegstad et al. 1998; Table 1) in that it "concentrates mg-sized particles into energy packets large enough to be eaten efficiently by seals, whales and birds" (Welch et al. 1992:351). In Lancaster Sound, Canada, alone, AMM and birds consume ~148 000 Mg/yr (metric tons per year) of Arctic cod (Welch et al. 1992).

Pelagic communities and food web

Much like those occurring in the ice, biological processes in the water column are mainly controlled by abiotic forcing. Seasonal fluctuation of light and ice melting and formation regularly alter growth conditions for phytoplankton. In early spring, increasing light and ice melt enhance water column stability; as a result phytoplankton blooms form in the marginal ice zones (MIZ) before algal growth occurs in the adjacent open ocean. These substantial MIZ algal blooms, which move across the shelves with the sea ice retreat, make up 50% of the total primary production in Arctic waters (Sakshaug 2004).

Total primary production rates in the Arctic can exceed values of >100 g C·m^{-2}·yr^{-1} on the shelves of the Barents, Chukchi, and Bering Seas (Sakshaug 2004). The highest production values are encountered on the Bering Shelf, where values are close to 5 g C·m^{-2}·d^{-1} or >500 g C·m^{-2}·yr^{-1} and are among the highest in the world's oceans. These very high rates reflect the high nutrient concentrations that allow the buildup of substantial phytoplankton biomass while Arctic shelves with lower nutrient availability (e.g., northern Barents Sea, East Siberian Sea, Kara Sea) exhibit much lower production values (15–70 g C/m^2; Sakshaug 2004). Primary production rates in the central Arctic Basin are one order of magnitude (<20 g C·m^{-2}·yr^{-1}) lower than on the shelves (Gosselin et al. 1997, Sakshaug 2004; Fig. 1). Within the ice pack, enhanced primary production rates were found in polynyas around Greenland, where yearly primary production estimates range between 20 and 50 g C/m^2.

In certain areas, the microbial food web plays an important role in the Arctic, based on locally very high concentrations of dissolved organic carbon (e.g., Sherr and Sherr 2003). From the perspective of AMM however, larger size classes, mainly herbivorous mesozooplankton, such as copepods and euphausiids, and fish are the most significant prey items within the water column. For example, the adults of some of the biomass-dominating marine Arctic copepod species, such as *Calanus glacialis* and *C. hyperboreus*, reach sizes larger than 1 mm. The Arctic pelagic herbivores adapted their life cycles to deal with the seasonally pulsed food supply (Hagen and Auel 2001). The storage of large amounts of lipids in form of either waxesters or triglycerids for either winter survival or spring reproduction (Hagen and Auel 2001) makes these copepods a rich food source for higher trophic levels from fish to AMM, among those in particular the bowhead whale (Tables 1 and 2). These copepods contribute the largest fraction to Arctic mesozooplankton biomass (Mumm et al. 1998). Besides copepods, typical Arctic zooplankton includes amphipods, chaetognaths, larvaceans, hydro- and scyphomedusae, and pelagic snails (Hopcroft et al. 2005). The biomass of Arctic mesozooplankton can exceed the phytoplankton biomass and shows a steep decline north of approximately 83° N from values of 8 g dry mass/m^2 in the Greenland Sea to ~1 g dry mass/m^2 in the High Arctic Nansen and Makarov Basins (Mumm et al. 1998). Similar latitudinal trends are obvious for the zooplankton productivity, as exemplified in Fig. 1.

Several of the dominant zooplankton taxa are linked in their occurrence to the Arctic hydrographical regime. The lipid-rich calanoid copepod species *Calanus glacialis* is endemic to polar waters, while *C. finmarchicus* is found in the Atlantic domain and, e.g., *Neocalanus cristatus* in the Pacific domain (Hopcroft et al. 2005). Similarly, the herbivorous euphausiid *Thysanoessa inermis* is abundant in the sectors influenced by Atlantic water and *T. longicauda* and *T. raschii* in Bering Sea water. Fluctuations or long-term changes in the large-scale hydrographical regimes will consequently alter the species spectra in the inflow shelves, which carry Atlantic and Pacific species, respectively. On a smaller scale, regional hydrographical processes, specifically freshwater runoff and consequent salinity changes, influence zooplankton composition and biomass, in particular on the shelves with large rivers (e.g., Deubel et al. 2003). For example, decreasing total zooplankton abundance and increasing contribution of smaller freshwater taxa were observed along a decreasing salinity gradient in the Lena River delta.

The food spectrum of copepods and euphausiids includes phytoplankton and microzooplankton but varies from species to species with actual ingestion rates frequently relating to the abundance of the prey (Hagen and Auel 2001). Depending on the availability of food and the abundance of mesozooplankton, their yearly grazing rates range between 1 and >18 g C/m^2 (Sakshaug 2004) and zooplankton production shows similar variability (Fig. 1). Increased primary productivity rates in specific regions such as marginal ice zones can sustain high densitites of mesozooplankton, which attract higher trophic levels such as plankton feeding birds and baleen whales (Bradstreet and Cross 1982).

Major AMM nekton prey include capelin, herring, walleye pollock, and squid (Table 1). In the southeastern Bering Sea walleye pollock is the single most abundant fish, and variations in its stock, therefore, percolate through the whole food web (Wepestad et al. 2000). Fish stock size is highly variable and, along with distribution, may be influenced by temperature. Walleye pollock, for example, currently a subarctic species, is dispersed across the Bering Sea shelf and even north of Bering Strait in warm but not in cold years and spends most time above 2°C, while Arctic cod inhabits areas of consistently colder waters (Wyllie-Echeverria and Wooster 1998). In the Atlantic sector of the Arctic, the distribution of forage fishes such as herring and capelin is influenced by climatic conditions in any given year (e.g., Loeng 1989). For example, capelin, a very energy-dense fish relative to walleye pollock (Table 2), was distributed more easterly and northerly in warm than in cold years in the Barents Sea. Adult capelin fed in both Atlantic and Arctic water masses in the Barents Sea with a preference for temperatures between −1°C and +2°C. Feeding area and growth were related, probably a function of temperature, with warmer temperatures and faster growth in southern areas. In the northwest Atlantic, the large capelin schools formed during the spawning season also make up a significant contribution of the diet of commercial fishes, marine mammals, and seabirds. Less is known about the pelagic fishes of the High Arctic shelves and Arctic deep sea. In a three-year study in the Beaufort Sea, Arctic cod (more on this species in *Sea ice communities and food web*), capelin, and liparids dominated epipelagic catches in coastal waters, with the 0+ age class being most abundant (Jarvela and Thorsteinson 1999). During approximately 15 pelagic dives of a remotely operated vehicle across the Canada Basin, few pelagic fishes were observed (R. Hopcroft, *personal communication*).

Among the squids, *Gonatus fabricii* is the most abundant species in Arctic and subarctic waters of the North Atlantic, where *Gonatus* predators apparently take advantage of aggregations of inactive females at their spawning sites (e.g., Bjørke 2001). While *Gonatus* juveniles inhabit the upper water column, the short-lived adults roam depths >400 m, where they are preyed upon by narwhals (Laidre and Heide-Jørgensen 2005), belugas, and other deep-diving mammals such as sperm whales, northern bottlenose whales, and long-finned pilot whales (Bjørke 2001). In the Bering Sea, where *Berrytheuthis magister* is the predominant squid species, squid are preyed upon by some mammals such as northern fur seals (Arkhipin et al. 1995).

Arctic benthic communities and food web

Major environmental determinants of Arctic benthic community structure include food supply, which largely originates in the surface waters and is highly seasonal in the Arctic, substrate type and grain size, salinity, temperature, and, in shallow water, ice scouring (Klages et al. 2004, Piepenburg 2005). Densities of sedimenting particles and their nutritional values range vastly from the nutrient-rich waters of the northern Bering, Chukchi, and Barents Seas to the oligotrophic deep waters of the Arctic Basins (Klages et al. 2004). Settling food particles add to the soft sediments predominating the Arctic and the grain size of these sediments, along with above-listed factors, determines faunal community composition (Grebmeier et al. 2006*a*). Exceptions to the soft bottoms in the Arctic are local accumulations of boulders, nearshore coastal regions, canyons, and High Arctic islands and Arctic fjords. In near-shore areas, benthic biomass and diversity intermittently decline due to ice scour, resulting in a patchwork of different successional stages (Piepenburg 2005). In addition, nearshore areas are under the influence of freshwater runoff, in particular the Laptev, Kara, and Beaufort Seas (Jørgensen et al. 1999, Deubel et al. 2003). Low numbers of euryhaline and brackish-water benthic species, some particularly well-adapted to high sedimentation rates (e.g., *Portlandia arctica*), dominated the shelf regions in estuaries (Deubel et al. 2003), where benthic biomass can be lower than under fully marine conditions (Jørgensen et al. 1999).

Arctic marine mammals prey on benthic species from the size classes macrofauna (mostly infaunal; >1 mm) to megafauna (large enough to be seen on seafloor images; mostly epifaunal). Benthic bacteria and meiofauna (<1 mm) are therefore excluded from this review. Arctic macrofauna is dominated, like most soft-bottom fauna in the world's oceans, by polychaetes, bivalve mollusks, and crustaceans, in particular amphipods, both on the Arctic shelves and in the central deep sea (e.g., Klages et al. 2004, Grebmeier et al. 2006*a*). Important macrofauna AMM prey species include bivalves taken by walrus, *Macoma* spp. and *Mya truncata*, and benthic amphipods utilized by gray whales and bearded seals (Table 1). Enhanced primary production at frontal systems, polynyas, and along the ice edge result in enriched benthic biomass with high water column productivity related to high benthic infaunal biomass in tightly coupled systems such as the Bering/Chukchi Seas. Benthic biomass is particularly high in the northern Bering Sea (~24 g C/m^2), the southern Chukchi Sea (~40–50 g C/m^2), and in the Gulf of Anadyr (~30 g C/m^2; Grebmeier et al. 2006*a*). In contrast, benthic infauna communities are depleted in biomass on the less productive Alaskan Beaufort Sea shelf (~4 g C/m^2) and in the eastern Chukchi Sea under influence of the nutrient-poor Alaska Coastal Current water (<10 g C/m^2; Grebmeier et al. 2006*a*). On the river-influenced Russian interior shelves, strong gradients of estuarine to fully marine conditions result in benthic biomass gradients (Deubel et al. 2003).

Arctic epibenthic communities include taxa with long life spans (several years to decades) and often slow growth rates such as echinoderms, crabs, and demersal fishes. These communities account for >25% of the overall benthic community respiration and, due to their often large size, contribute significantly to overall benthic biomass despite their patchy occurrence (Piepenburg 2005). At most locations studied, ophiuroids dominated the epibenthic megafauna with locally several hundred individuals per square meter. Other conspicuous epibenthic faunal elements, in varying abundances, included sea urchins, sponges, sea cucumbers, sea stars, crabs, and bryozoans (Piepenburg 2005). With the exception of crabs, shrimps, and molluscs, heavily calcified taxa tend to have little nutritional value (Table 2) and are rarely found on the AMM prey list. Several epifaunal organism groups are highly mobile and play an important role in the redistribution of pelagic carbon partitioned to the benthos and in organic carbon mineralization (Piepenburg 2005).

Benthic or demersal fishes preyed upon by AMM include mostly gadids, redfishes, and Greenland halibut (Table 1). Off Greenland, the demersal fish assemblage is dominated by Atlantic cod, golden and deep sea redfish, American plaice, Atlantic wolfish, and starry skate, although all underwent dramatic declines in abundance, biomass, and/or individual fish size from 1982 to 1996 (Rätz 1999). Greenland halibut, a major prey species of narwhals in Baffin Bay (Laidre and Heide-Jørgensen 2005), ranked 12th in average catch statistics off Greenland from 1982 to 1996 (Rätz 1999). Common and commercially fished demersal fishes in the eastern Bering Sea include Pacific cod, Greenland halibut (or turbot), yellowfin sole, arrowtooth flounder, and other flatfishes (Witherell 2000), a group which in that area does not seem to be among the preferred AMM prey items (Table 1). In High Arctic regions, benthic marine fishes have been poorly studied. Nevertheless, local subsistence fishing has a long tradition along the Arctic coasts and Barrow's native population, for example, is reporting more salmon catches in recent years (C. George, *personal communication*). In the northeastern Chukchi Sea, gadids made up 69–83% of the fishes in trawls in 1990 and 1991; cottids, pleuronectids, and zoarcids contributed much of the remaining catches (Barber et al. 1997). Two species of sculpin were dominant in the southern and northwestern Chukchi Sea in 2004, followed by Bering flounder and Arctic cod (C. W. Mecklenburg, B. A. Sheiko, D. L. Stein, N. V. Chernova, and B. A. Holladay, *unpublished manuscript*). Gadids and sculpins were dominant in a few bottom trawls in the Chirikov Basin in 2003 (R. Highsmith, C. O. Coyle, B. A. Bluhm, and B. Konar, *unpublished data*). The potential distribution and stock size changes in a warming Arctic climate may prompt more interest in Arctic fishes in the future.

Cryo-pelagic–benthic coupling

Coupling processes and interdependencies between ecosystem components are of great significance in the Arctic and are, therefore, stressed again here. The sea ice and pelagic and benthic realms are inherently linked through sedimentation of particles, animal migrations, life cycles, and direct food web interactions. The quantity and quality of particles produced in the sea ice or water column and settling out to the sea floor depend on nutrient availability and overall primary production in the water column, water stratification and mixed layer, midwater grazing rates, and bacterial degradation (Klages et al. 2004). If primary production is high in regions of high nutrient availability and zooplankton grazing is simultaneously low, coupling between the ice and/or pelagic and the benthic systems is tight, resulting in high benthic biomass (Grebmeier et al. 2006*a*). In a latitudinal comparison of energy flow partitioning, the benthic system received more energy in Arctic vs. temperate and tropical systems, although there are significant differences within the Arctic. A prime example for tight pelagic–benthic coupling can be found in the northern Bering and southern Chukchi Seas (Grebmeier et al. 2006*a*). Sediment trap measurements in the 1980s indicate that total particulate organic carbon (POC) flux in the northern Bering Sea is extremely high (253–654 mg $C{\cdot}m^{-2}{\cdot}d^{-1}$) and low C/N ratios of organic material in the sediment traps (4.9–7.4) indicate that fresh organic matter is reaching the benthic community. The latter utilizes the carbon directly and efficiently as indicated by a match of the mean vertical carbon flux (501 mg $C{\cdot}m^{-2}{\cdot}d^{-1}$) and the estimated organic carbon utilization at the seafloor (464 mg $C{\cdot}m^{-2}{\cdot}d^{-1}$; Grebmeier et al. 2006*a*). The high carbon flux is driven by high primary production, which was estimated at 250–300 g C/m^2 for the summer months or $\sim$2 g $C{\cdot}m^{-2}{\cdot}d^{-1}$. Those high production areas serve as feeding grounds for the bottom-feeding Pacific walrus, California gray whale, diving birds, and surface-feeding seabirds associated with feeding mammals (e.g., Oliver et al. 1983). In recent years, evidence is accumulating that change is underway, with less tight pelagic–benthic coupling and locally changing benthic biomass (Grebmeier et al. 2006*b*; see *Recent changes and fluctuations in Arctic marine food webs*).

RECENT CHANGES AND FLUCTUATIONS IN ARCTIC MARINE FOOD WEBS

The described characteristics of the ice, pelagic, and benthic realms provide a diverse spectrum of feeding habitats and prey communities for AMM. Variability and changes in environmental conditions (Walsh 2008) likely have different consequences for different trophic levels and species within them (Laidre et al. 2008). The growing concern about the potential impact of Arctic warming on the marine ecosystem stimulated major new large-scale biological climate studies and is one of the topics of the ongoing International Polar Year (IPY) 2007–2008. While Arctic systems have been described as well adapted or resilient to some degree of climate variation because of the frequent natural disturbances (Piepenburg 2005), the magnitude of change expected in this century makes the Arctic system vulnerable to climate change (ACIA 2004). It should be noted, however, that large changes are not necessarily (only) driven by climate. Arctic ecosystems are also impacted by high loads of pollutants and human exploitation (including harvest of fish and AMM), which have caused changes in Arctic food webs (e.g., AMAP 2003). The difficulty in documenting solid causal relationships between climate and biological populations lies in several factors, most importantly, the scarcity of long-term time series. Also, the best studied (sub-)arctic regions, the southern Bering and Barents Seas, are those that have undergone major climate variability, but are at the same time the most heavily exploited Arctic areas in terms of historic whaling, past and present fisheries, and/or oil and gas exploration.

Here we present examples of documented changes, attributed to climate variability or change, in subarctic and Arctic biological communities on a range of trophic levels. Examples will have a focus on subarctic regions, as biological investigations in the High Arctic have been too rare for analyses of interdecadal variabilities. Our current understanding of the High Arctic provides evidence for the close linkages between environment and marine food webs, but long-term time series are largely missing. Sporadic observations from the Central Arctic indicate substantial changes might be occurring already with the loss of sea ice and its attributed flora and fauna (Melnikov et al. 2001). Even today in the era of Arctic warming (ACIA 2004), no unified pan-Arctic long-term monitoring plan has been implemented to follow changes in the High Arctic marine food web composition and biomass. National programs, however, are underway, and so are efforts attempting to connect those in the framework of the IPY.

Pacific (sub-)arctic

A growing body of evidence suggests that regime shifts and long-term climate changes in the Bering and Chukchi Seas are coincident with alterations in biological regimes (Schumacher et al. 2003, Grebmeier et al. 2006*b*). Regime shifts are dynamic and can oscillate. The co-occurring biological changes can serve as model scenario indicators for effects of long-term climate change. The best understood example for climate-driven variability is the Bering Seas regime shift complex. The regime shift in 1997 had various effects on sea surface temperature, the extent of sea ice, and wind forcing of ocean currents in the Bering Sea. Since then, several coccolithophorid blooms have occurred in the Bering Sea and were intermittently thought to replace the previously occurring summer flagellate community (Schuhmacher et al. 2003). As a result, profound effects on consumer abundance and feeding types and on biogeochemical cycling were observed. As an example, zooplankton communities in the Bering Sea changed from crustacean-dominated communities to an increase in gelatinous plankton, which has since decreased again. The prey items of the dominant jellyfish species in the late 1990s and early 2000s, *Chrysaora melanaster*, includes euphausids, copepods, and amphipods, as well as juvenile pollock and, hence, overlaps with that of some Arctic marine mammals.

Shifts in fish and benthic community composition also occurred in recent decades (Hamazaki et al. 2005). In the heavily fished southeastern Bering Sea, flatfish and general groundfish biomass was higher in 1980–2000 than in 1960–1980. Catch per unit effort of total benthic epifauna (in particular crabs and sea stars) and fish (in particular flatfishes) increased from 1976 to 2002 in Norton Sound and from 1976 to 1998 in Kotzebue Sound. In contrast, a decrease in benthic infauna biomass and sediment oxygen uptake was observed south of St. Lawrence Island on the Bering Sea shelf (Grebmeier et al. 2006*b*). Here, the changes in the bivalve population composition by the late 1980s affected benthic predators, such as the spectacled eider, that heavily use this feeding ground. Between 1986 and 1988, ampeliscid amphipod biomass and production in the Chirikov Basin (northern Bering Sea) declined by ~20%, and by 2002–2003 production had further declined to ~50% of the highest value in 1986 (Coyle et al., *in press*). It is not fully resolved to what extent climate or whale predation is responsible for this decline. Indications for climate-related shifts in Arctic community composition are also evident from benthic studies in this region: Recent sampling in the Chukchi Sea suggests northern range extensions of some mobile epifauna species with climate warming as the suspected cause (B. Sirenko, B. A. Bluhm, and K. Iken, *unpublished manuscript*).

Arctic marine mammals have been used to understand long-term trends in ecosystem productivity in this region. The $\delta^{13}C$ stable isotope ratios in bowhead whale baleens support the hypothesis that the productivity of the Bering Sea declined by ~30–40% over the time period 1966–1997 (Schell 2000). Besides food web changes, ranges of AMMs might have changed as recent acoustic and visual observations documented temporally extended stays of gray whales in the Chukchi Sea all the way up to Barrow, potentially a consequence of warming trends (Moore et al. 2006).

Atlantic (sub-)Arctic

The variable inflow of comparatively warm North Atlantic water into the Barents Sea drives the variability of environmental conditions and of fish larval and zooplankton biomass in this area (e.g., Dalpadado et al. 2003). The North Atlantic Oscillation is thought to have an effect on the distribution and biomass of North Atlantic zooplankton. Over the last two decades the Barents Sea zooplankton biomass has undergone large changes with overall higher plankton biomass in relatively warm years such as 1994 than in cold years such as 1986. The biomass of the dominant copepod species, *Calanus finmarchicus*, was tightly linked to the supply of Atlantic water into the Barents Sea. With warming North Atlantic waters and stronger inflow into the Arctic, "warm-year" conditions may become prevalent in the future and extend northward. Zooplankton stock and growth fluctuations affect pelagic planktivorous fish such as capelin and herring, prey items of ringed seals and other AMM (Siegstad et al. 1998). More directly, a climate-related shift from large lipid-rich Arctic copepod species (Table 2) to smaller North Atlantic taxa might reduce the nutritional quality of the food present in areas affected by warming.

Similar linkages between warming and climate-related changes in benthic invertebrate and fish biomass and composition have already been observed in the Barents Sea half a century ago. Warming in the Barents Sea in the first half of the 20th century resulted in the restoration of the cod stock on Bear Island Bank after the species' practical absence for about four decades (Blacker 1957). Blacker also observed that several Atlantic indicator species had a northward range extension from 75° N to 78° N since 1878, apparently as a consequence of increased inflow of warm North Atlantic water. By 1978–1981, Dyer et al. (1984) noted that the same indicator species had further increased their temperature ranges in the same study region. In addition Arctic and Atlantic species overlapped more extensively in their ranges in the 1970s relative to the 1950s. Kiyko and Pogrebov (1997:330), in their analysis of pollution effects, observed decreases in polychaete biomass in the Barents and Kara Seas in the early 1990s relative to the 1920–1930s as well as a "redistribution of some organism groups." Although these authors interpret these changes as sampling effects and "natural population fluctuations," an analysis of these range changes in relation to climatic conditions still needs to be done.

Potential future scenarios for Arctic marine food webs

The Arctic Ocean will be, and to some extent already is, exposed to tremendous changes in the environmental boundary conditions, including loss of summer sea ice, increasing temperatures, and alterations in the precipitation and river runoff patterns (ACIA 2004, Walsh 2008). Detailed biological consequences of such changes on a species level are difficult to predict, as biological systems might react in unprecedented ways as learned from the described shifts between crustaceans and jellyfish in the Bering Sea. Here we describe three scenarios that, therefore, should be considered as thought experiments, providing inspiration to discuss possible effects on the Arctic marine food web and their implications for AMM and to pose related hypotheses. The underlying assumptions for the scenarios are based on published results from the literature described in the sections before; the scenarios themselves are, from our perspective, likely but not prognostic, each taking into account a particular set of parameters. We restricted ourselves to alterations outlined within the ACIA (2004) framework that assumes only slight modifications of the current Arctic Ocean hydrography; we excluded major alterations such as a potential loss of the Arctic halocline (Walsh 2008) and its subsequent impacts.

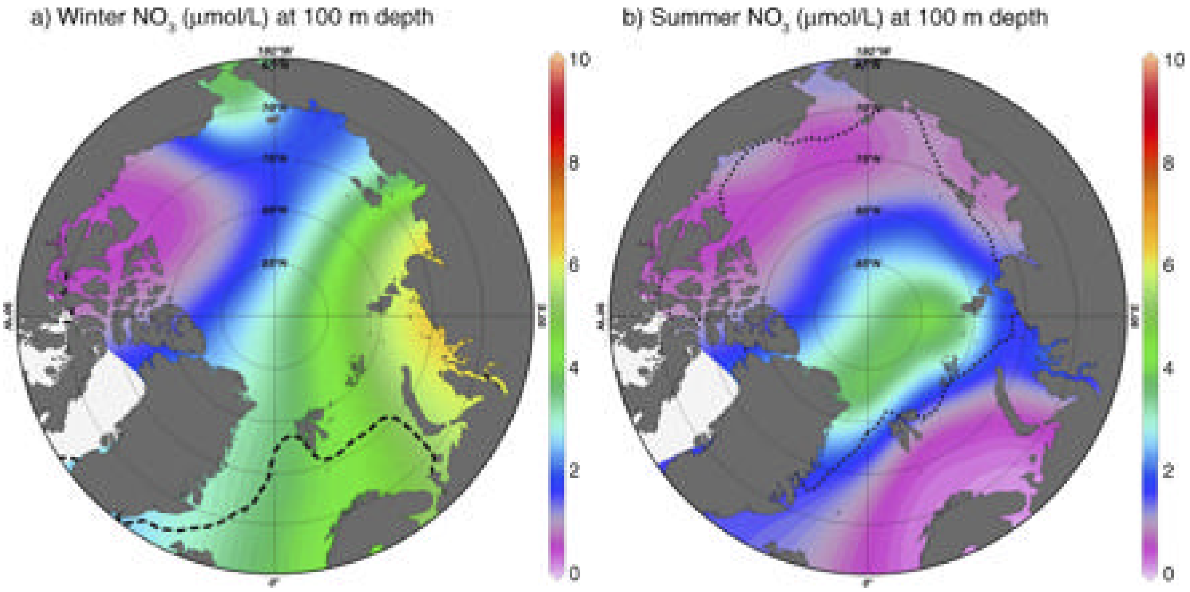

FIG. 2. (a) Winter and (b) summer nitrate concentration in the Arctic seas based on Colony and Timokhov (2001). Note that the data for winter are sparse (for details, see Colony and Timokhov [2001]). The dashed line indicates the long-term mean ice extent (concentration >50%) for (a) March and (b) September. The nutrient reservoir over the Central Arctic in the summer (blue and green areas) could support additional new primary production in an ice-free Arctic Ocean.

Changes in sea ice cover and resulting primary production.—The loss of summer sea ice cover will have immediate consequences for ice-dependent AMM. Examples include reduced reproductive success and survival chances of polar bears and the loss of insulation from snow and interruption of nursing in ringed seals due to early breakup (Kelly 2001, Laidre et al. 2008). The loss of the ice-based food web and the associated food sources such as amphipods and Arctic cod (Gradinger and Bluhm 2004) would additionally negatively impact the ice seals. For the Pacific walrus, the retreat of spring sea ice beyond the Arctic shelves into the deep basins will make ice no longer a resting and reproduction environment that is within the reach of their benthic prey (depth limit approximately 100 m; Kelly 2001).

On a broader ecosystem scale, the loss of sea ice will likely change the amount and characteristics of primary production in the Arctic seas. Several researchers (e.g., Anderson and Kaltin 2001) have proposed that the increased summer ice melt will increase the overall extent of marginal ice zones and lead to increased primary productivity in these regions. Increased primary productivity would supply more food for pelagic and benthic consumers, while the low productivity zone of the multiyear sea ice (MYI) would shrink. Also, ice retreat off the shelves may result in upwelling of nutrients or prey from the basins (Carmack et al. 2004). Based on the inorganic carbon availability, Anderson and Kaltin (2001) proposed an increase of up to 50 g C/m^2 integrated over the upper 100 m of the water column across the Arctic, mainly as a result of ice loss. Ultimately, however, nutrient availability, mainly nitrogen and phosphorous, determines the total amount of primary productivity possible in any given ocean.

Hence, we estimated the potential for increased primary productivity in the Arctic based on nutrient concentration data from the "Hydrochemical Atlas of the Arctic Ocean" (Colony and Timokhov 2001), which summarizes hydrographical and chemical data from drift ice stations and ship-based expeditions from 1948 to 2000. We selected nitrate concentration data from within the euphotic zone (10-m depth) to address the question of whether the removal of sea ice, and thus the increase in solar radiation in the water column, could indeed support an increase in primary production or whether the current nutrient resources are already completely consumed by phytoplankton growth. The large-scale nutrient regime in winter (Fig. 2a) shows three major features: (1) the oligotrophic Beaufort Gyre in the Canadian Basin, (2) the higher nutrient concentrations in the Transpolar Drift regime, and (3) the inflow of nutrients through the Bering Strait, the North Atlantic, and rivers on the Arctic shelves. The summer distribution (Fig. 2b), in contrast, shows a reduction of nitrate in the region south of approximately 80° N as a consequence of phytoplankton blooms in the dynamic marginal ice zones. North of 80° N, an area that currently overlaps with the MYI zone (Walsh 2008), summer nutrient concentrations remain higher, i.e., they are not completely utilized by phytoplankton. Based on the provided gridded data set, we calculated a mean nitrate summer concentration of 3.2 μmol NO_3 north of 80° N and of 0.8 μmol NO_3 between 70° and 80° N.

Assuming a typical phytoplankton C/N ratio of 7, the mean summer concentration of approximately 3.2 µmol NO_3 in the central Arctic would allow for an additional new production of 270 mg C/m^3 or 13 g C/m^2 (assuming a relatively shallow 50-m euphotic zone as typical for marginal ice zones, e.g., Sakshaug 2004) (Fig. 2b). This estimate is within the same order of magnitude as the current production estimates for the central Arctic Ocean (Gosselin et al. 1997), which according to our scenario would, hence, roughly be doubled. Similarly noteworthy is that the current nutrient regime would not allow for a substantial change in total primary productivity in the coastal and shelf regions using our assumptions.

In reality, total primary production will also depend on seasonal stratification, river runoff (see *Increased river runoff changes nearshore biological communities*), etc. Ice receding from the shelves could facilitate upwelling along the shelf breaks (Carmack et al. 2004), which in turn may support higher primary production on the shelves than suggested in our scenario that assumed constant nutrient concentrations. Nevertheless, we consider it reasonable to assume a primary production increase in the central Arctic Transpolar Drift system. Currently little of the Transpolar Drift system and the area north of 80° N is utilized by AMM (Laidre et al. 2008), but this might change under the outlined scenario. The fate of the above-described increased production at very high latitudes will depend on the food web structure. Currently, subarctic and Arctic pelagic and benthic communities (including AMMs) successfully exploit the seasonal ice systems of the Arctic shelves. Increased primary production in the Central Arctic might lead to higher biomass of zooplankton and/or benthos, depending on the reworking and sedimentation patterns. The great water depths in the Central Arctic will make remineralization of the majority of the production in the water column very likely, similar to current conditions in the Central Arctic (Fig. 1). From the perspective of AMM, benthic feeders such as gray whale and walrus will remain unable to exploit the Arctic basins because they are well beyond their diving depths. Pelagic feeders such as bowhead, fin, minke, and blue whales, in contrast, might be able to use the increased productivity. The question of whether jellyfish rather than (or in addition to) crustaceous zooplankton would increase in relative importance in subarctic and Arctic food webs, as documented in the Bering Sea and elsewhere, is open. Jellyfish and other gelatinous zooplankton are an integral part of the current High Arctic food web (Hopcroft et al. 2005) but have low caloric value for higher trophic levels (Table 2). Their increase would likely not lead to better feeding conditions for AMMs.

Increased river runoff changes nearshore biological communities.—A second scenario revolves around the potential effects of the observed and predicted increase in river runoff in the Arctic (ACIA 2004). Total freshwater inflow into the Arctic Ocean is on the order of 4523 km^3/yr (R-ArcticNet, *available online*)[2] and increased by ~7% from 1936 to 1999, with the potential for further increase with Arctic warming (ACIA 2004).

Increased freshwater discharge acts on biological communities through three major pathways (besides addition of organic dissolved matter): (1) nutrient transport, (2) turbidity, and (3) inflow of low salinity water (Pivovarov et al. 2003). All three effects can act on the levels of species richness, community composition, productivity, and biomass, and although these effects are tightly coupled, we will evaluate their current significance separately for clarity of the argument.

1) Arctic river runoffs differ in the amount of inorganic nutrients, both macro- and micronutrients. The injected macronutrients are consumed by phytoplankton within the river estuaries, as exemplified for both the Kara and the Beaufort Seas (e.g., Pivovarov et al. 2003). Additional nutrient input to the nearshore waters through either higher freshwater input (through changes in the hydrological cycle) or higher nutrient concentrations in the freshwater (through changes in the terrestrial environment; ACIA 2004) could increase the current productivity in coastal and estuarine areas, but this might be counteracted by the impact of decreased salinities and increased turbidity.

2) Increased river runoff, with its high levels of suspended inorganic material, will increase nearshore sedimentation and turbidity, which reduces light transmission for algae and can clog filtration apparatuses of filter-feeding animals (Thrush et al. 2004). Certain Arctic cumacean and bivalve species, e.g., *Portlandia arctica*, can endure high sedimentation rates (Syvitski et al. 1989) while many other species cannot. High turbidity reduces the capability of visual predators to find prey. Increased land use in the Arctic over the next decades due to resource exploitation and climate change has the potential to further increase the sediment load and impact the marine food web.

3) Increased freshwater discharge would likely result in larger areas inhabited by euryhaline and brackish-water species relative to marine species compared to the current situation. In general, species richness is related to salinity, with high numbers of species in fully marine and true freshwater conditions and the lowest number of species around 5–7 practical salinity units (PSU; Remane 1958; Fig. 3). Brackish-water species occur at a salinity range from close to 0 to ~20 PSU, but are not very numerous.

The structuring effect of freshwater runoff, with all features combined, on the biomass, productivity, and community composition of Arctic phytoplankton, zooplankton, and benthic taxa is reasonably well documented and outlined here, although some results are

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[2] ⟨http://www.r-arcticnet.sr.unh.edu⟩

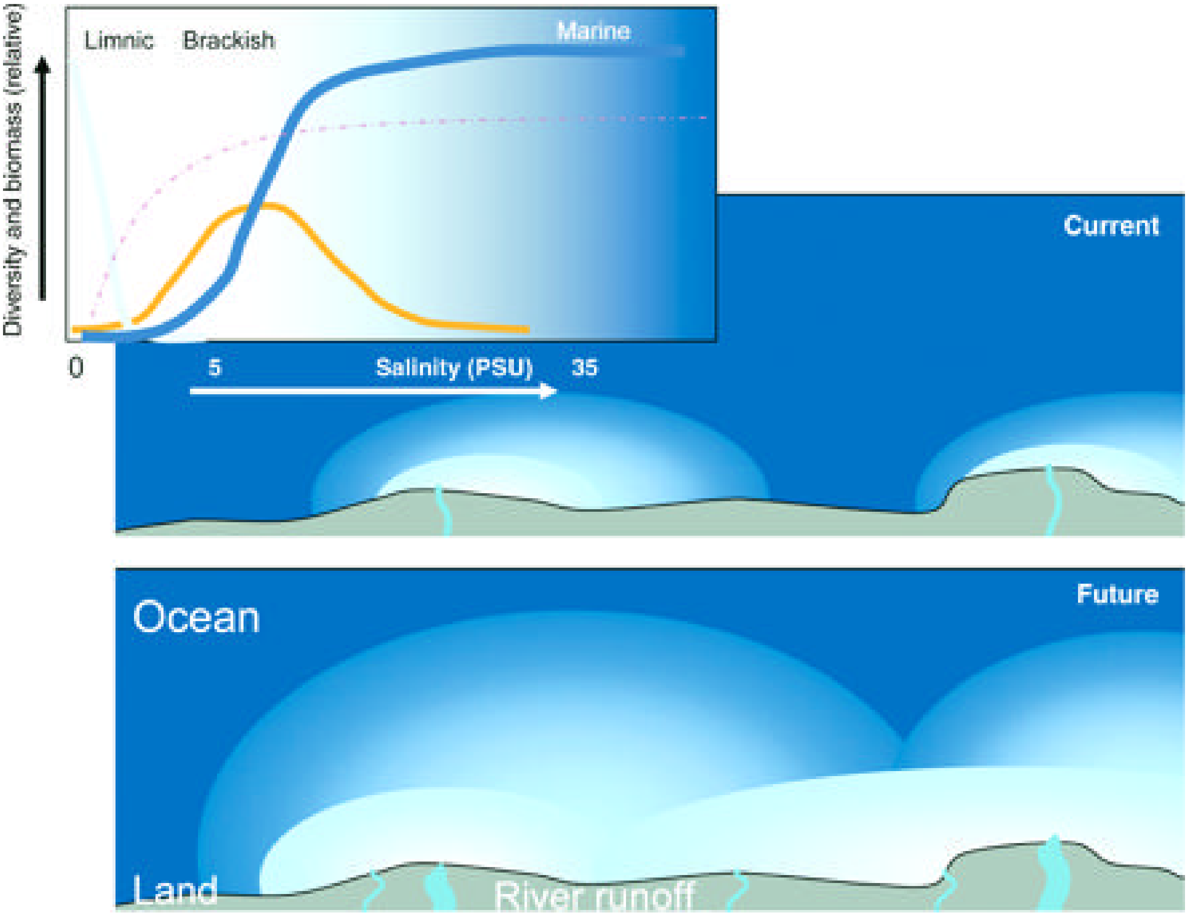

Fig. 3. Schematic representation of surface water salinity gradients in Arctic estuaries. Increased river runoff will decrease salinity over a broader area (indicated by light blue colors) in the nearshore Arctic Seas. This might lead to decreased diversity and biomass of the pelagic and benthic prey taxa of Arctic marine mammals. The relationship between water salinity and species diversity for freshwater (light blue line), brackish-water (orange line), and marine species (dark blue line), and biomass (pink line) is based on Remane (1953). For details see *Potential future scenarios…: Increased river run-off…*.

conflicting (Parsons et al. 1988, Deubel et al. 2003, Udalov et al. 2005).

In the pelagic realm, freshwater taxa currently dominate in the river mouths of the large Siberian rivers, and highest biomass was associated with the marine realm, where large copepods (*Calanus glacialis*) dominated the zooplankton (Deubel et al. 2003). In the near-mouth zone of an estuary in the White Sea, the concentration of suspended matter was higher than in the intermediate and marine zones, and the highest phytoplankton concentrations were observed in the marine zone, whereas the lowest occurred in the near-mouth zone (Dolotov et al. 2002). Similarly, minimum algal biomass (0.3 µg chlorophyll *a*/L) occurred close to the mouth of the estuary of Chesterfield Inlet in the Canadian Arctic, and maximum biomass (1.9 µg chlorophyll *a*/L) was observed near the estuary head (Roff et al. 1979). In the MacKenzie River estuary, the planktonic community near the river mouth experienced high dissolved organic carbon pools, high bacterial activity, and high amphipod biomass, while the more productive offshore community consisted of copepods, medusae, and ctenophores (Parsons et al. 1988).

Benthic infaunal species richness, biomass, and Shannon-Wiener diversity increased with salinity in the Kara Sea (e.g., Deubel et al. 2003). Arctic estuaries are dominated by few benthic species, as is typical for areas with large fluctuations in environmental conditions, such as the euryhaline polychaetes *Prionospio cirrifera* and *Marenzelleria arctica*, the cumacean *Diastylis* cf. *glabra*, and the bivalve *Portlandia* cf. *arctica* (Denisenko et al. 1999, Jørgensen et al. 1999). The biomass of micro- and macrozoobenthos also decreased with salinity in a White Sea estuary, whereas that of the meiozoobenthos increased in association with dramatic community composition changes: At salinity values <10 PSU, the proportion of nematodes dropped from 86% to 50% by abundance, while ostracods increased to up to 45% of the total abundance of meiobenthos (Udalov et al. 2005). Nematode and harpacticoid densities and biomass dropped dramatically below salinities of 3 PSU. These studies suggest that diversity and biomass in Arctic

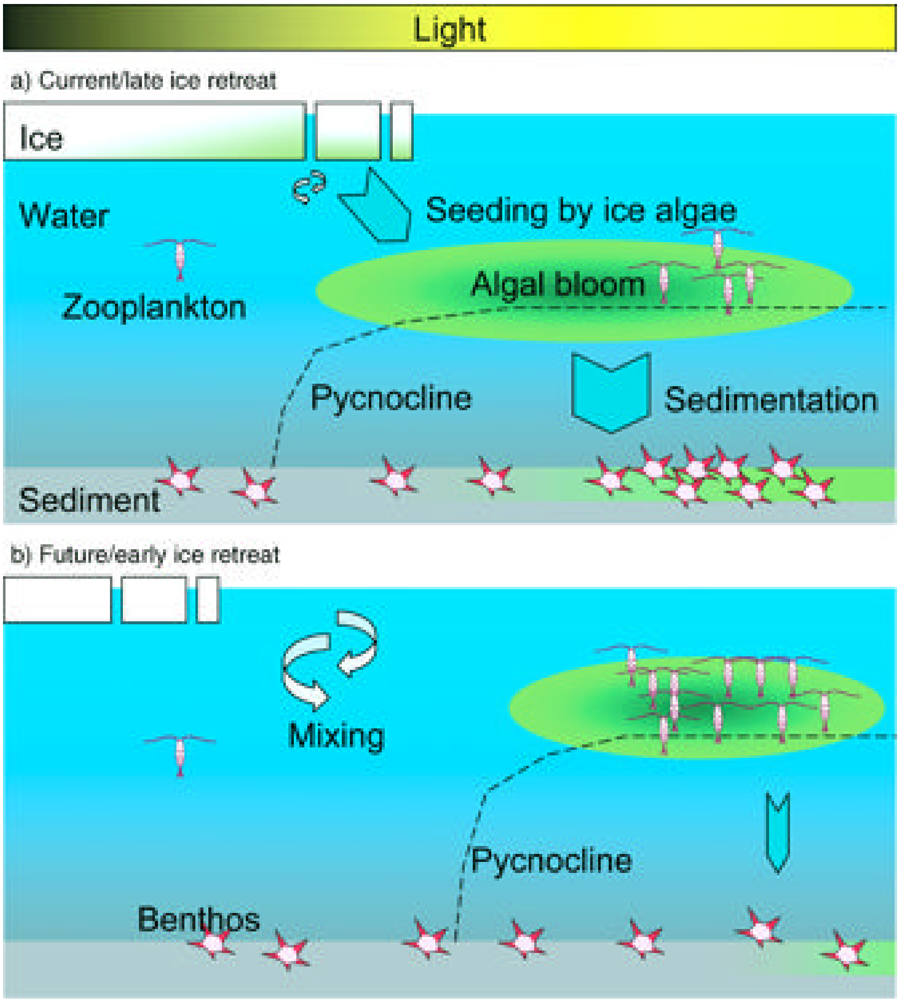

FIG. 4. Schematic representation of seasonal cycle of marine production in current/late ice retreat (a) and future/early ice retreat conditions (b). Early ice retreat allows for stronger wind mixing and causes later formation of the seasonal pycnocline. The delayed phytoplankton bloom is consumed by zooplankton, while, under current conditions on several Arctic shelves, it largely sinks directly to the sea floor, sustaining high benthic biomass.

estuaries often, but not always, covary along a salinity gradient with increasing biomass from the freshwater to the marine conditions and a diversity minimum at salinities of ~5 PSU (Fig. 3).

Applying the described relationships to the future situation for AMM, increased river runoff may be more likely to cause reduced rather than constant or increased benthic biomass and diversity, which would put benthic-feeding AMM at a disadvantage in the nearshore freshwater to brackish-water areas. Some studies suggest that reduced biomass may also be the trend in a fresher future pelagic realm. The total biological changes associated with the salinity gradient might cause AMM to prefer areas further offshore than they currently occupy, which could be harmful for the subsistence hunting activities of coastal Arctic communities.

Changes in cryo-pelagic–benthic coupling.—The extent of cryo-pelagic–benthic coupling varies in the Arctic, from regimes in which most of the primary production is consumed by pelagic zooplankton to regions with substantial flux to the seafloor and resulting high benthic biomass and production (Fig. 1; Piepenburg 2005, Grebmeier et al. 2006*a*). Two conceptual primary production scenarios have been suggested that relate to ice cover and may, therefore, have predictive value. In years of abundant sea ice (and, thereby, cold surface waters), herbivorous zooplankton is less abundant early in the season and has little grazing impact on the ice algal and marginal ice zone blooms (e.g., Carroll and Carroll 2003). As a result, primary production occurring in these well-stratified conditions is largely exported to the benthic community and can support a biomass-rich benthic community and benthic-dominated food web including bottom-feeding mammals and birds (Grebmeier et al. 2006*a*). In years or areas with less ice, in contrast, an open water and later-occurring phytoplankton bloom dominates over sea ice-related blooms. With zooplankton further along in their life cycles at this time and water temperatures slightly warmer, these phytoplankton blooms may be efficiently grazed by abundant zooplankton (Carroll and Carroll 2003; Fig. 4), which in turn are capable of supporting pelagic larval and juvenile fishes. The increased pelagic carbon utilization and recycling would result in a reduced flux of more refractory carbon to the seafloor.

These two contrasting scenarios imply that the ongoing trend of declining sea ice, earlier ice melt, and increased water temperatures in the Arctic (ACIA 2004) would make the pelagic food web-dominated scenario both more common and occur over a geographically larger area. The increased consumption of pelagic primary production by pelagic herbivores enhancing planktivorous fish abundance would increase the prey concentrations for pelagic-feeding AMM such as bowhead whales. Reduced carbon input to the benthic environment could have the reverse effect for benthic-feeding AMM such as walrus. Arctic marine mammal species currently flexible in their feeding mode and capable of utilizing both pelagic and benthic prey, e.g., bearded seals, may be less affected by the proposed alterations of the food web structure. In the extreme case of all benthic-feeding AMM species switching to pelagic feeding, if so capable, resource competition might be intensified.

Closing Remarks

Two if not all three of the suggested scenarios, although somewhat hypothetical at this point, propose higher pelagic rather than benthic prey availability to AMM in the future. Should these assumptions hold true, some AMM populations would need to adjust their feeding habits and/or location and timing of migrations for populations to maintain their current population levels. Several AMM (Table 1) are apparently capable of feeding in the pelagic and benthic realms within the same or in different geographic areas, e.g., bearded seals and gray whales. Other species, such as the walrus, may be less capable of changing to a different feeding mode and/or location and may hence be more vulnerable to changing conditions (Laidre et al. 2008). Besides changing food availability, the capability of shifting prey items and realms will ultimately depend on the trophic plasticity of AMM species with respect to their functional morphology, enzymatic and diving physiology, and foraging behavioral spectrum.

Our compilation shows that, for certain areas and species, sufficient information is now available on major prey selection patterns to produce pan-Arctic resource selection functions and preferred habitat models for AMM. Such approaches are underway for cetaceans on a worldwide scale and for selected vertebrate species on regional scales. These modeling efforts should be linked to historic data sets as currently compiled for cetaceans by the History of Marine Animal Population project and others in order to address effects of environmental change and human impact on a stronger data basis.

It should be noted that the various effects of environmental changes will occur simultaneously, which may provoke unpredicted and unprecedented developments. As pointed out previously, other changes that are not directly related to Arctic warming also influence AMM, but are not included in this paper. In our view, only holistic ecosystem monitoring approaches, combining ocean-observing systems and AMM and prey distribution and biomass surveys with modeling efforts, will provide the tools to detect, predict, and evaluate changes in the next decades.

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APPENDIX

A bibliographic list of additional sources (*Ecological Archives* A018-016-A1).

SC/A17/GW/06

Gray whale abundance estimates from shore-based counts off California in 2014/15 and 2015/2016.

John W. Durban, David W. Weller, Wayne L. Perryman

INTERNATIONAL
WHALING COMMISSION

Gray whale abundance estimates from shore-based counts off California in 2014/15 and 2015/2016.

JOHN W. DURBAN, DAVID W. WELLER, WAYNE L. PERRYMAN

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METHODS AND COUNT DATA

This paper presents updated counts and abundance estimates for gray whales (*Eschrichtius robustus*) migrating southbound off the central California coast between December and February 2014/15 and 2015/16. Counting and analytical methods followed those described by Durban *et al*. (2015) for four previous abundance estimates between 2006/7 and 2011/12. Counts were made from a shore-based watch station at Granite Canyon, California, by teams of observer pairs rotating from a larger pool. A total of 16 observers were used over the two years, 10 in 2014/15 and 12 in 2015/16; six observers counted in both years. Only five of these 16 observers were not involved in the previous independent counting experiments when the detection models were parameterized; in these cases, observer effects were predicted (with uncertainty) from the hierarchical model for observer effects (Durban *et al*. 2015).

Data were the total counts of whales from each 1.5-hour watch period that had acceptable weather conditions (see Durban *et al*. 2015). These comprised 179 watch periods in 2014/15 and 151 in 2015/16, totaling 269 and 226 hours of watch effort over 39 and 37 days, respectively (Table 1). The result was 2978 and 2666 whales counted in each of these years, the former representing the highest count since our new watch protocol was started in 2006/2007 (Durban et al. 2015).

Table 1: The number of whales recorded during the southbound gray whale surveys in 2014/15 and 2015/16. Data are the total counts of whales, hours and distinct days for watches during acceptable observation conditions.

Migration	Dates	Hours	Days	Whales
2014/2015	30-Dec-14 to 13-Feb-15	269	39	2978
2015/2016	30-Dec-15 to 12-Feb-16	227	37	2666

ABUNDANCE ESTIMATES AND DISCUSSION

Bayesian Markov Chain Monte Carlo (MCMC) sampling was used to simultaneously rescale counts for detectability and also smooth to abundance changes over the course of each migration (Durban *et al*. 2015). These abundance changes were described using Bayesian model selection between a parametric model for a Normally distributed migration trend that borrowed strength across years and a semi-parametric model that estimated the time trends independently for each year; the resultant migration curve was a weighted compromise between models, allowing for key departures from the common trend. The total number of whales passing during each migration was then estimated by summing the expected value (along with associated uncertainty, see error bars in Fig 1) from the model-averaged number of whales passing each day from time 0 (01 December) to 90 days, and these estimates were then rescaled to account for the differential passage rate at night (see Durban et al. 2015).

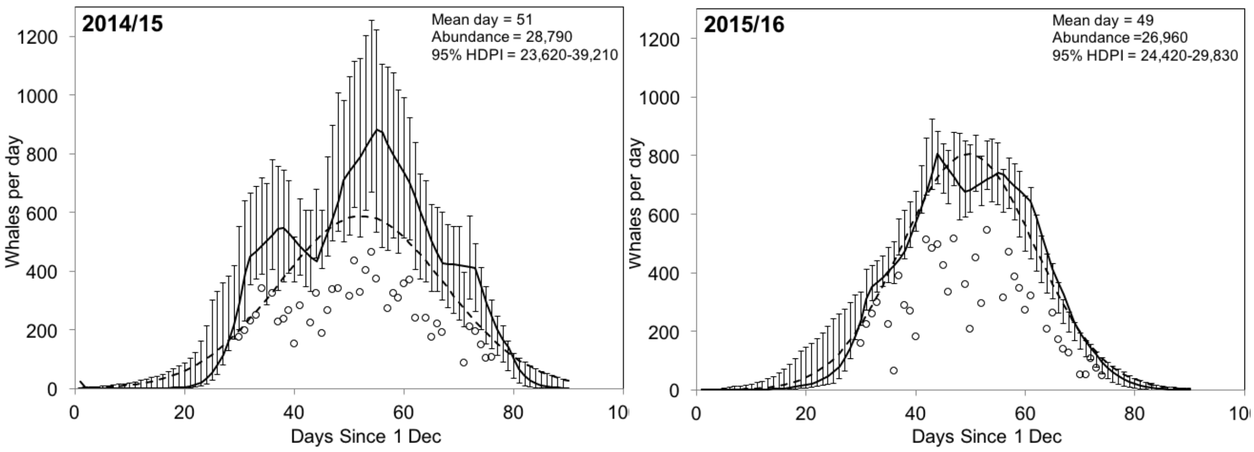

Figure 1. Observed whale passage rates expressed as total counts per day / proportion of day observed (circles) and fitted migrations models (lines) for two gray whale migration counts in 2014/15 and 2015/16. The broken line represents the median estimates from a hierarchical Normal model for migration and the solid line represents a semi-parametric model of penalized splines (see Durban et al. 2015). The abundance estimate for each day (95% highest posterior density interval shown by vertical lines) is a model averaged compromise between the migration models, and these were summed to estimate the overall abundance for the migrations.

To sample the full extent of the uncertainty associated with model parameters, inference was based on each 10th iteration of the MCMC sampler to generate a sample of 30,000 iterations following a burn-in of 10,000. There was consistency between the model predictions and observed counts for both years, with Bayesian P-values of 0.49 and 0.54, respectively; values close to 0.5 would indicate that the data were consistent with replications under the model such that the distribution of the predicted count would symmetrically overlap the observed count (Gelman *et al*. 1996). However, daily and total abundance in 2014/15 were subject to considerable uncertainty, as shown by the large error bars associated with each of the daily estimates (Figure 1) and the large coefficient of variation (CV = posterior standard deviation / posterior median; $CV^{2015} = 0.13$). This is likely explained in part by the results of model fitting, as significant departures from the Normal migration model (probability of Normal model <0.25) were estimated in 18/90 days in 2014/2015 compared to only 9/90 days in 2015/16. These departures, and the uncertainty associated with estimating an independent migration curve, constrained estimation of a precise migration curve. In contrast the $CV^{2016} = 0.05$ was consistent with previous estimates using this counting approach and model (CV = 0.04-0.06 for four previous estimates since 2006/2007), and this estimate was therefore more useful for interpreting in the context of the abundance time series. Differences in the CVs from the two years demonstrated the value of completing two counts and abundance estimates in back-to-back years, which provided a measure of redundancy.

The 2015/16 estimate of 26,960 (95% highest posterior density interval = 24,420-29,830) represented a 22% (5970 whales) increase in the five years since the 2010/11 estimate of 20,990. This is consistent with high estimates of calf production (Perryman *et al*. SC/67a), with a total of >6000 calves estimated during this period, including four of the highest years of calf production (>1000 calves per year) since our calf counts began in 1994. This increase in gray whale abundance also supports inference that gray whales have been experiencing a period of favorable feeding conditions in the Arctic due to a combination of expanding ice-free habitat (Moore 2016), increased primary production (Arrigo and Dijken 2015) and increased flow of nutrient-rich waters through the Bering Strait (Woodgate et al. 2012).

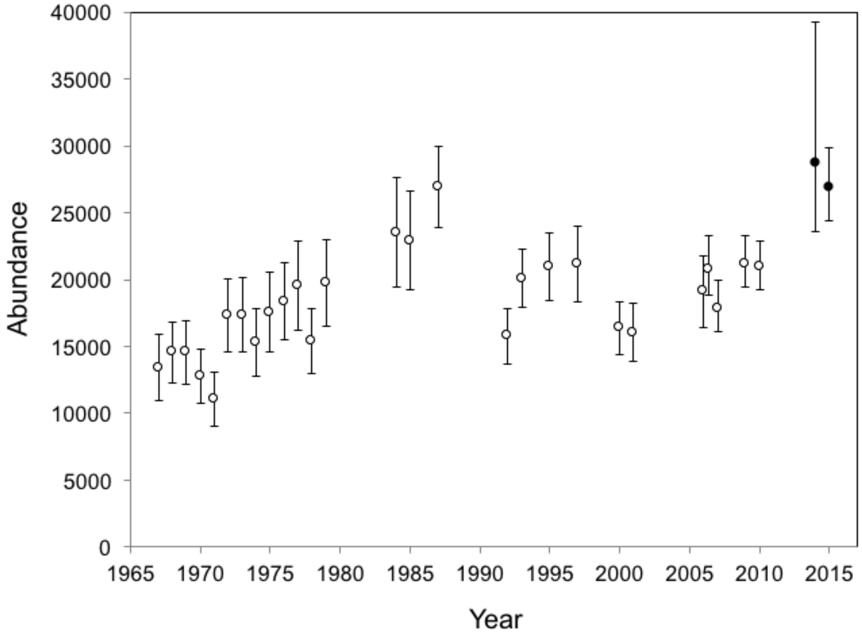

Figure 2: Gray whale abundance estimates for southbound migrations with an end year between 1967 and 2011 (open circles, with 95% confidence intervals; from Laake *et al.,* 2012 and Durban et al. 2015) together with the two recent migrations reported here for 2015 and 2016.

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Report of the Scientific Committee

Bled, Slovenia, 24 April-6 May 2018

**This report is presented as it was at SC/67b.
There may be further editorial changes (e.g. updated references, tables, figures)
made before publication.**

**International Whaling Commission
Bled, Slovenia, 2018**

Report of the Scientific Committee
Bled, Slovenia, 24 April - 6 May 2018

The meeting (SC/67b) was held at the Rikli Balance Hotel, Bled, Slovenia, from 24 April-06 May 2018 and was chaired by Caterina Fortuna. The next meeting of the Commission (IWC/67) will take place 4-14 September 2018. The list of participants is given as Annex A (about one-third of the Contracting Governments were represented by delegates).

1. INTRODUCTORY ITEMS

1.1 Chair's welcome and opening remarks

Fortuna welcomed the participants to the meeting. Although the meeting was not officially hosted by the Slovenian Government, she thanked it for welcoming them back and noted how pleased the Scientific Committee was to be once again in such a beautiful place. She thanked the IWC Secretariat staff for their hard work during the intersessional period, particularly Mark Tandy for organising the meeting under time pressure Stella Duff and Andrea Cooke for their assistance with meeting documents and Greg Donovan for all his support intersessionally. She thanked Sava Hotels for providing the meeting facilities and her Slovenian colleagues for helping meeting arrangements run smoothly. Fortuna also thanked the vice-Chair Robert Suydam, the Convenors (including those of intersessional groups) and Committee members for all their hard work since the last meeting.

Rebecca Lent, the new IWC Executive Secretary, welcomed participants to the meeting She noted this was her first IWC meeting, but already knew of its excellent global reputation and looked forward to attending many sessions. She noted her pleasure at joining the IWC at such an exciting time, with a busy year of meetings and several new initiatives. Two new coordinators have joined the Secretariat as part of the IWC work programmes endorsed by the Commission in 2016: Marguerite Tarzia as bycatch coordinator; and Karen Stockin as strandings coordinator. They will lead the Commission's work in these areas and will provide valuable input into the Scientific Committee's work.

Lent noted that the external "The IWC review – final report" (https://archive.iwc.int/?r=6890) undertaken as part of the IWC's Governance Review has recently become available and she noted that the Commission would welcome comments on it from the Scientific Committee, and that in particular, the Commission's Operational Effectiveness Working Group will take into consideration the comments from the Scientific Committee in making its recommendations to the Finance and Administration Committee; that Committee will then make recommendations to the Commission, which will determine the next steps in the governance review. Budget Management has become more challenging in recent years and there is much work to do to make sure the workplan of the Commission and all its subsidiary bodies is affordable going forward and into the long term. Finally, she thanked Scientific Committee members for their scientific input over the next two weeks and wished everyone a successful meeting.

The Committee was saddened to learn of the death of four scientists connected with the Scientific Committee:

(1) Greg Kaufman, a member of the Committee since 2006 and an active member of the sub-committee on whale watching and the Whale watching Working Group of the Conservation Committee;

(2) Doug Coughran, who although he did not attend Scientific Committee meetings, was a participant in numerous IWC workshops on entanglement and stranding response and was a charter member of both the IWC's entanglement and stranding expert (advisory) groups;

(3) Dale Rice, who although he has not attended IWC meetings in recent years, first represented the USA on the Scientific Committee as far back as 1960; and

(4) John Reynolds, who although not a member of the Scientific Committee, was a mentor to many Committee members.

The Committee paused in silence and respect for these scientists who had contributed directly and indirectly to the Committee's work and to whale conservation and management. Short obituaries can be found in Annex AA.

1.2 Appointment of rapporteurs

Donovan was appointed rapporteur with assistance from various members of the Committee as appropriate. Chairs of sub-committees and Working Groups appointed rapporteurs for their individual meetings.

1.3 Meeting procedures and time schedule

The Committee agreed to the meeting procedures and time schedule outlined by the Chair.

1.4 Establishment of sub-committees and Working Groups

The following pre-meetings were held:

1. the Standing Working Group on Environmental Concerns held a pre-meeting on 'Cumulative Effects' from 22-23 April; and
2. the sub-committee on Whale Watching held a pre-meeting on the IWC's 'Five Year Strategic Plan for Whale Watching' from 22-23 April.

Several sub-committees and Working Groups were established. Their reports were either made Annexes (see below) or subsumed into this report.

Annex D – Sub-Committee on the Revised Management Procedure;

Annex E – Standing Working Group on an Aboriginal Whaling Management Procedure;

Annex F – Sub-Committee on In-Depth Assessments;

Annex G – Sub-Committee on Other Northern Hemisphere Whale Stocks

Annex H – Sub-Committee on Other Southern Hemisphere Whale Stocks;

Annex I – Working Group on Stock Definition and DNA testing;

Annex J – Sub-Committee on Non-Deliberate Human-Induced Mortality of Cetaceans;

Annex K – Sub-Committee on Environmental Concerns;

Annex L – Standing Working Group on Ecosystem Modelling;

Annex M – Sub-Committee on Small Cetaceans;

Annex N – Sub-Committee on Whale Watching;

Annex O – Sub-Committee on Conservation Management Plans;

Annex P – Revised 'Annex P';

Annex Q – Standing Working Group on Abundance Estimates, Stock Status and International Cruises;

Annex R – *Ad hoc* working Group on Sanctuaries;

Annex S – *Ad hoc* Working Group on Photo-ID;

Annex T – Ad hoc Group on Global databases and repositories

Annex U – Statements on Special Permit discussions

Annex V – IWC-SORP – Southern Ocean Research Partnership

Annex W – Updated Rules of Procedure

Annex X – Comments on the 'Governance Review'

Annex Y – Intersessional groups

Annex Z – Minority Statements on the Agenda

1.5 Computing arrangements

Donovan outlined the computing and printing facilities available for delegate use.

2. ADOPTION OF AGENDA

The adopted Agenda is given as Annex B. Statements on the Agenda are given as Annex Z.

3. REVIEW OF AVAILABLE DATA, DOCUMENTS AND REPORTS

3.1 Documents submitted

The documents available are listed in Annex C. As agreed at the 2012 Annual Meeting, primary papers were only available at the meeting in electronic format (IWC, 2013a, pp 78-79).

3.2 National Progress Reports on research

The National Progress Reports have their origin in Article VIII, Paragraph 3 of the Convention. All member nations are urged by the Commission to provide Progress Reports to the Scientific Committee following the most recent guidelines developed by the Scientific Committee and adopted by the Commission. The report is intended to provide (1) a concise summary of information available in member countries and (2) advice on where to find more detailed information if required. In addition, the IWC holds several specialist databases (including, catches, sightings, ship strikes, images – see Item 23).

As agreed at the 2013 Annual Meeting (IWC, 2014), all National Progress Reports were submitted electronically through the IWC National Progress Reports data portal. Encouragingly, 18 countries (Argentina, Australia, Brazil, Croatia, Denmark, France, Germany, Iceland, Italy, Japan, Korea, Mexico, New Zealand, Netherlands, Norway, Spain, UK and USA) submitted reports this year compared to 12 last year. Information was provided on bycatch, entanglement, ship strikes, direct and indirect takes, sampling, sightings and tracking studies.

Nearly all the recommendations identified by the Committee in 2017 (IWC, 2018c) have been implemented although further guidance is required on the appropriate level of aggregation for some records (e.g. strandings) to simplify and accelerate data entry without losing valuable resolution.

Although data entry this year was hampered due to problems with the IWC server, this generic issue has already been resolved by the IWC Secretariat. Several suggestions for improvements, including the removal of default values, can be See Annex T for full details.

Attention: C, CG, S, SC

Despite the technical issues of the portal, the eighteen Progress Reports submitted to SC67b was an improvement on the twelve submitted to SC67a. Nevertheless, this represents a small proportion of IWC member nations. The Committee ***reiterates*** *that National Progress Reports are required under the Convention and they represent a useful tool and* ***recommends*** *that Contracting Governments to submit them annually through the IWC data portal (http://portal.iwc.int).*

National Progress Reports include records of reported bycatch and ship strikes. The Committee ***agrees*** *that the data collected in these reports are not intended to replace in-depth studies and they should be considered and used with great caution. However, it also* ***agrees*** *the reports have value because much of these data would not otherwise be available and the reporting process can assist in supporting national compilation of cetacean data.*

To address in part several of the issues and challenges described above the Committee ***agrees*** *to:*

(1) develop a strategy with the Scientific Committee Chair and Secretariat to raise awareness of National Progress Reports and promote reporting by member nations;
(2) produce a short summary explaining the utility of National Progress Reports and suggest including this text in the circular to member nations calling for data submission;
(3) request the Secretariat to issue the first call for data submission in February and repeat the call a few weeks prior to the start of the SC meeting;
(4) develop text acknowledging the likely limitations of the reported data (subsequently this text will be included in all reports and data downloads;
(5) further explore approaches (using R markdown) to produce PDF- formatted national reports.
This work will be conducted by the GDR Steering Group intersessionally (see Annex Y).

3.3 Data collection, storage and manipulation

3.3.1 Catch data and other statistical material

Table 1 lists data received by the Secretariat since the 2017 meeting.

Table 1
List of data and programs received by the IWC Secretariat since the 2017 meeting.

Date	From	IWC ref.	Details
18/05/2017	St Vincent&G: J. Cruickshank-Howard	E128 Cat2016	Information from St Vincent and the Grenadines aboriginal hunt 2016-17
3-10 7/2017	S. Kromann and Y. Ivashchenko	E127 C	Individual catch data for Taiyo Gyogyo, Japan in 1943-44. Copy of data held at NMML Seattle
16/08/2017	Y. Ivashchenko	E127	Extra details of N. Pacific sei whale catches by the USSR 1963-71
16/02/2018	Japan: K. Matsuoka	CD103	2017 POWER sightings cruise data (except photographs)
16/02/2018	Japan: K. Matsuoka	CD104	2017 ICR North Pacific dedicated sighting survey data.
04/04/2018	Canada: S. Reinhart	E130 Cat2017	Details of the Canadian bowhead harvest for the 2015-7 seasons and some information on the 2018 quota
11/04/2018	Japan: K. Matsuoka	E131	Data from the 2017-18 NEWREP-A dedicated sighting survey
18/04/2018	Iceland: G. Vikingsson	E130 Cat2017	Individual records of minke whales caught by Iceland 2017 [there was no fin whale catch]
18/04/2018	Norway: N. Øien	E130 Cat2017	Individual minke records from the Norwegian 2017 commercial catch. Access restricted (specified 14-11-00).
19/04/2018	USA: R. Suydam	E130 Cat2017	Individual records from USA Alaska aboriginal bowhead hunt 2017
20/04/2018	Japan: H.Morita	E130 Cat2017	Individual data for Japan's catch in 2017 in the N. Pacific (JARPN II) & 2017/8 in the Antarctic. (pdf format)

3.3.2 Progress of data coding projects and computing tasks

On behalf of Allison, Donovan reported that the 2017 catches and Japan coastal records in 1943-44 (data from NMML Seattle) have been added to the database. The changes agreed at the 2017 meeting, in particular to split out the catches taken *en route* to and from the Antarctic whaling grounds, have been implemented. Work on computing tasks with respect to work on the AWMP, RMP and in-depth assessments is reported under the relevant agenda items.

4. COOPERATION WITH OTHER ORGANISATIONS

Attention: C-A

The Committee ***stresses*** *the value of cooperation with other organisations when addressing the range of issues affecting cetacean conservation and management. In addition to the summaries below, co-operation is also discussed where relevant elsewhere in the agenda.*

4.1 African States Bordering the Atlantic Ocean (ATLAFCO)

There was no meeting of the Ministerial Conference of ATLAFCO during the intersessional period.

4.2 Arctic Council

4.2.1 PAME (Protection of the Arctic Marine Environment)

The PAME II-2017 meeting was held in Helsinki, Finland from 18-20 September 2017. No IWC observer attended the meeting. The Committee agrees that if possible an IWC observer should attend the next meeting of PAME.

4.3 Convention on Biological Diversity (CBD)

There was no meeting of the Conference of Parties during the intersessional period. The next meeting will take place 10-22 November 2018. The Committee agrees that if possible an IWC observer should attend the next meeting of CBD.

4.4 Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR)

The 36th Meeting of the CCAMLR Scientific Committee was held 16 - 20 Oct 2017 October 2016 in Hobart, Australia. Although no IWC observer attended the meeting, co-operation with CCAMLR remains an important component of the IWC's work and is discussed further under Item 16.1.

4.5 Convention on the Conservation of Migratory Species (CMS)

4.5.1 Scientific Council

The Second Meeting of the Sessional Committee of the Scientific Council was held 10- 13 July 2017 in Bonn, Germany. No IWC observer attended the meeting.

4.5.2 Conference of Parties

The Conference of Parties met 23-28 October 2017 in Manila, Philippines. No IWC observer attended the meeting.

4.5.3 Agreement on Small Cetaceans of the Baltic and North Seas (ASCOBANS)

The report of the observer to ASCOBANS is given as SC/67b/COMM01E. The following key activities have occurred since the last IWC Scientific Committee meeting:

(1) first Joint Meeting of the 13th Meeting of the Jastarnia Group (Baltic Sea harbour porpoises) and the 6th Meeting of the North Sea Group;
(2) best-practice workshop on 'Fostering Inter-regional Cooperation on Underwater Noise Monitoring and Impact Assessments in waters around Europe, within the context of the European Marine Strategy Framework Directive';
(3) 23rd Meeting of the Advisory Committee; and
(4) 14th Meeting of the Jastarnia Group.

The key ongoing ASCOBANS activities are:

(1) work on the three harbour porpoise Action Plans (Baltic, Belt and North Seas)- in place since February 2018;
(2) web-accessed database on marine mammal stranding and necropsy in preparation (ZSL/IOZ leading), 2018-2020;
(3) preparation of an action plan for common dolphins; and
(4) implementing a change in the national reporting cycle from annual (on all topics) to a four-year cycle (selected topics each year) - the intention is that all the key ASCOBANS working groups and meetings align their agendas to home in on these issues in the respective years of reporting (e.g. covering 2017 in 2018).

The Action Points at the last Advisory Committee meeting included:

(1) preparing a discussion on prey depletion and changes in prey quality on the agenda of the 24th Meeting of the Advisory Committee;
(2) co-organisation of a workshop with ACCOBAMS on strandings and marine debris (the report has been made to the Scientific Committee);
(3) future focuses will include the white-beaked dolphin and the white-sided dolphin.
(4) a draft Action Plan for the Common Dolphin is due to be presented at the 24th Advisory Committee Meeting.

The Committee thanked Simmonds for his report and **agrees** that he should represent the Committee as an observer at the next ASCOBANS meeting.

4.5.4 Agreement on the Conservation of Cetaceans of the Black Sea, Mediterranean Sea and Contiguous Atlantic Area (ACCOBAMS)

MEETING OF PARTIES

There was no Meeting of the Parties (MoP) to ACCOBAMS during the intersessional period. Donovan will represent the Committee as an observer at the next ACCOBAMS MoP.

SCIENTIFIC COMMITTEE

There was no meeting of the ACCOBAMS Scientific Committee during the intersessional period. Donovan will represent the Committee at the next ACCOBAMS Scientific Committee meeting.

4.6 Convention on International Trade in Endangered Species of Wild Flora and Fauna (CITES)

No relevant meetings of CITES have taken place during the intersessional period.

4.7 Food and Agriculture Organisation of the United Nations (FAO)

There was no meeting of The Committee on Fisheries (COFI) during the intersessional period. The next meeting will take place in Rome, Italy 9-13 July 2018.

4.8 Inter-American Tropical Tuna Commission (IATTC)

The 92nd meeting of the Inter-American Tropical Tuna Commission (IATTC) was held in Mexico City, Mexico 24-28 July 2017. No observer attended IATTC meetings in the intersessional period.

4.8.1 Agreement on the International Dolphin Conservation Program (AIDCP)

No observer attended IADCP meetings in the intersessional period.

4.9 International Committee on Marine Mammal Protected Areas (ICMMPA)

There was no meeting of ICMMPA task force during the intersessional period. The 5th International Conference will be held from 8- 12 April 2019 in Greece. It will evaluate progress in meeting the ICMMPA's long-standing goal of bringing the MMPA community closer together. A primary goal is to focus on the challenges ahead towards achieving effective place-based protection and management for marine mammals. It will build on previous initiatives to advance our understanding of science, management, and effective biodiversity conservation in protected areas. It will also provide updates on plans for the worldwide Important Marine Mammal Area (IMMA) initiative (*marinemammalhabitat.org*). Rojas-Bracho will represent the Committee at this meeting.

4.10 International Council for the Exploration of the Sea (ICES)

The report of the IWC observer documenting the 2017 activities of ICES is given as SC/67b/COMM01A. The ICES Working Group on Marine Mammal Ecology (WGMME) reported on recent information on status of, and threats to, marine mammal populations and briefly reviewed current knowledge of effects of plastics and underwater noise. Criteria for assessment of abundance trends in offshore cetaceans in the context of the Marine Strategy Framework Directive (MSFD) were reviewed, modifying the proposed indicator (previously based solely on the rate of decline) to make specific reference to baseline values. The group also considered the outcomes of the 2016 SCANS III survey[1]. All three SCANS surveys have arisen from individual projects. WGMME recommended that the surveys be co-organised and coordinated by Member States as part of their routine monitoring and that the frequency is increased to once every six years to match the MSFD reporting cycle.

A Workshop on Predator-prey Interactions between Grey Seals and other marine mammals (WKPIGS) focused on predatory behaviour of grey seals towards other grey seals, harbour seals and harbour porpoises in European waters. The workshop aimed to consolidate pathological indicators of grey seal predation events, collate data on the prevalence and distribution and discuss methods to aid in detection of predation events and potential population level consequences of reported incidences. Cases of predation on harbour porpoises peaked in spring months. Reported incidence has increased over the last decade although it is not known if this represents a true increase in prevalence, an increase in seal numbers or an increase in effort/reporting.

Highlights from the 2017 ICES Working Group on Bycatch of Protected Species (WGBYC) included: review of ongoing bycatch mitigation research projects; presentations on interdisciplinary bycatch monitoring programs in the US Northwest Atlantic northeast region; collaborations with other ICES working groups; positive advancements on WGBYC database development working jointly with the ICES Data Centre; and progress on summarising bycatch for the Baltic Sea and Bay of Biscay/Iberia fisheries overviews.

Four cetacean species were reported as bycatch from the 2015 member state reports (common dolphins, white-beaked dolphin, bottlenose dolphin, and harbour porpoise). The WGBYC continues to highlight the inconsistent submission and content of annual reports provided by some member states and the shortcomings to accurately reflect the full magnitude of cetacean bycatch in European fisheries. WGBYC is preparing for the transition away from regular member state reports as the primary source of data on bycatch of cetaceans over to data coming through the ICES regional database.

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[1] https://synergy.st-andrews.ac.uk/scans3/

The 2017 ICES Annual Science Conference (ASC) had no sessions devoted entirely to marine mammals. Nevertheless, some sessions had marine mammals included as an integral part - the most relevant sessions were: ‘microbes to mammals: metabarcoding of the marine pelagic assemblage’ and ‘from iconic to overlooked species: how (electronic) tags improve our understanding of marine ecosystems and their inhabitants’.

More information is available from the ICES website *www.ices.dk.*

The Committee thanked Haug for his report and **agrees** that he should represent the Committee as an observer at the next ICES meeting.

4.11 International Maritime Organisation (IMO)

The report of the observer is given as SC/67b/COMM01D. At IWC66, the Commission endorsed recommendations of the IWC Conservation and Scientific Committees for continued engagement with the IMO, including submission of a paper to the IMO Marine Environment Protection Committee (MEPC) providing an update of recent information related to the extent and impacts of underwater noise from shipping. This paper was written by an intersessional group appointed at SC67a and submitted to the IMO MEPC 72 meeting 9-13 April 2018 (MEPC 72/Inf.9).

The ship strike section of the IWC website now contains a list of the measures that have been put in place globally through IMO or national regulations, to reduce ship strike risks to whales. These include Traffic Separation Schemes, Areas to be Avoided, Recommended Routes, voluntary and mandatory speed restrictions. New measures relevant to ship strikes include three recommendatory areas to be avoided (ATBA) encompassing King Island, Nunivak Island, and St. Lawrence Island in the Bering Sea proposed by the United States (NCSR 5/3/8). The proposal noted that King Island is a biologically important site to the gray whale, while St. Lawrence Island’s ATBA would provide protection to bowhead whales, gray whales, and humpback whales. These areas were recommended for adoption (with a reduced size for the St. Lawrence ATBA) by the IMO Navigation, Communications and Search and Rescue sub-committee NCSR 5 in February 2018.

Members of the IWC Scientific Committee have attended IMO meetings in order to discuss how best to provide information on populations of marine mammals relevant to the marine mammal avoidance provisions of the IMO Polar Code. This is discussed further under Item 14.3.

The Committee thanked Ferris and Leaper for their report and **agrees** that they should represent the Committee at the next IMO meeting.

4.12 International Union for the Conservation of Nature (IUCN)

The report of the observers to IUCN is given as SC/67b/COMM01G. The IUCN Marine Mammal Protected Areas Task Force (*https://www.marinemammalhabitat.org*) held its 3rd regional workshop in Malaysia in March 2018 to identify, describe and map candidate areas for inclusion in the Important Marine Mammal Area (IMMA) e-Atlas (*marinemammalhabitat.org/imma-eatlas*). The 46 candidate IMMAs proposed by the workshop are currently undergoing independent review.

Cetaceans entries on the Red List are in the process of being updated. The first batch of updates covering 19 taxa was published on *redlist.org* in December 2017 and is summarised at *iucn-csg.org/index.php/page/3*. Most of the remaining mysticete species assessments and some subpopulation assessments, as well as around 10 more new assessments of small and medium-sized odontocetes, have been submitted for publication in the next Red List update in June 2018. Most of the remaining taxa are in the pipeline for publication in late 2018.

IUCN continues to convene the Western Gray Whale Advisory Panel (WGWAP), which provides advice to Sakhalin Energy Investment Company (SEIC) and other parties, especially on the mitigation of industrial and other impacts on the gray whales that feed each summer off Sakhalin Island, Russia. Details of the Panel’s recent work are given in Annex O, Appendix 3.

Regular news items on activities by members of the IUCN SSC Cetacean Specialist Group are posted on the CSG website, *www.iucn-csg.org*.

4.13 North Atlantic Marine Mammal Commission (NAMMCO)

Scientific Committee

The report of the IWC observer at the 24th meeting of the NAMMCO Scientific Committee (NAMMCO-SC) is given as SC/67b/COMM01B. The NAMMCO-SC discussed a current joint project, ‘Exploring marine mammal consumption relative to fisheries removal in the Nordic and the Barents Seas’. Preliminary results suggest that marine mammal consume around 15 million tons ± 50% of prey per year, predominantly targeting low and mid trophic level species (zooplankton and small pelagic fish). Fisheries remove around 4.3 million tons per year, targeting mid and top trophic levels (small pelagic fish and larger demersal and pelagic fish).

The NAMMCO By-Catch Working Group (BYCWG) met in May 2017. Methods used for collection of data and by-catch estimation were reviewed, and both the WG and the SC recommended methodological improvements to be implemented both in the data collection and the analysis before the bycatch estimates could be endorsed. Greenland is an atypical case because marine mammals that are caught, either directly or indirectly, are assumed to be reported as direct catch (with large whales being the exception where bycatch is reported as such). The primary concern is to ensure that any bycatch is included in the total number of removals to be used in population assessments.

The NAMMCO SC noted and appreciated that the IWC *Implementation Reviews* for North Atlantic fin whales and North Atlantic common minke whales are completed. The NAMMCO SC provided advice on sustainable catch levels fro these species in Icelandic waters (from 2018-2025) based upon application of the RMP. The NAMMCO SC also recommended that the *SLAs* that are developed in the IWC SC be used for advice for large whales in Greenland and provided advice on strike limits for West Greenland humpback whales for the 2019-24.

The NAMMCO SC received the results from an updated global review of monodontids and provided updated assessments and advice for white whales and narwhals in Greenland and Canada. It also received a new abundance estimate for bottlenose whales from the Faroese component of the 2007 T-NASS survey that was analysed together with data on deep diving species from the SCANS-II and CODA surveys. Sightings were mainly from the Faroese survey block.

Increased research on harbour porpoises in Norway is being driven by the concerns regarding bycatch. Bycaught harbour porpoises were collected in 2016 and 2017 by Norway for biological sampling, and a food-web model is being developed for the Vestfjord area close to Lofoten to study the role of the species in this area. An abundance estimate is now available from the SCANS-III survey which was extended from 62°N to include Vestfjorden, an area with high bycatch. Preliminary investigations using this new abundance estimate suggest that bycatch levels are within PBR.

NAMMCO's whale sighting surveys in the Northeast Atlantic in 2015 (NASS2015) included an intensive survey with the purpose of estimating the abundance of pilot whales around the Faroe Isles, an aerial survey of the coastal waters in East Greenland and a ship-based survey around Jan Mayen following methods developed for the Norwegian minke whale surveys. The next NASS survey should be in 2022-23. The NAMMCO SC strongly recommended that an attempt be made to conduct again a trans-Atlantic coordinated survey and charged the NAMMCO Secretariat to explore what are the present plans and how much flexibility they encompass.

Council
The report of the IWC observer at the 26th Annual Council meeting of NAMMCO held in Tromsø, Norway 7-8 March 2018 is given as SC/67b/COMM01C. Relevant items discussed at the Council meeting include the following:

> (1) A newly established working group on bycatch, entanglements and live strandings has started its work and will gather information on the matter from other organisations and develop recommendations for NAMMCO. The focus is animal welfare associated to non-hunting related activities, and how NAMMCO can best contribute to addressing significant adverse impacts of by-catch, entanglement and live strandings on marine mammals; and
>
> (2) The report of the Global Review of Monodontids (white whales and narwhals) reviewed the conservation status, threats, and data gaps for all stocks globally. The last review was in 1999.

The Committee thanked Moronuki for his report.

4.14 North Pacific Marine Science Organisation (PICES)

The report of the IWC observer at 2017 annual meeting of PICES is given as SC/67b/COMM01F.

The marine birds and mammals section (S-MBM) focussed on 'seasonal and climatic influences on prey consumption by marine birds, mammals and predatory fishes' Presentations were made on (1) significance of seasonal changes in prey consumption on energy budgets and ecosystem dynamics; (2) effects of changes in water temperature and other climatic variables on food requirements; (3) relationships between dietary shifts and population trends; (4) limits of plasticity in prey selection; and (5) how prey consumption of birds, mammals and predatory fishes is affected by the recent extreme climatic events. Overall, the collection of presented studies in this session contributed to the efforts of the S-MBM to estimate prey consumption of birds and mammals. They provided new methods to estimate prey consumption of marine mammals and gave insights into the existing databases of diets and population estimates that can be used to further this effort.

For 2018, the S-MBM will focus on 'diets, consumption and abundance of marine birds and mammals in the North Pacific'. Since the 2016 workshop, work on the agreed upon databases to estimate prey consumption has been initiated and will continue to be added to over the coming 12 months in anticipation of the 2018 workshop, when invited experts will review the compiled information. This process should result in near-complete databases of diets, abundances and energy requirements of marine birds and mammals in the North Pacific.

The 2018 annual meeting of the PICES will be held in Yokohama, Japan 25 October-4 November 2018. The Committee thanked Tamura for attending on its behalf and **agrees** that he should represent the Committee as an observer at the next PICES meeting.

4.15 Protocol on Specially Protected Areas and Wildlife (SPAW) of the Cartagena Convention for the Wider Caribbean

No observer attended SPAW meetings in the intersessional period.

4.16 Pacific Region Environment Programme (SPREP)
No observer attended SPREP meetings in the intersessional period.

5. GENERAL ASSESSMENT ISSUES WITH A FOCUS ON THOSE RELATED TO THE REVISED MANAGEMENT PROCEDURE (RMP)

Several assessment topics apply not only to the Revised Management Procedure (RMP), but to the work of the Scientific Committee as whole. This item focuses on general assessment issues, such as: (1) the relationship between MSYR_{mat} and MSYR_{1+}; (2) implications of RMP and AWMP simulation trials for consideration of 'status'; and (3) matters of relevance to special permits that involve RMP considerations including effects of catches upon stocks.

5.1 Evaluate the energetics-based model and the relationship between MSYR_{1+} and MSYR_{mat}
MSYR is a key parameter in the *Implementation Simulation Trials* used to evaluate the conservation and catch performance of alternative RMP variants for specific species and regions. In recent years, the Committee has been reviewing progress on an individual based energetics model (IBEM) to provide insights into the relationship between MSYR_{1+} and MSYR_{mat}. Two papers on the IBEM were reviewed by the Committee in SC/67b.

SC/67b/EM07 outlined enhancements to the IBEM since the last meeting. This included the ability to explicitly model the effects of feeding while on migration, which can have effects on the yield curve as well as MSYR and MSYL. The Committee discussed (Annex D, Item 2.1) several ways in which this model can potentially enhance understanding of the relationship between biological processes and MSYR.

SC/67/RMP01 reported on trials using the IBEM within the standard RMP testing framework. The results were consistent with the behaviour of the RMP *CLA* observed in less complex population models and will also provide a point of comparison for the emulator model for the IBEM currently under development. The Committee has previously agreed that a fully-developed emulator model could form the basis for future *Implementation Simulation Trials*.

Attention: SC

The Committee ***agrees*** *that work continue to develop an emulator model; assess whether it is possible to represent the trajectories from the IBEM using an emulator model; compare the yield curves from the IBEM with those from the emulator model; and develop guidelines for how to use an emulator model as the basis for a multi-stock, multi-area population dynamics model and how such a model could be conditioned given available data.*

5.2 Implications of ISTs for consideration of species' and populations' status
Last year, the Committee recommended that a set of *Implementation Simulation Trials* should be summarised using three statistics to provide information on status (IWC, 2018d). The Committee was advised that intersessional tasks toward that goal could not be completed prior to SC/67b due to computing workloads.

Attention: SC

The Committee ***agrees*** *that Allison should modify the control programs used for* Implementation Simulation Trials *to report the three measures of status agreed last year (IWC, 2018d). The RMP sub-committee, in conjunction with the Working Group on ASI, will review outcomes of the analyses at SC/68a. Punt and Donovan will develop draft updates to the Guidelines for* Implementations *and* Implementation Reviews *to reflect decisions on evaluation status of stocks for consideration at SC68a.*

5.3 General consideration of how to evaluate the effect of special permit catches on stocks and levels of information needed to show improved management performance
5.3.1 General issues
The Committee developed general guidelines on the levels of information needed to show improved management improvement, for proposals that identify this as an objective (Annex D; appendix 2). The guidelines are intended to assist proponents in proposal preparation and to facilitate the review process. It was stressed that these were guidelines not requirements. Proponents might request the establishment of an Advisory Group to provide comment on intersessional work, but this is not mandatory. An Advisory Group may most benefit nations which have not previously developed proposals or may be lacking analysts familiar with the modelling approaches commonly applied at the IWC.

Attention: SC

The Committee ***agrees*** *that the general guidelines on the levels of information needed to show improved management improvement, for proposals that identify this as an objective (Annex D; appendix 2), should be included as an Appendix to the Scientific Committee handbook.*

5.3.2 Specific issues
SC/67b/RMP03 provided draft specifications for RMP/IST type simulations to evaluate management procedures based on modified *CLA*s that use information on recruitment inferred from age data from Antarctic minke whales. This work originally arose from discussions of NEWREP-A and Recommendation 1 of the Panel Review of that proposal (and see Item 19). The Committee noted that SC/67b/RMP03 was a work-in-progress, and that several features of the operating models would need to be extended before final conclusions could be drawn. The author of SC/67b/RMP03 plans to continue this work and received several suggestions from the Committee to carry those efforts forward (Annex D, Item 2.3).

5.4 Work plan 2019-20
Details of work to be undertaken both before and during the 2019 Annual Meeting are given in Table 2.

Table 2

Work plan for general assessment matters with a focus on the RMP

Topic	Intersessional 2018/19	2019 Annual Meeting (SC/68a)	Intersessional 2019/20	2020 Annual meeting
Item 5.1: Conduct work to evaluate the energetics-based model and hence the relationship between MSYR1+ and MSYRmat	(a) Continue to assess whether it is possible to represent the trajectories from the IBEM using the emulator model (Annex Y); (b) Compare the yield curves from the IBEM with those from the emulator model (Annex Y); and (c) Develop guidelines for how to use an emulator model as the basis for a multi-stock, multi-area population dynamics model and how such a model could be conditioned given available data (Annex Y).	Continue to work to evaluate the energetics-based model and hence the relationship between MSYR_{1+} and MSYR_{mat}	Conduct follow-up analyses	Continue to work to evaluate the energetics-based model and hence the relationship between MSYR1+ and MSYRmat
Item 5.2: Implications of ISTs, for consideration of status	(a) Modify the control programs used for *Implementation Simulation Trials* to report the three measures of status (Allison) (b) Draft updates to the Guidelines for *Implementations* and *Implementation Reviews* to reflect decisions on evaluation status of stocks (Punt and Donovan)	Review the results of the projections Review the draft guidelines		
Item 5.3: levels of information needed to show improved management performance		Review progress implementing the suggested changes to the specifications of the model in SC/67b/RMP03 and any results.		

6. RMP – *IMPLEMENTATION*-RELATED MATTERS (RMP)
This agenda item includes the details of ongoing *Implementation Reviews* and preparation for new *Implementation Reviews*. For discussions related to the stock structure and abundance of these stocks, see also Items 11 and 12.

6.1 Completion of the *Implementation Review* of western North Pacific Bryde's whales
6.1.1 Report of the intersessional Workshop
The second intersessional Workshop on western North Pacific Bryde's whales was held in Tokyo from 14-16 February 2018 (SC/67b/Rep02). The objective was to facilitate completion of the *Implementation Review*. Much of the Workshop focussed on completing the final trial specifications, especially confirming the mixing matrices, updating the abundance estimates for the new sub-areas and confirming future sighting survey plans and whaling options. The Workshop reviewed preliminary conditioning results and agreed that they were satisfactory. It developed a workplan to try to ensure completion of the *Review* at SC/67b.

The Committee noted that the intersessional workshop had led to considerable progress towards completing the *Implementation Review*. It thanked Donovan for chairing the meeting, the Government of Japan for providing excellent facilities and all the participants for their contributions to the development of trial specifications and workplan.

The code and specifications for *Implementation Simulation Trials* were updated following the intersessional Workshop.

Attention: SC

The Committee ***agrees*** *to the updated trial specifications for the* Implementation Review *of western North Pacific Bryde's whales. These specifications are provided in Annex D, Appendix 3. It also* ***agrees*** *that conditioning has been achieved satisfactorily.*

6.1.2 Conclusions and recommendations

Once the trial specifications and conditioning had been agreed, the next step was to conduct projections under alternative RMP variants and survey plans. There was insufficient time during the meeting to complete all of the required projections and to check the associated calculations. Consequently, the remaining work will be completed intersessionally and reviewed and summarised by a Steering Group (Annex Y). This will occur well before SC/68a so that Japan has sufficient time to consider the results (e.g. with regard to its preferred survey options), prior to final conclusions being drawn. The Committee expects that this work can be completed before the end of 2018, but if complications arise conducting the projections, an extra day should be added to the 'First Intersessional Workshop for the western North Pacific minke whales' (see Item 6.2) to address outstanding issues.

Attention: SC

The Committee ***agrees*** *that the* Implementation Review *of western North Pacific Bryde's whales will be completed at SC/68a. Outstanding tasks will be completed intersessionally and the results reviewed and summarised by a Steering Group (Annex Y). This will occur well prior to SC/68a, and if complications arise then an extra day should be added to the First Intersessional Workshop for the western North Pacific minke whales (see Item 6.2) to address those issues.*

6.2 Start of the *Implementation Review* of western North Pacific common minke whales

6.2.1 Report of the intersessional Workshop

Donovan summarised the report of the preparatory Workshop for the Western North Pacific common minke whale *Implementation Review* (SC/67b/Rep05). Last year, the Committee recognised that the most difficult aspect of the last *Implementation Review* had been selecting, modelling and assigning plausibility to stock structure hypotheses. The objective of this Workshop was to begin to review work undertaken since the last *Implementation Review* and to develop, if necessary and possible, consensus advice on further analyses that will assist in the forthcoming *Implementation Review*. Stock structure discussions on common minke whales are detailed in Annex I, item 4.2.

This past lack of agreement with respect to the plausibility of existing stock structure hypotheses has, in part, revolved around how genetic analyses can be used to assign whales as part of the 'J' versus 'O' stocks. While some whales assign strongly to one of the two groups based on genetic data, the assignment of others is dependent on the assignment probability deemed sufficient to assign stock affinity. At the intersessional workshop (SC/67b/Rep05), the results of new stock structure-related analyses were reviewed by an advisory panel, and two recommendations were made with regard to additional genetic analyses needed to better understand stock structure. One of the recommended analyses involved evaluating the consistency of individual assignment probabilities when additional loci were genotyped. Progress with respect to that recommendation is discussed below.

The Workshop was also provided with an update to SC/67a/SCSP/13 that used information on the trend over time in the J:O stock ratio for common minke whale bycatches around Japan to draw various inferences, in particular about the value of the MSYR. The Workshop agreed that J:O stock ratios in bycatch will require attention when formulating stock distribution assumptions for the process of conditioning *IST*s in the coming *Implementation Review* and made some recommendations on how this could be achieved.

The Committee noted that the intersessional Workshop was held in an excellent spirit of co-operation among the participants and led to identification of additional data sets and analyses that should be taken forward. The Committee thanked Donovan for chairing the meeting, the Government of Japan for providing excellent facilities and all the participants for their contributions to progress the *Implementation Review*.

6.2.2 Progress since the intersessional Workshop

SC67b/SDDNA06 presented the results of the recommended analysis from the Workshop (see Item 6.2.1) and the Committee confirmed that the workshop's recommendation for this analysis had been properly completed.

Attention: SC

The Committee reviewed new results of genetic analyses that were recommended at the intersessional workshop (SC/67b/Rep05) to better evaluate the use of genetic data to assign stock affinity in North Pacific common minke whales. The Committee:

(1) ***agrees*** *that future analyses should incorporate a range of assignment thresholds to encompass uncertainty;*
(2) ***supports*** *the additional genetic analyses described in Annex I Appendix 5 relating to the second recommendation of the intersessional workshop and agrees that they should be performed prior to the next intersessional workshop; and*
(3) ***encourages*** *the inclusion of non-genetic biological data to inform stock structure where possible.*

SC/67b/RMP/02 aimed at suggesting a plausible range for $MSYR_{1+}$ for the western North Pacific common minke whales, and the relative plausibility of two stock structure hypotheses. The Committee thanked Kitakado for the updated analysis, which implemented some of the recommendations from the intersessional Workshop. Details of this paper and associated discussion can be found in Appendix D, Item 3.2.2. The Committee also discussed the analysis of genetic data conducted since the intersessional workshop (Annex I, Item 4.5).

Attention: SC, CG-A

The Committee ***agrees*** *that:*

(a) it is necessary to update the mixing matrices in the trial specifications to be more consistent with observed genetic and bycatch data, also taking into account sensitivity to alternative methods of genetic assignment to stock;
(b) whether it is possible to use the bycatch data to assign plausibility ranks to $MSYR_{1+}$ *values and stock structure hypotheses depends on assumptions regarding trends in fishing effort spatially and temporally; and*
(c) trials would need to consider different assumptions regarding the use of J:O bycatch ratios, including that these data do not provide information on $MSYR_{1+}$ *and the plausibility of stock structure hypotheses because of possible differential distributional changes by stock.*

The Committee therefore ***agrees*** *that scientists from Japan and Korea should provide data on the amount, location and timing (seasonal and annual) of fishing effort and bycatch to the First Intersessional Workshop (see item 6.2.3).*

6.2.3 Preparation for the First Intersessional Workshop

The Committee began preparations for the First Intersessional Workshop on the *Implementation Review* of western North Pacific common minke whales. It re-established the Steering Group (Annex Y) to organise this Workshop.

In accordance with the Committee's *'Requirements and Guidelines for Implementations and Implementation Reviews'* (IWC, 2012b), the primary objectives of the First Intersessional Workshop will be to: (a) consider plausible hypotheses and eliminate any hypotheses that are inconsistent with the data); (b) examine more detailed information in expected whaling operations, including options or suggested modifications to the pattern of those operations; (c) review the small geographical areas ('sub-areas') that will be used in specifying the stock structure hypotheses and operational pattern; and (d) specify the data and methods for conditioning the trials that will be carried out before the next annual meeting. An initial annotated agenda for the Workshop, highlighting the associated data and analysis requirements can be found in Annex D, appendix 5.

6.3 Workplan 2019-20

Details of work to be undertaken both before and during the 2019 Annual Meeting are given in Table 3.

Table 3

Work plan for RMP (*Implementation*-related matters)

Topic	Intersessional 2018/19	2019 Annual Meeting (SC/68a)	Intersessional 2019/20	2020 Annual meeting
Item 6.1: Western North Pacific Bryde's whales	Finalise the projections and the application of the criteria for evaluating which RMP variants are acceptable, borderline, and unacceptable	Complete the *Implementation Review*		
Item 6.2: Western North Pacific minke whales	(a) conduct the First Intersessional Workshop; (b) code the resulting trials and condition the trials	Conduct the work required for the First Annual Meeting	Conduct the Second Intersessional Workshop	Conduct the work required for the Second Annual Meeting

7. ABORIGINAL SUBSISTENCE WHALING MANAGEMENT PROCEDURE (AWMP)

This item continues to be discussed as a result of Resolution 1994-4 of the Commission (IWC, 1995), which has been strengthened by Resolution 2014-1 (IWC, 2016a). The report of the Standing Working Group (SWG) on the development of an aboriginal whaling management procedure (AWMP) is given as Annex E. The Committee's deliberations, as reported below, are largely a summary of that Annex, and the interested reader is referred to it for a more detailed discussion. The primary issues at this year's meeting comprised: (1) finalising the development of *SLA*s (*Strike Limit Algorithms*) for Greenlandic hunts, with a focus on fin and common minke whales; (2) finalising the work on the scientific components of the AWS (Aboriginal Subsistence Whaling Management Scheme); (4) completion of the *Implementation Review* for Bering-Chukchi-Beaufort Seas stock of bowhead whales; and (3) providing management advice for aboriginal hunts (see Item 8).

Considerable progress on items (1) and (2) was made because of intense intersessional work including two workshops in Copenhagen in October 2017 and March 2018, as well as a small technical meeting in December 2018 at OSPAR headquarters in London.

7.1. *SLA* development for the Greenland hunts

7.1.1 Fin whales

SC/67b/Rep06 incorporated the discussions of the two intersessional Workshops and the small working group meeting. Considerable progress was made in relation to (a) updated abundance estimates; (b) finalisation of the trial structure; (c) review and approval of conditioning; and (d) initial consideration of new *Strike Limit Algorithms* (*SLA*s) and results.

The Committee thanked Donovan, the Workshop chair and the participants for the excellent progress made.

The final trial specifications for the West Greenland fin whales are provided in Annex E (Appendix 2).

Table 4 below summarises the main factors considered in the *Evaluation Trials*. The most influential involve different stock structure hypotheses, different productivity rates (MSYR) and different 'need' envelopes (need envelopes incorporate scenarios where need remains constant at the present level for 100 years (termed A), where it increases linearly to twice the present level over the 100-year simulation period (termed B) and where it increases linearly to three times the present level over the 100-year period (termed C).

Table 4

Summary of the key factors considered in the fin whale trials

Factor
Stock structure hypotheses
Mixing matrices
MSYR rate
Survey bias
Need envelope

7.1.1.1 CANDIDATE *SLA*S

The Committee received two papers with candidate *SLA*s, SC/67b/AWMP13 and SC/67b/AWMP15. The general properties of the three *SLA*s presented in SC/67b/AWMP13 involve taking an inverse variance weighted average of the last three estimates as an estimate of abundance and calculating the strike limit as a growth rate fraction of a lower percentile of the abundance (conditional on a trend modifier), a snap to need feature and a protection level. The three variants relate to how they are 'tuned' (the trade-off balance between conservation and need).

The three *SLA*s presented in SC/67b/AWMP15 are based on a weighted-average interim *SLA* which uses all abundance estimates, but where the earlier ones are down-weighted. An adjustment to the multiplier of the abundance estimate in the interim *SLA* is applied which depends on the trend of the abundance indices. The three variants relate to how they are 'tuned' (the trade-off balance between conservation and need).

7.1.1.2 REVIEW FINAL RESULTS AND PERFORMANCE

In total, seven potential *SLA*s (which include the 'Interim' *SLA* – a modified version of the *Interim SLA* used to provide advice previously by the Committee until the final *SLA*s had been developed) were considered. The full range of conservation and need statistics were reviewed for the *Evaluation Trials*[2], noting that the initial focus is on meeting the Commission's conservation objectives. Those candidate *SLA*s that meet these are then evaluated on their ability to meet need satisfaction. In summary, conservation performance is deemed satisfactory if either the population is not at MSYL but it is increasing towards it or the population is above MSYL (in which case it may be increasing or decreasing towards MSYL). These concepts are captured in the 'D1' and 'D10' statistics (defined fully in Annex E, table 2) and can be visualised in bivariate plots given in Annex E.

The Committee agreed that the proposed *SLA*s had performed satisfactorily on the joint conservation statistics for the A and B (but not for the C) need envelopes for all trials. The focus was then to evaluate the need satisfaction performance over 20 and 100 years and consider stability in catch levels. This performance was captured by examining three statistics:

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[2] The Committee also examines the results of *Robustness Trials* to ensure that the *SLA* does not exhibit unusual behaviour in more extreme trials.

N9(20) the average need satisfaction over the first 20 years, N9(100) the average need satisfaction over the 100 years and N12 the mean down step statistic (these are also defined fully in Annex E, table 2). They can be visualised in 'Zeh' plots (e.g. see Annex E).

Given the present incorporation into the trial structure of two widely different stock structure hypotheses ('influx' and 'partial'- see Annex E, appendix 2) to explain the variability of the abundance estimates, the need satisfaction over 20 years was given more weight in the evaluation as it is likely that future *Implementation Reviews* may be able to remove one or other scenario.

After an examination of the full range of results, there was no obvious 'winner' between two of the *SLA*s (one from each developer). Depending on the trials considered, and which statistic was examined, they performed slightly differently but their performance overall was equivalent.

Following an approach originally adopted during the development of the *Bowhead SLA*, it was decided that an *SLA* which sets the strike limit to the average of the values obtained by the two *SLA*s[3] would be preferable, providing performance was as good or better than either individual *SLA*; no 'snap to need' for the averaged *SLA* has been applied. The results of the 'combined *SLA'* are summarised in Annex E, appendix 3[4].

7.1.1.3 CONCLUSIONS AND RECOMMENDATIONS

The management advice developed using this *SLA* is given under Item 8. 6.

Attention: C-A, SC

The Committee ***draws attention*** *to the extensive work undertaken over recent years to develop an* SLA *for the West Greenland hunt for fin whales. In concluding this work, the Committee:*

(1) ***agrees*** *that the combined* SLA *(which sets the strike limit to the average of the values obtained by the two best* SLAs *considered) performed satisfactorily in terms of conservation performance and was to be preferred over the individual SLAs in terms of need satisfaction;*
(2) ***recommends*** *that this* 'WG-Fin SLA' *be used to provide management advice to the Commission on the subsistence hunt for West Greenland fin whales (provided the need request falls within need scenarios A and B);*
(3) ***expresses*** *its great thanks to the developers, Brandão and Witting for the vast amount of work put into the development process and to Allison and Punt for their extensive work developing the operating models and running the trials; and*
(4) ***agrees*** *that one focus of the next* Implementation Review *will be to examine further stock structure in relation to the two hypotheses being considered at present, and especially the 'influx' model which was developed in the context of low abundance estimates in some years, rather than being based upon genetic information.*

7.1.2 Common minke whales (Greenland)

SC/67b/Rep06 incorporated the discussions of the two intersessional Workshops and a small working group meeting. Considerable progress was made in relation to (a) updated abundance estimates; (b) finalisation of the trial structure; (c) conditioning; and (d) initial consideration of new *Strike Limit Algorithms* (*SLA*s) and results.

The Committee thanked Donovan, the Workshop chair and the participants for the excellent progress made.

The final trial specifications for the West Greenland common minke whales are provided in Annex E (appendix 4).

Table 5 below summarises the main factors considered in the *Evaluation Trials* for common minke whales. The most influential involve different stock structure hypotheses, different productivity rates (MSYR) and different 'need' envelopes (see discussion under Item 7.1.1), where it increases linearly to twice the present level over the 100-year simulation period (termed B) and where it increases linearly to three times the present level over the 100-year period (termed C).

Considerable work was undertaken to finalise the list of trials, to ensure that the mixing matrices were correctly specified and to complete and agree conditioning. The final trial specifications are provided in Annex E, Appendix 4.

Table 5

Summary of the key factors considered in the common minke whale trials

Factor
Stock structure hypotheses
Mixing matrices
MSYR rate
Survey bias
Need envelope

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[3] tuned to a D10 of 0.8 for the influx trial F34-1B

[4] Final validation and archiving of results will be undertaken by Allison in Cambridge.

7.1.2.1 CANDIDATE *SLAS*

SC/67b/AWMP14 developed a candidate *SLA* for common minke whales off West Greenland similar to that used for fin whales in SC/67b/AWMP13. It operates on an inverse variance weighed average of the last three abundance estimates. The strike limit is calculated as a growth rate fraction of a lower percentile of the abundance measure, conditional on a ‘snap to need’ feature, and a protection level. It does not include a trend modifier.

It was tuned to have a 5th percentile of D10 of 0.80 for need envelope A for the most difficult *Evaluation Trial* (trial M04-1A – see Annex E, appendix 4), where there are two sub-stocks in the western North Atlantic in which the mixing between the Central and the Western stock, and mixing between the putative western sub-stocks, is minimal, and where the MSYR is 1%).

7.1.2.2 CONSIDERATION OF RESULTS

Conditioning of the *Evaluation Trials* was completed satisfactorily and a summary of the results of the is provided in Annex E (appendix 5[5]). Annex E, fig. 3 provides the bivariate plot.

In determining satisfactory conservation and need performance when evaluating *SLA*s, the Committee considers the full range of results across all the *Evaluation Trials*, not simply the worst-case scenarios. Conservation performance was satisfactory for all but the most extreme trial (trial M04-1A) where it was slightly below for the lower 5th percentile. This trial had low MSYR and two W-stocks; it had been originally considered in the context of investigating potential problems for the hunt to simulate possible local depletion in the hunting area rather than for conservation reasons. Genetic stock structure in the entire North Atlantic is subtle such that even an hypothesis of almost complete panmixia is not rejected by most of the analyses and thus differentiation among ‘C’ and ‘W’ is very low. This is even more true for substructure within the W stock (if, indeed, there is any). Given that trials are conservative in so far as they overrate isolation among stocks, and the very subtle differentiation among stocks and sub-stocks in the North Atlantic, a single trial (which implements two fully separate W sub-stocks, for which there is little evidence) not meeting the D1/D10 criteria is not of conservation concern.

The SWG (Annex E, item 2.2.3) had noted that given the unforeseen situation with Secretariat computing, there had been insufficient time for it to consider the results of the *Robustness Trials* during its meeting. Such trials are not needed to determine an *SLA* but are examined to ensure that the selected *SLA* has no unforeseen properties in extreme trials. These were subsequently run prior to the plenary discussions and the results showed no unexpected properties.

7.1.2.3 CONCLUSIONS AND RECOMMENDATIONS

The management advice developed using the *WG-common minke SLA* is provided under Item 8.5.

Attention: C-A, SC

The Committee ***draws attention*** *to the extensive work undertaken over recent years to develop an* SLA *for the West Greenland hunt for common minke whales. In concluding this work, the Committee:*

(1) ***agrees*** *that the tested* SLA *which performed satisfactorily in terms of conservation performance;*
(2) ***agrees*** *that this ‘WG-Common minke SLA’ be used to provide management advice to the Commission on the subsistence hunt for West Greenland common minke whales provided the need request falls within need scenario A (i.e. does not exceed 164 annually);*
(3) ***expresses*** *its great thanks to the developers, Brandão and Witting for the vast amount of work put into the development process and to Allison and Punt for their extensive work developing the operating models and running the trials; and*
(4) ***agrees*** *that one focus of the next* Implementation Review *will be to examine further stock structure in relation to the two hypotheses being considered at present, should be consideration of the results of analyses of genetic data using additional samples from Canada (as well as the additional samples that will become available from West Greenland and Iceland); and*
(5) ***agree****s to establish an intersessional advisory group (Annex Y) to facilitate issues relating to samples.*

7.1.3 North Pacific gray whales (Makah whaling)

7.1.3.1 MANAGEMENT PLAN PROPOSED BY THE U.S. FOR MAKAH WHALING

The Makah Indian Tribe has requested that the U.S. National Marine Fisheries Service (NMFS) authorise a tribal hunt for Eastern North Pacific (ENP) gray whales in the coastal portion of its ‘usual and accustomed fishing area’ in Washington State. The Tribe intends to hunt gray whales from the ENP population, which currently numbers approximately 27,000 animals (Durban *et al.*, 2017). However, at certain times of the year there is a possibility that the hunt may take animals from the PCFG (Pacific Coast Feeding Group) and/or the WNFG (Western North Pacific Feeding Group). In an updated management plan – known as the Makah Management Plan (the Committee had approved an earlier plan for this hunt in 2012 (IWC, 2013), NMFS has taken measures to restrict the number of PCFG whales that are struck or landed in a given 10-year period and to avoid, to the extent possible, striking or killing a WNFG gray whale. The Government of the USA requested the Committee to test this plan to ensure that it meets IWC conservation objectives.

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[5] Final validation and archiving of results will be undertaken by Allison in Cambridge.

This task was begun at the Fifth Rangewide Workshop on the Status of North Pacific Gray Whales (SC/67b/Rep07) from 28-31 March 2018. The major focus of the Workshop related to finalising the specifications for modelling, to enable results to be available for SC67b including incorporation of the Makah Management Plan (SC/67b/Rep07, Annex E, appendix 1) into the modelling framework. The factors taken into account in the trials are given in Table 6.

Table 6

Summary of the main factors considered in the Makah gray whale trials

Factor	
Model fitting related	Projection-related
Stock hypothesis	Additional catch off Sakhalin
MSYR	Catastrophic events
Mixing rate	Northern need in final year
Immigration into the PCFG	Struck and lost rate
Bycatches and ship strikes	Future effort
Pulse migrations into the PCFG	Factors related to obtaining and matching photographs

At the present meeting, the focus was on the conservation performance of the Makah Management Plan. Performance was evaluated in the same manner as described for the evaluation of the *SLA*s for West Greenland fin and common minke whales (see Items 6.1 and 6.2). The results can be found in Annex E (appendix 6). The only scenarios under which the plan might not perform adequately were considered to have low plausibility (e.g. a bycatch mortality of ~ 20 PCFG whales per year). Annex E, fig. 4 shows the bivariate plot.

7.1.3.2 CONCLUSIONS AND RECOMMENDATIONS

The management advice relating to the Makah Management Plan is provided under Item 8.2.

Attention: C-A, SC

The Committee reviewed a US Management Plan for a Makah hunt of gray whales off Washington State (the Committee had evaluated a previous plan in 2011 - IWC, 2011; 2012), using the modelling framework developed for its rangewide review of gray whales (SC/67b/Rep07). In conclusion, the Committee:

(1) ***agrees*** *that the performance of the Management Plan was adequate to meet the Commission's conservation objectives for the Pacific Coast Feeding Group, Western Feeding Group and Northern Feeding Group gray whales;*
(2) ***notes*** *that the proposed management plan is dependent on photo-identification studies to estimate PCFG abundance and the mixing proportions of PCFG whales available to the hunt (and to bycatch in its range);*
(3) ***stresses*** *that its conclusions are dependent on the assumption that these studies will continue in the future; and*
(4) ***expresses*** *its* ***great thanks*** *to Punt, Brandon and Allison for their excellent work in developing and validating the testing framework and running the trials.*

7.1.4 Conclusions on AWMP work

The Chair of the SWG on the AWMP, Donovan, noted that this meeting represented the end of a long journey – with the adoption of the two new *SLA*s, the SWG and the Committee has completed the development tasks it had been assigned by the Commission, originally in Resolution 1994-1. It was an immense task but a great pleasure to work with such dedicated and talented people. He thanked all of the scientists who have made such a wonderful contribution to this work over the years and especially Geof Givens, Kjartan Magnússon (sadly no longer with us), Eva Dereksdóttir, Lars Witting, Anabela Brandão, Doug Butterworth, Cherry Allison and André Punt – the SWG has, in his view, achieved ground-breaking work over the last two decades in a spirit of great collaboration and co-operation, even when there were disagreements, as inevitably there were. He also thanked the hunters and their representatives who had made major contributions in terms of not only data provision but also advice on the AWS (see Item 7.2). The Committee **concurred** that this was an excellent example of what the Scientific Committee could achieve with international collaboration. Finally, they **thanked** Donovan for his dedicated, good humoured and impartial leading of such a major piece of complex work over such a long period - this work has been central to the Committee's role in providing the best scientific advice to the Commission on aboriginal subsistence whaling hunts, bringing together conservation needs and the needs of the hunters.

7.2 Aboriginal Whaling Scheme (AWS)

7.2.1 Introduction

The Scientific Committee's Aboriginal Whaling Management Procedure (AWMP) applies stock-specific *Strike Limit Algorithms* (*SLA*s) to provide advice on aboriginal subsistence whaling (ASW) strike/catch limits.

ASW management (as part of an AWS, the aboriginal whaling scheme) incorporates several components, several of which have a scientific component:

(1) *Strike Limit Algorithms* (case-specific) used to provide advice on safe catch/strike limits;

(2) operational rules (generic to the extent possible) including carryover provisions, block quotas and interim relief allocations;
(3) Guidelines for *Implementation Reviews*; and
(4) Guidelines for data and analysis (e.g. guidelines for surveys, other data needs).

Considerable work on updating the AWS since the version presented (but not accepted by) to the Commission in 2002 (IWC, 2003) was undertaken by an intersessional correspondence group (SC/67b/AWMP 21) and at the intersessional workshops (SC/67b/Rep04).

7.2.2 Carryover request from the Governments of USA and Denmark/Greenland

The Governments of USA and Denmark/Greenland (SC/67b/Rep06, Annex F, appendix) had requested advice at the March intersessional Workshop on the conservation implications of carryover provisions allowed for a carryover provision that allowed use of unused strikes from the previous three blocks, provided that the number used in any year did not exceed 50% of the annual strike limit.

This request was tested on the two *SLA*s available for stocks hunted by the USA and Greenland at the time of the Workshop i.e. the *Bowhead SLA* (applicable to the Bering-Chukchi-Beaufort Seas stock) and the *WG-Humpback SLA* (applicable to West Greenland).

Three types of options were examined:

(1) baseline case - all strikes taken annually (i.e. no need for carryover);
(2) 'frontload' case - strikes taken as quickly as possible within block (+50% limit annually until the block limit is reached); and
(3) Two alternative scenarios where carryover strikes are accrued for one or three blocks, followed by a period of carryover usage subject to the +50% limit.

The three-block scenario considered in (3) served as a direct test of the provision described in the request of USA and Denmark/Greenland.

Attention: CG-A

The Committee received a request from the USA and Denmark/Greenland (SC/67b/Rep06, Annex F, appendix) on the conservation implications of carryover provisions that
'…allow for the carry forward of unused strikes from the previous three blocks, subject to the limitation that the number of such carryover strikes used in any year does not exceed 50% of the annual strike limit'.
The Committee reviewed the request using its simulation frameworks and the two SLA*s available for stocks hunted by the USA and Greenland available at the time of the Workshop i.e. the* Bowhead SLA *(applicable to the Bering-Chukchi-Beaufort Seas stock) and the* WG-Humpback SLA *(applicable to West Greenland) and*

(1) ***agrees*** *that a carryover provision for up to 3-blocks meets Commission's conservation objectives; and*
(2) ***reiterates*** *its previous advice, applicable for all* SLA*s, that interannual variation of 50% within a block with the same allowance from the last year of one block to the first year of the next is acceptable; and*
(3) ***agrees*** *to evaluate the above request for the other Greenland* SLA*s at the 2019 Committee meeting.*

7.2.3 Review proposed updates to the AWS

The proposed update to the previous AWS is provided in Annex E, appendix 8. It has sections on carryover, block quotas, interim relief allocation (and see Annex E, appendix 7), *Implementation Reviews* and guidelines for surveys and data.

7.2.4 Conclusions and recommendations

Attention: C-R

The Committee has been working for some years to update the scientific components of an Aboriginal Whaling Scheme. It has completed this work and ***recommends*** *the AWS provided in Annex E, appendix 8 to the Commission. It has sections on carryover, block quotas, interim relief allocation (and see Annex E, appendix 7), Implementation Reviews and guidelines for surveys and data. It* ***notes*** *that the Commission's AWS may include additional, non-scientific provisions.*

7.3 *Implementation Review* of BCB bowhead whales

According to the Committee's guidelines, the primary objectives of an *Implementation Review* are to:

(1) review the available information (including biological data, abundance estimates and data relevant to stock structure issues) to ascertain whether the present situation is as expected (i.e. within the space tested during the development of a *Strike Limit Algorithm* (*SLA*)) and determine whether new simulation trials are required to ensure that the *SLA* still meets the Commission's objectives; and
(2) to review information required for the *SLA*, i.e. catch data and, when available at the time of the *Review*, new abundance estimates (note that this can also occur outside an *Implementation Review* at an Annual Meeting).

The *Bowhead SLA* was adopted in 2002 (IWC, 2003, p.158) and there was an extensive *Implementation Review* completed in 2007 (IWC, 2008a, p.124) with a major focus on stock structure including three intersessional workshops. That included consideration of additional trials investigating management implications of assuming additional population structure even though these were considered of low plausibility. The Committee concluded that the *Bowhead SLA* remained the best tool to provide management advice. The next *Implementation Review* was completed in 2012 (IWC, 2013b, p.147); that concluded that there was no need to develop additional trials to those evaluated during the previous *Implementation Review* (IWC, 2008c).

The primary review was undertaken by the SWG on the AWMP (Annex E, Item 4) but the review benefitted from discussions within two other groups, SD-DNA (Annex I, Item X) and ASI (Annex Q, Item Y).

7.3.1 Stock structure: review new information

A full discussion of the work on stock structure can be found in Annex E (item 4.1) and Annex I. New information considered included genetic analyses (SC/67b/SDDNA 01) and telemetry results (SC/67b/AWMP04). SC67b/SDDNA01provided information on genetic analyses using samples from the BCB, Canadian and Okhotsk Sea stocks of bowhead whales. Within the BCB stock, no significant differences were identified in temporal or spatial comparisons, and age-related structure was not detected in comparisons between groups of large (old) versus small (young) whales. While comparisons of the BCB stock with the Okhotsk Sea stock revealed significant differences, there were only small, and in most cases statistically insignificant, differences between BCB and Canadian stocks. While this pattern could be related to historical connectivity between the two stocks, it could also, or additionally, be driven by some degree of contemporary gene flow.

Attention: SC

With respect to stock structure, considering the multiple lines of evidence, the Committee:

(1) ***agrees*** *that BCB bowheads comprise a single population, with no signs of substructure;*
(2) ***agrees*** *that there was no need to consider any new SLA trials regarding stock structure, since the trials conducted in 2002 and 2007 already covered all plausible stock structure hypotheses;*
(3) ***welcomes*** *the telemetry information provided, thanks the hunters involved for their skill and assistance;*
(4) ***encourages*** *additional telemetry efforts; and*
(5) ***agrees*** *with the suggestions for future genetic studies in the Arctic provided under Item 11.*

7.3.2 Abundance estimates: review new information

A new abundance estimate (SC/67b/AWMP) has been accepted for the year 2011 from a long-term photo-id capture-recapture study (27,133, CV=0.217; 95% CI from 17,809 to 41,337) that it has been agreed is suitable for providing management advice and for use in the *SLA* (Annex Q). The previously accepted, completely independent, 2011 abundance estimate from the ice-based survey (Givens *et al.*, 2016) is also acceptable for use in the *SLA* and has already been used in that regard (16,820, CV=0.052; 95% CI 15,176 to 18,643).

There are thus two independent estimates for the same year considered suitable for use in the *SLA* and this is considered under Item 8.3.

The Committee also discussed plans for future surveys (SC/67b/AWMP 12 and AWMP 16) in Annex Q (item 3.1.1.1). These plans are in accord with the AWS Guidelines that 'plans for undertaking a survey/census should be submitted to the Scientific Committee in advance of their being carried out, although prior approval by the Committee is not required.

7.3.3 Biological parameters: review new information

New and extensive information on biological parameters was received as discussed Annex E (item 4.3). These covered such matters: length at sexual maturity and pregnancy rate from hunted animals (SC/67b/AWMP 07); the potential use of samples from baleen plates to examine hormone cycles and pregnancy; and information on calves from aerial surveys (SC/67b/AWMP03).

Attention: SC

With respect to biological parameter information, the Committee:
(1) ***welcomes*** *the extensive information presented;*
(2) ***encourages*** *the continued collection of such data from the hunt;*
(3) ***encourages*** *the work on the baleen plate analyses to examine hormone levels and pregnancy;*
(4) ***encourages*** *continued aerial surveys under the ASAMM surveys and any future collaboration involving life history data from the harvest; and*
(5) ***agrees*** *that the information presented does not suggest the need to consider any new SLA trials regarding stock structure.*

7.3.4 Removals: review new information

The Committee received updated information about the 2017 harvest (SC/67b/AWMP 05) and long-term removals (SC/67b/AWMP 06). In 2017, 57 bowhead whales were struck resulting in 50 animals landed. The total landed for the hunt in 2017 was higher than the average over the past 10 years (2007-2016 mean of landed =41.7; SD=6.7). Efficiency (number landed / number struck) in 2017 was 88%, which was also higher than the average for the past 10 years (mean of efficiency=75.2%; SD=6.5%).

The Committee also received SC/67b/AWMP06 that provided a summary of bowhead whale catches in Alaska between 1974 and 2016. The authors pointed to the excellent cooperation and contribution of the whale hunters from the 11 villages that are members of the Alaska Eskimo Whaling Commission (AEWC). This information is discussed in Annex E (item 4.4).

From 2013 to 2017, four bowhead whales (2 females and 2 males) were harvested near Chukotka, mainly in Anadyr Bay (SC/67b/AWMP20). The average length was 14.5m (minimum 13.0m, maximum 17.0m). Although the portion of the annual strike limit allocated to Russia under their bilateral agreement with the USA is 5 animals, the actual annual take is usually only 1-2 whales per year, and this has been the case since at least 2004.

The Committee thanked the authors of the provision of this information, noting that catch and strike data are used in the *SLA* calculations (see Item 8.3).

7.3.5 Other anthropogenic threats and health: review new information

The Committee received extensive information related to threats and health ranging from entanglement, predation and health (body condition, pathology and parasite loads). The discussion of this can be found in Annex E (item 4.5).

Attention: SC

With respect to threats and health to the BCB bowhead whales, the Committee:
(1) ***welcomes*** *the extensive information presented;*
(2) ***agrees*** *that whilst the present level of unintentional human induced mortality is too low to require new Implementation trials or incorporation into the SLA calculations, the situation should continue to be monitored and evaluated at the next Implementation Review;*
(3) ***agrees*** *that the health analyses give no cause for concern with respect to the continued application of the Bowhead SLA; and*
(4) ***encourages*** *that the excellent work on health-related issues continues.*

7.3.6 Conclusions and recommendations (and, if needed, workplan to complete Review)

Attention: SC

With respect to the Implementation review of BCB bowhead whales, the Committee ***concludes*** *that:*
(1) the Implementation Review has been satisfactorily completed; and
(2) the range of hypotheses and parameter space already tested in Bowhead SLA trials was sufficient and therefore the Bowhead SLA remains the best way to provide management advice for this stock;
In addition, it ***thanks*** *the US scientists for the extremely hard work that they have put into providing comprehensive papers to facilitate this review.*

8. STOCKS SUBJECT TO ABORIGINAL SUBSISTENCE WHALING (NEW INFORMATION AND MANAGEMENT ADVICE)

The Committee noted that the Commission will be setting new catch/strike limits for at its 2018 biennial meeting in Brazil. It had received written or verbal requests for limits to be considered for each hunt as discussed below.

Attention: C-A

A general request had been received from the USA and Denmark (SC/67b/Rep06, annex F, appendix) for advice on whether there would be a conservation issue if there was a one-time 7-year block followed by a return to 6-year blocks to address logistical issues related to the Commission.

The Committee ***agrees*** *there are no conservation issues associated with this suggestion (and see the block quota section of the ASW in Annex E, appendix 8).*

8.1 Eastern Canada/West Greenland bowhead whales

8.1.1 New abundance information

Last year, the Committee had recommended that Canadian scientists attend the Committee to present the results of their work on abundance. It was very pleased that Doniol-Valcroze from Department of Fisheries and Oceans Canada, and the primary author of the paper on the 2013 aerial survey abundance estimate, was present at the meeting.

The Committee accepted, for the provision of management advice and use in an *SLA* (see Annex Q for details), the fully corrected abundance estimate (Doniol-Valcroze *et al.*, 2015) from a 2013 aerial survey of 6,446 bowheads (CV=0.26, 95% CI 3,722-11,200). The survey covered the major summering area for the Eastern Canada/West Greenland (EC/WG) stock.

The Committee recalled that the *WG-Bowhead SLA* had been developed on the conservative assumption that the abundance estimates for the West Greenland area alone (1,274 whales in 2012 (CV=0.12)) represented the abundance of the whole stock, as it believed that it was not possible to assume that a non-member country would continue with regular surveys. Doniol-Valcroze advised the Committee that the present management strategy of Canada does involves obtaining regular abundance estimates. The Committee noted it would be pleased to receive such estimates from Canada being presented to the Committee in the future.

Attention: SC

The Committee greatly appreciated the presence of a Canadian scientist at its meeting. The Committee:
(1) ***welcomes*** *the provision of the abundance estimate for the Eastern Canada/West Greenland stock and (see Item 8.1.2) the regular provision of information on catch data by Canada;*
(2) ***welcomes*** *the attendance of Canadian scientists at its meetings;*
(3) ***agrees*** *that consideration of how to incorporate abundance estimates from Canada should be one focus of the next Implementation Review for this stock;*
(4) ***notes*** *the regular collaboration of Canadian and Greenlandic scientists on other matters such as genetic sampling (inter alia for mark-recapture abundance estimation); and*
(5) ***encourages*** *further collaboration between Canada, Greenland and the USA for the study of bowhead whales across their range and the presentation of these results at future Committee meetings.*

8.1.2 New catch information

SC/67B/AWMP/10 provided an update of recent Canadian takes made in the Inuit subsistence harvest of the EC-WG bowhead whale stock. In the eastern Canadian Arctic, the maximum allowed take is 7 bowhead whales per year according to domestic policy, with no carry-over of unused takes between years. Since 2015, 5 strikes were taken and 4 bowhead whales were successfully landed (1 in 2015, 2 in 2016 and 1 in 2017). Witting reported that West Greenland hunters struck no bowheads in 2017. There was one 14.7m whale that died from entanglement in crab gear.

The Committee notes that the reported number of strikes was within the parameter space that was tested for the *WG-Bowhead SLA*, and encourages the continued collection of genetic samples from harvested whales.

8.1.3 Management advice

Attention: C-A

SC/67b/AWMP19 reported Greenland's plans for requesting aboriginal whaling provisions at IWC67 and no changes were requested for bowhead whales. The Committee therefore:

(1) ***agrees*** *that the WG-Bowhead SLA remains the best available way to provide management advice for the Greenland hunt;*
(2) ***notes*** *that this SLA had been developed under the conservative assumption that the number of bowhead whales estimated off West Greenland represented the total abundance between West Greenland and Eastern Canada;*
(3) based on the agreed 2012 estimate of abundance for West Greenland (1,274, CV=0.12), the catch of one whale in Canada in 2017, and using the agreed WG-Bowhead SLA, ***agrees*** *that an annual strike limit of two whales will not harm the stock and meets the Commissions conservation objectives; and*
(4) although the Committee has not yet had time to examine the request from the US/Denmark (SC/67b/Rep06, annex F, appendix) for the WG-Bowhead SLA, ***reiterates*** *its advice****,*** *applicable for all SLAs, that interannual variation of 50% within a block with the same allowance from the last year of one block to the first year of the next, is acceptable.*

8.2 North Pacific gray whales

8.2.1 New information (including catch data)

The Committee received considerable new information on the hunt off Chukotka as discussed in Annex E (item 5.2). In 2017, a total of 119 gray whales were struck in 2017 (37 males and 82 females). No whales were struck and lost, and no stinky (inedible) gray whales were taken. Similar whaling methods were employed as in recent years and the overall efficiency of the hunt was almost same as in 2016.

In advance of the gray whale *Implementation Review* that is scheduled to begin in 2019, the Committee reviewed new information regarding the stock structure of gray whales in the North Pacific (SC67b/SDDNA02 and SC67b/SDDNA03) – for details see Annex I. The results were based on whole genome sequence data from three individuals (one sampled off Barrow, Alaska and two sampled off Sakhalin Island, Russia) and SNP genotype data generated from larger sample sets representing whales sampled off Sakhalin and in the Mexican lagoons.

Attention: SC

*In reviewing the results of new genetic analyses of gray whales in the North Pacific, the Committee **agrees** that the genetic and photographic data for this species be combined to better assess stock structure-related questions. Given the potential for genomic data to aid in better evaluating the stock structure hypotheses currently under consideration for North Pacific gray whales, the Committee **encourages** the continuation of work to produce additional genomic data from sampled gray whales.*

8.2.2 Management advice

Attention: C-A

The Russian Federation (SC/67b/AWMP/17) had requested advice on the following provision:

'For the seven years 2019, 2020, 2021, 2022, 2023, 2024 and 2025, the number of gray whales taken in accordance with this sub-paragraph shall not exceed 980 (i.e. 140 per annum on average) provided that the number of gray whales taken in any one of the years 2019, 2020, 2021, 2022, 2023, 2024 and 2025 shall not exceed 140.'

The Committee therefore:
*(1) **agrees** that the* Gray Whale SLA *remains the best available way to provide management advice for the gray whale hunts;*
*(2) **advises** that an average annual strike limit of 140 whales will not harm the stock and meets the Commission's conservation objectives;*
*(3) **notes** that its previous advice that the interannual variation of 50% within a block with the same allowance from the last year of one block to the first year of the next remains acceptable;*
*(4) **advises** that the Makah Management Plan (see Item 2.3) also is in accord with the Commission's management objectives.*

8.3 Bering-Chukchi-Beaufort Seas bowhead whales

8.3.1 New information

New information (on abundance and catches) was considered as part of the *Implementation Review* discussed under Item 7.3.

The USA had indicated that it was proposing no changes to the present catch/strike limits although it may suggest changes to its carryover request in light of the advice received by the Committee as discussed at the intersessional workshop (SC/67b/Rep06).

The Committee noted that there are now two independent estimates of abundance for this stock in 2011 (see Item 7.3.1). Recognising the need to formally consider the general question of how best to combine estimates in such cases as part of the workplan in the next biennium, the Committee noted that if they are combined as a weighted average by the inverse of their variances, there is little difference (it is slightly higher) between the combined estimate and that from the ice-based census estimate; the ice-based approach has been the method used for the other estimates used in the *SLA*. Therefore, the ice-based census estimate for 2011 (16,820, CV=0.052; 95% CI 15,176 to 18,643) is considered the most recent estimate of abundance for use in the *Bowhead SLA* this year.

8.3.2 Management advice

Attention: C-A

The USA indicated that it requested advice on the existing catch/strike limits. The Committee therefore:

*(1) **agrees** that the* Bowhead Whale SLA *remains the best available way to provide management advice for this stock;*
*(2) **advises** that a continuation of the present average annual strike limit of 67 whales will not harm the stock and meets the Commission's conservation objectives; and*
*(3) **advises** that provisions allowing for the carry forward of unused strikes from the previous three blocks, subject to the limitation that the number of such carryover strikes used in any year does not exceed 50% of the annual strike limit, has no conservation implications (see SC/67b/Rep04).*

8.4 Common minke whales off East Greenland

8.4.1 New information on catches

In the 2017 season, nine common minke whales (3 males and 6 females) were landed in East Greenland, and one was struck and lost. Genetic samples were obtained from 8 of the landed whales. One common minke whale died from entanglement in fishing gear.

8.4.1 New information on abundance

The Committee endorsed the 2015 aerial survey abundance estimate of 2,762 (CV=0.47; 95%CI 1,160-6,574). This is only a small part of the wider Western and Central stocks from which catches may occur.

8.4.2 Management advice

Attention: C-A

SC/67b/AWMP19 reported Greenland's plans for requesting aboriginal whaling provisions at IWC67. It requested advice on an annual take of 20 animals (it had previously been 12). It had also requested advice on any conservation implications of a 12-month hunting season for common minke whales.

The Committee therefore:

*(1) **notes** that in the past its advice for the East Greenland hunt had been based upon the fact that the catch was a small proportion of the number of animals in the Central Stock;*
*(2) **notes** the process to develop an* SLA *for common minke whales off West Greenland resulted in a simulation framework that produces a considerably more rigorous way to provide advice for this hunt than before, by taking into account stock structure issues;*
*(3) **notes** that the results of the simulation trials that incorporated a continuing catch of 20 whales from East Greenland gave rise to no conservation concerns;*
*(4) **notes** that the 2015 aerial survey abundance estimate of 2,762 (CV=0.47; 95%CI 1,160-6,574) is only a small part of the wider western and central stocks;*
*(5) **advises** that a continuation of the present average annual strike limit of 20 whales will not harm the stock and meets the Commission's conservation objectives;*
*(6) **advises** that changing the length of the season to 12 months had no conservation implications; and*
*(7) **agrees** that an* SLA *should be developed for this hunt in the future; and*
*(8) **encourages** the continued collection of samples fro collaborative genetic analyses (and see Item 7.1.2.3).*

8.5 Common minke whales off West Greenland

8.5.1 New information on catches

In the 2017 season, 129 common minke whales were landed in West Greenland and four were struck and lost. Of the landed whales, there were 95 females, 33 males and one of unknown sex. Genetic samples were obtained from 104 whales, and the Committee was pleased to note that samples were already part of the data used in the genetic analyses of common minke whales in the North Atlantic. The Committee **encourages** the continued collection of samples and the collaborative approach of the genetic analysis.

8.5.2 New information on abundance

The Committee endorsed the 2015 aerial survey abundance estimate of 5,095 (CV0.46; 95%CI 2,171-11,961) as discussed in Annex Q.

8.5.3 Management advice

Attention: C-A

SC/67b/AWMP19 reported Greenland's plans for requesting aboriginal whaling provisions at IWC67. It requested advice on annual strikes of 164 animals (i.e. no change). It had also requested advice on any conservation implications of a 12-month hunting season for common minke whales.
The Committee therefore:

*(1) **agrees** that the WG-Common minke SLA is the best available way to provide management advice for this stock under need scenario A;*
*(2) **advises** that a continuation of the present average annual strike limit of 164 whales will not harm the stock and meets the Commission's conservation objectives;*
*(3) although the Committee has not yet had time to examine the request from the US/Denmark (SC/67b/Rep06, annex F, appendix) for this SLA, **reiterates** its previous advice**,** applicable for all SLAs, that interannual variation of 50% within a block with the same allowance from the last year of one block to the first year of the next is acceptable;*
*(4) **advises** that changing the length of the season to 12 months had no conservation implications; and*
*(5) **encourages** the continued collection of samples for collaborative genetic analyses (and see Item 7.1.2.3).*

8.6 Fin whales off West Greenland

SC/67b/AWMP19 reported Greenland's plans for requesting aboriginal whaling provisions at IWC67. It requested advice on annual strikes of 19 animals (i.e. no change).

8.6.1 New information on the catch
A total of seven fin whales (5 females and 2 males) was landed, and one was struck and lost, off West Greenland during 2017. The Committee was pleased to note that genetic samples were obtained from five of these, and that the genetic samples are analysed together with the genetic samples from the hunt in Iceland.

8.6.2 New information on abundance
The Committee endorsed the 2015 aerial survey abundance estimate of 2,215 (CV=0.41; 95%CI 1,017-4,823) for use in providing management advice and in the *SLA* as discussed in Annex Q (Item Y).

8.6.3 Management advice

Attention: C-A

SC/67b/AWMP19 reported Greenland's plans for requesting aboriginal whaling provisions at IWC67. It requested advice on annual strikes of 19 animals (i.e. no change). It also requested advice on whether there were any conservation implications of removing length limits (while retaining the prohibitions relating to calves.
The Committee therefore:

(1) ***agrees*** *that the WG-Fin SLA is the best available way to provide management advice for this stock;*
(2) ***advises*** *that a continuation of the present average annual strike limit of 19 whales will not harm the stock and meets the Commission's conservation objectives; and*
(3) although the Committee has not yet had time to examine the request from the US/Denmark (SC/67b/Rep06, annex F, appendix) for this SLA, ***reiterates*** *its advice****,*** *applicable for all SLAs, that interannual variation of 50% within a block with the same allowance from the last year of one block to the first year of the next is acceptable;*
(4) ***advises*** *that removing the length limits had no conservation implications; and*
(5) ***encourages*** *the continued collection of samples for collaborative genetic analyses (and see Item 7.1.1.3).*

8.7 Humpback whales off West Greenland
8.7.1 New information on catches
A total of two (both female) humpback whales were landed and none were struck and lost in West Greenland during 2017. Genetic samples were obtained from all the landed whales. The importance of collecting genetic samples and photographs of the flukes from these whales is emphasised.

Five humpback whales were observed entangled in fishing gear in West Greenland in 2017. Of these, one died, two became free and one was successfully disentangled by a disentanglement team. The remaining animal was alive and still entangled when it was last sighted.

Inclusion of bycaught whales had been incorporated into the scenarios for the development of the *Humpback SLA*. If high levels continued, then this will need to be taken into account in any *Implementation Review*. The Committee noted the IWC efforts with respect to disentanglement and prevention and welcomed the news that the Greenland authorities requested IWC disentanglement training that took place in 2016 and that they successfully disentangled one humpback whale.

8.7.2 New information on abundance
The Committee endorsed the 2015 aerial survey abundance estimate of 993 (CV=0.46; 95%CI 434-2,272) as discussed in Annex Q (Item Y) for use in the provision of management advice and in the SLA.

8.7.3 Management advice

Attention: C-A

SC/67b/AWMP19 reported Greenland's plans for requesting aboriginal whaling provisions at IWC67. It requested advice on annual strikes of 10 animals (i.e. no change).
The Committee therefore:
(1) ***agrees*** *that the* WG-Humpback SLA *is the best available way to provide management advice for this stock;*
(2) ***advises*** *that a continuation of the present average annual strike limit of 10 whales will not harm the stock and meets the Commission's conservation objectives;*
(3) ***advises*** *that that provisions allowing for the carry forward of unused strikes from the previous three blocks, subject to the limitation that the number of such carryover strikes used in any year does not exceed 50% of the annual strike limit' has no conservation implications (see SC/67b/Rep04); and*
(4) ***encourages*** *the continued collection of samples and photographs for collaborative analyses.*

8.8 Humpback whales off St. Vincent and The Grenadines
The alternate Commissioner for St Vincent and the Grenadines advised that no change to the present limits were envisaged.

8.8.1 New information on catch
It was reported that one humpback whale was struck and landed in 2017 by St. Vincent and The Grenadines.

8.8.2 New information on abundance

Last year, the Committee had requested that the USA provide a new abundance estimate for the western North Atlantic based upon the available NOAA data. A progress report on this work was provided with a focus on information on abundance estimates generated by the MONAH study, conducted in 2004 and 2005 on Silver Bank (a breeding ground in the West Indies) and in the Gulf of Maine feeding ground. The best estimate around 12,300, similar to the Committee endorsed best estimate from the YONAH project from 1992/93, which was 10,400 (8,000, 13,600). The lack of strong population growth was unexpected given information on rates of increase from some other areas of the North Atlantic, and may reflect either a true rate of increase, unidentified sampling bias, and/or the idea that Silver Bank as a habitat has reached maximum capacity. It is not clear whether the MONAH estimate is representative of the entire population, nor the extent to which the full estimate can be applied to the southeastern Caribbean in the context of the St Vincent hunt. However, four animals from the Gulf of Maine have been linked to animals seen in the southeastern Caribbean (including one that was caught in the hunt).

The Committee also noted several endorsed recent abundance estimates of humpback whales in parts of the North Atlantic including: 993 (95% CI: 434-2,272) in West Greenland in 2015; 4,223 (95% CI: 1,845-9,666) in East Greenland in 2015; and 12,879 (95% CI 5,074; 26,455) in the Iceland-Faroes region in 2007.

It has now been nearly two decades since the IWC has done an In-Depth Assessment on North Atlantic humpback whales. The Committee **agrees** that it would be a valuable exercise to perform a North Atlantic Rangewide review of humpback whales, similar in scope to the Rangewide Review for North Pacific gray whales and taking into account recent work on stock structure including that of Stevick *et al.* (2018).

8.8.3 Management advice

Attention: C-A

The alternate Commissioner for St Vincent and the Grenadines advised that no change to the present limits were envisaged. The Committee therefore:

(1) ***notes*** *that is does not have an approved abundance estimate for western North Atlantic since that in 1992;*
(2) ***notes*** *that in accord with the advice provided in the AWS (see Annex E, Appendix 8), it therefore considered the available evidence to see if was sufficient to provide safe management advice;*
(3) ***advises*** *that, given the information above on recent abundance in the North Atlantic combined with the size of the requested catch/strikes (an average of four annually), continuation of the present limits will not harm the stock;*

The Committee also ***reiterates*** *its previous advice that:*

(1) the status and disposition of genetic samples collected from past harvested whales be determined and reported next year;
(2) photographs for photo-id (where possible) and genetic samples are collected from all whales landed in future hunts; and that
(3) the USA (NOAA, NMFS) provides an abundance estimate from the MONAH data as soon as possible for the Committee.

8.9 Workplan 2019-20

Table 7 summarises the work plan for work related to aboriginal subsistence whaling. The Committee also established an Intersessional Correspondence Group to work on ASW related issues (Annex Y).

Table 7

Work plan for matters related to aboriginal subsistence whaling

Topic	Intersessional 2018/19	2019 Annual Meeting (SC/68a)	Intersessional 2019/20	2020 Annual meeting
(1) Annual review of catch/strike limits		Carry out		Carry out
(2) *Implementation Review*		Gray whales based upon rangewide review		West Greenland humpback whales
(3) *SLA*s		Consider development of an *SLA* for the hunt of common minke whales off East Greenland based on operational models developed for the West Greenland hunt		Adopt *SLA* if it is decided one is necessary
(5) Interim relief allowance testing	Run trials for gray whale hunts	Review results	Run trials for West Greenland common minke whales and fin whales	Review results
(6) Carryover (US/Denmark request)	Run trials for remaining Greenland hunts (West Greenland common minke whales, bowhead whales and fin whales	Review results		

9. WHALE STOCKS NOT SUBJECT TO DIRECTED TAKES

9.1 In-depth Assessments

Donovan gave a presentation explaining a streamlined procedure hereby the Committee, via its sub-groups, can undertake Comprehensive Assessment (traditionally the first time an assessment is undertaken for a particular species/ocean basin) or an in-depth assessment (assessments subsequent to a comprehensive assessment). This can be found as SC/67B/GEN04 and is summarised in Fig. 1. The objective is to provide a consistent approach (including methods) that initially focusses on ensuring that sufficient data are available to undertake an assessment (the pre-assessment approach that will normally be undertaken at annual meetings) and then follows this with a concentrated effort (ideally two workshops and two annual meetings, with no new data) to complete the assessment. The objective is to provide Commission with robust information on present status. This involves identifying:

(1) if populations are recovering, recovered or if there is cause for concern;

(2) factors that may be or are affecting status so that conservation and management needs can be determined; and

(3) information gaps and ways to address these in order to reduce uncertainty at the next assessment.

9.1.1 Comprehensive Assessment of North Pacific humpback whales

Work towards a Comprehensive Assessment of North Pacific humpback whales began in 2016, and included an intersessional workshop held in April 2017 (IWC, 2018b). After the 2017 Committee meeting, an intersessional steering group continued preparing the input data and assessment model (IA/67b/IA03). The assessment model is a simplified age-aggregated model of the breeding and feeding grounds. The development of the input data (stock structure, abundance, catches, and life history parameters) continued during the year but given the slower than initially expected progress, particularly with respect to narrowing down the number of stock structure hypotheses, the steering group had agreed that it was premature to hold the anticipated workshop prior to SC67b.

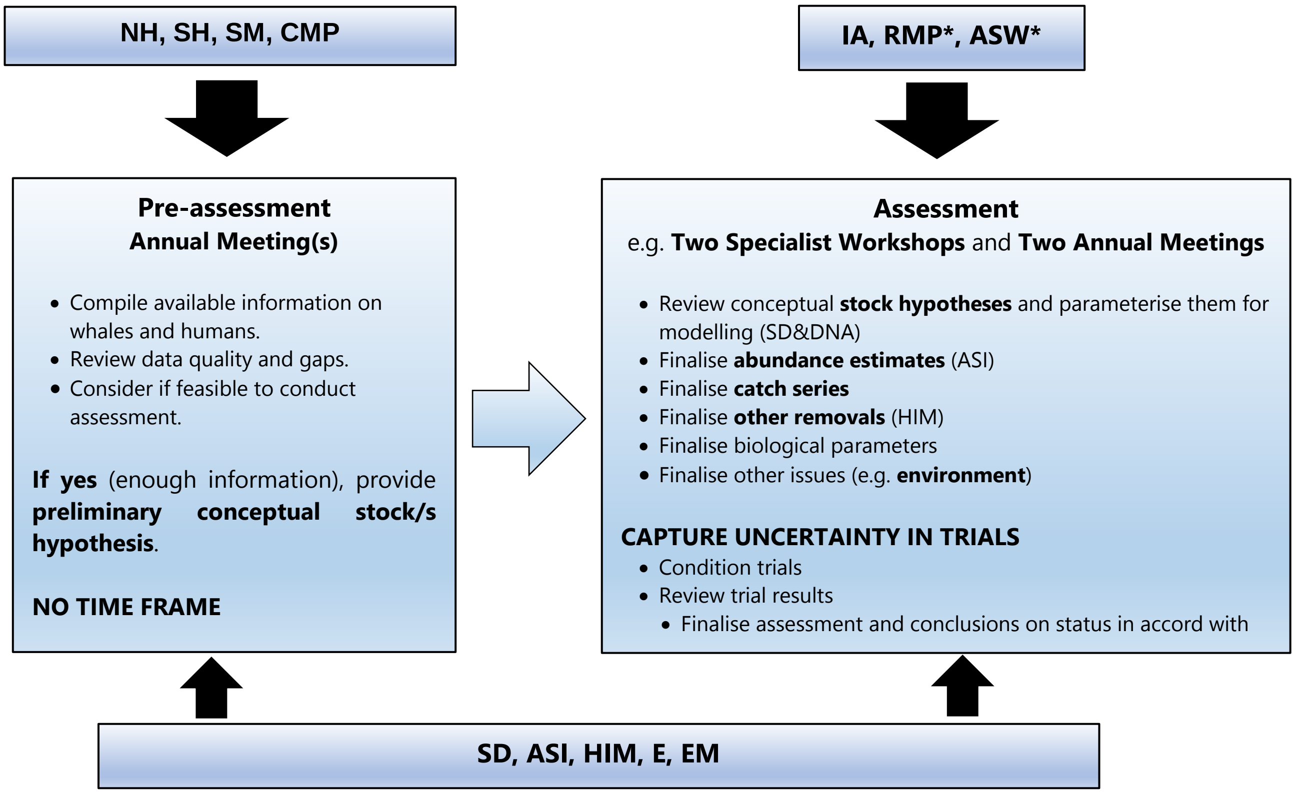

Fig. 1. Schematic of the approach to conduct assessments within the Scientific Committee. Acronyms refer to sub-groups. Normally the final assessment will take place in the sub-committee on in-depth assessments but for stocks subject to direct catches it may occur in the context of the RMP or AWMP sub-groups as appropriate.

Work continued at this meeting and the detailed discussions can be found in Annex F (item 4). The subdivisions of the North Pacific humpback whale feeding and breeding grounds in Annex F (fig. 1) are broadly consistent with existing data; identified uncertainties will be addressed in the assessment by evaluating four scenarios with different numbers of feeding and breeding grounds. This work will be greatly assisted by undertaking comparisons of humpback whale photographs from the Pacific obtained after the conclusion of the photographic component of the SPLASH (Structure of Populations, Levels of Abundance and Status of Humpback Whales) programme in 2005 (e.g. see Calambokidis *et al.*, 2008).

The general underlying structure of the assessment model has been developed but before the model can be run the input data (e.g. catches and abundance estimates) need to be updated and allocated for each stock structure hypotheses and mixing matrices developed and parameterised.

Attention: SC, G

The Committee is undertaking a Comprehensive Assessment of North Pacific humpback whales. To complete this assessment the Committee ***agrees*** *that:*

(1) a large-scale matching effort of post-2005 photo-identifications should be undertaken (see Annex F, item 4 for methods); and
(2) this matching effort will (a) help clarify the connections among the feeding/breeding areas within the North Pacific; and (b) assist in developing updated abundance estimates where appropriate.
The Committee ***stresses*** *that to obtain the most robust assessment and thus conservation advice, all available data should be included in the matching effort. Therefore, the Committee* ***strongly encourages*** *all catalogue holders to participate in this exercise, after the appropriate data sharing agreements are made.*

The Committee also ***welcomes*** *the provision of new abundance estimates (e.g. those from the IWC-POWER surveys and from local areas in Japan), noting that they will also need to be adjusted for the various stock structure hypotheses.*

The Committee ***agrees*** *that the next assessment workshop should take place at a time prior to SC68b when the intersessional Steering Group (Annex Y) decides sufficient progress has been made.*

9.1.2 Comprehensive Assessment of North Pacific sei whales

The Committee began what was called an in-depth assessment of North Pacific sei whales in 2015 (IWC, 2016c) but, in keeping with the discussion under Item 9.1 will now be termed a Comprehensive Assessment for consistency. Work has focussed since then on finalising the stock structure hypotheses (two have been agreed for use in the assessment - a single-stock hypothesis and a five-stock hypothesis), developing an appropriate population model and finalising the model inputs in accordance with these hypotheses (including catches, mark-recovery locations, abundance estimates, estimates of mixing between sub-areas, and life history parameters).

Considerable progress was made with this work intersessionally and at this meeting as discussed in Annex H, item 3.

Attention SC, G

The Scientific Committee intends to complete the Comprehensive Assessment of North Pacific sei whales within the next biennial period. It notes the progress made at this meeting with respect to stock structure, abundance estimates, marking data, catch history, life history parameters and the assessment model. To complete this work, the Committee ***agrees*** *to:*

(a) the work undertaken to finalise input data for the assessment (Annex F, appendices 2-7);
(b) support the modelling work identified in Annex F; and
(c) re-establish the intersessional steering group to oversee the assessment.

In addition, the Committee ***encourages*** *telemetry work in waters outside the 'pelagic' sub-area to assist in quantifying the movement patterns of animals.*

9.1.3 In-depth Assessment of Indo-Pacific Antarctic minke whales

An intersessional correspondence group under Murase completed its task to finalise a document synthesising the results of the 2001 - 2014 in-depth assessment of an eastern Indian stock (I-stock) and a western South Pacific stock (P-stock) of Antarctic minke whales distributed between 35°E and 145°W.

The Committee **commends** the authors for completing this paper and submitting it to the *Journal of Cetacean Research and Management.* As the paper has just entered the review process, the intersessional correspondence group (Annex X) has been re-established to see the paper through to publication.

9.1.4 Workplan 2019-20

The work plan for Comprehensive and in-depth assessments for the next biennium is provided in Table 8.

Table 8

Work plan for in-depth assessments

Topic	Intersessional 2018/19	2019 Annual Meeting (SC/68a)	Intersessional 2019/20	2020 Annual meeting (SC/68b)
In-depth Assessment of Indo-Pacific Antarctic minke whales	Complete review of paper submitted for publication	-	-	-
Comprehensive Assessment of North Pacific sei whales	Re-establish the ISG (Annex Y) to further data preparation and development of the assessment model	Review progress of intersessional work and continue the assessment	Finalise preparation of assessment	Review progress of intersessional work and finalise the assessment
Comprehensive Assessment of North Pacific humpback whales	Re-establish the ISG (Annex Y) to further data preparation, development of the assessment model and hold a Workshop	Review progress of intersessional work and continue the assessment	Finalise /continue preparation of assessment	Review progress of intersessional work and continue/finalise the assessment

9.2 Evaluation for potential new Comprehensive or In-Depth Assessments

9.2.1 North Pacific blue whales

The Committee welcomed the report of an intersessional group that had been determining the data that are available on items required to carry out a Comprehensive Assessment of blue whales in the North Pacific. The status of the eastern North Pacific population is well known and a stock assessment was reviewed and accepted by the Committee in 2016 (Monnahan and Branch, 2015). However, information from the central and western North Pacific is sparser. Information presented at this meeting concerned stock structure, catch history, biological parameters, photo-identification, Discovery marks and sighting surveys. Details can be found in Annex G (item 6.1).

Several papers and datasets were discussed including: the use of blue whale sounds to identify stocks; morphological data; genetic data; sightings data (SC/67b/IA02; SC/67b/SCSP06; SC/67b/SCSP07; SC/67b/NH08).

Attention: SC

*The Committee **agrees** the following priorities to progress the pre-assessment:*

(1) obtain abundance estimates from the IWC-POWER surveys;
(2) obtain abundance estimates from the JARPN and JARPNII surveys;
(3) analyse and compare genetic samples from ENP, IWC-POWER and ICR biopsy samples to determine stock structure throughout the North Pacific;
(4) compare photo-identification data from POWER, JARPN/JARPNII and other ENP catalogues;
(5) Review new acoustic locations and information and conduct fine-scale analysis of song features for central Pacific blue whale calls, with particular focus on calls around Japan;
(6) Obtain better life history parameters (especially age at sexual maturity and calving interval) from the Cascadia Research Collective, the Mingan Island Cetacean Study Research Station and the CICIMAR-IPN photo-ID dataset;

*With respect to (3), the Committee **requests** the collection of about 20 biopsy samples if possible during the NEWREP-NP surveys in the western North Pacific to improve the power to evaluate stock structure and **encourages** genetic analysis of the existing Japanese samples.*

*With respect to (5), the Committee **requests** a reanalysis of recordings from the Northern Mariana Islands (Saipan and Tinian) collected by the Pacific Islands Fisheries Science Center to look for the presence or absence of the new song type recorded from Japan. It also **encourages** passive acoustic data collection during surveys (e.g. IWC-POWER, university/training cruises) from the region of high blue whale density southeast of the Kamchatka Peninsula to determine the song type produced by animals in that region.*

*The Committee **agrees** that the intersessional correspondence group continue to review data needed for an assessment of North Pacific blue whales be reappointed under Branch (Annex Y).*

9.2.2 Non-Antarctic Southern Hemisphere blue whales

9.2.2.1 SOUTHERN HEMISPHERE POPULATION STRUCTURE

The Committee is currently preparing for a Comprehensive Assessment of pygmy blue whales. For this reason, it continues to gather information on population structure (see Item 3.1, IWC, 2018a). This year, the web-based pygmy blue whale song library funded by the IWC will be launched (SC/67b/SH12). This will enable researchers to compare their acoustic recordings with validated song archetypes and greatly assist the determination of Southern Hemisphere blue whale distribution patterns and stock structure. Photo-ID and genetic evidence support the idea that each distinct pygmy blue whale song represents a geographically and genetically distinct population of pygmy blue whales around the Southern Hemisphere. A full description of the discussion of the use of songs in this pre-assessment is given in Annex H (item 3.1), including comparison with genetic and photo-identification data. The Committee also received information from whale bones and notes that further analysis of blue whale bones from old whaling land stations will be helpful to establish the past distribution of these stocks.

Assessments require catches to be allocated to populations and in 2016 the Committee funded an examination of regional catches to assign them to each putative population (Item 5.1, IWC, 2017a). The results of this work are provided in SC/67b/SH23 and discussed in Annex H (item 3.1). Total pygmy blue whale catches were estimated at 12,184 with totals for each population of 1,228 (Northern Indian Ocean), 6,889 (South West Indian Ocean), 3,646 (South East Indian Ocean) and 421 (South West Pacific Ocean).

The Committee also discussed an intersessional effort to identify and standardise genetic markers used in Southern Hemisphere blue whale research (only four loci were common across all research laboratories) and received a progress report (SC/67b/PH04) on matching within the Southern Hemisphere Blue Whale Catalogue, which has been supported by funding from the Committee (Item 10.2.2, IWC, 2017a). This helps understanding of blue whale movements between regions, and allows estimation of regional abundance. The catalogue is currently being migrated to IWC servers (and see Item 23.2.3.2).

Attention: SC, G

In order to progress its work towards an assessment of pygmy blue whales, the Committee:

(1) ***agrees*** *that further work is needed to identify high and base case catch scenarios for pygmy blue whales;*
(2) ***encourages*** *deployment of more acoustic recorders in the southern Indian Ocean;*
(3) ***agrees*** *that further population modelling is needed to assess pygmy blue whale populations;*
(4) ***strongly encourages*** *blue whale research groups to publish the metadata associated with their sequences in order that levels of sample overlap can be established and datasets compared;*
(5) ***agrees*** *that the Southern Hemisphere Blue Whale Catalogue should be continued to help understand blue whale movements, with a priority focus on matching photographs within regions to measure regional abundance of pygmy blue whales.*

9.2.2.2 INDONESIA/AUSTRALIA BLUE WHALES

The Australian blue whale photo-ID catalogue data have now nearly all been uploaded and matched within the Southern Hemisphere Blue Whale Catalogue, at which point quality control analysis can begin. This will allow the potential for using these data for mark recapture abundance estimation to be assessed. The Scientific Committee was informed that mark-resighting data from the Perth Canyon (Australia) will be analysed intersessionally, to provide a new estimate of Australian blue whale abundance which assist in a future assessment of this population.

Attention: SC, G

The Committee ***encourages*** *analysis to provide an estimate of Australian blue whale abundance using mark-resighting data.*

9.2.2.3 MADAGASCAR BLUE WHALES

The Committee was informed that passive acoustic monitoring of blue whales in the Mozambique Channel detected both South West Indian Ocean (SWIO) and Antarctic blue whale song types, as well as fin and Antarctic minke whales (SC/67b/SH14). In addition, SC/67b/SH24 reported an unidentified blue whale song off Oman. A full discussion of the results of these papers can be found in Annex I (item 3.3.2).

This new information means that the blue whale catch allocations for the Indian Ocean, currently only ascribed to a single ‘NIO’ population in the Northern Indian Ocean, will need revision to take this new acoustic pattern into account.

Attention: SC, G

The Committee notes that the distribution and population isolation of blue whales is poorly understood in the northern and western Indian Ocean. The Committee therefore:

(1) ***strongly encourages*** *further acoustic work in the western Indian Ocean and Arabian sea to better understand the distribution, seasonality and overlap of blue whale calls;*
(2) ***strongly encourages*** *the collection and analysis of available tissue samples for analysis of genetic population structure in this region to assist with characterising these populations; and*
(3) ***agrees*** *that catch allocations of blue whales be revised to include the new blue whale song in the northwest Indian Ocean as a potential distinct ‘stock’.*

9.2.2.4 NEW ZEALAND BLUE WHALES

Three papers were presented on blue whales off New Zealand (see Annex H, item 3.3.4 for a full discussion).

SC/67b/SH09 reported a recent study of blue whale movement and habitat use in the Taranaki region of New Zealand in which two animals were tagged. However, due to the small sample size and La Niña conditions, it is uncertain how representative these movements are for blue whales in New Zealand waters.

SC/67b/SH05 summarised a multi-disciplinary study included acoustics, genetics and photo-identification in the same area, and provided a conservative estimate of blue whale population abundance (see Annex Q, item 3.1.1.9), to consider if this estimate can be used in the upcoming regional assessments of pygmy blue whales. SC/67b/SH04 reported projects underway to assist regional conservation management, including a description of fine-scale habitat use during summer months in the South Taranaki Bight, and response to local acoustic disturbance.

Attention: SC, G

With respect to information on blue whales off New Zealand, the Committee:

*(1) **welcomes** the work being undertaken to understand abundance and connectivity, which will contribute towards the pygmy blue whale population assessments; and*
*(2) **agrees** that New Zealand photo-identifications should be combined with others within the Southern Hemisphere Blue Whale Catalogue to provide the fullest possible assessment of regional abundance and connectivity*

9.2.2.5 SOUTHEAST PACIFIC BLUE WHALES

The Committee received two papers relevant to blue whales off Chile and the full discussion can be found in Annex H (item 3.3.1). SC/67b/SH03 presented a morphometric analysis of Chilean blue whales which reinforces the argument that Chilean blue whales should be considered a separate sub-species from the Antarctic and pygmy forms. (Bedrinana-Romano *et al.*, 2018) reported distribution modelling of blue whales using Chilean Northern Patagonia waters. Preliminary delimitations of possible blue whale conservation areas in this region overlap with highly used vessel navigation routes and areas allocated for aquaculture. The Committee was also informed that predictions of southeast Pacific blue whale habitat following Redfern *et al.*, (2017) will be completed intersessionally.

Attention: SC, G

In view of the recent identification of movements of Chilean blue whales into the South Atlantic and ongoing questions about the distribution of this population, the Committee:

*(1) **encourages** further satellite tracking and surveys (including collection of photo-ID and genetic data) to assess the population limits, habitat use and abundance and sub-species identity of blue whales in Chile;*
*(2) **encourages** compilation of morphometric data available for northeast Pacific blue whales and comparison with Chilean data, to assess morphological differentiation of these whales in the eastern Pacific and evaluate sub-species identity; and*
*(3) **welcomes** plans for further photo-ID catalogue matching within this region to assist with regional abundance estimation.*

9.2.2.6 WORK PLAN

The work plan for all Southern Hemisphere blue whales is given in Table 9.

9.2.3 Antarctic blue whales (Areas III and IV)

Undertaking a regional population assessment of Antarctic blue whales is challenging due to the scarcity of whales and logistical challenges. The Committee received new information this year on sightings, abundance and genetic studies.

SC/67b/SH08 presents a preliminary estimate of abundance (the first using photo-ID data) and this is discussed in Annex Q (see item 3.1.19) where suggestions were made to refine the analyses. Reports from two 2017/18 NEWREP-A summer cruises included sightings of blue whales and information on biopsy sampling (SC/67b/SP08 and SC/67b/ASI07). An IWC-SORP Southern Ocean blue whale-focussed cruise is planned for January to March 2019 (140°E-175°W), which intends to describe krill swarms in relation to blue whale density and distribution (SC/67b/SH07).

With respect to genetic work, IWC-SORP funded work on blue whale bones to compare past and current genetic diversity levels is reported in SC/67b/SH02 and discussed in Annex I (item 4.4.2). The Committee was also updated about ongoing work to analyse a collection of 1,626 baleen plates (roughly 50:50 blue and fin whales) from the Japanese whaling in the 1940s and held at the Smithsonian Natural History Museum, USA. A pilot study has established that mitochondrial DNA can be sequenced from these plates. Further analyses including of stable isotope and hormone levels are planned for these samples.

Attention: SC, G

*The Committee **welcomes** the progress being made towards being able to undertake am in-depth assessment of Antarctic blue whales. The Committee:*

*(1) **encourages** further work to update the abundance estimate for Antarctic blue whales following Committee recommendations;*

(2) ***strongly encourages*** *continued opportunistic photo-ID data collection in the Antarctic to assist with developing estimates of population abundance for this subspecies; and*
(3) ***encourages*** *continued collection and analysis of bone and baleen from historical Antarctic commercial whaling samples and sites to evaluate loss of genetic diversity and shifts in population structure.*

9.2.3.1 WORK PLAN

The work plan for all Southern Hemisphere blue whales is given in Table 9.

Table 9.

Workplan for Southern Hemisphere Antarctic and pygmy blue whales

Topic	Intersessional 2018/19	2019 Annual Meeting (SC/68a)	Intersessional 2019/20	2020 Annual meeting
Antarctic blue whales				
Catalogue matching	Catalogue matching of photo-IDs (Annex Y)	Report	Catalogue matching (opportunistically collected photos)	Report
Abundance estimation	Mark recapture modelling work to update SC/67b/SH08 Annex Y	Report		
Photo-ID outreach material	Create photo-ID information booklets for distribution via IAATO operators	Report		
SH non-Antarctic blue whales				
Population assessment	Improve catch separation model, explore alternative catch allocation models (Annex Y)	Report	Population assessment. Analyse minimum and extrapolated recovery status of all populations for which abundance is available	Report
Catalogue matching	Catalogue matching of photo-IDs within southeast and central east Pacific (Annex Y)	Report	Catalogue matching (opportunistic photos from citizen scientists and collaborators) if funds are available	Report
Blue whale song library	Finish implementation of blue whale song library (Annex Y)	Report		
Australian abundance estimate	Analyse Perth Canyon abundance using mark recapture data (Annex Y)	Report		

9.2.4 Southern Hemisphere fin whales

9.2.4.1 POPULATION STRUCTURE

As part of its pre-assessment work, the Committee is gathering information on Southern Hemisphere fin whales in order to: (1) clarify the subspecies status of these whales (currently two Southern Hemisphere subspecies are recognized, Committee on Taxonomy, 2017); and (2) measure population differentiation around the Southern Hemisphere to establish whether any distinct populations exist.

A summary of available data on Southern Hemisphere fin whale structure was presented in SC/67b/SH15 and is discussed in detail in Annex H (item 4.1). The only evidence for any structure comes from acoustics. A genetic study from the southeast Pacific (SC/67b/SH13) found high local diversity in Chile, with no significant differentiation from the other Southern Hemisphere datasets. The Committee noted however that genetic differentiation can be difficult to detect when diversity levels are high and genetic differentiation is low (see Annex H, item 4.1).

Attention: SC, G, S

Knowledge of population structure is essential to future efforts to assess Southern Hemisphere fin whales. To determine the differentiation and potential sub-species structure among fin whales the Committee:

(1) ***agrees*** *that analysis of concurrently collected acoustic recordings of fin whales, to assess song variation around the Southern Hemisphere, is a priority;*
(2) ***agrees*** *that a review of all Discovery mark data published on fin whales to assess population connectivity patterns should be carried out; and*

(3) ***requests*** *that the Secretariat provide a letter of support for a study examining the evidence for* B. physalus patachonica, *which requires access to the holotype for this species from the Bernardino Rivadavia Natural Sciences Museum in Buenos Aires.*

The Committee also ***encourages:***

(1) analysis of fin whale distribution and geographic aggregations using all available catches;
(2) strategic biopsy sampling and analysis to measure the genetic differentiation of fin whales around the Southern Hemisphere;
(3) further biopsy sampling and sequencing of multiple nuclear loci to establish Chilean fin whale differentiation patterns, with co-collection of photo-IDs and body length measurements to establish population identity;
(4) satellite telemetry to discern seasonal movements; and
(5) photo-identification to understand site fidelity and residency patterns and linkages between high- and low-latitude grounds.

9.2.4.2 DISTRIBUTION AND ABUNDANCE

The Committee welcomed a review of the available metadata on Southern Hemisphere fin whales (SC/67b/SH19), compiling data from dedicated and opportunistic surveys, moored acoustic recorders, sonobuoy surveys, photo-identifications, satellite tagging and biopsy sampling. The Committee also welcomed a summary of recent work by the Brazilian Antarctic Program to conduct dedicated fin whale research using sighting surveys, photo-ID, biopsy sampling and telemetry.

Reports from two 2017/18 NEWREP-A summer cruises included sightings of fin whales and information on biopsy sampling (SC/67b/SP08 and SC/67b/ASI07). A new abundance estimate for fin whales using sightings data from the third IDCR-SOWER circumpolar survey is expected to be available for review at next year's meeting.

SC/67b/14 provided information on the presence of fin whales in the Mozambique Channel and a new lower-latitude song. Details of the discussions can be found in Annex H (item 4.2).

The Committee was also informed that an analysis has suggested that Antarctic fin whales are sufficiently well marked to enable to use in photo-ID projects (SC/67b/PH01) and this is discussed in Annex S (item 4.1).

Attention: SC, G, CG-A

With respect to obtaining information on the distribution, movements and abundance of Southern Hemisphere fin whales for use in a future assessment, the Committee:

(1) ***encourages*** *a meta-analysis of the Antarctic Peninsula and Scotia Sea sightings data, to measure recent fin whale distribution, density and habitat use;*
(2) ***strongly encourages*** *continued work by the Brazilian Antarctic Program towards the understanding of fin whale population structure, movements and habitat use*
(3) ***agrees*** *that a new abundance estimate for fin whales from the IWC IDCR/SOWER programme should be presented for review at next year's meeting,*
(4) ***welcomes*** *news that fin whales can be used in photo-ID studies, and* ***encourages*** *further photo-ID data collection at high latitudes.*

9.2.4.3 WORK PLAN

The work plan for Southern Hemisphere fin whales is given in Table 10.

Table 10

Work plan for Southern Hemisphere fin whales

Topic	Intersessional 2018/19	2019 Annual Meeting (SC/68a)	Intersessional 2019/20	2020 Annual meeting
Fin whale acoustic structure	Review fin whale call patterns across Southern Hemisphere, investigate call variation (Annex Y)	Report	Complete review of fin whale call patterns (Annex Y)	Report
Discovery marks	Review available Discovery mark data on fin whales (Pastene and Jackson)	Report		
Catch maps	Update fin whale catch model to include Soviet catch data (de la Mare)	Report		

9.2.5 North Atlantic sei whales

The Committee welcomed information on two separate habitat-based density modelling efforts, using visual survey data to produce seasonal abundance estimates for sei whales from the purported 'Nova Scotia' stock, ranging from Nova Scotia to the southeastern USA (SC/67b/NH07). There was also some consideration of passive acoustic and strandings data from the US eastern seaboard. No new data are available from around Iceland or Norway, partially due to difference in timing between surveys and species' arrival in regional waters. This information was discussed in Annex G (item 6.2). An intersessional correspondence group (Annex Y) will compile additional information this species in the North Atlantic and the Committee looks forward to a further update on reanalysis of historical data, particularly related to stock structure and strandings, next year.

9.2.6 North Atlantic right whales

Since 2016, the Committee has recommended a comprehensive update on North Atlantic right whales. SC/67b/NH05 summarised the information on the status of the North Atlantic right whale. This population has been slowly declining since 2010 and the abundance at the end of 2015 was estimated to be around 460 individuals (Pace *et al.*, 2017[6]). Of particular concern is the lower annual survival rate of females than males and poor recent calving (five in 2016/17 and none so far in the 2017/18 calving season). The observed number of dead whales in 2017 was 17 whales, several showing signs of death from fishing gear or blunt force trauma. These clearly represent minimum numbers and there was some discussion as to whether it was possible to scale minimum observed mortalities to an overall estimate but several confounding factors preventing this were identified (see Annex F, item 6.3 and Annex J, item 2.1.2).

Due to the increased 2017 Canadian interactions in the Gulf of St. Lawrence, on 19 April 2018 the Government of Canada implemented mitigation measures to reduce future interactions (DFO, 2018), including: closing a large part of the Gulf of St. Lawrence snow crab fishery on 30 June; creating a dynamic 15-day fishing closure; introducing a 10 knot speed restriction when any single right whale sighting in any area is detected; putting in place mandatory gear marking and reporting of any lost gear; minimising the allowable amount of floating line at surface; and using vessel monitoring systems that reports the boats position every 5 minutes.

A substantial increase in collaboration and data sharing between the US and Canada has occurred as a result of these mortalities.

Attention: C-A, CC

The Committee reiterates its serious concern over the status of the western North Atlantic stock of right whales as it is probably the only viable population of this species, for which entanglements and ship strikes have long been identified as key threats.

This year, the Committee:
(1) ***recognises*** *that entanglements have now replaced ship strikes as the primary cause of deaths (Kraus et al. 2016);*
(2) ***reiterates*** *its recommendation for the USA to submit a comprehensive update on the status of North Atlantic right whales (IWC, 2017:40) including an update of the Pace* et al. *abundance estimate, prior to the 2019 meeting;*
(3) ***stresses*** *that this update will allow time for explanations or additional analyses to be undertaken before the proposed 2019 Workshop on the Comparative Biology, Health, Status and Future of North Atlantic Right Whales: Insights from Comparative with other Balaenid Populations (including bowheads);*
(4) ***encourages*** *updates from the US Large Whale Take Reduction Team (ALWTRT) on progress of the Whale Safe Rope and Gear Marking Feasibility Subgroups; and*
(5) ***requests*** *that the Commission asks the IWC Executive Secretary to write to the U.S. National Marine Fisheries Service (NMFS) and the Canadian Department of Fisheries and Oceans, informing them of the Committee's serious concerns over the declining population trend of this species, and stressing that,* ***as a matter of absolute urgency****, every effort be made to reduce human induced mortality in the population to zero.*

9.2.7 North Pacific right whales

The Committee received a report of a dead right whale caught in a set net off Izu, Japan in 2018 (SC/67b/NH06) – the first in a set net since one in Korea in 2015 (Kim *et al.*, 2015).

The Committee welcomed information on a single sighting off Hokkaido (and a biopsy sample) from a Japanese national cruise (SC/67b/ASI10). It also welcomed information on North Pacific right whales from the visual, acoustic and biopsy sampling components of the 2017 IWC-POWER cruise in the eastern part of the Bering Sea. A total of 9 schools and 18 individuals (including 2 duplicate schools of 3 individuals) of right whales were sighted with photo-identification of 12 individuals and biopsy samples from 3 individuals. Discussion of these sightings can be found in Annex G (item 6.4).

In response to a recommendation made last year (IWC, 2018c), US and Japanese scientists presented the results of new genetic analyses of right whales in the North Pacific. Comparison of whales sampled in the eastern and western North Pacific revealed statistically significant differentiation based on mtDNA data, supporting presumed separation of the two stocks based on gaps in the spatial distribution of sightings (and also see discussion in Annex I, item 4.3).

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[6] Any revised estimate from the Pace *et al.* 2017 paper will be reviewed by the ASI sub-committee during SC68a.

Attention: SC

The results of new genetic analyses support the recognition of separate stocks of right whales in the eastern and western North Pacific. Given the importance of this work and the precarious situation of this species, especially in the eastern North Pacific, the Committee ***encourages*** *the publication of this information as soon as possible.*

9.2.8 Workplan 2019-20

The Committee agreed to the two-year workplan in Table 11.

9. 3 New information and workplan for other northern stocks *(NH)*

9.3.1 North Pacific fin whales

The Committee received new information on studies of North Pacific fin whales. New sightings of fin whales were reported in the papers (SC/67b/ASI12, SC/67b/ASI10, SC/67b/SCSP06) during the POWER cruise in the Bering Sea and the two surveys in the western North Pacific (Areas 7, 8 & 9). Over 260 schools found, many individuals were photo-identified and biopsy samples were obtained from 28 whales.

9.3.2 Omura's whale

The Committee welcomed the new information on this species (SC/67b/NH09) from the west coast of Madagascar, supporting the current understanding that the population is resident and non-migratory with strong site fidelity. Likely threats to the Madagascar population include entanglement in local fisheries, impacts from oil and gas exploration, and most imminent the risk of coastal water contamination from a recently initiated mining operation for Rare Earth Elements. Future work should include a long-term latitudinal study that incorporates multiple methodologies to investigate all aspects of the species biology and conservation threats to the population.

Kim and colleagues reported on the first confirmed documentation of Omura's whale in the waters of South Korea. Two of six large baleen whales bycaught were confirmed by genetic analysis to be Omura's whale. This bycatch reinforces the concept that this coastal species is vulnerable to anthropogenic impacts, especially entanglement in fishing gear.

Attention: SC, G

The Committee notes that little information is available to assess the status of Omura's whale. The Committee:

(1) ***recognises*** *the significant contribution the research efforts off Madagascar have made to the understanding of this species and* ***encourages*** *this work to be continued and expanded into the future; and*
(2) ***encourages*** *identification of study sites that are suitable for long-term comparative study on Omura's whales in other parts of its range (e.g. New Caledonia, Komodo Islands, Indonesia, and the Bohol Sea, Philippines).*

Table 11

Workplan for other Northern Hemisphere stocks

Topic	Intersessional 2018/19	2019 Annual Meeting (SC/68a)	Intersessional 2019/20	2020 Annual meeting
North Pacific blue whales	Data collection and review with focus on catches and stock structure	Review especially stock structure	Develop proposal for stock structure	Agree stock structure hypotheses
North Atlantic sei whales	Review distribution, strandings, sightings and stock structure	Review new information for assessment	Develop proposal for stock structure	Agree stock structure hypotheses
North Atlantic right whales		Review status and mortality data		Review status and mortality data
North Pacific right whales		Review new information for assessment		Review new information for assessment
North Atlantic humpback whales		Consider information for new assessment		Develop plans for new assesssment
Gulf of Mexico Bryde's whale		Review new information on mortality		Review new information on mortality
All other stocks		Review new information		

9.3.3 North Atlantic Bryde's whales

SC/67b/ASI01 presented sightings collected during recent coastal surveys off Guinea, Sierra Leone and Liberia in March 2018. During this survey, two groups of five individual Bryde's whales were observed.

The Committee welcomed this information and **encourages** future surveys in this region.

9.3.4 North Atlantic blue whales

The Committee welcomed new information from the USA on blue whales in the North Atlantic including recent sightings, serious injuries or mortalities, seasonal occurrence based on acoustics. Lesage *et al.* (2018) provides an extensive summary of recent data collected in Canadian waters. This is discussed in Annex G (item 7.6) where it was noted that multiple new datasets (including from passive acoustic monitoring) have been recently collected and may provide more information on blue whale distribution in North Atlantic waters

Attention: SC, G

The Committee notes that there has been a recent increase in information available on North Atlantic blue whales. The Committee:

(1) ***draws attention to*** *the lack of data on interchange between blue whales in the eastern and western North Atlantic and* ***recommends*** *that U.S., Canadian and Icelandic colleagues conduct a new comparison of blue whale photo-identification catalogues and present this information at SC/68a; and*
(2) ***encourages*** *Canadian colleagues to generate a new population abundance estimate as soon as feasible, and looks forward to updates on new passive acoustic and visual sightings data SC/68a.*

9.3.5 North Atlantic humpback whales

The Committee received new information (NOAA, 2018b) on humpback mortalities along the US coast (vessel strikes and entanglements were noted as the primary causes of anthropogenic mortality). An ‘Unusual Mortality Event’ was declared by the USA for humpback whales in April 2017. This is discussed further in Annex G (item 7.7. New abundance estimates for parts of the North Atlantic are discussed in Annex Q (item 3.1.1.3) and presented in Item 12.1. Consideration of the need for a new in-depth assessment of North Pacific humpback whales is given in Annex E (item 5.8.2) and Item 8.7.3.

9.3.6 North Atlantic bowhead whales not subject to aboriginal subsistence whaling

No new information was available to the Committee.

9.3.7 North Pacific bowhead whales not subject to aboriginal subsistence whaling

No new information was available to the Committee.

9.3.8 North Pacific sperm whales

Three papers (SC/67b/ASI10,12 and SC/67b/SCSP06) provided new information of sperm whale occurrence and distribution was collected during 2017 in the western North Pacific, eastern Bering Sea. An intersessional correspondence group to examine possible ways to assess sperm whales has been reappointed (Annex Y)

9.3.9 Gulf of Mexico Bryde’s whales

9.3.9.1 NEW INFORMATION

The Committee received an update on activities related to monitoring and new research plans for the critically endangered Gulf of Mexico sub-species of Bryde’s whale. The Southeast Fisheries Science Center undertook a shipboard survey in the northern Gulf of Mexico in 2017, including known habitat of the Gulf of Mexico Bryde’s whale. Passive acoustic data were collected in historic habitat of the central and western Gulf from June 2016 to June 2017. The In the USA, there is legislation that provides funds to restore and protect ecosystems of the Gulf of Mexico following the Deepwater Horizon oil spill (2010); this work will include research on the Gulf of Mexico Bryde’s whale.

Attention: SC, G

The Committee ***agrees*** *that the NOAA scientists working with this sub-species should present results from shipboard and acoustic data analyses to the IWC at the 2019 Scientific Committee meeting and looks forward to receiving a report from the Workshop held in conjunction with the initiation of research associated with funds to restore and protect ecosystems of the Gulf of Mexico following the Deepwater Horizon oil spill.*

The Committee also ***encourages*** *U.S. and Mexican scientists to collaborate in efforts to determine whether any of these whales occur in Mexican waters (e.g. Bay of Campeche) where a major oil spill of three million barrels occurred in 1979. This should include consideration of the use o9f passive acoustics as well as visual surveys focusing on areas of habitat similar to that found in the core known range in the north-eastern Gulf. It was further noted that passive acoustic data or specimen records from the northern coast of Cuba would be useful to determine potential occurrence of this subspecies in that region.*

9.3.9.2 CONSERVATION ADVICE

Attention: CG-R, S
The small population size, known human related mortality, restricted range and low genetic diversity place the Gulf of Mexico sub-species of Bryde’s whale (added to the Critically Endangered category of the IUCN Red List in 2017) at significant risk of extinction. The Committee ***reiterates*** *its previous* ***recommendations*** *that US authorities:*

(1) make full and immediate use of available legal and regulatory instruments to provide the greatest possible level of protection to these whales and their habitat;
ensure that seismic surveys and associated activities that degrade acoustic habitat are excluded from the region of the eastern Gulf of Mexico inhabited by these whales, including an appropriate geographic buffer against acoustic impacts from activities in the Central Planning Area and active leases in the Eastern Planning Area;
(2) characterise the degree of overlap between the whales' currently known preferred habitat and ship traffic, and immediately implement appropriate measures to reduce the risk of ship strikes (e.g. re-routing, speed restrictions);
(3) based on the known distribution of these whales and overlap with certain fisheries, improve understanding of potential for interaction with fishing gear, and expand and implement appropriate measures, such as area closures, to reduce the risk of entanglement throughout their range;
(4) develop and implement restoration projects (with funds from the Deepwater Horizon oil spill settlement) for these whales and their habitat as a priority and ensure that a robust monitoring and adaptive management plan is in place to evaluate the effectiveness of all restoration efforts;
(5) design and conduct research programmes (sighting surveys, acoustic monitoring, genetic mark-recapture, photoidentification if feasible, satellite tagging if feasible, health studies if feasible) to further investigate these whales' distribution, movements, habitat use, health, survival and fecundity - this should include efforts to better document the whales' total geographic range and to document causes of mortality through necropsies when carcasses are reported; and
(6) *ensure that information about core known habitat and movements in the Gulf of Mexico is transmitted to the U.S. Coast Guard, shipping industry trade organizations, and Gulf of Mexico port authorities (e.g. in Tampa, Florida) for their consideration to mitigate ship-strike risk.*

In addition, the Committee ***reiterates*** *its recommendation that the IWC Secretariat (i) communicate the above concerns and recommendations to range state authorities and (b) specifically explore in collaboration with the International Maritime Organization the feasibility of providing internationally recognized forms of protection to these whales (e.g. designation of an Area to be Avoided) that would reduce the risk of ship strike and help mitigate degradation of acoustic habitat by ship noise.*

9.3.10 Other stocks - Northern Indian Ocean sperm whales

No new information was available to the Committee.

9.3.11 Workplan 2019-20

The Committee agreed to the two-year workplan in Table 11.

9.4 New information and workplan for other Southern stocks

9.4.1 Southern Hemisphere humpback whales

9.4.2.1 BREEDING STOCK D

The assessment of the Breeding Stocks D (West Australia), E1 (East Australia) and Oceania was completed in 2014 (IWC, 2015a), but there were substantial associated problems in obtaining a reliable estimate of absolute abundance for Breeding Stock D. See Annex H (IWC, 2017a; 2018a) for a detailed discussion of these issues. Last year (IWC, 2018c), the Committee had agreed that efforts should focus on designing and implementing a new 'survey' (perhaps using new approaches such as drones), and recommended that prior to implementation, an assessment of the feasibility of such a 'survey', focusing in particular on the study conducted by du Fresne *et al.*, (2014), is conducted.

Attention: SC, G, CG-R

The Committee ***agrees*** *that obtaining a reliable estimate of absolute abundance for humpback whale Breeding Stock D (west Australia) is a priority for any future in-depth assessment. The Committee* ***reiterates*** *its recommendation that an evaluation of abundance survey feasibility be carried out for this population, focusing in particular on the study conducted by du Fresne et al. (2014), with a view to implementing a new survey of this population in the future.*

9.4.2.2 WORK PLAN

The work plan for Southern Hemisphere humpback whales is given in Table 12.

Table 12.
Work plan for Southern Hemisphere humpback whales

Topic	Intersessional 2018/19	2019 Annual Meeting (SC/68a)	Intersessional 2019/20	2020 Annual meeting
Survey feasibility	Reanalyse pilot study to assess feasibility of future West Australia surveys (Kelly)	Receive report		

9.4.3 Southern Hemisphere right whales not the subject of CMPs

The Committee would like to progress regional population assessments for southern right whales (Item 10.8.1.5, IWC, 2017b) This requires a good understanding of population structure, abundance, trend and past exploitation levels. It was agreed that Australia should be the highest priority region for the next assessment (Item 9, IWC, 2018a).

9.4.3.1 SOUTH AFRICA

SC/67a/SH01 provided the results of the 2017 survey of southern right whales flown along the coast of South Africa, part of a long-term monitoring programme since 1979. Since 2015 there has been a marked decline in the presence of unaccompanied adults and cow-calf pairs for unknown reasons (see discussion in Annex S, item 5.1.3). Photo-ID analyses indicated an increasing occurrence of apparent 4- and 5-year calving intervals since 2014. SC/67b/SH22 applied a life history model to photo-ID data collected from 1979 to 2017. They showed that a model variant which allows the probability of a resting female remaining in the resting phase (rather than having a calf) to vary through time provided a better fit to the data than a time-invariant model. They calculate an annual population growth rate of 6.5% and measure first year survival at 0.852, with subsequent annual survival of 0.988.

Attention: SC, G, C-A, CG-A

The Committee is ***concerned*** *that the future of the exemplary long-term monitoring programme of right whales in South African waters remains uncertain. The Committee therefore* ***reiterates*** *that it:*

(1) ***strongly recommends*** *continuation of the survey;*
(2) ***requests*** *the Commission to urge South Africa to do all it can to ensure the long-term future of this vital monitoring programme; and*
(3) ***encourages*** *South African scientists to investigate the offshore movements and locations of southern right whales with future surveys.*

9.4.3.2 AUSTRALIA

The Committee was informed about the latest of a series of aerial surveys conducted in South and West Australia in 2017. The 2017 counts were the highest yet in the series and an exponential increase of ~6% per year remains a good description of the data. Funding has been obtained for the next three years of surveys. The Committee was also informed about: (a) a 26-year cliff-top study conducted at the Head of the Great Australian Bight (south Australia) on right whale population trends and identifications (Charlton *et al.*, In prep); and (b) an aerial survey in southeast Australia where small numbers of whales have been sighted (Watson *et al.*, 2015). Right whales in southeast Australia are genetically and geographically distinct from the large population in south/southwest Australia (e.g., Carroll *et al.*, In press).

The Committee was advised that the Australian Government has recently allocated funds towards a two-year project that will provide an abundance estimate for Australia's two southern right whale populations. It will investigate life history characteristics as well as connectivity between breeding areas on the eastern, southern and western coasts of Australia.

Attention: SC, G, CC, CG-A

The Committee ***recognises*** *the value of the Australian long-term right whale monitoring programmes to understand right whale population trends and dynamics, and* ***recommends*** *that this monitoring continues.*
In regard to right whales in southeast Australia, the Committee ***reiterates*** *concerns expressed in 2017 that abundance remains low despite this area having been a significant historic calving ground. The Committee therefore:*

(1) recommends an assessment of the likely effects of fish farms and other developments in hindering population recovery in this region; and
(2) encourages further work to estimate the abundance of the southeast Australia population.

9.4.3.3 NEW ZEALAND

The Committee welcomed information that surveys will be conducted in the Auckland Islands in 2020/21 to estimate abundance (updating the last estimate from 2009), to assess trend and population age structure, as well as changes in genetic diversity of right whales using this calving ground.

9.4.3.4 FEEDING GROUNDS

The Committee welcomed the results of a visual and acoustic survey of southern right whales off South Georgia/Islas (SC/67b/SH20). SC/67b/SH06 used genotypic markers to assess re-sight rates and sex ratios from biopsy samples (*n*=157) collected during 14 summer surveys in Antarctic Area IV. A preliminary abundance estimate was calculated using these data and further mark recapture analyses will be conducted intersessionally to provide an abundance estimate for review at next year's meeting. To further investigate linkages it was suggested that these high latitude data be compared the western Australia stock to investigate what population component is using this high latitude area.

Attention: SC

The Committee ***encourages*** *further mark recapture analysis of the genotype data of the 14-year dataset collected in the high latitudes of Area IV, to estimate the abundance of southern right whales in this feeding area and* ***agrees*** *that this will be considered at next year's meeting.*

9.4.3.5 PROGRESS TOWARDS POPULATION ASSESSMENT

This year, the Committee reviewed newly available information on population structuring of southern right whales around the Southern Hemisphere (Carroll *et al.*, In press) which further confirms the genetic differentiation of regional calving grounds off Argentina, South Africa, New Zealand and Australia, showing limited migratory movements between these areas (see Annex H, item 5.1,).

The Committee was provided with updates on trends and distribution for calving grounds off South Africa and off south and southwest Australia. Recent published data on population size and trend for calving grounds across the Southern Hemisphere were summarised in Annex H (table 2); this will be reviewed at next year's meeting. Given the trends in abundance and calving rates reported this year (Items 9.4.3.1 and 9.4.3.2), integration of these analyses in a common modelling framework was suggested as a useful way to evaluate common patterns and changes in demography and investigate the relative importance of environmental drivers in determining these patterns.

Another important aspect of population assessment is to update the pre-modern catch series for southern right whales, to better reflect patterns of regional exploitation. The Committee was informed that substantial new data are available on offshore whaling patterns and extent, particularly from American and British voyage logbooks (see Annex H, item 5.2,), which are likely to increase regional catch estimates and provide revised estimates of the numbers of whales struck but lost at sea by the different fisheries.

Attention: SC, G

To better understand patterns of right whale population dynamics around the Southern Hemisphere, and further the work on updated assessments, the Committee:

(1) ***agrees*** *that analysis of three southern right whale calving grounds (Head of the Bight and southwest Australia, southwest Atlantic and south Africa) should be undertaken using the same life-history model, to estimate regional demographic parameters and investigate commonalities in the population dynamics of these populations; and*
(2) ***supports*** *the compilation of new data on pre-modern right whale catches, and the organisation of a workshop to investigate regional right whale catches and rates of whales struck but lost by fisheries, in order to proceed toward regional population assessments.*

9.4.3.6 WORK PLAN AND BUDGET REQUESTS FOR 2019-2020

The work plan for southern right whales not the subject of a CMP is given in Table 13.

Table 13.

Workplan for southern right whales that are not the subject of a CMP

Topic	Intersessional 2018/19	2019 Annual Meeting (SC/68a)	Intersessional 2019/20	2020 Annual meeting
Southern right whales	Examine southern right whale demographic parameters across multiple calving grounds using a common modelling framework	Review progress		Complete comparison
Southern right whales	Plan right whale catch series workshop	Progress update	Organise catch series workshop	Workshop report

10. STOCKS THAT ARE OR HAVE BEEN SUGGESTED TO BE THE SUBJECT OF CONSERVATION MANAGEMENT PLANS (CMPs)

10.1 Stocks with existing CMPs

This item covers stocks (with a focus on progress with scientific work and information) that are either: (1) the subject of existing CMPs; or (2) are high priority candidates for a CMP. It also considers stocks that have previously been considered as potential CMPs, recognising that the Commission has stressed the need for Range States to support any IWC CMPs.

10.1.1 SE Pacific southern right whales

10.1.1.1 NEW INFORMATION

The Committee received information on advances with respect to sightings (SC/67b/CMP20) and acoustic monitoring (SC/67b/CMP08; SC/67b/CMP18) of the critically endangered population of SE Pacific southern right whales. This information is discussed in detail in Annex O (item 2.1.1). Four confirmed observations were made off Chile in 2017 (three opportunistic sightings and one entangled carcass) and there was another, as yet unconfirmed sighting involving adults and calves. Analysis to date of acoustic data collected off the southwestern tip of Isla de Chiloe in 2012 has provided valuable new information about call parameters and patterns.

10.1.1.2 PROGRESS WITH THE CMP

The Committee received information on progress in implementing priority actions of the CMP (SC/67b/CMP20) as discussed in Annex O (item 2.1.1.2).

This progress includes:

(1) deployment of Passive Acoustic Monitoring (PAM) devices along the coast of Chile and Peru (SC/67b/CMP18) in two locations that will also be used as the focus of educational and capacity-building activities in communities near the monitoring sites;
(2) additional capacity-building and awareness efforts (including posters, press releases and social media) including advice on how fishermen and the public can provide information to the national sighting network; and
(3) additional training towards increasing the capacity of range states to respond to entanglements.

Attention: SC, CC

The Committee ***reiterates*** *the importance of the CMP for the conservation of this critically endangered population of southern right whales in the southeastern Pacific,* ***welcomes*** *the progress being made in its implementation by Chile and Peru. It therefore:*

(1) ***commends*** *the scientific work and international co-operation being undertaken for the PAM project and looks forward to receiving the results of the acoustic studies such that future sighting surveys will be more informed and baseline information on the location of breeding grounds will be available; and*

(2) ***advises*** *that satellite imagery be explored as an additional means to inform the design of sighting surveys because it is likely that line-transect surveys would not successfully identify whales in some areas even if they were present.*

10.1.2 Southwestern Atlantic southern right whales

10.1.2.1 NEW INFORMATION

The Committee was pleased to receive a considerable amount of new information on the southwest Atlantic population of southern right whales; this is fully discussed in Annex O (item 2.1.2.1).

With respect to abundance, SC/67b/CMP/05 suggested that although the population has continued to increase, the rate may have been slowing, perhaps as a consequence of changes in distribution due to density-dependence processes (SC/67b/CMP02).

The Committee has for some time been focussing on the die off at Peninsula Valdes (e.g. IWC, 2011; 2015) and the excellent work of the Southern Right Whale Health Monitoring Program. New and updated information was presented this year on strandings and investigations related to health including examination of levels of stress hormones in baleen and kelp gull attacks (SC/67b/CMP04) and nutritional condition (SC/67b/CMP03). This work is ongoing.

Information was received on telemetry studies (one animal in 2016 and 8 in 2017) as part of an ongoing long-term study to understand the migratory routes and destinations of southern right whales wintering off the coast of Argentina (SC/67b/CMP17. Tracks reveal that these animals are found across a vast extent of the South Atlantic and each season visit multiple potential feeding areas.

The Committee also received the report of a land-based survey of whales near Miramar on the southwest coast of the Buenos Aires Province, Argentina, where there has been a recent expansion of right whales into the region where they have been seen from May to October with peaks in August and September (SC/67b/CMP21).

Attention: SC, G

The Committee ***reiterates*** *the importance of continued monitoring of the southwestern Atlantic population of southern right whales and research into threats that it may face. The Committee therefore:*

(1) ***commends*** *the work being undertaken on understanding the mortality events and* ***encourages*** *its continuation;*
(2) ***encourages*** *the researchers working on stress hormones in baleen to increase their sample size, consider suggestions for additional studies provided in Annex O (item 2.1.2.1) and present a full report to the Committee when it becomes available;*
(3) ***commends*** *the telemetry work,* ***encourages*** *its expansion and draws attention to additional analyses that could be addressed using the telemetry data suggested in Annex O (item 2.1.2.1).*

10.1.2.2 PROGRESS WITH THE CMP

The overall objective of the southern right whale CMP is to protect their habitat and minimise anthropogenic threats to maximise the likelihood that the population will recover to healthy levels and recolonise its historical range. The Committee was pleased to receive information on progress with the actions of the CMP from Argentina (SC/67b/CMP14), including the work described under Item 10.1.2.2, and Brazil (Annex O, appendix 2). Work in Brazil includes long-term monitoring via sightings and strandings networks, mitigation of entanglements and the development of a management plan for whalewatching (see Annex O, item 2.1.2.2).

Attention: SC, CC

The Committee ***reiterates*** *the importance of the CMP for the conservation of the southwestern Atlantic population of southern right whales. The Committee therefore:*

(1) ***welcomes*** *the progress being made in the implementation of the CMP reported by Argentina and Brazil and supports its continuation;*
(2) ***encourages*** *the continued co-operation and collaboration amongst range states towards implementing the CMP and addressing mortality evens in this population; and*
(3) recognising the report of a ship-struck southwestern Atlantic southern right whale in the range of the southeastern Pacific (Estrecho de Magallanes), ***encourages*** *co-operation with those involved in the southeastern Pacific CMP to facilitate a regional assessment; and*
(4) ***encourages*** *the research work identified under Item 10.1.2.1.*

10.1.3 North Pacific gray whales

10.1.3.1 RANGEWIDE ASSESSMENT

Donovan summarised the report of the Fifth Rangewide Workshop on the Status of North Pacific Gray Whales (SC/67b/Rep07) held at the Granite Canyon Laboratory, California of the Southwest Fisheries Science Center from 28-31 March 2018. The primary tasks of the workshop were to (a) review the results of the modelling work identified at the fourth rangewide workshop (IWC, 2018a) and the 2017 Scientific Committee meeting (IWC, 2018b), (b) examine the new proposed Makah Management Plan (submitted by the USA – given as Annex E, Appendix 1) for gray whaling off Washington state and (c) to update as possible, and develop a workplan for, updating the scientific components of the Conservation Management Plan (CMP) for western gray whales.

A full discussion of the workshop can be found in Annex O (item 2.1.3.1). The Workshop finalised its work on (a) prioritising stock structure hypotheses, (b) finalising inputs for the modelling work especially related to bycatch; and (c) incorporating the Makah Management Plan (SC/67b/Rep07, Annex E, Appendix 1) into the modelling framework.

Two stock structure hypotheses (3a and 5a) were given priority whilst others were used in sensitivity tests. In summary, Hypothesis 3a assumes that whilst two breeding stocks (Western and Eastern) may once have existed, the Western breeding stock is extirpated. Whales show matrilineal fidelity to feeding grounds, and the Eastern breeding stock includes three feeding aggregations: Pacific Coast Feeding Group (PCFG), Northern Feeding Group (NFG), and the Western Feeding Group. Hypothesis 5a assumes that both breeding stocks are extant and that the Western breeding stock feeds off both coasts of Japan and Korea and in the northern Okhotsk Sea west of the Kamchatka Peninsula. Whales feeding off Sakhalin include both whales that are part of the extant Western breeding stock and remain in the western North Pacific year-round, and whales that are part of the Eastern breeding stock and migrate between Sakhalin and the eastern North Pacific.

In discussion of the report and intersessional progress, the Committee thanked Donovan, Punt and the participants for the progress made, approved the conditioning results developed after the workshop, noted the preliminary results from the modelling and agreed a strategy for obtaining conservation advice (see recommendation below under Item 10.3). The management implications of the results for the Makah Management Plan are found under Item 7.1.3.

10.1.3.2 REGIONAL STUDIES

The Committee was pleased to receive recent information from long-term studies in the breeding lagoons of Mexico (SC/67b/CMP09) as discussed in Annex O (item 2.1.3.1.1).

The Committee received several updates on work undertaken in the Russian Federation (see Annex O, item 2.1.3.2). It welcomed the annual update of activities from the IUCN Western Gray Whale Advisory Panel (see Annex O, appendix 3) which highlighted work to develop a monitoring and mitigation plan for a 2018 seismic survey being undertaken near the feeding grounds off Sakhalin Island, Russia and issues related to fishing gear. SC/67b/CMP07 updated findings from the long-term monitoring programme carried out by the Russian Gray Whale Project off Sakhalin Island, Russia. The research programme run in the same area by two oil companies was presented in SC/67b/ASI04 and discussed in Annex S (item 4.2).

The recent status of conservation and research on gray whales in Japan was reported in SC/67b/CMP12. During May 2017-April 2018, no anthropogenic mortalities were reported from the adjacent waters off Japan, while two opportunistic sightings of gray whales were made near Aogashima Island in May 2017 and February 2018.

Finally, SC/67b/CMP11 reported on the possible occurrence of a gray whale off the east coast of Korea; work is continuing to try to confirm the species identification; if confirmed it will be the first record in these waters in over 40 years.

Attention: CG-R, SC, G

The Committee ***reiterates*** *the importance of long-term monitoring of gray whales,* ***recommends*** *that range states support such work and* ***welcomes*** *the information provided this year. In particular, the Committee:*

(1) ***commends*** *the work in the breeding lagoons and urges its continuation;*
(2) ***encourages*** *an additional calf-count survey for Punta Banda to address apparent differences in numbers of calves observed in the lagoons with counts from California;*
(3) ***reiterates its concern*** *at the risk of whales becoming entangled in gear placed by the salmon trap-net fishery off Sakhalin Island, recognises that disentanglement training has occurred but* ***recommends*** *that measures to be taken to reduce risk;*
(4) ***encourages*** *continued genetic analyses to assist in stock structure discussions especially related to a western breeding stock;*
(5) ***welcomes*** *the continued provision of information from Japan and* ***encourages*** *researchers to continue to collect as much information on sightings as possible, including, if feasible, attempting to obtain biopsy samples; and*
(6) ***welcomes*** *the information from Korea and the willingness of researchers to investigate sightings from social media as a form of 'citizen science', which can be especially valuable for areas where occurrence is very rare animals in areas with little to no information on critically endangered species.*

10.1.3.3 PROGRESS WITH THE CMP

As noted above, one of the objectives of the fifth rangewide workshop was to progress work with updating the scientific components of the original IWC/IUCN CMP in the light of the results of the rangewide review. Although some work was undertaken, there was insufficient time at the workshop to complete this although a workplan to achieve it was suggested (see SC/67b/Rep07). The Committee concurred with this view and this is incorporated into the workplan below.

Another important component of the CMP effort is the need for a stakeholder workshop (tentatively forecast to occur in 2019) to finalise the CMP and develops a strategy for its implementation. The plan is for a workshop, co-sponsored by IWC, IUCN and the signatories to the Memorandum of Cooperation, to: (1) review and updating of the CMP; (2) establishing a stakeholder Steering Group to monitor CMP implementation, (3) arrange for a coordinator of the CMP and (4) establish a work plan and consider funding mechanisms to implement the actions of the plan.

Attention: C-A, CG-R, CC, SC

The Committee ***reiterates*** *the importance of the CMP for the conservation of western gray whales. The Committee therefore:*

(1) ***recognises*** *the tremendous work undertaken in the rangewide assessment and the value of the modelling framework developed;*
(2) ***agrees*** *that the next part of the process is to develop conservation-related questions and to use the framework to address these with a view to examining results at SC68a;*
(3) ***agrees*** *that a small group meeting (see Item 27) attended by at least the national co-ordinators of the Memorandum of Co-operation on gray whales, Reeves, Punt and Donovan be held to: (a) draft an update to the CMP; and (b) identify conservation-related questions to be addressed by the modelling framework and to present results at SC68a;*
(4) ***requests*** *those signatories to the Memorandum of Co-operation on western gray whales who have not yet named a national co-ordinator to do so promptly; and*
(5) ***supports*** *the holding of a stakeholder workshop in 2019 co-sponsored by the IWC, IUCN and the states that have signed the Memorandum of Co-operation and* ***welcomes*** *the valuable assistance of IUCN in organising the workshop.*

10.1.4 Franciscana

10.1.4.1 NEW INFORMATION

The Committee received valuable new information on franciscana at this meeting related to fisheries and bycatch from five localities in North Espírito Santo State, Brazil (SC/67b/SM30) – bycatches of Guiana dolphins was also reported. Additional information was presented assessing fisheries that operate in Fisheries Management Area (FMA) Ib for their compliance with Brazilian ordinance (IN) 12 (e.g. with respect to gill-net regulations and no-take zones) and risk of bycatch (SC/67b/SM05) – compliance was limited and enforcement poor. Both projects were funded by the IWC Small Cetacean Fund and the Government of Italy. This information is discussed in Annex O (item 2.1.4.1) and a related recommendation is given under Item 10.4.2.2.

10.1.4.2 PROGRESS WITH THE CMP

The overall objective of the CMP, submitted by Argentina, Brazil and Uruguay (IWC/66/CC11) and adopted in 2016, is to protect franciscana habitat and minimise anthropogenic threats, especially bycatch. It includes seven high priority actions, ranging from public awareness and capacity building through research to mitigation. Coordination with Uruguay to implement the CMP in this area will be initiated during a workshop that will take place in May 2018 with the main stakeholders (SC/67b/CMP16). The CMP is funded by the IWC CMP Voluntary Funds and the World Wildlife Fund.

Attention: CG-R

The Committee ***emphasises*** *the importance of the CMP for the conservation of franciscana in the waters of Argentina, Uruguay and Brazil. The Committee therefore:*

(1) ***stresses*** *the value of the actions included in the CMP towards future assessments of the status of franciscana, which is imperative for determining the effectiveness of conservation efforts;*
(2) ***recommends*** *that research be undertaken to estimate the abundance of franciscana dolphin off Buenos Aires province, Argentina; and*
(3) ***recommends*** *that additional research be undertaken to determine the effectiveness of management measures, such as that described in SC/67b/SM05 for other ports (e.g. Macaé, Tamoios (Cabo Frio) and Armação dos Búzios – the fishery in Tamoios coincides with a high diversity of marine megafauna).*

The Committee established an intersessional correspondence group that will help co-ordinate the presentation of CMP projects for this species across sub-committees at SC/68a (Annex Y).

10.2 Progress with identified priorities

10.2.1 Humpback whales in the northern Indian Ocean including the Arabian Sea

10.2.1.1 NEW INFORMATION

The Committee received several papers that improved knowledge of Arabian Sea humpback whales and a full discussion can be found in Annex O (item 2.2.1). It welcomed the information on the progress of work being undertaken by the Arabian Sea Whale Network (ASWN) formed in 2015 (SC/67b/CMP10). The ASWN is an informal collaboration of researchers, consultants and conservation and governmental organisations interested in the conservation of whales in the Northern Indian Ocean. A primary goal of the ASWN is to promote and foster research and collaboration in previously unsurveyed parts of the Arabian Sea humpback whales' suspected range, as well as in Oman where surveys have been conducted since 2000. Work has focused on collecting data on whale distribution and status (including through increased awareness and an observer programme – described in SC/67b/CMP15)), the introduction and implementation of a regional online data platform (SC/67b/PH03) and providing updates on research activities in Oman, India, Pakistan and Sri Lanka (SC/67b/INFO07). Two marine protected areas have been established in Pakistan (Astola Island and Indus Canyon).

Madhusudhana *et al.* (2018) reported on and compared humpback whale songs recorded off India, Oman, Reunion Island and Comoros Islands in the southwest Indian Ocean. The results highlighted (a) the distinct nature of the Arabian Sea population and (b) that SW Indian Ocean whales may move into the Arabian Sea more commonly than previously thought.

SC/67b/CMP13 reported on a humpback whale tagged off Oman that moved to the southern tip of India and back again - the first recorded movement of a whale across the Arabian Sea. Four additional satellite tags were deployed where the whales remained over the continental shelf of central and southern Oman.

Attention: G, SC

The Committee ***welcomes*** *the new information from the region on this critically endangered population and* ***commends*** *the researchers for their initiatives and collaborative efforts. In light of the information presented, the Committee:*

(1) ***encourages*** *the collection of genetic information which would be helpful for identifying stock structures within the area;*
(2) ***recommends*** *future use of unoccupied aerial systems to (i) measure whale health, (ii) develop long-term health metrics, (iii) compare body condition to stock C in the Southern Hemisphere, which is the presumed 'source' population for whales in the Arabian Sea and (iv) assess for evidence of anthropogenic threats;*
(3) ***commends*** *the use of fishing crew as observers and* ***advises*** *that the crew-based observer programme continue, recognising that it is not clear if the timing of the sightings reflects the seasonal distribution of whales or the seasonal nature of fishing effort and* ***encourages*** *future research to tease apart timing of the distributions using targeted surveys;*
(4) ***advises*** *that capacity building for local scientists be continued such that surveys can be deployed in suspected areas of humpback whale distribution and data can be gathered for future assessments;*
(5) ***advises*** *the continuation of monitoring songs of Arabian Sea humpback whales and that additional data sets be acquired comparison purposes, particularly from the southwest Indian Ocean, if they exist, to further (i) detect the movement of southwestern Indian Ocean animals in Boreal winter, (ii) document potential diffusion of southwestern Indian Ocean song, (iii) provide a long-term data set for the comparison of songs across Oman, Pakistan and India to assess continuity of whales in the Arabian Sea and (iv) evaluate the unprecedented temporal stasis of song in the Arabian Sea; and*
(6) ***agrees*** *that an intersessional correspondence group (Annex Y) be formed to review the methods used for the preliminary estimates of abundance, in order to increase their robustness by taking into account the non-random survey approach that violates some key assumptions of mark-recapture models.*

10.2.1.2 PROGRESS WITH INTERNATIONAL CO-OPERATION AND REGIONAL MEASURES SUCH AS CMPS

A Concerted Action for Arabian Sea humpback whales under the Convention on Migratory Species (CMS; SC/67b/INFO06) was drafted and passed with wide support from Arabian Sea range states at the CMS COP in October 2017. It is hoped that this Concerted Action can be implemented in conjunction with a CMP as a means to translate current research and conservation efforts and plans into concrete, government-supported conservation measures in Arabian Sea humpback whale range states.

Attention: *C-A, S*

The Committee ***reiterates*** *its serious concern about the status of the endangered Arabian Sea humpback whale population and the anthropogenic threats it faces. It therefore:*

(1) ***commends*** *efforts to develop the Concerted Action under the CMS, noting that it covers many of the elements required for a CMP;*
(2) ***stresses*** *the value of regional initiatives and* ***encourages*** *range states to explore future sources of collaboration; and*
(3) ***encourages*** *continued efforts between range states and Secretariats to work toward a joint CMS-IWC CMP.*

10.2.2 Mediterranean fin whales

The ACCOBAMS Meeting of Parties has endorsed the development of a CMP, ideally jointly with the IWC, for fin whales in the Mediterranean Sea. A small group will meet in the summer of 2018 to draft an outline for a CMP that can be presented at SC/68a. ACCOBAMS is also considering the development of CMPs for other species in the region.

10.2.3 South American River Dolphins

Advice was sought regarding the development of a CMP for South American river dolphins, which currently have several actions plans endorsed by various range states.

Attention: CG-A

The Committee ***advises*** *that the applicable range states work towards developing a draft CMP for presentation at SC/68a.*

10.3 Workplan 2019-20

The workplan on matters related to stocks that are or might be the subject of CMPs is given as Table 14.

Table 14

Summary of the work plan on conservation management plans.

Topic	Intersessional 2018/19	2019 Annual Meeting (SC/68a)	Intersessional 2019/20	2020 Annual meeting
Southeast Pacific right whales	.	Review progress with scientific aspects of the CMP		Review progress with scientific aspects of the CMP
Southwestern Atlantic right whales		Review progress with scientific aspects of the CMP		Review progress with scientific aspects of the CMP
Gray whales	Hold workshop on scientific aspects of CMP and use of modelling framework.	Review results and provide advice on scientific aspects of CMP	Stakeholder workshop	Review scientific aspects of results of stakeholder workshop
Franciscana		Pre-assessment for in-depth review		Continue pre-assessment and develop plan for in-depth assessment
Humpback whales in Northern Indian Ocean	Intersessional email group (Annex Y) on abundance estimates	Review new information and progress towards CMP		Review new information and progress towards CMP
Mediterranean fin whales	Develop outline draft	Review draft and progress towards CMP		Review progress towards CMP
South American river dolphins		Review new information and progress towards CMP		Review new information and progress towards CMP

11. STOCK DEFINITION AND DNA TESTING

This agenda item merges two previously separate sub-groups, the Working Group on Stock Definition and the Working Group on DNA. During SC67b, the Stock Definition and DNA Testing Working Group assessed genetic methods used for species, stock and individual identification, including matters associated with the maintenance of DNA registers (see 11.1); continued to develop and update guidelines for preparation and analysis of genetic data within the IWC context (see 11.2); and provided the Committee with feedback and recommendations concerning stock structure related methods and analyses (see 11.4), including those relevant to other sub-committees (see 11.3). The Report of the Working Group is given as Annex I.

11.1 DNA testing

This item has been considered since 2000 in response to a Commission Resolution (IWC, 2000).

11.1.1 Genetic methods for species, stocks and individual identification

The Committee received two papers relating to the use of genetic methods for species, stock and individual identification. The first paper (Carroll *et al.*, 2018) provided a review of how technological advances, particularly those associated with the development of high throughput sequencing (HTS) technology, can aid in genetic monitoring. Of particular interest to the Committee was discussion of targeted capture approaches that allow for microsatellite genotyping via HTS (e.g. De Barba *et al.*, 2017). Much of the past genetic work has relied on generating microsatellite datasets, including the work to maintain DNA registries of bycaught or direct catches (see Items 11.1.2 and 11.1.3). These 'legacy' datasets may include microsatellite genotypes for thousands of individuals. While technical challenges exist, microsatellite genotyping via HTS could 'bridge the gap' by maintaining the utility of these legacy datasets while also taking advantage of the newer HTS approaches.

The second paper (Baker *et al.*, In press) presented the results of a study confirming the potential to detect environmental DNA (eDNA) in seawater collected from the wake of killer whales. This is a new approach for detecting and identifying cetacean species, including those that may be elusive to study using other methods. Although eDNA has been more broadly used to detect the occurrence of species in an area (i.e. DNA barcoding), it could provide sequence data useful for stock-level identifications of cetaceans under certain circumstances (e.g., when a single animal is present). It was noted, however, that its utility in addressing questions requiring individual identification via multi-locus genotyping is, at least currently, limited for scenarios in which the water sample could contain DNA from multiple individuals.

Attention: SC

The Committee ***welcomes*** *the opportunity to review papers that take advantage of technological advances to improve the ability to detect and identify species, stocks, and individual cetaceans. It* ***encourages*** *the submission of similar papers in the future and recognises the relevance of these techniques to the Committee's work.*

11.1.2 'Amendments' of sequences deposited in GenBank

While *GenBank*[7] is an important scientific resource, it is an uncurated database of DNA sequences and thus contains sequences that are misidentified or have other annotation problems. While retaining the 'raw data' represented in *GenBank* is valuable, less-experienced users may be unaware that additional sequence validation may be needed when incorporating *GenBank* sequences into a study. The Committee has agreed (IWC, 2018c, p. 228) that its revised DNA quality guidelines will contain a section discussing the precautions that should be taken when including GenBank sequences in a study. This text has been drafted and will be incorporated into the revised guidelines (see Item 11.2).

11.1.3 Collection and archiving of tissue samples from catches and bycatches and
11.1.4 Reference databases and standards for diagnostic DNA registries

The Committee previously endorsed a new standard format for the updates of national DNA registers to assist with the review of such updates (IWC, 2012a, p. 53), and the new format has worked well in recent years. This year, the update of the DNA registers by Japan, Norway and Iceland were based again on this new format. Details are given in Annex I (appendices 2-4) for each country, covering the period up to and including 2017. Almost all samples in the three registries have been analysed for microsatellites, and work on unanalysed samples is continuing. Almost all samples in the registries of Japan and Iceland have also been analysed for mtDNA.

During last year's discussion of the Norwegian minke whale DNA register (IWC, 2018c, p. 228-229), the Committee was informed that mtDNA analysis on Norwegian samples had been discontinued and that microsatellite typing would eventually be replaced by SNP analysis. The Committee had expressed concern regarding the comparability of the DNA registers in the future. This year, the Committee noted that Norway had discontinued mtDNA typing of samples and substituted it with SNP genotyping.

Attention: CG-A

The Committee ***expresses appreciation*** *to Japan, Norway and Iceland for providing updates to their DNA registries using the standard format agreed in 2011 and providing the detailed information contained in their DNA registries.*

11.2 Guidelines and methods for genetic studies and DNA data quality

Two sets of guidelines have been developed for reference in the Committee's discussions of stock structure. The most recent version of the guidelines for genetic data analyses are in press with the Commission's *Journal of Cetacean*

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[7] https://www.ncbi.nlm.nih.gov/genbank/

Research & Management. The DNA data quality guidelines address DNA validation and systematic quality control in genetic studies, and are currently available as a 'living document' on the IWC website[8]. In recent years, it has become common for the Committee to review papers using data derived from Next Generation Sequencing (NGS) approaches, including SNPs, to address stock structure questions (see Item 11.3).

Attention: SC

The Committee ***emphasises*** *the importance of keeping its guidelines related to genetic data quality and analyses up to date. It therefore:*

(1) ***reiterates*** *the need to update these guidelines to incorporate the discussion of data quality measures used for Next Generation Sequencing data; and*
(2) ***agrees*** *to continue the intersessional correspondence group (Annex Y) to review revised sections of the DNA data quality guidelines that apply to data generated from next generation sequencing platforms, including SNPs and whole genome sequencing, with the goal of posting an updated version of the guidelines on the website next year.*

11.3 Provide advice on stock structure to other sub-groups

The Working Group on Stock Definition and DNA also has the task of discussing high-priority stock related papers from other sub-committees and working groups to provide them with stock structure related feedback and recommendations. These discussions often refer to the genetic analysis guidelines and genetic data quality documents.

The discussions (see Annex I for details) are summarised under the relevant stock agenda items in this report. Two, more general issues arose from discussions of Southern Hemisphere stocks and North Atlantic common minke whales. These are considered below.

11.3.1. Southern Hemisphere whale stocks and use of samples

The Committee reviewed the results of genetic analyses of Southern Hemisphere whale stocks, including Southern Hemisphere blue, fin, right and sei whales. These results highlighted the value of existing collections of tissue samples to address stock structure questions.

Attention: SC

In reviewing the results of stock structure analyses of Southern Hemisphere whale stocks, the Committee expresses ***concern*** *regarding the depletion of tissue samples in existing collections (including those collected during the IWC SOWER surveys, although the Steering Group does take this into account when reviewing requests). Given recent advances in high throughput sequencing technology, the Committee* ***agrees*** *that an intersessional correspondence group (Annex Y) should be formed to provide recommendations on genomic approaches to maximise the utility of these samples for future studies.*

11.3.2. North Atlantic common minke whales

The Committee reviewed the results of genetic analyses pertaining to the stock structure of North Atlantic minke whales (SC/67b/Rep06). The analyses presented involved the use of a new approach to evaluate stock mixing proportions by (1) identifying a 'reference' year in which mixing of stocks was considered low based on a lack of heterogeneity in genetic characteristics estimated for each area, and (2) using principal component analysis of the genetic data to assign stock affinities in the non-reference years based on proximity to mean values in the reference year.

Attention: SC, C-A

The Committee reviewed the use of a new approach that used ordination analyses of genetic data to assign stock mixing proportions. Recognising that this new approach requires making certain assumptions about the data, the Committee:

(1) ***agrees*** *that the inference of mixing rates was informative for AWMP/RMP simulation trials in the absence of empirical data; and*
(2) ***encourages*** *the attempt to use genetic data to estimate mixing rates in the context of other IWC-related tasks.*

11.4 New statistical and genetic issues relating to stock definition

11.4.1. Simulation tools for spatial structuring

TOSSM was developed with the intent of testing the performance of genetic analytical methods in a management context using simulated genetic datasets (Martien *et al.*, 2009), and more recently the TOSSM dataset generation model has been used to create simulated datasets to allow the plausibility of different stock structure hypotheses to be tested (Archer *et al.*, 2010; Lang and Martien, 2012). The Working Group noted that while TOSSM has been particularly valuable in

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[8] http://iwc.int/scientific-committee-handbook#ten

informing the interpretation of results of stock structure related analyses, it has not been broadly used within the IWC Scientific Committee for this purpose.

In recent years, a wide-range of software packages have become available for producing simulated datasets that can be used for statistical inference and/or validating statistical methods (Hoban, 2014, and see ; IWC, 2017c p.44), and in 2016 the Committee agreed to expand this item (formerly specific to TOSSM) to include a broader range of tools (IWC, 2016c p.44).

Attention: SC

The Committee noted that while simulation-based approaches have been particularly valuable in informing the interpretation of results of stock structure-related analyses, they have not been broadly utilized within the Committee for this purpose. The Committee ***agrees****:*

(1) to continue an intersessional review via an email correspondence group (Annex Y) of the available simulation tools and their potential utility to the Committee; and
(2) to consider bringing in invited expertise to present an overview of the applicability of such approaches in order to expedite progress on this agenda item.

11.4.2. Terminology

Defining and standardising the terminology used to discuss 'stock issues' remains a long-standing objective of the Working Group, in order to help the Committee report on these issues according to a common reference of terms (IWC, 2014 p.287-8). At SC67b, the status of the existing draft glossary on key terms related to stock definition was revisited.

Attention: SC

The Committee ***agrees*** *to establish an intersessional correspondence group (Annex Y) to revisit terminology with specific reference to the implications of inferred stock structure in other sub-committees, particularly those that deal with large whale assessments, and suggest revisions where appropriate for consideration at SC68a.*

11.4.3. Close-kin mark-recapture

An overview of the close-kin mark-recapture (CKMR) approach (Bravington *et al.*, 2016) was presented to the Committee last year (IWC, 2018c p.40). CKMR uses multi-locus genotyping to find close relatives among tissue samples from dead and/or live animals; the number of kin-pairs found, and their pattern in time and space, can be embedded in a statistical mark-recapture framework to infer absolute abundance, parameters like survival rate, and stock structure. No papers applying the CKMR approach were reviewed by Committee this year, although the value of integrating data from epigenetic aging (see 11.4.4) into CKMR was noted.

Attention: SC, G

Given that close-kin mark-recapture has multiple applications that fall within the Committee's scope of work, the Committee ***encourages*** *the submission of papers using this approach in the future.*

11.4.4. Epigenetic ageing

Information on estimated age of individuals can be used in many aspects of the Committee's work, including (1) discriminating between the parent and offspring among genetically identified parent-offspring pairs, which can inform both assessment of stock structure as well as genetic mark-recapture estimates of abundance (e.g. CKMR); and (2) integrating age information into the population modelling exercises integral to assessment work (e.g. on RMP implementation). Recently, epigenetic (DNA-methylation) ageing has been successfully used to estimate age in humpback whales (Polanowski *et al.*, 2014). This year, the Committee invited Jarman, the lead scientist on the humpback whale work, to give an overview presentation to the Committee. This session was organised as a special evening session in order to enable participation across sub-committees and Working Groups. He covered issues specific to age estimation in cetaceans, including how DNA methylation-based age estimation are likely to perform in cetaceans and what current and near-future prospects there are for this class of methods (see Annex I, item 5.5).

The Committee also reviewed the results of a study to evaluate the feasibility of using the DNA-methylation technique to estimate age in Antarctic minke whales (SC/67b/SDDNA04). This study was initiated in response to a recommendation made during the Expert Panel review of the NEWREP-A proposal (SC66A/REP06, p17). DNA-methylation rates were examined for seven methylation sites (CpG sites) within three genes, and regressions of each CpG methylation site against age determined by earplug were conducted. When all sites were incorporated, the assay predicted age from skin samples with a standard deviation of about 8.9 years. While some sites showed age-related effects, others did not show such correlation. Thus, using only those loci that appear to have an age-related effect might reveal a stronger relationship between methylation rates and age.

During the discussion (Annex I, item 5.5) it was noted that the humpback whale age assay, which used the same sites, reports a precision of 2.99 years, measured as the average of the absolute values of the differences between known and estimated ages (Polanowski *et al.*, 2014). During the presentation, the precision as measured by the standard deviation for absolute age prediction was reported as 4.8 years. That was a preliminary study demonstrating the fundamental feasibility of this approach, and is not as accurate or precise as tests developed for humans and mice based on analysis of many more CpG sites. While precision is expected to improve with the inclusion of more CpG sites, the maximum precision possible for any DNA methylation-based age estimator is likely limited by the imperfect relationship between chronological age and biological age. To date, that precision has ranged from 3.9% in humpback whales (Polanowski *et al.*, 2014 assuming a 95-year lifespan), to 3.2% of lifespan in humans (e.g. Horvath, 2013) and 1.7% of lifespan in mice (Stubbs *et al.*, 2017). These observations indicate that the SD and 95% CI for age estimation described in Polanowski *et al.* (2014) and in SC67b/SDDNA04 could be substantially improved before an inherent limit is reached. These precision estimates adhere to age determination in individual specimens. Hence, averaged age estimates over cohort will improve over larger sample sizes and may be more precise.

The Committee noted that the implications of this upper limit on precision in estimating age for individuals would need to be evaluated in the context of the specific application for which the age data were being used. For example, although additional precision is helpful, CKMR studies may be informed by relatively crude estimates of age allowing the parent to be discriminated from the offspring (i.e. ordinal age).

Attention: SC

The Committee welcomed the results of the study to evaluate the feasibility of using epigenetic techniques to estimate age in Antarctic minke whales and ***agrees****:*

(1) that the current set of loci did not provide sufficient precision for use in the population dynamics modelling exercise recommended for NEWREP-A; and
(2) that identification of additional sites with an age-related DNA-methylation pattern is encouraged, as it would likely allow more precise estimates of age to be made in the future; and
(3) given that there is an upper limit to the degree of precision that can be achieved using this technique, the utility of epigenetic age estimation to the Committee should be further evaluated by the sub-committees concerned with regard to the degree of precision needed for the specific application of interest.

11.5 Workplan 2019-20

The details of the workplan are given in Table 15.

Table 15

Workplan on topics related to genetics.

Topic	Intersessional 2018/19	2019 Annual Meeting (SC/68a)	Intersessional 2019/20	2020 Annual meeting
3.1 DNA quality guidelines	Intersessional group (Annex Y) to review recent revisions to the DNA quality guidelines that pertain to data produced using NGS approaches.	Report and finalise updated guidelines		
4.4.2 Recommendations to avoid sample depletion	Intersessional email group to provide recommendations on genomic approaches to maximize the utility of tissue samples that are in danger of becoming depleted in the future.	Report and provide advice		
4.5 North Pacific minke whale stock structure	Perform genetic analyses detailed in Appendix 5; report results at intersessional workshop on the North Pacific minke whale IR.	Review results and provide advice		
5.1 Simulations	Intersessional email group to review software packages and evaluate utility to the Committee.	Report	Continue as needed	Report (if needed)
5.3 Terminology	Intersessional email group to continue discussions of the use of stock structure-related terms within the Committee.	Report	Continue as needed	Report (if needed)

12. CETACEAN ABUNDANCE ESTIMATES, STOCK STATUS

The Committee received new information from the Standing Working Group on Abundance Estimates, Status and International Cruises (ASI) that had been established (IWC, 2017c, p. 94) to formally review and agree on the status of the abundance estimates submitted to the Scientific Committee across all of the Committee's sub-committees and working groups. It also assists the Committee and the Secretariat in developing a biennial document reporting to the Commission on the abundance and status of whale stocks.

12.1 Summary of abundance estimates and update of IWC consolidated table

Appendix 3 of Annex Q provides detailed information about abundance estimates agreed by the Committee, including estimates received prior to and during 2017, as well as ones evaluated this year. The Secretariat maintains a consolidated table.

Broadly, cetacean abundance estimates are usually obtained in one of three ways. Line transect surveys require observers on ships or aircraft to detect animals while the observers are traveling on paths traversing the survey area. Statistical methods are used to estimate how many animals were not seen, usually by evaluating how detection deteriorates as sighting distance increases and by extrapolating to survey areas beyond visual detection distance. Mark-recapture studies require multiple attempts to 'capture' individuals that are mixing between attempts. For cetaceans, individual animals are usually identified - and hence 'captured'- on the basis of matching photographs of whale markings, or by genetic analysis of biopsy samples of live animals. Statistical methods are used to estimate how many animals were never captured, based on information about the probability of capture, which is inferred from instances when the animal was sometimes captured and sometimes not. Population model based abundance estimates use information from a variety of sources to build a mathematical model of how a population changes over time. Important data and parameters in such models include survival rates, productivity rates, and previous abundance estimates. By fitting (and possibly projecting) this model, an estimate of current abundance is achieved.

Many sophisticated abundance estimation methods are hybrids or extensions of these basic approaches.

This year, the Committee **endorses** the following:

(1) a photo-id mark-recapture estimate of 2011 abundance for Bering-Chukchi-Beaufort Seas bowhead whales;
(2) an aerial line transect estimate of 2013 abundance of East Canada / West Greenland bowhead whales;
(3) aerial line transect estimates of 2015 abundance of East Greenland and West Greenland North Atlantic humpback whales;
(4) ship-based line transect abundance estimates of North Atlantic humpback whales in Iceland/Faroe Islands in 2007 and 2015;
(5) aerial line transect abundance estimates of East Greenland (2015) and West Greenland (2007 and 2015) North Atlantic minke whales;
(6) ship-based line transect abundance estimates of North Pacific Bryde's whales for several areas and time periods;
(7) aerial line transect abundance estimates of East Greenland (2015) and West Greenland (2005, 2007 and 2015) North Atlantic fin whales; and
(8) genetic mark-recapture abundance estimates for Maui's dolphins in New Zealand for several years.

Table 16 summarises key information about the **agreed** abundance estimates. Full details are given in Annex Q (item 3 and appendix 3).

Attention: SC, S, C-A

Abundance estimates are a key parameter in determining status. The Committee:

(1) ***endorses*** the new abundance estimates *presented in Annex Q, Appendix 3 for inclusion in the IWC Table of Accepted Abundance Estimates;*
(2) ***agrees*** *that they should be incorporated into that table and uploaded to the IWC website; and*
(3) ***agrees*** *that the table should continue to be updated intersessionally by the Steering Group (Annex Y).*

12.2 Process to review abundance estimates

Abundance estimates are needed to assess the status of cetacean populations and are used extensively by the Committee, including for providing management advice. These estimates are often computed by standard, but technically advanced methods. In addition, because of the high scientific standards found within the Committee's work, it is not uncommon for the Committee to receive estimates of abundance computed using novel methods and non-standard software/code. The review of these estimates can be complex and time consuming. At last year's meeting, the Committee noted that adequate time is needed to review abundance estimates and agreed that a process to facilitate the review of these estimates be developed (IWC, 2018c). In addition, the Committee noted that reviews would benefit if minimum requirements for the presentation of abundance estimates are established.

Table 16

Abundance estimates, CVs and 95% confidence intervals for estimates agreed at the 2018 meeting.

Whale and Region	Year	Estimate	CV	95% Confidence Interval
North Pacific Bryde's whales				
Area 1W	1995	12,149	0.41	5,579-26,454
	2000	6,894	0.47	2,872-16,549
	2011	25,158	0.38	12,202-51,872
Area 1E	1995	15,695	0.42	7,079-34,801
	2000	19,200	0.56	6,929-53,204
	2011	9,315	0.33	4,957-17-505
Area 2	1995	4,340	0.45	1,876-10,039
	2000	6,083	0.61	2,030-18,229
	2014	6,491	0.36	3,254-12,950
North Atlantic common minke whales				
East Greenland	2015	2,762	0.47	1,160-6,574
West Greenland	2007	9,066	0.39	4,333-18,973
	2015	5,095	0.46	2,171-11,961
North Atlantic fin whales				
East Greenland	2015	6,440	0.26	3,901-10,632
West Greenland	2005	9,800	0.62	3,228-29,751
	2007	15,957	0.72	4,531-56,202
	2015	2,215	0.41	1,017-4,823
North Atlantic humpback whales				
East Greenland	2015	4,223	0.44	1,845-9,666
West Greenland	2015	993	0.44	434-2272
Iceland/Faroe Islands	2007	18,105	0.43	7,226-45,360
	2015	10,031	0.36	4,962-20,278
Bowhead whales				
Bering-Chukchi-Beaufort Seas	2011	27,133	0.22	17,809-41,377
East Canada / West Greenland	2013	6,446	0.26	3,722-11,200
Gray whales				
Western North Pacific	1995	74	0.05	66-81
	2015	200	0.03	187-211
Maui's dolphin				
North Island, New Zealand	2016	57	n/a	44-75

This year, the Committee developed a process to improve the review of abundance estimates, including a prioritisation of the estimates according to the timeline they need to be used by the Committee. This process is described in detail in Annex Q, item 2.1. In addition, minimum requirements to present abundance estimates for review by the Committee were established. Details are given in item 2.2 of Annex Q.

The Committee noted that validation may be needed before estimates computed using novel methods and non-standard software are used to provide management advice (Annex Q, item 2.3). The Committee also noted the need to consider how estimates of abundance from population models are reviewed before they are included in the Table of Accepted Abundance Estimates (Annex Q, item 2.4).

Attention: SC, S

*The Committee **reiterates** the importance of using high quality, fully reviewed abundance estimates for its work. To achieve this the Committee **agrees**:*

(1) to adopt the process to improve the review of abundance estimates given in Annex Q (item 2.1);
(2) the minimum requirements for the presentation of estimates for review by the Committee given in Annex Q (item 2.2);
(3) to host a pre-meeting before next year's meeting (SC68a) to develop (a) a process to validate abundance estimates computed with non-standard methods, noting the value of simulated datasets in this process; (b) a process to review estimates of abundance computed with population models is needed.

12.3 Methodological issues

12.3.1 Model-based abundance estimates (and amendments to RMP guidelines)

The Committee noted that there was a need for RMP guidelines to be modified in order to incorporate spatial modelling approaches to estimate abundance.

Attention: SC

*The Committee noted that whilst much progress has been made with respect to considering model-based estimates (IWC, 2016c), the 'Requirements and Guidelines for Conducting Surveys and Analysing Data within the Revised Management Scheme' need to be modified. The Committee **agrees** that an intersessional steering group (Annex Y) will develop instructions and select a candidate to modify the Guidelines.*

12.3.2 Review new survey techniques/equipment

The Committee received information on the use of unmanned aircraft vehicles (UAVs) to improve estimation of abundance of river dolphins in the Amazon. Details are provided in Annex Q, item 5.

Attention: SC, G

The Committee ***looks forward*** *to receiving information on new survey technologies used to improve estimates of abundance of cetaceans.*

12.4 Consideration of the status of stocks

The Committee noted that further consideration on how to report status of cetacean stocks is needed.

Attention: SC

The Committee ***recognises*** *the need to further consider how to report status of stocks to the Commission in a consistent manner and* ***agrees*** *to address this topic at a pre-meeting to be held prior to next year's SC meeting (SC68A).*

12.5 Workplan 2019-20

The Committee **agrees** to the workplan given in Table 167

Table 17

Workplan on abundance estimates and status.

Topic	Intersessional 2018-19	SC68a	Intersessional 2019-20	SC68b
Review of Abundance Estimates	Review estimates identified at SC67B (New Zealand Blue Whales, Arabian Sea humpback whales) – Annex Y	Review intersessional progress and estimates available at SC68A	Review estimates identified at SC68A	Review intersessional progress and estimates available at SC68A
Upload the estimates accepted at the annual meeting to the IWC website and continue to update the IWC Abundance Table	Update the table with estimates accepted at SC67B (Annex Y)		Update the table with estimates accepted at SC67B	
Review and provide advice on plans for future surveys		Receive, review and provide feedback to research plans to conduct abundance estimates		Receive, review and provide feedback to research plans to conduct abundance estimates
Pre-meeting to consider: (a) validation of non-standard software and methods, (b) estimates of abundance computed from population models and (c) Status of populations	Meeting Preparation	Review of progress		
Amend the RMP Guidelines to consider abundance estimates computed with model-based methods.	Identify a candidate to update the RMP Guidelines (Annex Y)	Review an updated document of the Guidelines		
Develop simulation software to evaluate methods for abundance estimates		Review Progress		

13. BYCATCH AND ENTANGLEMENTS

13.1 Review new estimates of entanglement rates, risks and mortality (large whales)

The Committee received three papers relating to the bycatch of large whales. SC/67b/HIM03 provided information on stranded humpback whales stranded along the southeastern coast of Brazil in 2016 and 2017 including records of entanglements over the São Paulo coast. SC/67b/HIM09 focussed on ten baleen whale populations for which bycatch appears to be a component of substantial conservation problems and the authors categorised priorities for action. SC/67b/AWMP08 provided information on Bering-Chukchi-Beaufort Seas stock of bowhead whales. Discussion can be found in Annex J (item 2.1).

13.2 Reporting of entanglements and bycatch in National progress reports

Reports of large whale bycatch are summarised in Annex J (item 2.4) and the issue of partial reporting discussed. Issues related to reporting and progress reports is given under Item 3.2.

13.3 Mitigation measures for preventing large whale entanglement

Mattila, the IWC's technical advisor for reducing unintended human impacts, reported on relevant activities under the entanglement initiative. Details can be found in Annex J (item 2.5). Since last year's meeting, IWC entanglement trainings have been conducted in Sakhalin (Russia), Arica (Chile), Sortland (Norway) and Bahía Solan (Colombia). This brings the total number of trainees in this initiative to 1,130 from 27 countries. In addition, two apprentices were hosted this year, one from Chile and one from Oman. Mattila also presented the IWC's work with entanglement in two workshops at the Society for Marine Mammalogy Biennial conference (2017). The Committee thanked Mattila for his exemplary work in coordinating the Global Whale Entanglement Response Network.

13.4 Review proposal for global entanglement database

The Committee considered progress with the development of a dedicated entanglement database. This will be considered further at the June 2018 meeting of the Global Whale Entanglement Response Network (see Annex J, item 2.3).

13.5 Estimation of rates of bycatch, risks of, and mortality for small cetaceans

13.5.1 Small cetacean bycatches in Peru

The Committee received a report (SC/67b/HIM01) summarising monitoring efforts of beach-cast cetaceans in 11 locations along the Peruvian coast from 2000-2017. Full discussion can be found in Annex J (item 2.1.2) that showed clear evidence of continued high bycatch rates and some intentional takes. Burmeister's porpoises accounted for 66% of the specimens and the low proportion (25%) of dusky dolphins contrasted with 1985-1990 statistics, when dusky dolphins accounted for three quarters of all cetacean captures. This reiterated prior concerns (Van Waerebeek, 1994) about a persistent long-term trend of a significant decline in prevalence of Peruvian dusky dolphin in catch and stranding records.

The observed high mortality levels in Burmeister's porpoise are a serious concern, and action is needed to avoid the same critical situation as with the closely related vaquita. Burmeister's porpoise is already included in a preliminary list for potential Conservation Management Plan development (Genov *et al.*, 2015), and dusky dolphin could potentially also be included. The Committee reiterated recommendations from 2008 regarding bycatch monitoring programmes and mitigation efforts in these fisheries (IWC, 2009, p. 323).

Attention: C-A, CC

*The Committee **draws the attention** of the Commission to its **serious concern** over the high mortality levels from bycatches in Peru and especially those of the Burmeister's porpoise and dusky dolphin. It **stresses** that action is needed to avoid the same critical situation for Burmeister's porpoise as with the closely related vaquita. In this regard the Committee:*

*(1) **reiterates** its advice (IWC, 2009, p. 323) on bycatch monitoring and mitigation in these fisheries;*
*(2) **reiterates** that the Burmeister's porpoise is a potential candidate for a Conservation Management plan;*
*(3) **highlights** opportunities to focus on the bycatch of small cetaceans in Peru through the new IWC Bycatch Mitigation Initiative and **recommends** that they are considered as a potential pilot project; and*
*(4) **offers its assistance** to the Government of Peru; and*
*(5) **requests** that the Commission, through the Secretariat, transmits the Committee's concern and offer of assistance to the Government of Peru.*

13.5.2 Franciscana bycatch in Brazil

Considerable information was provided on the Santos Basin Beach Monitoring Project required by the Brazilian authorities for licensing oil and gas production and transport (see Annex J, item 2.1.2). This provided information *inter alia* on stranded franciscana. From October 2015 to September 2017, 1,123 carcasses were recorded stranded in the area and interactions with fishing gear was reported for over 85% of necropsied individuals with signs of human activities.

Attention: CG-A

*The Committee **draws attention** to the fact that the franciscana remains under strong pressure from human activities, especially bycatch, in Brazilian waters despite fishing net regulations established by the government. The Committee:*

*(1) **advises** that the existing regulation on gillnets, implemented in 2012, is either not being effectively enforced or is not effective in reducing bycatch; and therefore*
*(2) **recommends** the need for this to be investigated further by the Brazilian authorities.*

13.5.3 Estimating bycatch from strandings data

Estimates of common dolphin mortality in the Bay of Biscay based on strandings data (Peltier *et al.*, 2016) had been discussed at SC67a. SC/67B/HIM/05 and SC/67B/HIM/08 provided further analyses related to using stranding data to make inferences about small cetacean mortality. An intersessional group was established at SC67a to provide advice on consistent ways to estimate bycatch across both large and small cetaceans, and specifically, to review the methods applied in Peltier *et al.* (2016) focused on small cetaceans. Discussion of the report of the intersessional group and some additional related papers (SC/67b/ HIM05 and SC/67b/HIM08) can be found in Annex J (item 2.1.2).

In discussion of other ways to estimate bycatch, the Committee noted that Bartholomew *et al.* (2018) had concluded that Remote Electronic Monitoring can provide a time- and cost-effective method to monitor target catch in small-scale fisheries and can be used to overcome some of the challenges of observer coverage. This requires consideration by the Committee.

Attention: CG-A, SC, G

With respect to methods for obtaining bycatch estimates the Committee:

(1) ***agrees*** *with the recommendations of its intersessional group regarding (a) uncertainties in bycatch estimates derived from strandings; (b) the use of bycatch estimates derived from strandings; and (c) assessing whether strandings can identify gaps in observer coverage;*
(2) ***notes*** *the importance of observer programmes, including electronic monitoring, and the limitations of stranding information for determining the type of fishing gear implicated in a bycatch event, or in determining reliable bycatch estimates;*
(3) ***recognises*** *that in small scale fisheries (a) observer programmes are particularly complicated, given the small size of vessels and (b) electronic monitoring may not capture the animals falling from the net during hauling*
(4) ***advises*** *that a robust evaluation of the effectiveness of bycatch mitigation measures requires a combination of monitoring measures, including well-designed and effectively implemented observer programmes, electronic monitoring and stranding programmes;*
(5) ***advises*** *that the above advice is relevant to the situation of the franciscana in Brazil; and*
(6) ***agrees*** *that given the increased use of Remote Electronic Monitoring techniques and the rapid development of camera and associated electronic technology, these techniques should be a focus topic at SC68a.*

13.6 Scientific aspects of mitigation measures

13.6.1 The IWC Bycatch Mitigation Initiative

The Committee considered the outcomes of an assessment on the potential work areas for the new IWC Bycatch Mitigation Initiative (SC/67b/HIM12). This resulted in several recommendations for the Committee in relation to potential work areas, including:

(1) identification of priority fisheries/sites/species/populations to be considered for pilot projects based on conservation need and the establishment of bycatch baselines for relevant cetacean populations where mitigation is to be trialled;
(2) leading in communicating the need for increased research on mitigation measures/management approaches for cetaceans to the broader scientific community;
(3) annually reviewing mitigation measure tables;
(4) providing technical assistance to the coordinator and the expert panel in the development of scientific trials/monitoring programmes to evaluate mitigation measures; and
(5) collaborating with researchers identifying fishing effort using vessel monitoring and tracking systems and assessing bycatch risk, with a focus on small scale fisheries.

With respect to the identification of priorities, five criteria for the selection of pilot projects were identified:

(1) urgency of conservation situation driven by bycatch or concern over situations with little or no data on bycatch, but suspected overlap between high risk fishing gears and vulnerable cetacean species;
(2) enabling conditions necessary for success;
(3) scope for IWC to contribute (e.g. enhanced international cooperation);
(4) ability to monitor effectiveness of mitigation actions; and
(5) potential for the project to contribute to mitigation of bycatch in other areas.

A list of information sources (including SOCER) was created at the meeting to assist Tarzia, the new BMI coordinator, to identify potential projects, after which she will consult with the expert panel to apply the above criteria, including contact with any of the governments involved, to select the projects for review by the initiative's Standing Working Group which can be presented to the Commission. The Committee suggested that identified fisheries in the Republic of Congo, Peru, Ecuador, Pakistan and India appear to fulfil many of the criteria and are locations where past or present IWC work is being carried out which is relevant to bycatch.

Attention: C-R, SC, CC

The Committee discussed the strategic assessment of the Bycatch Mitigation Initiative (BMI) and the role of the Committee. The Committee:

(1) ***welcomes*** *the progress made thus far under the BMI, including the Strategic Assessment;*
(2) ***thanks*** *Tarzia for the excellent work she has carried out since her appointment as co-ordinator;*
(3) ***agrees*** *to incorporate in its workplan the five work areas listed in its report under Item 13.6.1 and also consideration of 'rapid bycatch and risk assessment' tools;*
(4) ***agrees*** *to the criteria listed in its report under Item 13.6.1 when identifying priority fisheries/sites/species/populations; and*
(5) ***recommends*** *to the Commission that the BMI continues and is supported, including the provision of ongoing support for the BMI coordinator.*

13.6.2 Collaboration with FAO

FAO held an Expert Workshop on Means and Methods for Reducing Marine Mammal Mortality in Fishing and Aquaculture Operations in March 2018 which had been attended by several members of the Committee. The workshop report contained a review of mitigation measures and a decision tree providing guidance on choosing a bycatch mitigation pathway. The IWC Executive Secretary and BMI Coordinator will attend the FAO Committee on Fisheries (COFI) meeting in July 2018 where the report will be reviewed.

Attention: C-R, S

The Committee ***welcomes*** *the efforts of the FAO to consider cetacean bycatch and* ***recommends*** *that the IWC Secretariat continues to collaborate with the FAO on this issue.*

13.7 New information on cetacean bycatch in the Western, Central and Northern Indian Ocean

Last year (IWC, 2018c, p. 46), the Committee had recommended that in light of the scope and scale of cetacean bycatch in the Western, Central and Northern Indian Ocean and the considerable data gaps associated with intensive and extensive gillnet fisheries, the topic be included in the work plan for this meeting and the Secretariat establish communications on the issue with the Indian Ocean Tuna Commission (IOTC). SC/67B/HIM/07 provided updated information on this topic, as discussed in Annex J (item 2.7). The IWC's Executive Secretary provided an update on engagement with the IOTC, including a recent teleconference with the IOTC Executive Secretary.

Attention: C-A, CC, SC

With respect to bycatches of cetaceans in the Indian Ocean, the Committee:

(1) ***reiterates*** *its willingness to collaborate with the IOTC on this issue; and*
(2) ***encourages*** *the Secretariat to continue to work with the IOTC Secretariat.*

13.8 Workplan 2019-20

The Committee's workplan on bycatch and entanglement is given in Table 18.

14. SHIP STRIKES

14.1 Review estimates of rates of ship strikes, risk of ship strikes and mortality

The Committee received information on a pilot study to better characterise ship strikes in Southeastern Alaska (see Annex J, item 3.1) and looks forward to further updates on this work.

14.1.1 Review progress on ship strike database

The IWC continues to develop a global database of ship strike incidents as discussed in Annex J (item 3.1.1). The primary task is ongoing review of previously reported records by two data coordinators in conjunction with a data review group (SC/67b/HIM11). It is expected that the review process for all historical records will be completed in the next biennium.

Attention: C-R, S

The Committee ***reiterates*** *the importance of the global ship strikes database to its work. It therefore:*

(1) ***welcomes*** *the work undertaken thus far;*
(2) ***recommends*** *the continuation of this work including (a) that of the co-ordinators and Data Review Group on the review of historical records and (b) the Secretariat on upload tools.*

Table 18

Workplan on bycatch and entanglement related issues.

Topic	Intersessional 2018/19	2019 Annual Meeting (SC/68a)	Intersessional 2019/20	2020 Annual meeting
Bycatch Mitigation Initiative		Review aspects relevant to Committee and respond to requests for advice		Review aspects relevant to Committee and respond to requests for advice
Rates and risks		Review new estimates of entanglement rates, risks and mortality		Review new estimates of entanglement rates, risks and mortality
Mitigation		Review new information on mitigation		
Inferences from strandings	Consider new information and issues that need to be addressed at SC68a	Review new information		
Rapid risk assessment		Consideration of 'rapid risk assessment' tools and outputs		
Electronic monitoring		Consideration of remote electronic monitoring and vessel tracking		
Mitigation measures tables		Develop table of mitigation measures for small cetaceans and update table for large whales from 2017 if needed.		
Global disentanglement database	Discussion at GWERN workshop	Review Progress	Advance database development if considered feasible	Review Progress
Collaboration with FAO	Secretariat attend COFI meeting	Review FAO outputs on bycatch	Continue collaboration	Continue to review
Encouraging innovative research on mitigation	BMI through existing networks, at conferences, workshops and with students – all members of Committee with relevant expertise	Review progress		

14.2 Mitigation of ship strikes in high risk areas

The Pelagos Sanctuary in the Mediterranean is a recognised high risk area for ship strikes to fin and sperm whales. In France, the REPCET reporting system became mandatory on 1 July 2017 for French passenger, cargo vessels (SC/67b/HIM04). As discussed in Annex J (item 3.2.1), 'alerting' systems such as REPCET require a trained observer and a subsequent avoidance action of some sort by the vessel in order to be a considered as a mitigation tool.

The Committee had previously agreed that the available data supported a proposal to IMO to move the shipping lanes off the southern coast of Sri Lanka to reduce the risks of ship strikes to Northern Indian Ocean blue whales. In 2017, major shipping organisations represented at IMO also wrote to the Sri Lankan government requesting the routing change to reduce ship strike risks and improve maritime safety. So far, there has been no response from Sri Lanka.

The Hellenic Trench west of Greece is also an identified high risk area for sperm whales and in 2015 (IWC, 2016d), the Committee recommended that interested parties (including Greece, ACCOBAMS and the shipping industry) move forward with Greece in order to develop a proposal for routing measures.

The IUCN Marine Mammal Protected Areas Task Force process for identifying Important Marine Mammal Areas (IMMAs) may assist in identifying high risk areas for ship strikes. The Committee and the IWC's Ship Strike Standing Working Group have previously encouraged cooperation on this between the IUCN Task Force and the IWC.

Attention: C-A, CC, SC, G

The Committee has continued its work on identifying high risk areas for ship strikes and potential mitigation measures. In this regard the Committee:

(1) ***recommends*** *continued work to develop and evaluate mitigation measures, such as speed restrictions, that might be associated with the designation of a Particularly Sensitive Sea Area (PSSA) in the Pelagos Sanctuary area;*
(2) ***reiterates*** *its previous recommendations on the importance of evaluating the efficacy of the REPCET system for reducing the risk of ship strikes;*
(3) ***requests*** *the Commission, via the Secretariat, to remind the authorities in Sri Lanka of its previous offer of assistance from the IWC on this issue;*
(4) ***requests*** *the Commission via the Secretariat, to follow up on previous correspondence on the ship strike risks to sperm whales off Greece;*
(5) ***agrees*** *to support a workshop to evaluate how the data and process used to identify IMMAs can assist the IWC to identify areas of high risk for ship strikes; and*
(6) ***agrees*** *to continue ongoing IWC engagement with the process to identify IMMAs, including consideration of their utility to address other threats.*

14.3 Co-operation with IMO Secretariat and relevant IMO committees

The Committee has long recognised the importance of co-operation with IMO on matters related to shipping including ship strikes.

Attention: C-R, S

*The Scientific Committee **reiterates** the importance of cooperation with IMO and:*

*(1) **welcomes** the ongoing co-operation the Secretariat has maintained with IMO and its Secretariat on ship strike issues, including meetings during IMO MEPC 72; and*
*(2) **recommends** that this dialogue continue.*

14.4 Work Plan

The Committee's work plan on matters related to ship strikes is given as Table 19.

Table 19

Workplan on matters related to ship strikes

Topic	Intersessional 2018/19	2019 Annual Meeting (SC/68a)	Intersessional 2019/20	2020 Annual meeting
Rates and risks		Review estimates of rates of ship strikes, risk of ship strikes and mortality		Review estimates of rates of ship strikes, risk of ship strikes and mortality
Mitigation		Review new information on mitigation		
Advice on routing measures related to ship strike risk	Provide advice as required (Annex Y)	Review advice	Provide advice as required (Annex Y)	Review advice
Follow up on previous contacts offering IWC assistance regarding high risk areas	Secretariat to contact Sri Lankan and Greek authorities	Review progress on identified high risk areas in IWC Ship Strike Strategic Plan		
Continued co-operation with IMO	Secretariat to maintain dialogue with IMO Secretariat. Attend relevant IMO meetings.	Review cooperation		
Ship strike database	Continue ongoing data entry into Ship Strike Database and validation of records	Review progress against specific deliverables and time line	Continue ongoing data entry into Ship Strike Database and validation of records	Review progress against specific deliverables and time line
Provision of AIS data	Secretariat to develop MOU with Marine Traffic for provision of data	Consider best way to handle requests for data through the MOU		
Use of IMMAs to identify high risk areas for ship strikes	Hold workshop to evaluate how the data and process used to identify IMMAs can assist the IWC to identify areas of high risk for ship strikes.	Review workshop report		

15. ENVIRONMENTAL CONCERNS

The Commission and the Scientific Committee have increasingly taken an interest in the environmental threats to cetaceans. In 1993, the Commission adopted a resolution on research on the environment and whale stocks and on the preservation of the marine environment, IWC Resolution 1993-12 (e.g. IWC, 1996; 1997; 1998; 1999; 2010). As a result, the Committee formalised its work by establishing a Standing Working Group that has met every year subsequently. This year, it has been established as a sub-committee and its report can be found in Annex K.

15.1 Pollution 2020

15.1.1 Review on intersessional progress on the Pollution 2020 initiative

The individual based model to investigate the effects of pollutants on cetacean populations (SPOC) has been finalised. A peer-reviewed paper detailing the model and applying it to a number of case studies has been published in *Environmental Pollution* (Hall *et al.*, 2018) and the model's R code is available through the repository associated with the paper. The web-based, user-friendly version is now available through the Sea Mammal Research Unit, University of St Andrews server (*http://www.smru.st-andrews.ac.uk/reports/*) and a link will be added to the IWC webpages on the Chemical Pollution page. There are new data on the combined effects of persistent organic pollutants (POPs) on the immune system of killer whales (Desforges *et al.*, 2017) and this will be integrated into the model in the next year.

As noted in Annex K (item 2.1), the contaminant mapping tool will be completed next year, with the inclusion of the data on the concentrations of mercury in cetacean tissues by time and region. This online resource that will be made available through the IWC website and will be updated with new information identified in the SOCER annual reviews.

Research to estimate how long it is likely to take for POPs in the blubber of cetaceans to observably decline, following a reduction in environmental levels, will be completed next year.

Attention: SC

*The Committee **agrees** that the Pollution 2020 initiative should be completed and presented at SC/68a. It also **encourages** a paper to be presented at SC/68a summarising the potential mitigation measures for reducing exposure of cetaceans to polychlorinated biphenyls (PCBs) in particular and persistent organic pollutants (POPs) in general.*

15.1.2 Report on mercury in cetaceans

The impact of mercury exposure is still an issue of concern for cetaceans. SC/67b/E08, reviewed mercury in cetaceans, in response to Commission Resolution 2016-4, 'Resolution on Minamata Convention'. The paper (see discussion in Annex K, item 2.2) highlights continued global exposure and potential effect of mercury on cetaceans. Although cetaceans have a unique detoxifying mechanism which may protect them from the health effects of organic mercury, the resulting mercuric-selenide complexes may cause adverse effects in individuals experiencing other physiological and metabolic challenges. Research into identifying the toxic thresholds for mercury in cetaceans is still required.

The Committee also received several papers presenting information on mercury in cetaceans including river dolphins (SC/67b/E06), humpback whales (SC/67b/E09) and gray whales off Chukotka (SC/67b/E03). The Committee highlighted the need for standardisation in reporting units. It also discussed preferred tissues for mercury analyses. Discussion of these papers can be found in Annex K (item 2.2)

Attention: SC, CG-R

The Committee continued to work on mercury in cetaceans in response to Resolution 2016-4. It therefore:

*(1) **encourages** the continued provision of information on mercury and cetaceans;*
*(2) **encourages** researchers presenting such information to report concentrations on both wet and dry weight bases; and*
*(3) **recommends** that Contracting Governments support the continued monitoring of mercury in cetaceans, as this is required in order to assess the medium- and long-term impact of the Minamata Convention.*

15.1.3 Impact of heavy fuel oils on cetaceans

There is a paucity of information on the impacts of heavy fuel oils on cetacean health (Annex K, item 2.3). However, some new information comparing the occurrence of cancer and elevated PAH levels in St Lawrence Estuary white whales with similar cancers in the local human population, was highlighted. In addition, behavioural changes in white whales in the White Sea following exposure to oil have been observed.

Attention: CG-A, SC, G

The Committee:

*(a) **reiterates** the need to estimate the risk and impact of oil spills, particularly to cetaceans in the Arctic;*
*(b) **notes** that heavy fuel oil could pose an environmental threat in many regions due to its high viscosity and chemical composition;*
*(c) **notes** that heavy fuel oil poses a special threat in the Arctic due to difficulties in recovery and potential impacts of some recovery measures (e.g. dispersant use and in situ burning); and*
*(d) **encourages** the collection of baseline data for cetaceans, including standardisation of measures.*

15.1.4 Other pollution issues

Understanding the effects of oil dispersants and dispersed oil on cetaceans is a gap in our current knowledge. To address this need, the Coastal Response Research Center (CRRC) in the USA has co-ordinated a discussion among scientists with dispersant research expertise, as well as those with Arctic expertise, to determine the state-of-science regarding dispersants or dispersed oil, as it applies to Arctic waters. The Committee looks forward to the publication of the final report.

Attention: CG-A, SC, G

*The Committee **draws attention to** the lack of data the effects of oil dispersants and dispersed oil on cetaceans. It therefore:*

(1) ***encourages*** *Contracting Governments to support research on the effects of dispersants or dispersed oil to the Arctic and other ecosystems; and*
(2) ***requests*** *that the results of such research be brought forward to future meetings of the Scientific Committee.*

15.2 Cumulative effects

The Committee welcomed the summary of the Cumulative Effects Workshop (see Annex K, item 3) and looked forward to receiving the report. Overall, the Workshop found that there is considerable uncertainty in addressing this topic and thus in developing assessments and management advice.

The Scientific Committee also received a report on a workshop entitled 'Towards understanding the overlap of selected threats and Important Marine Mammal Areas (IMMAs) across the Mediterranean Sea', which was held jointly by the IUCN Joint Species Survival Commission/World Commission on Protected Areas (SSC/WCPA) Marine Mammal Protected Areas Task Force (the 'Task Force') and by the Agreement on Conservation of Cetaceans of the Black Sea, Mediterranean Sea and contiguous Atlantic area (ACCOBAMS). The workshop provided the opportunity to support the ongoing effort to map specific threats to cetaceans in the ACCOBAMS area by overlaying the Mediterranean IMMAs with the available area-explicit information on shipping and seismic surveys, thereby giving preliminary indications of new Cetacean Critical Habitats in the ACCOBAMS area and facilitating the implementation of conservation actions at the regional level.

Attention: SC, G

The Committee ***recognises*** *the importance of understanding cumulative effects of threats on populations of cetaceans, as well as its complexity. It therefore:*

(1) ***concurs*** *with the Cumulative Effects Workshop recommendations (see Annex K, item 3) to improve our knowledge and enable quantitative assessments;*
(2) ***highlights*** *the recommendation that consideration needs to be given to 'developing a widely applicable approach for providing precautionary advice for populations in which cumulative effects are of concern';*
(3) ***agrees*** *to establish cumulative effects as a standing item on its agenda;*
(4) ***notes*** *the work on Important Marine Mammal Areas (IMMAs) and* ***encourages*** *additional efforts to identify the relevant threats in these, in order assist with the management of cumulative effects;*
(5) ***endorses*** *the results of the recent IUCN/ACCOBAMS workshop entitled 'Towards understanding the overlap of selected threats and Important Marine Mammal Areas (IMMAs) across the Mediterranean Sea';*
(6) ***encourages*** *that such an effort – aimed at overlaying different sources of threat and pressure on existing Important Marine Mammal Areas (IMMAs) – be continued and carried out in more detail in the other marine regions where IMMAs have already been identified; and*
(7) ***offers*** *its assistance in such assessments.*

15.3 Strandings and mortality events

15.3.1 Update on the IWC Strandings Initiative

The IWC strandings initiative was agreed by the Commission at its 2016 meeting (IWC, 2017d) and details can be found in Annex K (item 4.1). It noted that the rescue and welfare aspects of live strandings will be addressed by the Strandings Initiative but that this aspect is not within the purview of the Committee.

Attention: C-R, S, SC

The Committee ***reiterates*** *the importance of the IWC Strandings Initiative. It therefore:*

(1) ***welcomes*** *the excellent progress that has been made in the Strandings Initiative and the appointment of Sandro Mazzariol (Italy) as the Chair of the Strandings Expert Panel and Karen Stockin (New Zealand) as the Stranding Coordinator;*
(2) ***recommends*** *that the Commission (a) endorses the Strandings Initiative governance structure in Annex K (appendix 2) and (b) endorses the continuation of the Strandings Coordinator position for another two years (until IWC68) subject to available funding and requests the Secretariat make the necessary arrangements;*
(3) ***recommends*** *that the Strandings Initiative Steering Committee and Expert Panel, with the support of the Secretariat, should explore the best ways to gather information on strandings events and what basic data about these events should be recorded, focussing on what is useful for the Committee and the Commission;*
(4) ***agrees*** *that a phased approach to this, starting with an initial pilot project, will assist in this endeavour; and*
(5) ***agrees*** *that criteria for allocating funds for emergency responses should be developed by the Steering Committee and the Expert Panel and should be presented to the Committee at SC/68a.*

15.3.2 New information on unusual mortality events

Cetacean morbillivirus continues to be a major disease issue for cetaceans and a cause of unusual mortality events in dolphins in and around the Atlantic. Focus this year was on an outbreak of cetacean morbillivirus in the South Atlantic Ocean (SC/67b/E14) that is discussed in Annex K (item 4.2).

Attention: CG-R, SC

The Committee ***commends*** *the impressive rapid and comprehensive response to the cetacean morbillivirus outbreak in Brazilian Guiana dolphins. It therefore:*

(1) ***encourages*** *further work on the longer-term impact of the outbreak and the investigation of the occurrence and impact of this disease in cetaceans across different geographical areas;*
(2) ***draws attention to*** *the large number of animals that died during the outbreak (particularly mature females) and the historical high levels of human impacts affecting Guiana dolphins in Rio de Janeiro state, such as bycatch, chemical and noise pollution;*
(3) ***recommends*** *that immediate actions should be taken to protect affected populations in order to increase the chances of population recoveries;*
(4) ***draws attention to*** *the increase in Guiana dolphin deaths reported in Sao Paulo and Espirito Santo states in the weeks following the onset of the cetacean morbillivirus outbreak in Rio de Janeiro; and*
(5) ***encourages*** *the monitoring of the virus presence in neighbouring coastal dolphin populations, particularly species and populations in which immunosuppressive conditions or cumulative threats are identified.*

15.4 Noise

The Committee welcomed an update on international efforts addressing anthropogenic noise and their impacts on cetaceans, particularly regarding the appropriate assessment and protection of acoustic habitat quality as discussed in Annex K (item 5), and commended IWC engagement with organisations such as IMO and the UN.

Guidelines developed by the Convention on Migratory Species (CMS) Secretariat, also on behalf of the ASCOBANS and ACCOBAMS Secretariats, for Environmental Impact Assessments for noise-generating offshore industries were presented to the Scientific Committee. These guidelines had been endorsed through CMS Resolution 12.14 on Adverse Impacts of Anthropogenic Noise on Cetaceans and Other Migratory Species, and provide a pathway to implementing the Best Available Techniques (BAT) and Best Environmental Practice (BEP).

The Committee also considered the results of a study utilising modelling approaches to evaluate relative levels of communication masking for four baleen whale species in the Stellwagen Bank National Marine Sanctuary, in Massachusetts Bay, USA Cholewiak *et al.* (In press).

Attention: SC, G, CG-A

Recalling its previous recommendations on noise and the importance of addressing its impacts on cetaceans, the Committee:

(1) ***welcomes*** *and* ***draws attention*** *to the Convention on Migratory Species Family Guidelines on Environmental Impact Assessments for Marine Noise-Generating Activities (https://www.cms.int/en/guidelines/cms-family-guidelines-EIAs-marine-noise), noting that these guidelines will help improve global standards for environmental impact assessments;*
(2) ***recommends*** *that levels of anthropogenic noise and its effects on marine species be explicitly considered in the management of marine protected areas;*
(3) ***welcomes*** *the information received on using marine soundscape planning strategies to reduce interference between hydroacoustic instrumentation (e.g. echosounders and airgun arrays) and marine mammals, and* ***encourages*** *work to further develop this approach;*
(4) ***recognises*** *the commonalities identified among the concurrent efforts of multiple international bodies to develop national guidance on noise strategies, and* ***encourages*** *continuing efforts to identify synergies and develop priorities for actions to reduce exposure of cetaceans to anthropogenic noise;*
(5) ***welcomes*** *the work on modelling cetacean communication space, and* ***encourages*** *scientists engaged in the development of modelling techniques that address multiple anthropogenic impacts, such as noise and entanglement in fishing gear to bring these forward to the Scientific Committee;*
(6) ***agrees*** *that a pre-meeting on noise be organised for SC/68b and that an intersessional steering group be convened (Annex Y) to develop the agenda for that pre-meeting.*

15.5 State of the Cetacean Environment Report – SOCER

The Scientific Committee **thanks** the editors of the State of the Cetacean Environment Report (SOCER) for their work and commended them on compiling this information on the Mediterranean and Black Seas. Next year's region will be the Atlantic Ocean. The Scientific Committee would welcome input from the members for information on this region. A 5-year global compendium is being produced in cooperation with the Secretariat that will receive a dedicated webpage on the IWC website in time for presentation to the 2018 Commission meeting.

15.6 Update on other standing topics

15.6.1 Marine debris[litter]

The Committee received and discussed a number of papers relating to several aspects of marine debris as discussed under Annex K (item 7.1). Exposure to marine debris and microplastics in cetaceans is now widespread and common. However the impacts on cetacean health and populations is not fully understood.

Attention: C-A, SC

The Committee ***draws attention*** *to the fact that marine debris remains a threat, and that in particular, exposure to plastics (including microplastics) is a rapidly emerging area of concern.* It therefore:

(1) ***agrees*** *that an intersessional workshop on Marine Debris should take place, preferably to coincide with the World Conference on the Biology of Marine Mammals in Barcelona in December 2019.*

15.6.2 Climate change

Climate change was highlighted at SC/67a as being an overarching issue that is important to various topics, and that where relevant its impact should be discussed in conjunction with that topic (see discussion in Annex K, item 7.2). Notwithstanding that, the Committee may want to initiate a specific activity related to climate change in future (see intersessional correspondence group in Annex Y).

Attention: C-A, CG-A, SC

The Committee ***draws attention*** *to the fact that climate change remains a threat that interacts with other threats and stressors impacting cetacean populations.*

15.6.3 Cetacean diseases of concern

Monitoring health and disease agents in large whales in the Arctic is continuing to provide important information on changing patterns in prevalence, environmental status, and potential impacts. In addition, morbillivirus and Brucella continue to be important pathogens causing disease and increased mortality in cetaceans in the Atlantic.

Remote methods for assessing health and condition using visual and aerial photography (e.g. SC/67b/CMP13), is a major rapidly developing field, due to the widespread availability and reduced cost of unmanned aerial vehicles (UAVs). Standardisation efforts (e.g. see Annex S) for measuring body condition using UAVs for photogrammetry, and for collecting blow samples, should progress to ensure this useful tool can provide comparable data across studies, taking into account the differences between the various platforms available. Cross-validation with current methods for assessing body condition from visual health assessments is essential.

Attention: SC

The Committee ***agrees*** *to hold a focussed session next year (SC/68a) on our current understanding of the pathology and epidemiology of morbillivirus and* Brucella *and the potential for identifying and understanding the cumulative effects of exposure to other immunosuppressive stressors in cetaceans.*

15.7 Progress on previous recommendations

15.7.1 Pollution

The SC/67a recommendations were to (a) make the effect of contaminants on cetacean populations (SPOC) model available to the public; (b) review mercury in cetaceans; and (c) include new data into the contaminant mapping tool. These have all been completed.

15.7.2 Cumulative effects

As recommended last year, a workshop on understanding the cumulative effects of multiple stressors was held as a pre-meeting to SC/67b.

15.7.3 Diseases of concern

The Committee noted that the content on the Cetacean Diseases of Concern (CDoC) website will now be utilised and merged with the Strandings Initiative for the development of their training and outreach materials.

Whilst the recommended quarterly CDoC updates remain of interest to the Committee, a means of progressing this on a voluntary basis has not yet been identified although efforts to find such assistance are ongoing.

15.7.4 Strandings

The Strandings Initiative has progressed as recommended at SC/67a and a full progress report can be found in Annex K, Appendix 2.

15.7.5 Noise

In response to a previous recommendation, that Committee has received the recently developed seismic survey guidelines by the New Zealand government, a link to the technical working group reports created during the NZ seismic guidelines review is now available (*http://www.doc.govt.nz/our-work/seismic-surveys-code-of-conduct/work-of-the-technical-working-groups/*). However, these guidelines have not yet been discussed by the Committee.

As recommended and noted earlier under Item 15.5, the intersessional group assisted in the development of a summary of the IWC recommendations relevant to shipping noise for presentation to the International Maritime Organization's Marine Environment Protection Committee in 2018.

15.7.6 Thanks

The Committee would like to thank Teri Rowles for her exceptional support and hard work as Chair of the sub-committee on environmental concerns over recent years. Her extensive knowledge, expertise and guidance has been most appreciated and will be missed.

15.8 Workplan 2019-20

The Committee's workplan on environmental concerns is given as Table 20.

Table 20

Work plan for matters related to environmental concerns (for more details see Annex K, Appendix 4).

Item	SC68a	SC68b
Pollution 2020 (including oil spills)	If new information	Primary topic (including oil spills and mercury), summary report to Commission
Cetacean diseases of concern (incl. HAB toxins)	Primary topic	Primary topic
Strandings	If new information	Primary topic
Noise		Noise focus session
Marine litter	Pre-meeting on litter and plastics focus session	If new information
Cumulative impacts	If new information	If new information
Emerging issues	If new information	If new information
SOCER	Receive report	Receive report
Climate change	Over-arching topic	Over-arching topic

16. ECOSYSTEM MODELLING

The report of the Working Group on Ecosystem Modelling is given as Annex L. This group was first convened in 2007 (IWC, 2008b). It is tasked with informing the Committee on relevant aspects of the nature and extent of the ecological relationships between whales and the ecosystems in which they live.

Each year, that Working Group reviews new work on a variety of issues falling under three areas:

(1) reviewing ecosystem modelling efforts undertaken outside the IWC;
(2) exploring how ecosystem models can contribute to developing scenarios for simulation testing of the RMP; and
(3) reviewing other issues relevant to ecosystem modelling within the Committee.

16.1 Cooperation with CCAMLR on multi-species modelling

The Committee has been considering plans for joint workshops with CCAMLR on ecosystem modelling for some time (e.g. see IWC, 2017c, p.56), although this has not yet happened, the Committee remains interested.

Attention: SC

The Committee ***reiterates*** *its interest in holding joint workshops with CCAMLR. It* ***agrees:***

(1) that a two-year delay in the occurrence of the workshop will provide the opportunity to pursue and complete the relevant work with input from CCAMLR as needed; and
(2) that collaboration between SC-IWC/SC CCAMLR should be on going, and that the revised plan for the workshops (IWC, 2018e) be implemented.

16.2 Applications of species distribution models (SDMs) and ensemble averaging

The Committee had agreed in 2015 to review the application of species distribution modelling (SDM) and associated techniques as they pertain to the goals of the Committee and to develop good practice guidelines and recommendations. While the review has occurred (IWC, 2016b), there has been no significant progress in the intersessional correspondence group set up to develop the guidelines.

Attention: SC

The Committee ***reiterates*** *the importance of developing good practice guidelines and recommendations for species distribution modelling and* ***agrees*** *that this should be pursued by an intersessional correspondence group (Annex Y) with a view to reviewing and adopting guidelines within the next biennium.*

16.3 MODELLING OF COMPETITION AMONG WHALES

16.3.1 Individual-based energetic models

Enhancements to an individual-based energetics model (IBEM) were presented to the Committee (SC/67b/EM07). These included the explicit modelling of feeding on migration, individual dives and searching for prey schools. Results showed that carrying capacity and productivity were sensitive to the level of food available during migration, making it important that ecosystem models to cover the entire migratory range of the species. This is an important contribution to the determination of species' function response, which can play a pivotal role in ecosystem modelling. This approach is also discussed under Item 5.1.

16.3.2 Modelling of relationship between whales and prey

The Committee reviewed three papers relevant to modelling of the relationships between whales and prey, SC/67b/EM04, SC/67b/EM06 and de la Mare *et al.* (*in press*). The discussion of these can be found in Annex L (item 3.2).

16.3.3 Modelling of competition among baleen whales

The Committee noted that multi-species individual based energetic models (IBEM) such as those described under Items 16.3.1 and 16.3.2 could be used to model direct and indirect competition of different whale species in the same environment, and that relevant modelling work was nearing completion.

16.3.4 Stable isotope analyses

The Committee received preliminary results of the analysis of stable carbon (δ13C) and nitrogen isotope ratios (δ15N)) on samples from the edge of baleen plates in Antarctic minke whales (SC/67b/SP09). The details can be found in Annex L (item 3.5).

16.4 Standing topics

16.4.1 Effects of long-term environmental variability on whale populations

How long-term environmental variability might affect stock assessments is of particular interest to the Committee. Given the need for a literature review on the subject to facilitate discussions, an intersessional correspondence group (Annex Y) has been established.

16.4.2 Update on body condition analyses for the Antarctic minke whales

For several years, the Committee has been discussing whether there has been a statistically significant (5% level) decline in the blubber thickness and fat weight of Antarctic minke whales over the course of the JARPA surveys. In 2014, the Committee had agreed that there had been such a decline (IWC, 2015b). Since then, scientists from Australia, Japan and Norway have presented a series of models both supporting and challenging this conclusion. There has been collaboration over this period and significant development in the types of models used. In addition, there have been in-depth discussions regarding the proper handling of data, the explanatory variables to be included in the analysis and the appropriateness of various statistical methods.

New analyses were presented this year and detailed discussions can be found in Annex L, item 2. This year the debate focused on three points; (1) the use of a new variable of primary interest (the 'accumulated blubber thickness in each feeding season); (2) the use of FIC and (3) the appropriate handling of the data.

Attention: SC, G

The Committee has been discussing whether there has been a statistically significant (5% level) decline in the blubber thickness and fat weight of Antarctic minke whales over the course of the JARPA surveys for several years. In conclusion, the Committee ***agrees****:*

(1) that, for the data set considered as a whole, all approaches result in point estimates reflecting a decline when fit to a linear trend in time;
(2) however, the extent of the decline estimated differs amongst the methods, and is not statistically significant at the 5% level for all approaches;
(3) for some approaches, when the data are disaggregated by gender and/or area, some point estimates of trend are not negative;
(4) there are some indications of temporal variation that is more complex than linear.

In addition, the Committee:

(1) ***encourages*** *the authors to publish the results of their study in peer-reviewed journals; and*
(2) ***agrees*** *that this matter will not be considered during the forthcoming biennium.*

In discussion of the above, Norwegian scientists stated that since an error in parts of the Australian scientists' calculations has recently been acknowledged by them, and parts of the Australian scientists' conclusion and appendix had recently been withdrawn, the overall position regarding the blubber thickness and fat weight analyses now became as follows. There are no new analyses from the Australian scientists on the five response variables which have been considered and discussed in the Committee from 2011 to 2017. The results presented this year by the Norwegian scientists (SC/67b/EM02), which took into account some of the queries from the Australian scientists from last year, confirmed results presented by the Norwegian scientists earlier. Thus, the conclusions by the Committee in 2014 and 2017 on these variables remain valid. For this meeting the Australian scientists had presented analyses related to a new difficult dependent variable 'increase in blubber thickness during summer feeding in Antarctic waters' estimated from the blubber thickness at position BT11. The conclusion above about variables with a non-significant decline now pertains to the new variables only (points (2) and (3) above). The Norwegian scientists' position is that the conclusion drawn above was heavily influenced by the results of the calculations subsequently withdrawn, so that parts of those conclusion are no longer valid.

In response, the Australian scientists stated that results of some calculations carried out earlier were withdrawn because of a previously unidentified problem with a standard statistical package failing to converge on a solution without giving an error message. Subsequent collaborative checking with the Norwegian scientists led to the discovery of this problem. Withdrawing this calculation (which the Australian scientists had carried out to illustrate a property of the Norwegian scientists' methods) had no effect on the main results which the Australian scientists had presented in SC/67b/EM03. Nor did this retraction affect the results of analyses the Australian scientists had presented in 2017 showing non-significant trends in fat weight and blubber thickness (De La Mare *et al.*, 2017a; 2017b). The Australian scientists held the view that the assertion by the Norwegian scientists that "There are no new analyses from the Australian scientists on the five response variables which have been considered and discussed in the SC from 2011 to 2017" was not correct; the Australian scientists had provided full results of fitting models to BT11 in SC/67b/EM03. The main results in SC/67b/EM03 were based on differences between early- and late-season predictions from models with BT11 as the dependent variable. This difference was a simple measure of feeding in Antarctica. The earlier conclusion should not be materially affected by withdrawing the Australian scientists' compromised demonstration in relation to the Norwegian scientists' methods.

16.4.3 Review the information on krill distribution and abundance by NEWREP-A

The Committee received the results of the krill and oceanographic surveys during the third NEWREP-A survey in Area V-E and VI-W (SC/67b/EM05). Discussion of this information can be found in Annex L (item 6.1).

16.4.4 Ecosystem functioning

Resolution 2016-3 tasked the Committee with investigating the contribution of cetaceans to ecosystem functions. Last year, the Committee noted that its focus would be on scientific aspects of the issue and it established an intersessional correspondence group to progress this work. Progress made by that group, including development of a final terms of reference, can be found in Annex L, item 6.2. The Committee notes that the Conservation Committee will focus on the conservation and social science aspects of this issue.

It was noted that there is broad interest in understanding the role of cetaceans in ecosystem functions, and that the Committee's expertise relates to the scientific aspects of the issue. Given the broad international interest, it is suggested that the Committee work in collaboration with interested parties (e.g. CMS, CCAMLR, SCAR and SCOR) to share information and avoid the duplication of work.

C-A, CC, SC

Commission Resolution 2016-3 tasked the Committee with investigating the contribution of cetaceans to ecosystem functions. The Committee notes that the Conservation Committee will focus on the conservation and social science aspects of this issue. In responding to the Resolution 2016-3, the Committee ***advises*** *the Commission that with respect to the scientific aspects on the contribution of cetaceans to ecosystem functioning:*

(1) it is unlikely that the ultimate goal of reliably determining the contribution of cetaceans to ecosystem functioning could be achieved in under a decade, given the complexity of the issue and the data gaps; and
(2) a more immediate and achievable goal is the carrying out of a gap analysis to identify knowledge gaps and to develop a plan to address them.

To further this work, the Committee ***agrees****:*

(1) to hold a workshop to (a) define short- and medium-term objectives to be addressed and (b) to identify what further research is required in order to begin initial modelling of the contribution of cetaceans to ecosystem function; and
(2) that the Secretariat in conjunction with the Steering Group (Annex Y) should contact CMS to determine their interest in participating in such a workshop.

16.6 Workplan 2019-20

The Committee's work plan on ecosystem modelling is provided in Table 21.

Japan referred to its statement on the adoption of the Agenda (Annex Z) and considered that several of the items for the proposed workshop (Item 16.4.4 and Item (7) in Table 1) are outside the competence of IWC. Therefore, it cannot support the proposed workshop or associated funding from the Committee's budget.

Table 21

Summary of the two-year work plan on matters related to ecosystem modelling

Item	Intersessional 2018/19	2019 Annual Meeting (SC/68a)	Intersessional 2019/20	2020 Annual meeting (SC/68b)
(1) Ecosystem modelling in the Antarctic Ocean	Continue further analyses.	Review results of further analyses	Continue further analyses.	Review results of further analyses
(2) Application of species distribution models (SDMs)	Intersessional group activity (Annex Y)	Review progress		
(3) Effect of long-term environmental variability on whale populations	Continue further analyses. Intersessional group activity (Annex Y)	Review results of further analyses. Review progress	Continue further analyses	Review results of further analyses
(4) Further investigation of individual-based energetic models	Continue further analyses	Review results of further analyses	Continue further analyses	Review results of further analyses
(5) Modelling of competition among whales	Continue further analyses	Review results of further analyses	Continue further analyses	Review results of further analyses
(6) Update of any exercises on krill distribution and abundance	Conduct NEWREP-A krill survey and an international cooperative krill survey. Conduct simulation analyses to resolve issues on survey design.	Review results of survey and analyses.	Conduct NEWREP-A krill survey. Conduct analysis of data taken by the international survey.	Review results of survey and analyses.
(7) Cetaceans & Ecosystem Functioning: a gap analysis workshop or pre-meeting	Review relevant scientific studies before the workshop in addition to preparation of workshop (Annex Y).	Review outcomes of workshop and develop clear work plans with priorities.	Continue analyses	Review results of analyses.

17. SMALL CETACEANS

The report of the Committee on Small Cetaceans is given as Annex M.

17.1 Overview of taxonomy, distribution and abundance for *Inia* and *Sotalia*

In this assessment, two species and two sub species of dolphins were considered, some of which have several common names. In addition, a new species has been proposed but has not yet been recognised (Table 22).

Table 22

Summary of names used in the description of *Inia* and *Sotalia*

Scientific name	Common Name
Inia geoffrensis	boto, Amazon River dolphin
I. g. boliviensis	Bolivian bufeo
I. g. geoffrensis	Common boto
I. araguaiensis	Araguaian boto
(proposed species)	(from the Tocantins and Araguaia basins)
Sotalia fluviatilis	tucuxi, delphín gris, bufeo negro
Sotalia guianensis	Guiana Dolphin

The river and estuarine dolphins of South America are subject to various threats from habitat degradation, competition with fisheries, bycatch and direct exploitation. A major threat to river dolphins in South America is population fragmentation, altered habitat productivity and regulation of natural river flow as a result of dam construction. The cumulative impacts from this type of infrastructure at the macrobasin scale exacerbate the threats to river dolphins and their habitat in the Amazon and Orinoco basins. It was estimated that more than 50% of the range of Araguaian *Inia* is affected by damming.

Two genera were discussed in depth, *Inia* and *Sotalia,* from the vast and convoluted systems within the Amazon, Orinoco, Tocantins and Araguaia River basins. In the case of *Sotalia,* two species are recognised: *Sotalia guianensis* (marine) and *Sotalia fluviatilis,* (freshwater) in the Amazon basin. *S. guianensis* in the Orinoco basin likely represents an independent population unit as it is isolated from other coastal populations. Two intersessional workshops have been proposed that aim to elucidate the status of *S. guianensis* and it is that divisions within this genus will be clearer on the completion of this work in 2020. The taxonomoy of *Inia* has a complex history and at this time, one species and two sub species are recognised: *Inia geoffrensis*, the Amazon river dolphin, *I. g. boliviensis*, the Bolivian bufeo, and *I. g. geoffrensis*, the common boto. There is a third putative subspecies, *I. g. humboldtiana*, in the Orinoco basin of Venezuela and Colombia. The information currently available suggests that *I. g. boliviensis* should be elevated to species level and that *I. g. humboldtiana* should be recognised. Another new species, *I. araguaiensis*, has been proposed for the dolphins that inhabit the Tocantins and Araguaia basins of central Brazil as this area is geologically and hydrologically separate from the Amazon basin.

Attention: SC, G

Given the incomplete resolution of Inia *taxonomy, the importance of clarifying and solidifying recognition (or elevation to species) of the* Inia *subspecies found in different river basins, the possibility that in such complex habitats localised specialisation is likely, and the need to focus attention on the conservation of demographically independent populations, the Committee* ***encourages*** *support for efforts to resolve* Inia *spp. taxonomy in light of the significant and diverse threats affecting the populations inhabiting the Amazon-Orinoco-Tocantins/Araguaia drainages.*

17.1.1 Inia

For *Inia*, there are estimates of abundance for some rivers, however, there is little information on population trends. It was suggested that new technologies, such as Unmanned Aerial Vehicles (UAV), may help to better refine population survey techniques. From telemetry studies and two long term studies some information on population parameters is available. In particular, the Committee commends an ongoing telemetry study as it begins to address some of the most important scientific questions concerning *Inia* ecology, habitat use, behaviour and, particularly movements.

In addition, and central to IUCN assessments, a generation time for *Inia* has been calculated as 24.8 years from a long-term mark and recapture study. Given the estimated rate of population decline, this equates to a loss of 82% per generation and in excess of 99% over three generations. Such values are well above the threshold for a Red List assessment of a species as Critically Endangered. Concern was also expressed at the high rate of mortality of <1 year calves in one study site, where examined carcasses show evidence of both deliberate killing and net entanglement.

The information presented on population parameters were based on direct observations in a very small geographic area of the Amazon and therefore, a very small proportion of the total range of *I. geoffrensis.* As such, extrapolation to the whole region would be unwarranted, nonetheless these results and their implications for population decline are alarming.

Attention: CG-A, G

The Committee ***draws attention*** *to declines in Inia numbers documented in two study areas and the lack of abundance surveys in most parts of its range. The Committee therefore* ***encourages*** *the collection of data, calculation of abundance estimates and undertaking of analyses to estimate population trends for* Inia *throughout its range, for use in assessments of the status of the species, subspecies, and regionally isolated populations.*

17.1.2 Sotalia

Sotalia fluviatilis, known as tucuxi (Brazil) delphín gris (Colombia) or bufeo negro (Peru and Ecuador) is restricted to the Amazon basin in Ecuador, Peru, Colombia and Brazil and has a more limited distribution than *Inia*. *Sotalia guianensis*, the Guiana dolphin, occurs mainly in nearshore and estuarine waters of the Atlantic from southern Brazil, along the coast of Central America, to Nicaragua and possibly Honduras. Small populations in Lake Maracaibo and in the lower reaches of the Orinoco River, Venezuela, were highlighted as being heavily impacted.

In the Mamirauá Reserve, Brazil, the population of *S. fluviatis*, has shown a precipitous decline in abundance over a 22-year study period. Using the average observed decline of 7.4% per year, and, from literature, a generation time estimate of 15.6 years, the Mamirauá population trend equates to a 97% reduction over 3 generations, qualifying this population as Critically Endangered under IUCN Red List criteria. Unlike *Inia*, which is heavily exploited for use as bait in the piractaninga fishery, the primary driver of the decline in Sotalia in this region is gillnet entanglement.

17.1.3 Threats shared by dolphins in the Amazon and Orinoco River systems and Lake Maracaibo

Throughout the range of both genera, illegal hunting was highlighted as a transnational problem, making it difficult to create and enforce effective conservation measures. This issue is severe for *Inia* throughout its range and, for *Sotalia* in the Orinoco River and particularly in Lake Maracaibo, Venezuela.

Attention: C-A, G, CC

The Committee ***draws attention to*** *the serious situation reported for Lake Maracaibo in Venezuela, where both directed takes and oil pollution are thought to be having serious impacts on populations of* S. guianensis. *The Committee* therefore ***recommends*** *that NGOs and researchers focus on documenting the threats to* Sotalia *and work with local communities to mitigate the impacts on these dolphin populations.*

In addition to direct exploitation, there are numerous other threats to both species throughout their habitat in South America: the recent increase in deforestation effects their prey species, as there is no deposition of seeds and fruits into the rivers to support productivity and sustain fish stocks; hydropower developments and channel dredging affects flows regimes, the connectivity of rivers, the migrations of fish and can fragment dolphin populations, as has already occurred in the Tocantins River basin; heavy metals, such as mercury, have been measured in high concentrations in dolphin tissues; negative interactions with fisheries, in addition to directed takes for use as bait and food, also include bycatch, deliberate poisoning and 'control' killing.

Attention: CG-A, G, CC

The Committee ***draws attention to*** *the multiple threats associated with development, habitat degradation and fragmentation, and pollutants facing river dolphins in the Amazon, Orinoco and Tocantins basins. It therefore:*

(1) ***advises*** *the Brazilian, Bolivian and Peruvian Governments, as they carry out their reviews of proposed construction of new dams for hydroelectric energy production, to explicitly consider the potential impacts on river dolphins (e.g. isolation, loss of genetic diversity, habitat degradation;*
(2) ***discourages*** *water pumping in the Araguaia-Tocantins river basin for agricultural use as such a practice causes dramatic decreases in water levels in rivers, thereby increasing the probability that dolphin populations will be extirpated;*
*(3) e****ncourages*** *range states of the Amazon basin and its tributaries to support and carry out baseline research into the impacts of the development of commercial waterways in the Amazon (hydrovias) and their potential impacts on dolphin populations and habitats, including but not limited to the ecological impacts of dredging, noise pollution, channelisation by embankments, altered sediment suspension and transfer, and changes in turbidity, light, oxygen availability and primary productivity, and (b) work to minimize or at least mitigate these impacts;*
*(4) e****ncourages*** *(a) a review of the status of dolphins trapped within dammed stretches of the Tocantins and Madeira rivers and (b) evaluation of possible relocation (translocation) of animals when environmental conditions create a high likelihood that they cannot continue to survive in this severely compromised habitat; and*
*(5) e****ncourages*** *the review of the effects and the scale of contaminant and heavy metal (e.g. mercury) pollution on river dolphins in key areas of the Amazon (Japura/Caquetá, Içá/Putumayo, in Brazil and Colombia) and Orinoco (Venezuela) basins.*

17.2 *Tursiops* populations occurring in estuarine areas in southern Brazil

Discussion focused on two populations of Lahille's bottlenose dolphins (*Tursiops truncatus gephyreus*) in Patos Lagoon Estuary (PLE) and Laguna (LGN), Brazil. Both have been the focus of long-term ecological studies that provide a good source of information on the conservation status of the subspecies. Mark-recapture studies indicate year-round residency and permanent emigration is unlikely. Population sizes are small (85 dolphins in PLE and 60 in LGN) with low to moderate genetic diversity (mtDNA and nuclear DNA variation) in both areas. Pollutant analyses indicated moderate levels of persistent organic pollutants (POPs). Of additional concern is a chronic dermal infection which is apparent in 14% of the LGN population, which may be related to pollution but this is not clear. The greatest threat to both populations is bycatch in artisanal gillnet fisheries. Whilst there is no clear evidence of a negative trend in abundance, there is a high probability of population decline in the near future, given the small population, the high degree of residency and the continuing mortality as a consequence of IUU (illegal, unreported, unregulated) fishing and other human activities in these areas.

In Santa Catarina, Paraná, and São Paulo provinces, Brazil, north of LGN and PLE, a total of 119 bottlenose dolphins (sub species unknown) and 442 Guiana dolphins were recorded stranded over 2 years. There was strong evidence that entanglement was indicated as the cause of death for bottlenose dolphins. The Committee was informed that the Brazilian Government is looking into this issue and is seeking ways to improve legislative effectiveness in protecting dolphins and other threatened species in these locations.

Attention: SC, CG-R

The Committee draws the attention of the range states (Argentina, Brazil, Uruguay) to its conservation concerns over the entire sub-species of Lahille's bottlenose dolphins (T. t. gephyreus) given their relatively small population sizes and constricted ranges, the high levels of bycatch and the high incidence of individuals with chronic dermatitis. The Committee therefore recommends:

(1) immediate action to reduce the level of bycatch in the southern Brazil populations;
(2) continued monitoring and photo-identification work on the populations throughout the subspecies' range to refine survival estimates and to assess trends in abundance and the prevalence and etiology of the chronic skin infections; and
(3) that the conservation status of the subspecies be prioritised for assessment in the future.

17.4 Franciscana CMP

In 2016, the IWC created a Conservation Management Plan (CMP) for the franciscana – see Item 10.1.4. In 2019, a review will be presented to the Committee. The review will be jointly conducted by the SM and CMP sub-committees and will include input from other relevant sub-committees.

17.5 Report of the 2018 *Tursiops* Taxonomy Workshop

In 2014 (IWC, 2015b) it was agreed that the Committee would undertake a review of taxonomy and population structure in the genus *Tursiops*, over several meetings. Understanding whether there is any consistency in the derivation of various local forms across the range, and to which taxonomic or population unit(s) they belong, has been challenging, and the taxonomy of the various forms is still unresolved. An additional aim of this exercise was to develop a widely applicable taxonomy assessment framework for small cetaceans. The review process concluded with an intersessional workshop, held in La Jolla in January 2018.

The 3-year review and workshop brought together researchers and experts from around the world to discuss this topic, motivated focussed research, and promoted new collaborations. Results from studies presented at previous meetings (2015-2017) and at the workshop itself were compiled and formed the basis for evaluation of taxonomic and population distinction issues in each geographic region.

Attention: SC, G

Having reviewed the extensive information included in the 2015-2017 review and 2018 workshop for evaluation of Tursiops *species, subspecies and population distinctions, the Committee* ***draws attention to*** *the need for* Tursiops *research in the areas identified as data deficient (the African coast of the eastern Atlantic, southern and eastern Mediterranean Sea, eastern South Pacific, Pacific coast north of California and off the Mexican mainland, Central American coast of the eastern North Pacific, Central American Atlantic and Caribbean Sea and Atlantic coast of northern and north-eastern Brazil, eastern Australia and in the western Pacific the islands of Micronesia, Melanesia, Polynesia, the Philippines and Vietnam). The Committee therefore* ***encourages****;*

(1) collection of additional data, including morphometrics, and high-resolution genetic analyses (e.g. ddRAD which may also be useful in other areas where there are similar questions requiring high-resolution analysis), to better characterise divergence between coastal and offshore forms in the western South Atlantic Ocean, to help confirm whether subspecies or species classification is more appropriate for T. t. gephyreus;
(2) further investigation of T. aduncus *lineages in the Indian Ocean and western South Pacific to assess potential subspecies recognition, extending the geographic coverage to include eastern Africa, the region between Pakistan and Indonesia, and the region between Australia and China;*
*(3) continued study of the genetics and morphology of southern Australia bottlenose dolphins with the "*T. australis*" mtDNA lineage, in the context of both* T. truncatus *and* T. aduncus;
(4) examination of the level of male-mediated gene flow between the coastal and offshore forms in the western North Atlantic to determine whether the coastal form should be elevated to species or subspecies status;
(5) more comprehensive morphometric analyses comparing T. truncatus in the Mediterranean, Black Sea, and eastern Atlantic to integrate with genetic data and evaluate whether any regions in addition to the Black Sea (T. t. ponticus) harbour a taxonomic unit above the level of population;
(6) comprehensive morphometric analyses of coastal and offshore T. truncatus in the eastern North Atlantic and comparison to those from the western North Atlantic to better evaluate potential regional differences;
(7) morphometric analyses of Gulf of California coastal and offshore dolphins relative to those from California and the eastern tropical Pacific, with a particular focus on the level of divergence of coastal dolphins in the upper Gulf of California to other areas; and
(8) the collection of additional genetic and morphological data throughout the eastern South Pacific and further studies to investigate coastal versus offshore forms throughout the region, including coastal and offshore waters from Central America to Mexico, and if possible around the southern tip of South America to Argentina.

The Committee also ***agrees*** *to continue compilation of specimen, study, and researcher details, and concentrated effort to improve our understanding of* Tursiops *in data-deficient areas.*
Finally, after reviewing the 2018 Tursiops *Taxonomy Workshop's evaluation of the support provided for taxonomic (subspecies, species) and population-level distinctions proposed in the publications reviewed, the subcommittee* ***concludes*** *that:*

(1) the current taxonomy provided for Tursiops *by the Society for Marine Mammalogy's Committee on Taxonomy is well supported by morphological and molecular genetic data, as well as ecological and distributional data; and*
*(2) discordance in currently available results from morphometric analyses and across different genetic markers of the recently described '*T. australis*' from southern Australia calls into question its validity at this time.*

In addition to the information and recommendations on *Tursiops*, the Committee noted that the review provided an opportunity to formulate some generic conclusions on taxonomic issues related to small cetaceans.

Attention: SC, G

After reviewing the development and use of a strategy for objective evaluation of species, subspecies, and population-level distinctions by the 2018 Tursiops *Taxonomy Workshop, the Committee:*

(1) ***agrees*** *with the strategy implemented at the workshop for the evaluation of species, subspecies and population level distinctions;*
(2) ***encourages*** *use of the criteria and guidelines in Reeves et al. (2004) for the assessment of species-level taxonomy, in Taylor et al. (2017) for subspecies-level taxonomy, and in Martien et al. (2015) for Demographically Independent Populations; and*
(3) ***concludes*** *that future taxonomic questions should be examined within an appropriately wide and inclusive geographic context and that multiple lines of evidence are necessary when positing taxonomic changes.*

The Committee applauded Natoli, Rosel and Cipriano for their considerable work and organisational skills during this effort.

17.6 Poorly documented takes for food, bait or cash and changing pattern of use

17.6.1 Intersessional Workshop on the use of Small Cetaceans for Food and Non-Food Purposes in South America

The poorly documented take of small cetaceans for use as wildmeat has been assigned as a priority topic. An ICG (and see Annex Y) has been tasked with the development of a toolbox of techniques that could guide and co-ordinate research into this topic, and as such a series of workshops were proposed to fulfil this task. The second of these workshops focused on South America and incorporated a detailed review of the use of Amazon river dolphins as bait in the piracatinga fishery, which, in turn, fed into the priority topic of the 2018 meeting.

Information was summarised for all countries, except Guyana and Suriname, and it was recognised that products from small cetaceans have been used throughout the region for both food and non-food purposes. This type of use is referred to as ‘aquatic wildmeat’. The usefulness of various tools and techniques was discussed, including data gathering techniques and forensic investigation. A database, comprising more than 3000 references, was used to map existing knowledge and understand data gaps. A framework was also established that had the purpose of standardised future data collection. The workshop participants populated a database from which regional patterns were mapped. Areas that were highlighted as a cause of conservation concern were; Bolivia, Brazil, Colombia, Costa Rica, Ecuador, Peru and Venezuela.

The take of Amazon river dolphins as bait in the piracatinga fishery was also reviewed. All range countries of *Inia* and *Sotalia* have laws in place to protect dolphins and prohibit intentional killing. Fishing for piracatinga is banned in Brazil and its trade is prohibited in Colombia, due to its impact on river dolphins and other wildlife. The practice of using dolphins as bait has recently expanded to Peru, Bolivia and Venezuela, following the imposition of restrictions in Brazil, however, no other range country has developed specific legislative or regulatory action, beyond the general protection of river dolphins, in response to the emergence of this practice.

The workshop concluded that some species and population required urgent attention both due to the extent of their use as wildmeat and from other threats.

17.6.1.1 SCIENTIFIC CONCLUSIONS AND RECOMMENDATIONS

Attention: SC, G, CG-A

The Committee ***endorses*** *the scientific conclusions and recommendations from the recent intersessional workshop on the use of Small Cetaceans for Food and Non-Food Purposes in South America aimed at improving regional knowledge and conservation research. In particular, the Committee:*

(1) ***agrees*** *that potential divisions within the genus* Inia *should be evaluated and genetic conservation units established;*
(2) ***agrees*** *that an evaluation of historical data on river dolphins should be undertaken to better understand other threats (e.g., from bycatch), to provide further insights into current trends;*
(3) ***encourages*** *the use of new technologies, such as drones and satellite telemetry, to establish trends, habitat use and dispersion patterns of Inia within Amazon River Basin and*
(4) ***encourages*** *new efforts to improve regional research capacity.*

The Committee ***draws attention*** *to the evidence showing that several small cetacean species and/or populations are being negatively impacted by their use as wildmeat in South America, and therefore* ***recommends*** *that abundance and distribution surveys, in tandem with investigation into the magnitude of aquatic wildmeat use, be conducted on these species. Appropriate survey designs should be implemented that consider the statistical power required to detect trends and the resultant data should then be used to estimate the impact of deliberate take for wildmeat on the following populations:*

(1) Boto in Purus and Japurá rivers, Brazil, and Içá/Putumayo river in both Brazil and Colombia, using previously established standardised methods (studies should also be expanded into other areas where take for bait may be a cause for concern);
(2) Chilean dolphin in Chile;
(3) Burmeister's porpoises in both Chile and Peru, noting that current evidence suggests that the Peruvian population is distinct;
(4) Dusky dolphins in Peru, noting that evidence shows that landings of this species has decreased and populations may have been heavily impacted;
(5) Guiana dolphins and other small cetaceans in Amapá, Pará, Maranhão, Piauí, Ceará, Espírito Santo, São Paulo and Paraná, in Brazil, where there is a documented use of bycatch for wildmeat purposes;
(6) Bottlenose dolphins and pantropical spotted dolphins) in Bahia Solano, Colombia, noting that deliberate takes for a long line fishery is ongoing;
(7) Tucuxi throughout its range, in Brazil, Colombia, Ecuador, as it shares most of the same threats as Inia geoffrensis, *and may also be used as bait in the piracatinga fishery; and*
(8) Guiana dolphin (Sotalia guianensis) in Lake Maracaibo in Venezuela, noting that deliberate take for food is ongoing.

The Committee also ***draws attention to*** *the Boto dolphins that have been isolated within the dam system of the Tocantins and Maderia Rivers in Brazil. Given the confined condition of the dolphins' habitat, the Committee* ***agrees*** *that the status of these dolphins be evaluated, to include abundance, genetic, habitat, prey availability assessments, with a view to developing a translocation protocol, including under what circumstances such a protocol should be enacted.*
Finally, given the concerns over the extensive habitat modification that will result from the Mega Project 'Arco Minero del Orinoco', a large scale mining operation proposed along the river and watershed of Venezuela, the Committee ***recommends*** *that population sizes and trends of both* Inia geoffrensis *and* Sotalia guianensis, *in the Orinoco River basin, be monitored before and during this project.*

17.6.1.2 CONSERVATION AND MANAGEMENT ISSUES

Attention: CG-R, S, CC

The Committee ***draws attention to*** *the management recommendations within the Report of the Workshop on the Use of Small Cetaceans for Food and Non-Food Purposes in South America, in particular, the need to have a regionally co-ordinated fisheries management plan for the Amazon River basin and a regional strategy for the conservation of river dolphins. Given continued concern over the use of dolphins as bait in the piracatinga fishery, the Committee:*

(1) ***commends*** *the Government of Brazil on its swift action in declaring a moratorium on the piracatinga fishery and respectfully requests that it maintains the moratorium to allow sufficient time to evaluate the effectiveness of protective measures and ensure the necessary protection of river dolphins;*
(2) ***reiterates*** *previous recommendation of the IWC Scientific Committee that range states (Bolivia, Brazil, Colombia, Peru and Venezuela) engage in a co-ordinated effort to strengthen legislative, enforcement, management and scientific efforts to ensure protection of the Amazon River dolphins;*
(3) ***encourages*** *range state authorities to work together and exchange information on the movement of piracatinga products across international borders; and*
(4) ***requests*** *that progress reports be submitted to the Scientific and Conservation Committees.*
(5) ***recommends*** *that the Commission asks the IWC Secretariat to send a letter to the Buenos Aires Group highlighting the issue of dolphins being used as bait in the piracatinga fishery and requesting joint efforts to enhance enforcement on wildlife and trade laws.*

17.6.2 Wildmeat Database

In 2016 (IWC, 2017) an intersessional group was established to work with the IWC Global Database Repositories Convenor, to develop an overarching aim for any future cetacean wildmeat database and identify the specific questions that such a database might address. The results of this work were presented, including a research agenda the formulation of key questions that could be addressed through the development and analysis of an aquatic wildmeat database. The Aquatic Wildmeat Database, developed independently of the IWC, was presented again and the Committee was updated on its improvements made following suggestions made last year. The future value of this data repository was highlighted and this and related issues will be considered intersessionally (see Annex Y).

The work of the Steering Group (see Annex Y) will continue and a third workshop, focusing on Africa, will be conducted intersessionally. The framework for an IWC Wildmeat database established at the workshop in South America will be further refined and will be used at the forthcoming workshop.

17.7 Small cetacean task team

The Scientific Committee continues to support the Task Team Initiative and the latest Task Team, for the South Asia River Dolphin, is in the process of being established with Dipani Sutaria and Nachiket Kelkar nominated as co-conveners. The task team currently comprises 14 members with representation from Bangladesh, India, Nepal and Cambodia and includes university associated researchers and NGOs (WWF and the Wildlife Institute of India).

Under its Task Team Initiative (e.g. IWC, 2016), the Committee ***strongly supports*** *the work of a Task Team for the South Asia River Dolphin and* ***agrees*** *that its first meeting which will occur before the 2019 meeting, if sufficient funding is available.*

17.8 Progress on previous recommendations

17.8.1 Vaquita

The Report of the Tenth Meeting of the International Recovery Team for Vaquita (CIRVA-10) was summarised and the results of the acoustic monitoring program for vaquitas were presented (SC/67b/SM01). This shows a continued decline in vaquita detections with no change in the trend since the last report in 2016. A brief review of the VaquitaCPR project was presented. This initiative, conducted in October and November 2017, aimed to capture vaquitas and bring them into human care. Ninety experts from nine countries were involved, including researchers experienced in the capture and handling of harbour porpoises, animal care professional, and veterinarians. Two vaquitas were successfully captured (an immature female [V01F] and an adult female [V02F]). In both cases, medical and behavioural evaluations were conducted to determine the suitability of the animals for transport to the floating pen or shore-based facility. Through the whole process the animals' health was continuously monitored by a team of experienced marine mammal veterinarians. The first vaquita caught (V01F) was in good condition initially, but did not acclimate to either the vaquita care centre pool or to the sea-pen facility, and the vaquita was released. V02F was also considered to be in good condition for transport to the sea-pen, however, after initially showing signs of adapting to the facility, the animal stopped swimming and an emergency release was initiated. The release was unsuccessful and the vaquita was quickly recaptured for administration of emergency care. Following three hours of emergency response, the animal went into cardiac arrest and did not respond to resuscitation attempts. Analyses of tissues and material obtained from VH02 is ongoing and a full report on VaquitaCPR will be reported at SC68A.

The survival of the vaquita depends on gillnet-free habitat and efforts to remove gillnets, both derelict and active, have increased dramatically in the last three years, particularly, during the ongoing 2017-18 totoaba season. The net removal programme demonstrates that illegal totoaba gillnets are still routinely set in great numbers in vaquita habitat. Despite enhanced enforcement efforts, there is a continued failure to prevent illegal fishing. CIRVA have stated that immediate action is needed to improve the situation through implementation of a series of recommendations. In particular, CIRVA recommended that the Government of Mexico establish an enhanced enforcement area, extending the boundaries of the existing vaquita refuge.

Attention: SC, CC, CG-R

The Committee has stressed for many years that the vaquita population is at a critically low level, and the most recent evidence demonstrates that the cause of the decline – use of illegal large-mesh gillnets – continues, making extinction in the wild increasingly likely; *the long-term decline in the vaquita reported previously has continued in 2017.* The Committee yet again **re-emphasises the serious concerns** it has raised on the status of the vaquita, and in particular its recommendations of the past two Committee meetings. Whilst again **commending** the Government of Mexico for its attention and response to the CIRVA findings and recommendations, the Committee:

(1) respectfully ***requests*** *that reports continue to be provided annually to the IWC Scientific Committee on actions and progress towards saving the vaquita;*
(2) ***strongly endorses*** *the recommendations of CIRVA10 that:*

(a) the CIRVA10 acoustic monitoring programme, critical for evaluating the effectiveness of conservation actions, be continued as in previous years to provide an annual empirical estimate of population trend;
(b) all Mexican enforcement agencies increase their efforts on land and in water immediately and continue this enhanced enforcement programme for the duration of the period of illegal totoaba fishing (at least until June 2018) to eliminate all setting of gillnets in the range of the vaquita;
(c) emergency regulations be promulgated immediately to strengthen the current gillnet ban and enhance enforcement and prosecution by:

- *(i) eliminating all fishing permits for transient fishermen and limiting fishing access to only those fishermen who can demonstrate residency in the fishing villages;*
- *(ii) confiscating any vessel that does not have the appropriate vessel identification, permits, and the required vessel monitoring system;*
- *(iii) requiring vessel inspection for each fishing trip at the point of departure and landing;*
- *(iv) prohibiting the sale or possession of gillnets on land and at sea within the area of the current gillnet ban and on adjacent lands within a specified distance of the coastline.*
- *(v) requiring that all gillnets be surrendered or confiscated and destroyed.*

(vi) eliminating the exemptions for all gillnet fisheries, including the curvina and sierra fisheries.

(d) efforts to remove gillnets from vaquita habitat be continued and enhanced and the numbers and locations of new nets recovered be published monthly;
(e) the number of inspections, interdictions, arrests, sentences, and other enforcement actions be published monthly, together with information on observed levels of illegal activities obtained from intelligence operations, for example from drones;
(f) successful prosecution and subsequent penalties be sufficient to deter illegal fishing; and
(g) development of gillnet-free fisheries be enhanced and linkages to incentivise the conversion of the fleet to gillnet-free operations be strengthened.

17.8.2 Yangtze finless porpoise

A rangewide survey of Yangtze finless porpoises (*Neophocaena asiaeorientalis asiaeorientalis*) was conducted in 2017, giving a preliminary abundance of around 1,000 individuals. This indicates that the rapid decline observed between 2006 and 2012 has now slowed, and that numbers may even be increasing in some areas. Nevertheless, the Critically Endangered status of this species remains unchanged. The survey results were encouraging and regarded as a possible indication that *in situ* conservation of Yangtze finless porpoises is feasible, given the marked increase of the number of individuals in Dongting and Poyang Lakes. For the population to make a sustained recovery in both numbers and range, current measures directed towards improving the habitat in the Yangtze River as well as the Dongting and Poyang Lakes must be continued and expanded. The Government of China was commended for the efforts undertaken to improve the YFP habitat. Nevertheless, concern remain over threats such as vessel strikes, bycatch, underwater noise and bridge construction. In addition, the planned construction of a dam across the channel connecting Poyang Lake to the river is an additional concern.

Attention: SC, CG-R

Given the extensive and pervasive nature of the threats facing the Yangtze finless porpoise population, the Committee:

*(1) **commends** the efforts of the Government of China to improve its habitat; and*
*(2) **reiterates** that the primary conservation actions should focus on (a) restoring and maintaining suitable habitat throughout the Yangtze River and associated lakes, including the maintenance of a network of* in situ *reserves and (b) ensuring that genetic diversity is preserved and that harmful human activities are limited.*

17.8.3 Maui Dolphin

The Government of New Zealand reported that its review of management measures is scheduled for later this year. An update was provided on observer coverage of the set net fishery in Taranaki and the trawl fisheries adjacent to existing closure areas (95.5%, and 88.3%, respectively). Outside of this target coverage area, an additional 114 trawl fishing days were observed. No captures of Māui dolphins were reported by observers or fishermen in commercial fisheries in the 12-month reporting period to 31 March 2018. A species-specific, spatially explicit, multi-threat risk assessment is being developed for Māui and Hector's dolphins, the results of which will inform an updated Threat Management Plan later in 2018.

Attention: SC, CG-R, CC

The Committee notes that no new management action regarding the Māui dolphin has been enacted since 2013. It therefore concludes, as it has repeatedly in the past, that existing management measures in relation to bycatch mitigation fall short of what has been recommended previously and expresses continued grave concern over the status of this small, severely depleted subspecies. The human-caused death of even one individual would increase the extinction risk. In addition, the Committee:

*(1) **re-emphasises** that the critically endangered status of this subspecies and the inherent and irresolvable uncertainty surrounding information on most small populations point to the need for precautionary management;*
*(2) **reiterates** its previous recommendation that highest priority should be assigned to immediate management actions to eliminate bycatch of Māui dolphins including closures of any fisheries within the range of Māui dolphins that are known to pose a risk of bycatch to dolphins (i.e. set net and trawl fisheries);*
*(3) **notes** that the confirmed current range extends from Maunganui Bluff in the north to Whanganui in the south, offshore to 20 n. miles, and it includes harbours - within this defined area, fishing methods other than set nets and trawling should be used;*
*(4) **welcomes** the update on Maui dolphins provided and looks forward to receiving the species-specific, spatially explicit, multi-threat risk assessment in 2019.*
*(5) **respectfully encourages** the New Zealand; Government to commit to specific population increase targets and timelines for Māui dolphin conservation,*
*(6) **respectfully requests** that reports be provided on progress towards the conservation and recovery goals as updates become available.*

17.8.4 Cruise report from North Western Africa

For the third year, survey results were reported from cruises conducted in north western Africa waters. Fourteen schools comprising some five species and totalling 433 individuals were sighted, including bottlenose dolphins, both pantropical and Atlantic spotted dolphins and, spinner dolphins. This area is poorly surveyed and the continuation of this work was encouraged. The Committee **suggests** that a more substantive analysis of the data from all surveys be conducted and reported back next year, particularly as SC68A priority topic will be on African small cetacean species.

17.8.5 Monodontids Workshop Report

NAMMCO hosted a workshop and produced a Global Review of Monodontids. Researchers and subsistence hunters from across the Arctic and subarctic participated. Several IWC scientists also participated, including Litovka, Reeves, and Suydam. The report[9], summarises what is known about the status of 12 stocks of narwhals and 22 stocks of white whales. There may be more stocks than this as information on stock structure is incomplete for some areas. The summary information and identification of threats and concerns within the report will be helpful in prioritising future research. Some stocks are doing well, but conservation actions are desperately needed for some others. The IUCN Red List status and documentation for both species was updated to Least Concern in December 2017 and that the information summarised in the NAMMCO review was very useful for those assessments.

Attention: C-A

The Committee ***welcomes*** *the report of the NAMMCO workshop reviewing the monodontids[9]. It* ***draws attention to*** *the recommendations contained in the report and* ***encourages*** *their implementation, particularly those pertaining to the stocks of greatest concern.*

17.9 Takes of small cetaceans

7.9.1 New information on takes

The Committee received the summary of takes of small cetaceans in 2016–17 extracted from the online National Progress Reports and prepared by the IWC Secretariat, in addition to information obtained online.

No direct takes of small cetaceans were reported in the 2017 National Progress Reports. The Committee **notes** that it would be helpful if the Secretariat encouraged all member countries and IGOs (e.g. NAMMCO) to submit information on direct takes as a routine procedure.

The content of the Japan Progress Report on Small Cetaceans, a public document available from the website of the Fishery Agency of the Government of Japan[10], was summarised. It was noted that catch statistics in the Japan Progress Report on small cetacean cover catches in the calendar year, that is, from 1 January to 31 December, following the guidelines for IWC National Progress Report, while the catch quota of small cetacean fisheries are set seasonally. Thus, in some cases, the calendar yearly catch may exceed the seasonal (yearly) catch in appearance, but in such cases, the actual seasonal catch is aligned with the allocated catch quota. The Committee noted that the catch of 1,057 Dall's porpoises in the hand harpoon hunt was significantly lower than previously recorded reported and below the quota. It was stated that this is a result of the destruction of the community that conducts this hunt, rather than a change in the cetacean population, following the earthquake and tsunami of 2011.

7.9.2. Live captures

The Pacific Scientific Research Institute of Fisheries and Oceanography (TINRO) will consider a quota of 13 killer whales for 2018 and a public hearing was held on 3 May 2018 to make comments on this plan. This proposed new quota considers killer whales in the Sea of Okhotsk as one population, which is estimated to have an abundance of over 3,000 individuals. This number is considered minimal as only 50% of the sea was surveyed. In addition, the information available to the Russian Government on colour and fin patterns, feeding behaviour and distribution do not allow clear identification of different ecotypes, and that all genetic samples analysed to date belong to a single population. It was noted that most published information on Okhotsk Sea killer whale abundance and stock structure is in Russian-language literature, or as part of internal documentation.

Attention: C-A, CG-A
With respect to live captures, and specifically the capture of killer whales from the Sea of Okhotsk, the Committee:

(1) ***reiterates*** *its long-standing recommendation that no small cetacean removals (live capture or directed harvest) should be authorised until a full assessment has been made of their sustainability;*
(2) ***notes*** *that this is especially important for killer whales because populations are generally small and have strong social bonds and removals have unknown effects on their demographic structure; and*
*(3) r****eiterates*** *its concern that removals of killer whales are occurring from the Okhotsk Sea population.*

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[9] https://nammco.no/wp-content/uploads/2018/05/report-global-review-of-monodontids-nammco-2018_after-erratum-060518_with-appendices_2.pdf
[10] *http://www.jfa.maff.go.jp/j/whale/w_document/attach/pdf/index-9.pdf*

In light of the verbal report received at this meeting that Russian authorities intend to proceed to consider limits of allowable live-capture removals of killer whales in the Sea of Okhotsk on the basis that there is no stock structure and there are no ecotype differences between the populations in this region, the Committee:

(1) ***encourages*** *more extensive effort to examine these issues; and*
(2) ***requests*** *that relevant analyses be provided for the Scientific Committee's consideration at its next meeting.*

17.10 Status of the voluntary fund for small cetacean conservation research

In 2017, donations for the Voluntary Fund for Small Cetacean Conservation Research totalling £13,122 were received from the Government of Italy. At the end of the financial year 2017, this brought the total of the fund to £81,077.

The Committee **expresses its sincere gratitude** for Italy's contributions and notes that these funds support critical conservation research projects of direct relevance to the work of the Committee.

Five projects were offered funding in 2016 and were implemented in 2017. One of the projects has since been withdrawn and one project, the Indus river dolphin abundance survey, was completed and reported on in 2017. The remaining three projects, on the 'Chilean Dolphin' in Chile, the 'Use of small cetaceans as wildmeat in China' and the 'Development of a business model for sustainable fisheries in the Upper Gulf of California, Mexico', are all near completion and will be reported on fully next year. Updates are available on the IWC website.

17.11 Work plan and budget requests

17.11.1 Priority topics for 2019 to 2024

The sub-committee on Small Cetaceans discussed ongoing priorities and will continue the development of these intersessionally; however, given the location of the meeting it is likely that the focus will be on African species or areas during 2019-20. Other potential priorities identified in discussions were *Inia* (e.g. taxonomy), *Sotalia guianensis*, *Phocoena phocoena*, *Delphinus delphis*, southern hemisphere beaked whales, *Steno bredanensis*, Northwest Pacific *Orcinus orca* and 'the Caribbean'.

17.11.2 Work plan for 2019 – 2020

The workplan on issues related to small cetaceans is given in Table 23.

Table 23

Work plan on small cetaceans

Topic	Intersessional 2018/19	2019 Annual Meeting (SC/68a)	Intersessional 2019/20	2020 Annual meeting
Franciscana CMP	ICG (Annex Y) to co-ordinate outcomes of CMP across sub-committees	Report	ICG (Annex Y) to synthesis actions from 2019 SC report and develop a work plan	Report
Wildmeat	ICG (Annex Y) to plan and conduct African Workshop.	Report	ICG (Annex Y) group to summarise workshop series and develop future work plan.	Report
Small Cetacean Task Team	Intersessional Workshop on South Asian river dolphins.	Report	Act on recommendations from 2018/19 River dolphin workshop.	Report
Sotalia	SG (Annex Y) to plan and conduct workshop #1 (at SOLOMAC)	Report	SG (Annex Y) to plan and conduct workshop #2	Report

18. WHALE WATCHING[11]

The report of the sub-committee on whale watching is given as Annex N.

18.1 Assess the impacts of whale watching and swim-with-whale operations on cetaceans

18.1.1 Review progress of Modelling and Assessment of Whale Watching Impacts (MAWI)

Modelling and Assessment of Whale Watching Impacts (MAWI) has been on the Committee's agenda for several years. In April 2018, an intersessional workshop was held to identify the key research questions for understanding the potential impacts of whale watching on cetaceans (SC/67b/Rep03). A number of issues were highlighted, including: (a) the need to better understand the impact of recreational whale watching vessels as compared to commercial vessels; (b) the importance of looking at the potential impact of whale watching at short-term (e.g., behaviour change), mid-term (e.g., shift in habitat use) and long-term (e.g., population dynamics) time scales; (c) the use of existing and new data to explore the mid- and long-term impacts, as opposed to replicating short-term studies; and (d) the importance of building scientific capacity in the locations where the research would take place. More information can be found in Annex N, item 2.1.

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[11] In response to a request from the Chair of the Whale Watching Working Group of the Conservation Committee, we have changed our past practice of treating whalewatching as a single word to the use of two words.

Attention: SC, C-R

The Modelling and Assessment of Whale Watching Impacts (MAWI) initiative held a workshop in Italy in April 2018, in conjunction with the 32nd European Cetacean Society conference.

The Committee ***endorses*** *the following recommendations from this workshop:*

(1) the incorporation of both social and natural sciences to better understand whale watching impacts;
(2) the development of a Strategic Framework, supported by a Decision Tree, to aid in the prioritisation of policy and research choices;
(3) the development of toolkits and resources that can be accessed globally; and
(4) the standardisation of data collection.

The Committee also ***agrees*** *that a third MAWI workshop be held intersessionally, ideally just before or after the 2nd World Marine Mammal Science Conference in 2019, in Barcelona, with the following objectives:*

(1) to determine in detail which data should be collected to best answer the natural and social science research questions developed in SC/67b/Rep03;
(2) to identify the best locations for conducting research projects that address these questions; and
(3) to continue to develop modelling approaches for assessing the long-term impacts of whale watching on cetacean populations (using data on short- and mid-term impacts).

18.1.2 Review specific papers assessing impacts

The Committee received several papers regarding impacts to cetaceans from whale watching activities. Those papers included (1) efforts to assess stress hormones in baleen of southern right whale calves, (2) ‘solitary sociable’ cetaceans, (3) land-based observations in the Canary Islands to assess and mitigate potential impacts of whale watching vessels on cetaceans, (4) a Whale Welfare Assessment Tool (also presented and discussed in Plenary) and (5) the 15th year of a summary of papers published in the previous year related to a better understanding of impacts, mitigation and compliance to regulations. Additional details on these papers and projects can be found in Annex N, item 2.2.

Attention: SC, CG-A

The term ‘solitary sociable dolphin’ or cetacean is usually taken to apply to cetaceans that have little or no contact with conspecifics and who regularly closely approach humans, often including touch, social, sexual and play behaviours (Wilke et al.*, 2005). Given that solitary sociable cetaceans often end up in circumstances where they are harmed and killed and that they may come to present a threat to human swimmers, the Committee:*

(1) ***agrees*** *to continue intersessionally to monitor the phenomenon of solitary sociable cetaceans as part of its work;*
(2) ***advises*** *that, where these animals occur, research be conducted to determine whether the emergence of harmful behaviours either to the animal or to people can be reversed; and*
(3) ***advises*** *local authorities and other concerned parties to keep people away from them in order not to encourage behaviour that may prove harmful to the animal or swimmers.*

In addition, the Committee ***agrees*** *that the Whale Welfare Assessment Tool (currently being developed at the Royal Veterinary College, University of London, in the context of the IWC Whale Killing Methods and Welfare Issues Action Plan), for which a hypothetical whale watching case study was trialled (Annex N, item 2.2), be applied to real-world whale watching situations. The southern resident killer whales in Washington, USA and the bottlenose dolphins in Bocas del Toro, Panama were proposed. These two populations are subject to intense whale watching pressure and may be suffering welfare and health impacts related to this pressure. Both locations have data relevant to the assessment tool and therefore seem ideal as pilot projects for its application.*

18.1.3 Consider documented emerging areas of concern (e.g., habituation, new areas/species, new technologies, in-water interactions) and how to assess them

The Committee received several papers about emerging areas of concern regarding whale watching, including (1) human-induced behavioural changes, (2) impacts from recreational in-water interactions with cetaceans and (3) purposeful and inadvertent feeding by humans.

The Secretariat for the Convention of Migratory Species (CMS) submitted several documents to SC/67b including a global review of in-water interactions with aquatic mammals. That review had resulted in a CMS resolution that encouraged Parties to facilitate research allowing for an assessment of the long-term effects and biological significance of disturbances from ‘swim-with-marine-mammal’ programmes. The topic of swimming with cetaceans is also addressed under Item 18.6.

The Committee received reports about several studies to assess the impacts and compliance with regulations of commercial ‘swim-with-whale’ operations in Australia. The discussion of this issue can be found in Annex N, item 2.3.

Attention: SC, CC, S

*The Committee **agrees** that the habituation intersessional correspondence group, now named human-induced behavioural changes of concern, should continue (see Annex N, table 3).*

Given the substantial effort the Convention on Migratory Species (CMS) Secretariat has made in preparing several documents for the Committee to consider this year, the Committee:

*(1) **recommends** a continuation and an expansion of this exemplary collaboration between the IWC and CMS Secretariats and their various committees;*
*(2) **endorses** the intention of CMS to work with the IWC Scientific Committee on guidelines for in-water interactions with aquatic mammals and **offers** to provide the scientific underpinning for these guidelines;*
*(3) **agrees** that the Committee's intersessional correspondence group on swim-with-whales work intersessionally with the CMS Aquatic Mammals Working Group to develop draft guidelines; and*
*(4) **offers** to review draft guidelines when they are ready, with a view to **agreeing** a joint product of the IWC and CMS and hosted by both websites as a global resource.*

See also Item 18.6 for additional recommendations related to swimming with cetaceans.

18.2. Consider information from platforms of opportunity of potential value to the Scientific Committee

The Committee received examples of several platforms of opportunity where data have been collected concerning habitat use, behaviour, changes in distribution and potential risks from shipping for multiple different species in several different areas. Of particular interest was Peninsula Valdés, Argentina, where approximately 460,000 photographs have been taken from whale watching boats and provided to researchers from the Instituto de Conservación de Ballenas and Ocean Alliance (SC/67b/WW04). See Annex N, item 3.

The Committee offered numerous suggestions as to how to handle the large number of images and **encourages** the researchers to network with other researchers around the world, particularly humpback whale researchers dealing with similarly large numbers of photographs and multiple catalogues, to improve the processing time of the photographs.

18.3 Whale watching in east Africa and the wider Indian Ocean

A proposal for Concerted Action for Arabian Sea humpback whales was passed by CMS with strong support from range states. This was discussed in Annex N, item 4.

Attention: CC, S, CG-A

Noting the Committee's discussions over several years on the status of the Arabian Sea humpback whales (see Item 10.2.1), the Committee:

*(1) **welcomes** the CMS proposal for Concerted Action for Arabian Sea humpback whales;*
*(2) **notes** that humpback whales are the target of one emerging whale watching operation in the south of Oman and **highlights** the likelihood that the population could become the target of future whale watching activities;*
*(3) **emphasises** the need for regulators and scientists to work with the industry to ensure that whale watching does not add to the many other pressures on this small, isolated, non-migratory and endangered population.*

The Committee therefore:

*(1) r**ecommends** that building capacity to conduct needed research and to ensure consistent training of whale watching operators be a high priority for Omani authorities and other parties working on the recovery of the endangered Arabian Sea humpback whale population;*
*(2) **notes** that boat operators for cetacean watching operations appear to turn over at a high rate in this area, and **recommends** that training workshops should be regularly offered and conducted;*
*(3) **welcomes** the offer from the Pacific Whale Foundation to help organise and conduct another training workshop, but **recommends** a more comprehensive plan be implemented by the Omani authorities, working with the IWC and other interested parties, to build local capacity for such training; and*
*(4) **agrees** to retain a review of whale watching in east Africa and the wider Indian Ocean region in its work plan (see Annex N, table 4) and to conduct an intersessional review of whale watching in these areas, to be presented at SC/68a.*

18.4 Review Whale Watching Strategic Plan (2018-2024) and joint work with the Conservation Committee

18.4.1 Review and provide recommendations on the draft Strategic Plan

At SC/67a, the Conservation Committee's SWG on Whale Watching requested the Scientific Committee to review a draft of the next iteration of the IWC's Strategic Plan (2018-2024) on Whale Watching (see SC/67b/WW02). This was accomplished primarily during a SC/67b pre-meeting and then further discussed in Annex N (item 5 and appendix 2).

Attention: CC

The Committee ***draws the attention*** *of the Conservation Committee's Standing Working Group on Whale Watching (SWG) to Annex N, appendix 2, which provides a full set of comments on the draft Strategic Plan (2018-2024) on Whale Watching. The most important comments and recommendations from the appendix are highlighted below:*

(1) The addition of an Action 1.5: Develop a communications strategy to actively promote IWC whale watching resources (e.g., the Handbook, reports and training opportunities), with approaches tailored to target key audiences. These audiences include the public and whale watching managers, researchers, operators, and on-board naturalists. Communication actions could include preparing publicly accessible summaries of IWC whale watching reports, improving the whale watching pages on the IWC website (which is already underway with the new Whale Watching Handbook, see Item 18.5), and promoting resources on social media, at key meetings and via press releases to industry bodies and trade publications. The implementation of this action could be coordinated intersessionally via the Secretariat. A joint intersessional working group, which includes key Secretariat staff, could develop a communications strategy for consideration at IWC/67 (the Brazil Plenary meeting) and/or the joint session of the CC/SC at SC/68a.

(2) The replacement of the actions of Objective 2 in the draft Strategic Plan with the following:

a) Action 2.1 – Continue the Modelling and Assessment of Whale Watching Impacts (MAWI) initiative, to develop tools and methodologies to assist researchers and managers in their efforts to assess potential impacts of whale watching on cetaceans and to mitigate them. This initiative is ongoing and could focus on:

i) Investigating modelling methods to link short- (e.g., behavioural reactions) and medium-term (e.g., changes in population distribution) responses with potential impacts from whale watching to long-term (i.e., >10 to 20 years) consequences (e.g., vital rates).

ii) Establishing standard data collection methodologies, including from platforms of opportunity.

iii) Identifying key locations for whale watching research projects and programmes, taking into consideration logistics, capacity and management urgency;

b) Action 2.2 – Develop a long-term integrated research programme to better understand the potential impacts of whale watching on the demographic parameters of cetacean populations. Seek to:

i) Investigate whether there is a causal relationship between whale watching exposure and the survival and vital rates of exposed cetacean individuals and populations;

ii) Understand the mechanisms involved in causal effects, if they exist, in order to define a framework for improved management;

c) Action 2.3 – Develop processes and mechanisms for whale watching activities to collect and provide scientifically robust and useful data to researchers and research programmes; and

d) Action 2.4 – Develop an approach (e.g., hold an intersessional workshop; establish a joint intersessional working group) to integrate social and ecological scientific research within the IWC to inform whale watching management and promote potential benefits. This is a coordinated action between the SWG and the sub-committee.

In particular, Action 2.2 will require a dedicated person to guide and coordinate the development and implementation of a research programme or plan. The best option would be for the SWG to contract with someone, full- or part-time, to carry out this task, whilst recognising the budgetary concerns. Therefore, the Committee ***recommends*** *that the search for funding for this and all other actions in the Strategic Plan be focused, broad-ranging, and innovative. An alternative, if budgetary issues are prohibitive, is to have the research programme developed intersessionally by an intersessional correspondence group or the convenor and co-convenor of the Committee's sub-committee on whale watching.*

Lastly, the Committee ***reiterates*** *its previous recommendation to improve the coordination between the SWG and the Committee's sub-committee on whale watching in the development and implementation of a Strategic Plan on Whale Watching. This year's 21 April pre-meeting to review the draft Strategic Plan was intended to improve coordination and provided an opportunity to contribute to the draft Strategic Plan but it did not completely achieve the goal of coordination, as a limited number of SWG members were able to attend the pre-meeting.*

18.4.2 Develop procedures to provide scientific advice as requested in the plan (including the online handbook) and make the Committee more effective at providing information to the Commission

The revised Actions 2.1-2.4 in Item 18.4.1 outline how the sub-committee on whale watching will collect information needed to inform the Conservation Committee's SWG on Whale Watching. Procedures for providing this advice will be discussed and determined cooperatively with the Conservation Committee, during the joint meeting immediately after SC/67b and intersessionally through the intersessional correspondence group (see Annex N, table 3,).

18.5 Whale watching handbook

18.5.1 Review and provide comments on the IWC's Whale Watching Handbook

The Whale Watching Handbook (Handbook) was presented. Before being made available to the public it will also be translated into French and Spanish with support from CMS. Annex N (item 6) provides additional comments and suggestions for fine-tuning and improving the already-admirable Handbook.

Attention: CG-R, SC, S, CC, C-R

The Committee ***welcomes*** *the presentation of the online Whale Watching Handbook and* ***agrees*** *that it is comprehensive, scientifically substantive, user-friendly and well designed.*

To ensure the IWC Whale Watching Handbook comes to the attention of the international whale watching community, including managers, operators and the public, the Committee ***recommends*** *that all Contracting Governments provide a link to the Handbook on the relevant agency pages of their own government websites once the Handbook goes 'live'.*

The Committee also ***recommends*** *that the Conservation Committee and the Commission develop a plan for identifying and securing long-term funding for the further development (e.g., translations into additional languages, writing additional case studies or country profiles) and the ongoing maintenance (e.g., periodic reviews of content) of the IWC Whale Watching Handbook. The Handbook must be updated regularly to remain a vibrant, living document.*

18.6 Review reports from intersessional correspondence groups

The Committee received information from the intersessional correspondence groups (ICG) of swim-with-whale operations and communication with IORA. Annex N provides details of (1) the discussion related to the intersessional work of the ICG on swim-with-whale operations (item 7.1) and (2) the discussion related to the intersessional work of the ICG on IORA communication (item 7.2).

Attention: S, SC, CC, CG-A, CG-R

Regarding swim-with-cetacean operations, the Committee:
(1) ***agrees*** *that the intersessional correspondence group on swim-with-whale operations (Annex N, table 3) should continue;*
(2) ***draws attention*** *to guiding principles for whale watching, including in-water interactions, that are being or have been developed by various regional bodies, such as the Convention on Migratory Species and UNEP in the Wider Caribbean (see Annex N, item 2.3 and UNEP-CEP, 2012), that advise that swimming with cetaceans be discouraged where it is not already established; and*
(3) ***recommends*** *that, in jurisdictions where swim-with-cetacean activities have not been occurring or are just starting, this practice be prohibited until there is scientific evidence that supports allowing it, noting that the risks to both humans and cetaceans are substantial if operators are inexperienced and not following any relevant guidelines; and*

The Committee also ***welcomes*** *the increased communications between IORA and the IWC over the past year. The IORA Sustainable Whale and Dolphin Watching Tourism Network was established and Australia will convene the Network in its first year of operation and will produce a biannual newsletter. Consequently, the Committee:*

(1) ***agrees*** *that the intersessional correspondence group on communication with IORA (Annex Y) should continue; and*
(2) ***encourages*** *greater engagement between the IWC and IORA on whale watching, beyond the exchanges amongst the intersessional correspondence group (Annex N, table 3).*

18.7 Review progress on scientific recommendations

18.7.1 Global influence of recommendations

The Committee received information about the influence of previous recommendations in numerous countries. Details can be found in Annex N, item 8.1.

18.7.2 Tracking progress on previous recommendations

The sub-committee on whale watching reviewed 27 of its recommendations and agreed statements from the past two years. Of those, 15 were completed or partially completed, nine are on-going, and three have not yet been addressed. Annex N, item 8.2, provides details about those recommendations and agreed statements. There is also ongoing work to update and finalise the terms of reference for the sub-committee on whale watching.

18.7.3 Update on dolphin watching in Bocas del Toro, Panama

Concern continues about the number of dolphins from the small population in Bocas del Toro, Panama that are found dead. Nine deaths in 2016 and 2017 are known to have occurred, five of them confirmed boat strikes. These losses are unsustainable. Research to better understand impacts on the population includes measuring stress hormones in biopsy samples and acoustic monitoring. A regulatory update to strengthen management of whale and dolphin watching in Panama, including Bocas del Toro, was released in October 2017, with the support of the Ministry of Environment.

Attention: SC, C, CG Panama

The Committee ***reiterates*** *its grave concern regarding the intense and uncontrolled dolphin watching in Bocas del Toro, Panama. This concern has been expressed and reiterated for several years due to continuing mortalities, including from vessel strikes, in this small population (probably fewer than 100 animals). In this regard, the Committee:*
(1) ***welcomes*** *the ongoing research to monitor this dolphin population and the impacts it is facing from dolphin watching;*
(2) ***reiterates*** *its welcome of Panama's increased responsiveness to protect the local dolphin population by minimising negative impacts from dolphin watching (IWC, 2018a) and* ***welcomes*** *the regulatory update, supported by the Ministry of Environment, which is meant to lead to stronger management of whale and dolphin watching in Panama, including Bocas del Toro; and*

(3) ***expresses serious concern*** *at the number of deaths reported in 2016 and 2017 and* ***recommends*** *action from the Government of Panama as a matter of urgency, including the immediate and committed implementation of the updated regulations.*

18.8. Work plan and budget requests for 2019-2020

18.8.1 Work plan for 2019-2020

The work plan for matter related to whalewatching is shown in Table 24.

Table 24

Summary of the work plan for matters related to whale watching. Many of these items have intersessional correspondence groups (ICG) or intersessional advisory groups (IAG). Those groups will work intersessionally and provide updates at SC/68a (see Annex X)

Topic	Intersessional 2018/19	2019 Annual Meeting (SC/68a)	Intersessional 2019/20	2020 Annual meeting
Assessing impacts	-	Papers to be presented	-	Papers to be presented
Third MAWI workshop	Workshop planning	Receive update on planning	Workshop (Annex Y)	Report
Update IWC whale watching guidelines and principles	Revise guidelines and principles	Review	Continue if needed	Receive update
Indian Ocean review	ICG (Annex Y)	Papers to be presented	-	-
East Africa review	Work to prepare review	Paper to be presented	-	-
Intersessional correspondence groups	See Annex Y	Receive reports	See Annex Y	Receive reports
Joint meeting with Conservation Committee Standing Working Group on Whale Watching (SWG) to discuss incorporation of social science in joint work streams	Meeting planning	Receive update	Meeting planning	Joint meeting with SWG
IWC Whale Watching Handbook	-	Receive updates	-	Receive updates

19. SPECIAL PERMITS

19.1 General considerations on improving the evaluation process

This issue is considered as part of the process to revise ‘Annex P’ (see discussion in Item 28.3).

19.2 NEWREP-A

Summaries of NEWREP-A papers are given in Annex U1.

19.2.1 Report on ongoing research

In plenary, the Committee received and briefly discussed four papers on ongoing work – as indicated below, some of these were discussed more fully in sub-groups.

SC/67b/SP08 presented the results of the third biological field survey of NEWREP-A during the 2017/18 austral summer season. In discussion, it was noted that the high apparent pregnancy rate (95.3%; 122 of 128 mature females) of Antarctic minke whales was consistent with previous results (e.g. from JARPA and JARPA II).

SC/67b/ASI07 presented a summary of results of the NEWREP-A dedicated sighting survey during the 2017/18 austral summer season whilst SC/67b/ASI11 presented the research plan for the next systematic vessel-based sighting survey in the Antarctic under NEWREP-A 2018/19. The new NEWREP-A 2018/19 sighting survey plan has been endorsed by the Committee; Annex Q (item 4.2) provides more details on both these papers.

SC/67b/EM05 presented results of the krill and oceanographic surveys undertaken during the third NEWREP-A survey in Area V-E and VI-W (see Annex L, item 6.1 for details).

19.2.2 Update on previous recommendations

19.1.2.1 AGE DATA AND RMP/IST (RECOMMENDATION 1)

SC/67b/RMP03 provided updated draft specifications for an RMP/IST type simulation exercise to evaluate management procedures based on modified catch limit algorithms that use information on recruitment inferred from age data from Antarctic minke whales. Details and discussion are given in Annex D, section 2.3.2.

Attention: S

The Committee ***agrees*** *that methods currently used or proposed to be used in the Committee that use age data should (as necessary) be investigated to evaluate the relationship between their results and the accuracy and precision of the age data that they use where this is pertinent to the results of import from these methods. The Committee* ***agrees*** *to include this as an agenda item for next year’s meeting.*

19.1.2.2 BIOPSY SAMPLING AND TELEMETRY FEASIBILITY STUDIES (RECOMMENDATIONS 4 AND 5)

SC/67b/SP04 summarised the results of a feasibility study on biopsy sampling and satellite tagging of Antarctic minke whales under NEWREP-A. The authors concluded that in the context of the NEWRREP-A objectives, (a) the efficiency of biopsy sampling is much lower than that of lethal sampling for Antarctic minke whales and (b) that the amount of tissue derived from biopsy samples is insufficient to conduct the suite of biomarkers targeted by NEWREP-A. They therefore concluded that biopsy sampling was not a feasible approach to fulfil the objectives of NEWREP-A.

This paper prompted considerable discussion in the Committee, both with respect to 'efficiency' of the method and the amount of material required.

One issue raised was that there was the need for better clarification of terminology used in the paper (e.g. 'sampling' versus 'killing) in order, for example, to interpret properly the conclusion that biopsy sampling took approximately three times longer than lethal sampling. It was not clear, for example, whether the median times for biopsy and lethal sampling provided were truly comparable because of the lack of information on when the time for these methods started and ended. In particular, handling time for lethal sampling appeared to not be included in the total time calculations.

The authors responded that in SC/67b/SP04 'the efficiency' of sampling techniques was defined as 'Success Proportion' rather than 'Time of Experiment' because 'Success Proportion' represents a better indicator of the efficiency. To fulfil the purposes of NEWREP-A, random sampling is required in which generally only one animal from a school is sampled. Notwithstanding this clarification, they provided definitions of 'Time of Experiment' (see details in Yasunaga *et al*. in Annex U2).

Another issue raised was that the NEWREP-A review workshop (ref) had suggested 'involving people with expertise in successfully biopsy sampling common minke whales in the North Atlantic', meaning collaborating in the field with experienced foreign experts. However, Table 2 of SC/67b/SP04 showed an ongoing decline in success proportion (number of biopsy samples / number of targeted whales which were chased for sampling by the SSVs) between 2015/2016 and 2017/2018 rather than the increase one would expect with increasing experience. The authors responded that they had consulted with foreign scientists although they were not on the vessels, that they used experienced marksmen and that the decline was an artefact of weather and sea state conditions under which samples were collected. However, the counter-comment was made that in authors' analyses, the best model did not include "weather conditions" as a significant factor.

In response the authors provided results of a GLM analysis based on the binomial distribution assumption to examine the differences in success proportion in the biopsy sampling experiment using research seasons as explanatory variables. The coefficients for each year were not significant, suggesting that the differences of success proportions among the seasons are not statistically significant and consequently provide no evidence that shooters' efficiency has decreased significantly over the three research seasons (see details in Yasunaga *et al*. in Annex U2).

Some Committee members (see Clapham et al. I, in Annex U2) disagreed with the authors' conclusion that the study revealed that biopsy sampling was not feasible for the NEWREP-A programme. Rather, they believed that it showed that it was both feasible and appropriate. They also disagreed that the amount of tissue obtained was insufficient, citing the large number of research programmes that successfully use biopsy samples to fulfil research objectives including using a single sample for a variety of biomarkers (e.g. stable isotopes, fatty acids, hormones, genetics).

In response, the authors agreed that the amount of epidermal tissue collected by biopsy sampling is enough for the requirement of genetic, epigenetic and stable isotope analyses. However, they stressed that the amount of adipose tissue collected by biopsy sampling was not large enough to measure progesterone, lipid content and fatty acid in the context of the objectives of NEWREP-A (see details in Yasunaga *et al*. in Annex U2).

In their closing comments, the authors stated that in response to the recommendation of the Expert Panel, dedicated experiments for biopsy sampling of Antarctic minke whales had been carried out which had generated the results presented at this meeting and from which the authors had drawn their conclusions. No further dedicated time for biopsy experiments was planned at this stage, but this could be reconsidered at the mid-term review. Meanwhile, NEWREP-A will only collect additional biopsy samples opportunistically.

With respect to the best approach to assess the efficiency of biopsy versus lethal sampling, a standard approach for measuring the efficiency of biopsy sampling and to compare this to the process of lethal sampling was proposed (Clapham et al. II, in Annex U2).

Attention: S

The Committee had last year agreed on establishing an intersessional Advisory group tasked 'to provide advice on developing an experimental protocol for ascertain whether it is possible to reliably biopsy minke whales and, if so, under what circumstances (experience, vessel type, equipment, environmental conditions, etc.). This group could use as starting point the advice provided by the Expert Panel' (JCRM 19 suppl:431-490). Due to a clerical error the group did not convene. Attention was drawn to a protocol to evaluate non-lethal techniques presented to SC66b (Mogoe et al., 2016). This protocol included four questions to help identify the feasibility and practicability of non-lethal methods.

The Committee ***agrees*** *to re-establish the Advisory group (Annex Y), under Palka for consideration at SC68a. It also* ***agrees*** *that suggestions for refining questions in the method used by Mogoe and colleagues (2016) should be added to the tasks of this group.*

19.1.2.3 EPIGENETIC AGEING (RECOMMENDATION 8)

Recently, epigenetic (DNA-methylation) ageing has been successfully used to estimate age in humpback whales (Polanowski *et al.* 2014). As noted under Item 11.4.4, this year, the Committee invited Jarman, the leading specialist in this technique to give an overview presentation to the Committee as a special night session. This covered topics such as current and future prospects for this class of methods (see Annex I, item 5.5).

SC/67b/SDDNA04 presented a feasibility study on epigenetic ageing in Antarctic minke whales in response to Recommendation 8 from the Expert Panel (for details see Annex I, item 5.5).

Some suggestions were made on how to improve resolution (in particular, evaluate more loci and then restrict to those loci highly correlated with age); the current set of loci do not provide sufficient precision for use in the population dynamics modelling exercise recommended for NEWREP-A. Given that there is an upper limit to the degree of precision that can be achieved using this technique, the Committee noted that the utility of epigenetic age estimation (and other methods of age determination) will depend on the degree of precision needed for the specific application of interest (see recommendation under Item 11.4.1).

19.1.2.4 DETERMINING SEXUAL MATURITY IN BLUBBER (RECOMMENDATION 9)

SC/67b/SCSP05 presented results from the NEWREP-A research component focused on determining sexual maturity in female Antarctic minke whales, during the feeding season based, on concentrations of progesterone in blubber. The authors concluded that the progesterone concentration in blubber samples cannot be used as a diagnostic index to discriminate between mature and immature female Antarctic minke whales and that lethal sampling is required to obtain information on sexual maturity for use in population dynamic models.

Some members of the Committee disagreed with that conclusion, as they demonstrated that the amount of misclassification in immature versus mature females would be small (~1%, see Wade *et al.* in Annex U2) and thus that progesterone levels in biopsy samples would allow discrimination between mature and immature animals.

They noted that the stated purpose of the study was to discriminate between immature and mature females for fitting population dynamics models such as the catch-at-age analysis; the only misclassification that occurred was a total of 3 (out of 230) whales between the resting and the immature classes, and therefore the only misclassification rate that is important remains ~1% of the total sample.

Some other members noted, also in relation to recommendation 10, that misclassification for discriminating between resting and immature animals was higher and thus the method less reliable for that task.

In response to a request, the authors provided a histogram showing the numbers of immature, resting, ovulating and pregnant animals (Figure 1 of Yasunaga *et al.* in Annex U2). Based on the assumption of cut off values (1.0 ng/g) of progesterone set in Wade *et al.* (see in Annex U2), six of 56 immature whales and three of 11 resting whales were misclassified. Misclassification ratios were thus10.7% and 27.2%, respectively, and these were not considered negligible by the authors (see details in Yasunaga *et al.* in Annex U2).

19.1.2.5 SAMPLE SIZES REQUIRED TO DETECT CHANGE IN ASM (RECOMMENDATION 26)

SC/67b/SCSP01 focused on the need to complete NEWREP-A recommendation 26 on the calculation of sample size. The Committee discussed its previous conclusions in this regard. In 2016, the Committee assessed that three of six aspects of the Expert Panel's recommendations had been adequately addressed in relation to sample sizes. Some members of the Committee consider that until the proponents fully implement the Expert Panel recommendations for calculating sample sizes, the proponents have not demonstrated that they are able to meet their stated objectives in relation to the NEWREP-A programme. The proponents' position and that of some Committee members is that the work has been completed to a reasonable level and that any further work on sample sizes will be afforded a low priority.

The Proponents reiterated their position regarding the work on and status of recommendation 26 ('Provide a thorough power analysis of sample sizes required to detect change in ASM and follow the other recommendations in this item') from the NEWREP-A Review Workshop (IWC, 2016). In view of the proponents, the work on recommendation 26 has been completed to a reasonable level. Details can be found in GOJ (2015; 2016a) and GOJ (2016b). The IWC SC has already concluded that the approach being taken to address the recommendation is appropriate (IWC 2018). Consequently, the proponents have concluded that the reasonableness of the proposed sample size (333) has been adequately demonstrated. The proponents recognize that in 2016 the Scientific Committee suggested some further refinement work; however, they consider that such refinement work goes beyond the original scope of recommendation 26 from the NEWREP-A review workshop. Nevertheless, in deference to the Committee, it was the proponent's intention to address the refinement work for this year's Scientific Committee. However, because of unanticipated specialist personnel unavailability, this has had to be postponed. The proponent's intention is to continue contributing to this work subject to logistical constraints and the availability of specialist analysts.

19.1.2.6 COMMITTEE'S ADVICE

The table in Annex U4, provides a detailed update of the Committee's view of progress on previous recommendations. An overview is given in Table 25.

Table 25

NEWREP-A – Overview on progress with recommendations.

Recommendations in are not in priority order. Recommendations that relate to purposes A, B, C and D are higher priority for completion. Recommendations coded uniquely as "*E: Relevant to improve existing components of the proposed programme*" are excluded from this table as they were optional. Key for 'Purpose': *A: To evaluate the contribution of a particular objective or sub-objective of the programme to meet conservation and management needs*; *B: To evaluate the feasibility of particular techniques (whether lethal or non-lethal)*; *C: Relevant to a full evaluation of whether any new lethal sampling is required*; *D: Relevant to issues related to sample size (irrespective of method used to obtain data).*

Recommendation	Purpose	Deadline	Proponents self-evaluation on progress as of SC67b	Committee's comments
(1) Age data and RMP/IST	A, C, D	August 2016	Completed to a reasonable level	SC66b: A range of opinions as to the extent to which this recommendation has been addressed. SC67a: No new information. SC67b: Some information presented (See section 19.1.2.1).
(2) Stock definition	A, D	May 2016	In progress.	SC66b: No progress. SC67a: As in SC66b. SC67b: As in SC66b.
(3) Mixing rates (simulations on precision and bias)	A, D	May 2016	To be completed by the mid-term review.	SC66b: No progress. SC67a: As in SC66b. SC67b: As in SC66b.
(4) Biopsy feasibility study	B, C, D, E	Field season 2017-2018	Completed.	SC66b: Some progress (SC/66b/IA05). SC67a: Some progress (SC/67a/ASI07). SC67b: Partially completed, further refined analysis is needed (see 19.1.2.2). A WG was formed to review and improve methods.
(5) Telemetry feasibility study	B, E	Field season 2018-2019	Completed.	SC66b: Some progress (SC/66b/IA05). SC67a: Some progress (SC/67a/ASI07). SC67b: Completed.
(8) DNA methylation ageing technique	B, C, D	March 2017	Completed.	SC66b: No progress. SC67a: As in SC66b. SC67b: Partially completed, further refined analysis is encouraged. See section 19.1.2.3.
(9) Hormones in blubber and sexual maturity	B, C, D	March 2018	Completed.	SC66b: No progress. SC67a: As in SC66b. SC67b: Blubber hormones analysis completed. On accuracy see section 19.1.2.4.
(10) SCAA and misassignment 'resting' females/immature females.	A, C, D	August 2016	To be completed by the mid-term review*.	SC66b: No progress. SC67a: As in SC66b. SC67b: New information presented (SC/67b/SCSP05).
(11) SCAA, density- dependence, and stock mixing	A, C, D	May 2016	Completed*.	SC66b: Partially completed: updates on stock mixing and mixing rates still necessary. SC67a: As in SC66b. SC67b: As in SC66b.
(12) Time-varying natural mortality and SCAA	A, C, D	August 2016	To be completed by the mid-term review*.	SC66b: No progress. SC67a: As in SC66b. SC67b: As in SC66b.
(13) Time varying ASM data and SCAA	A, C, D	May 2016	To be completed by the mid-term review*.	SC66b: No progress. SC67a: As in SC66b. SC67b: As in SC66b.
(15) Krill acoustic sampling	B, E	March 2017	Completed.	SC66b: Completed.
(17) Power analysis for krill abundance	A, E	August 2016	To be addressed.	SC66b: Will be addressed in consultation with CCAMLR specialists SC67a: No progress. SC67b: As in SC66b.
(18) Stomach contents vs krill survey	A, B, C	May 2016	To be addressed.	SC66b: Will be addressed in consultation with CCAMLR specialists SC67a: No progress. SC67b: As in SC66b.
(22) Energy intake (requirements)	A, B, D	August 2016	To be addressed. Need clarification from the IWC SC	SC66b: No Progress. SC67a: As in SC66b. SC67b: As in SC66b.
(23) Stable isotopes in baleen plates	B	August 2016	Completed.	SC66b: Will be addressed in consultation with other research institutions. SC67a: Some progress presented. SC67b: Completed.
(26) Sample sizes required to detect change in ASM	D	May 2016	Completed to a reasonable level	SC66b: Overall, the approach being taken to address the recommendation is appropriate, but some further refinements are required. SC67a: No Progress. SC67b: As in SC67a.

*See note in Table #, Annex U4.

19.3 JARPN II

The new information provided on JARPN II is relevant only to the discussion of the NEWREP-NP 'non-lethal vs lethal' feasibility study (see Item 19.3).

19.4 NEWREP-NP

19.4.1 Report on ongoing research

Three papers were presented on progress made during the 2017 surveys of different aspects of the NEWREP-NP programme (SP03, 06, 07, see Annex U3 for summaries).

In particular, SC/67b/SP03 reported the results of the satellite tagging ofn North Pacific sei whales. A total of 44 tagging attempts were made using SPOT6 tags with the LKArts attachments system. A total of 15 tags were deployed on sei whales, and eight whales were tracked. Two sei whales were tracked for more than 35 days, and both showed longitudinal movement. The authors concluded that the tagging experiment showed that deploying such tags from sighting/sampling vessels was practical, but identified technical improvements to try to increase the tracking period.

In discussion, it was noted that the proportion of successful deployments was low (7 failures in 15 attempts); and suggestions on how to improve this included: (a) strategic placement of tags on the upper body of whales to ensure tag longevity and reduce potential physical impacts (e.g. lesions) and (b) replacement of the current screw-on anchor system with an integrated tag design to decrease the possibility of tag breakage. It was noted that guidelines for cetacean tagging should become available within the next year and published in the IWC Journal. It was noted by the authors that the cause of the failures in SP03 were difficult to evaluate since a tag in an optimal position on the whale had also failed. New tags with a modified anchor system and stopper will be used during the next season.

The Committee welcomes new information on the feasibility of satellite tagging sei whales and notes the valuable movement data collected from two of the longer-term (>35 days) deployments. The Committee **encourages** the collection of more telemetry data and notes that this may help improve abundance estimation (by providing information on correction factors) and provide inferences on stock structure.

SC/67b/ASI10 presented a summary of results of the NEWREP-NP dedicated sighting survey in the western North Pacific in 2017 whilst SC/67b/ASI06 presented the research plan for the next systematic vessel-based sighting survey in the western North pacific under NEWREP-NP in 2018 and 2019. As indicated under Item 24.3, the new NEWREP-NP sighting cruise plan has been endorsed by the Committee; Annex Q (item 4.2) provides more details on both these papers.

19.4.2 Update on previous recommendations

The table in Annex U4, provides a detailed update of the Committee’s view of progress on previous recommendations. An overview is provided in Table 26 (see next page).

Table 26

Summary of status of recommendations relevant to NEWREP-NP

No. of recommendation	Priority by the Committee	Timeline	Proponents self-evaluation on progress as of SC67b	Scientific Committee Evaluation
(1) Lethal vs non-lethal quantitative review of data	Very high	Before start	SC67a: Completed.	SC67a: Different opinions as to whether the recommendation has been met. SC67b: No progress.
(3) Sexual maturity (blubber and serum)	High	Before start	SC67a: Completed.	SC67a: The Proponents demonstrated intention to include analysis of blubber for progesterone, but there are few details of how. SC67b: Partially addressed.
(4) Sightings surveys	High	Before start and annually	Addressed and ongoing.	SC67a: Completed: survey plan was presented. SC67b: Completed: survey plan was presented.
(5) Stomach contents	High	Before start	SC67a: Completed.	SC67a: Completed.
(7) Immune function assays	High	Before start	SC67a: Completed.	SC67a: Completed.
(8) Lipophilic compounds	High	Before start	SC67a: Completed.	SC67a: Completed.
(10) Coordination with IWC-POWER	High	Before start and annually	Addressed and ongoing	SC67a: Completed annually.
(11) Coastal component: sampling strategy	High	Before start	Disagree with Panel	SC67a: No progress as proponents disagree with Panel. SC67b: No progress.
(12) Offshore components: sampling strategy	Very high	Before start	SC67a: Completed.	SC67a: Completed.
(13) downweight historical age-composition data	Very high	Before start	Disagree with Panel.	No progress.
(15) efficiency of biopsy sampling (additional captures unnecessary)	Very high	High priority ASAP in 2017	Disagree with Panel.	No progress.
(17) Telemetry	High	Before start	Ongoing	SC67a: Partially addressed. SC67b: New information (SC/67b/SCSP03).
(21) Sample size (potential reduction of lethal sample size)	Very high	Before start	To be considered by the mid-term review.	SC67a: The possibility for further work has been considered. SC67b: No progress.
(22) Sample size (in general)	Very high	Before start	Not relevant.	SC67a: Small progress. SC67b: No progress.
(23) Impact of catches on common minke whales (subset of 2013 *Implementation*)	Very high	Before start	Disagree with Panel.	SC67a: Major concerns addressed. SC67b: Completed. Refined analyses were presented. It could be reconsidered in the next *Implementation Review.*
(24) Impact of catches on common minke whales (new abundance)	Very high	Before start	Disagree with Panel.	SC67a: Major concerns addressed. SC67b: Completed. Refined analyses were presented. It could be reconsidered in the next *Implementation Review.*
(25) Sei whale (abundance, $MSYR_{1+}$=1%, $MSYR_{mat}$=4%)	Very high	Before start	SC67a: Completed.	SC67a: Completed.
(27) Higher priority to analyses and modelling	High	Before start	Ongoing	SC67a: It is not clear that additional qualified personnel have been hired. SC67b: No progress.
(28) Sample and data archiving, relational database(s)	High	Before start	Ongoing	SC67a: Partially addressed for DNA data and associated biological information.
(29) Contingency plan	High	Before start	Ongoing	SC67a: Partially addressed.

20. WHALE SANCTUARIES

20.1 Review of the Southern Ocean Sanctuary Management Plan

The Schedule amendment establishing the Southern Ocean Sanctuary (SOS) requires the Sanctuary to be reviewed at succeeding ten-year intervals, unless otherwise revised by the Commission. The first review of the SOS took place in 2004 (IWC, 2005) and the second review was completed in 2016 (IWC, 2017). In 2014 (IWC, 2015c), the Commission adopted eight objectives for the SOS (summarised in Annex R, item 3). The Commission also provided terms of reference for the review to be undertaken by the Scientific and Conservation Committees. The Scientific Committee review made several recommendations (IWC, 2017c). These recommendations were taken into account in a draft Southern Ocean Sanctuary Management Plan (SC/67b/SAN01) developed by Australian scientists and discussed in Annex R (item 3). It was noted that, while the draft Plan does contain performance measures, it does not contain criteria for its own review.

The purpose of the draft Management Plan is twofold: (1) to inform the Commission and public about the sanctuary objectives and actions planned for the next ten years; and (2) to propose strategies toward the achievement of the SOS's goals using the best means available and provide clear performance measures for each proposed action.

The operative part of the Plan is a Research and Action Plan that involves assessing and addressing threats and research on the recovery of whale populations and their habitats. The Research and Action Plan is structured based on the Commission's agreed objectives for the SOS. Each objective is linked directly to a measurable objective, action or approach and performance measure.

The Committee also discussed the potential contributions that data and results from the Japanese whale research programme in the Southern Ocean (NEWREP-A) could make to the objectives and goals of the Plan and the Committee agrees to incorporate reference to NEWREP-A under Objectives 4-6.

The amended Plan, with Objectives 1 and 8 (relating to policy) and the chapeau of Objective 5 redacted to clarify that the Committee did not address these elements of the Plan, is given as Annex R (Appendix 2).

A statement from the Government of Japan regarding its position on the SOS and this draft Management Plan is attached as Annex R, Appendix 3.

Attention: C-A, CC, SC,

The Committee reviewed the components of a draft Management Plan for the Southern Ocean Sanctuary (SOS) that are related to science and therefore within its remit and:

(a) ***endorses*** *the measurable objectives, approach/actions and performance measures of Objectives 2 -7 of the amended draft Southern Ocean Sanctuary (SOS) Management Plan (Annex R, appendix 2); and*
(b) ***agrees*** *to include a new standing item on the agendas of all relevant sub-committees and working groups: 'new information relevant to the SOS Management Plan' in order to assist the Commission in monitoring and measuring progress on the scientific objectives of the Plan.*

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21. SATELLITE TAGGING DEVELOPMENT AND BEST PRACTICES

21.1 Tag Workshop Meeting, Silver Spring, MD, USA 6-8 September 2017

A workshop on cetacean tag development, tag follow-up and tagging best practices was held at the National Marine Fisheries Service in Silver Spring, Maryland, USA from 6-8 September 2017. The workshop was co-sponsored by the Office of Naval Research (ONR), the International Whaling Commission (IWC), and the National Oceanic and Atmospheric Administration's National Marine Fisheries Service (NOAA/NMFS). The purpose of the workshop was to review and evaluate progress in tag design and attachment since the 2009 ONR Cetacean Tag workshop (ref - attached), with an emphasis on (a) recent tag attachment improvements, (b) follow-up studies that examined the effects of tagging, and (c) reviewing and providing input on draft cetacean tagging best practices guidelines.

Several presentations were made, with a focus on sharing information and discussion of the best available science of design and effects of tagging to facilitate future advancements in tag design and application, maximising attachment durations to the extent required to answer the questions being posed, whilst minimising potential impacts to the animals.

Discussion on the status of tag attachment development and follow-up studies occurred, along with extensive discussion regarding the cetacean tagging best practices guidelines. While much was accomplished towards the collective goals of the workshop, one item not covered in sufficient detail was discussion on the future directions in tag attachment technology. Therefore, a second smaller workshop will be convened in June of 2018 with a subset of the original attendees that focus specifically on tag attachments. The final report will merge the results of the September 2017 workshop and the June 2018 workshop.

22. IWC LIST OF RECOGNISED SPECIES

The Committee has agreed to follow the guidance of the Society for Marine Mammalogy's Committee on Taxonomy. This year (see Item 17.5), in completing its review of the taxonomy of *Tursiops*, the Committee noted that the current taxonomy provided by the SMM Committee for *Tursiops* was well supported by morphological and molecular genetic data, as well as ecological and distributional data.

23. IWC DATABASES & CATALOGUES

23.1 Guidelines for IWC catalogues and photo-ID databases

At last year's meeting, the Committee agreed IWC Guidelines for Photo-identification Catalogues (IWC, 2018f), noting that adding technical Appendices would be valuable in the future. Draft items for inclusion as Appendices were discussed by the *Ad hoc* Working Group on Photo-identification (Annex S, item 5.1) covering five issues: (1) cataloguing software; (2) image matching software; (3) seminal papers defining individual identification, by species; (4) photo quality guides; and (5) photo/data collection apps. Work will continue on developing these appendices intersessionally (Annex Y).

23.2 Progress with existing or proposed new catalogues

23.2.1 Integration of eastern South and Central Pacific blue, humpback, and fin whale photo-catalogues

There was no new information specific to this item this year.

23.2.2 Southern Hemisphere and Indian Ocean humpback whale catalogues

23.2.2.1 ANTARCTIC HUMPBACK WHALE CATALOGUE

The Antarctic Humpback Whale Catalogue (AHWC), maintained at College of the Atlantic, USA, was established in 1987 and during the past 30 years its data have been used in dozens of studies and publications (Stevick *et al.*, 2017). With a recent loss in funding, the catalogue database is now 'frozen' and is not being actively updated. The Working Group expressed strong disappointment at this news as well as the hope that the AHWC's funding situation will change and enable the catalogue to continue.

Attention: SC, G

The Scientific Committee has been informed that due to a loss of funding, the Antarctic Humpback Whale Catalogue curated by the College of the Atlantic, USA will no longer be updated. The Committee:

(1) ***draws attention*** *to the great value this catalogue (established in 1987) has provided to the Committee, including receiving photographs from the IWC IDCR and SOWER cruises and providing information for the Committee's Comprehensive Assessment of Southern Hemisphere humpback whales;*
(2) ***welcomes*** *news that the existing catalogue will remain a resource for scientists; and*
(3) ***encourages*** *potential funders to support future continuation of the catalogue.*

The Committee also received an update on the development and status of 'Happywhale', a web-based marine mammal photo-ID crowd-sourcing platform (SC/67b/PH05)[12]. This is discussed in Annex S (item 2.2). In recent months Happywhale provided images to catalogues relevant to the IWC and IWC-SORP of Southern right whales, Antarctic blue whales, and Antarctic killer whales. It will also contribute to the ongoing in-depth assessment of North Pacific humpback whales (see Annex F item 4.2.1).

23.2.2.2 ARABIAN SEA WHALE NETWORK'S FLUKEBOOK

In 2016 (IWC, 2017), the IWC approved funding for the development of a regional data platform for the Arabian Sea Whale Network (ASWN), to be implemented in collaboration with Wild Me, the developers of Flukebook. This year the Committee received information SC/67B/PH/03 that described Flukebook, a non-profit, open source cetacean data archiving and photo matching tool as discussed in Annex S (item 2.1; SC/67B/PH/03). The ASWN is joining Flukebook with two primary objectives: (1) to consolidate and more effectively manage humpback whale and other cetacean data collected in Oman over the past 20 years; and (2) to provide an online platform that will allow comparison and regional-level analysis of cetacean data collected by different research groups throughout the Arabian Sea (so far photographs are mainly from Oman, with a few from Pakistan and India). The Committee **looks forward** to updates on this work.

23.2.3 Southern Hemisphere Antarctic and pygmy blue whales: Catalogues and databases

23.2.3.1 SOUTHERN HEMISPHERE BLUE WHALE CATALOGUE (SHBWC)

The SHBWC has become the largest repository of Southern Hemisphere blue whale photo-identifications. It now includes a total of 1,519 individual blue whale photo-identifications from areas off Antarctica, Chile, Peru, Ecuador-Galapagos, Eastern Tropical Pacific (ETP), Australia, Timor Leste, New Zealand, southern Africa, Madagascar and Sri Lanka. The Committee received information on the progress made with the catalogue (SC/67B/PH/04), especially in light of the recommendations made last year to conduct catalogue comparisons in the Indo-Australian region (IWC, 2018b). This is discussed in more detail in Annex S (item 3.2). Comparison work (SC/67B/SH16) found (a) no matches between Australia, New Zealand and Sri Lanka, reinforcing the hypothesis of separate populations; and (b) exchange within Australia, suggested a single population; and (c) re-sights found in New Zealand suggest some site fidelity. Additional work is underway. The relevance of the catalogue to population assessments is discussed in Annex H Item 7.1.1.2.

23.2.3.2 ANTARCTIC BLUE WHALE CATALOGUE (ABWC)

In 2017, the Antarctic Blue Whale Catalogue compared photographs from the IWC IDCR/SOWER cruises in 1989/1990, 1993/1994, and 1997/1998 as well as opportunistic photographs collected by collegial scientists, naturalists, and tourists 2015-2018. The catalogue now contains almost 460 individuals. The results of the comparison of new Antarctic blue whale identification photographs to the ABWC is summarised in SC/67B/PH02 and discussed in Annex S (item 3.1); 17 new individual blue whales were identified. The collection of Antarctic blue whale identification photographs provide data for capture-recapture estimates of abundance (SC/67B/SH08) as well as information on the movement of individual blue whales within the Antarctic region. The relevance of the catalogue to population assessments is discussed Annex H, Item 7.1.1.1.

Attention: SC

(1) The Southern Hemisphere Blue Whale Catalogue provides data useful for estimating abundances and examining connectivity between feeding and breeding grounds. The Committee ***agrees*** *that the catalogue continue.*
(2) The Committee ***agrees*** *that the Antarctic Blue Whale Catalogue continue its work collecting adding photo-identification data to the catalogue in order to assist with developing estimates of population abundance for Antarctic blue whales.*
(3) The Committee ***agrees*** *that the development of a simple guide (physical and electronic versions) to help tourists and naturalists take photos that are suitable for photo-identification should be undertaken. This will support the photo-ID*

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[12] https://happywhale.com

catalogues from the Antarctic region for use in population assessments by the IWC, particularly for blue whales, right whales, fin whales, and humpback whales.

23.2.4 Southern Hemisphere fin whale photo catalogues

The Committee received information on on a new photo-identification catalogue of Antarctic fin whales. Photographs from SOWER cruises 2004-2008 are included as well as those collected opportunistically near the South Orkney Islands during a Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) fisheries research voyage (SC/67B/PH01). This is discussed in Annex S (item 4.1). The catalogue serves as a foundation for future photo-ID studies, especially those proposed for the western Antarctic Peninsula. The relevance of the photo-identification of fin whales to population assessments is discussed Annex H, Item 7.1.2.

Attention: S, SC

1) The Committee ***encourages*** *continuation of the Antarctic Fin Whale Catalogue which can potentially provide data toward estimating abundance or identifying movement patterns.*
2)The Committee ***agrees*** *that an exhaustive search be conducted to locate SOWER photos that are missing from the IWC archives, including those of fin whales.*

23.2.5 Western Pacific gray whale photo catalogues

The Committee received information on two photo-identification catalogues relating to the Sakhalin Island feeding aggregation: one (SC/67B/ASI04), based on work undertaken as part of an industry-sponsored Exxon Neftegas Limited-Sakhalin Energy Investment Company joint monitoring program discussed in Annex S, item 4.2); and the other conducted by the Russia gray whale project (SC/76b/CMP/7) discussed in Annex O (item 2.1.3). The Committee welcomed news that the two catalogues would be unified under the auspices of the IWC.

23.3 Work plan

The work plan on work related to catalogues is provided in Table 27.

Table 27

Work plan on issues related to catalogues.

Topic	Intersessional 2018/19	2019 Annual Meeting (SC/68a)	Intersessional 2019/20	2020 Annual meeting
Appendices for IWC Guidelines for Photo-identification	Continue compilation	Appendices ready for review	Continue compilation	Appendices ready for review
Upload all available New Zealand blue whale identification photographs to SHBWC (also pertains to Annex H item 7.1.1)	Cross-reference between separate area catalogue holdings before uploading to SHBWC avoid duplication; intersessional correspondence group (Annex Y)	Included in SHBWC report	-	-
Development of how-to photo-ID materials for naturalists and citizen scientists (also pertains to Annex H item 7.1.1.2)	Prepare hard copy and PPT photo-ID guides	Guide completed and available (pending funding)		
4) Search for missing SOWER photographs, especially fin whale photos from 2006/2007	Search Secretariat archives and contact SOWER researchers for personal copies of photos	Report		

23.4 Potential future IWC databases

23.4.1 Global database for disentanglement activities

As discussed under Item 13.2, development of a dedicated entanglement database will be considered further at the June 2018 meeting of the Global Whale Entanglement Response Network (see Annex J, item 2.3).

23.4.2 Global bycatch database

No new information was presented on the development of a global bycatch database was presented this year. Consideration of such a database could take place as part of the Bycatch Mitigation Initiative and should it be taken further, follow the guidelines for the proposal of new databases developed last year (IWC, 2018, pp. 403-404).

23.4.3 Development of simple technical guidelines for new proposals

No changes were suggested to the guidelines developed at last year's meeting (IWC, 2018, pp. 403-404).

24. IWC MULTINATIONAL RESEARCH PROGRAMMES AND NATIONAL RESEARCH CRUISES THAT REQUIRE IWC ENDORSEMENT

24.1 IWC-POWER

The Committee received the results of the 8th annual IWC-POWER cruise conducted between 3 July and 25 September 2017 in the eastern Bering Sea. Researchers from Japan, USA and IWC participated on the surveys (SC/67b/ASI12). The Committee also received the report of the planning meeting for the 2018 IWC-POWER cruise, which will be conducted in the central Bering Sea, and cruise plans for the 2019 and 2020 cruises (SC/67b/Rep02). Details and preliminary results of the 2017 IWC-POWER survey and future plans for 2018, 2019 and 2020 are provided in Annex Q, item 4.1.

Attention: SC, C-A, CG-R

The Committee ***reiterates*** *to the Commission the great value of the data contributed by the IWC-POWER cruises which cover many regions of the North Pacific Ocean not surveyed in recent years and so address an important information gap for several large whales. The Committee:*

(1) ***thanks*** *Japan who generously supplies the vessel and crew, for their continued support of this IWC programme;*

(2) ***thanks*** *the USA who provided an acoustician and acoustic equipment for the 2017 cruise and will do so for the 2018 cruise;*

(2) ***agrees*** *that the 2017 cruise was duly conducted following the requirements and guideline of the Committee (IWC, 2012) and looks forward to receiving abundance estimates based on these data;*

(3) ***endorses*** *the plans for the 2018, 2019 and 2020 POWER cruise and* ***recommends*** *a meeting of the Technical Advisory Group along with the planning meetings for 2019 and 2020 cruises;*

(4) ***strongly recommends*** *that Russia facilitates the proposed research by providing permits for the IWC-POWER cruise to survey the Russian Exclusive Economic Zone in 2019;*

(5) ***looks forward*** *to receiving a report from the 2018 survey at the next SC meeting.*

24.2 Southern Ocean Research Partnership (IWC-SORP)

The Southern Ocean Research Partnership (IWC-SORP) was established in March 2009 as a multi-lateral, non-lethal scientific research programme with the aim of improving the coordinated and cooperative delivery of science to the IWC. The Partnership currently has 13 member countries: Argentina, Australia, Belgium, Brazil, Chile, France, Germany, Italy, New Zealand, Norway, South Africa, the United States of America, and Luxembourg was welcomed at this meeting. New members are warmly welcomed.

There are five ongoing IWC-SORP themes:

(1) ‘The Antarctic Blue Whale Project’;

(2) ‘Distribution, relative abundance, migration patterns and foraging ecology of three ecotypes of killer whales in the Southern Ocean’;

(3) ‘Foraging ecology and predator-prey interactions between baleen whales and krill’;

(4) ‘Distribution and extent of mixing of Southern Hemisphere humpback whale populations around Antarctica?’ focused initially on east Australia and Oceania; and

(5) ‘Acoustic trends in abundance, distribution, and seasonal presence of Antarctic blue whales and fin whales in the Southern Ocean’.

Bell presented the IWC-SORP Annual Report 2017/18 on the continued progress of research undertaken researchers involved in the five themes since last year (SC/67b/SH21). This progress includes the production of 33 peer-reviewed publications during 2017/18, bringing the total number of peer-reviewed publications related to IWC-SORP since the start of the initiative to 126. In addition, 125 IWC-SORP related papers have been submitted to the Scientific Committee, 22 of them this year.

Fieldtrips were undertaken to a variety of places during the past year, including the western Antarctic Peninsula, Marion Island, the Ross Sea, the Chesterfield-Bellona Reef complex west of mainland New Caledonia, and the Great Barrier Reef, Australia. Thousands of images for photo-identification have been collected; a variety of satellite tag-types deployed on Antarctic minke whales, humpback whales and killer whales as well as biopsy samples collected from these same species; video suction cup tags have been deployed on Antarctic minke whales and humpback whales; and hundreds of hours of acoustic recordings have been made and analysed. The support of tour companies in providing opportunistic research platforms to facilitate these activities and external data contributors were acknowledged by the Committee.

Attention: SC, G

The Committee reiterates the great value of the IWC-SORP (Southern Ocean Research Partnership) programme to its work. The Committee:

(1) ***encourages*** *the continuation of the Southern Ocean Research Partnership programme;*

(2) ***commends*** *the researchers involved who are key to the overall success of the Partnership in IWC-SORP for:*

(a) the impressive quantity of work carried out across diverse member nations;

(b) their contributions to the work of the Committee; and

(3) ***encourages****:*

(a) the continued development, testing and implementation of leading edge technology; and

(b) the continued development of collaborations between ships of opportunity and external bodies that can provide platforms for research and/or contribute data, inter alia, photo-identification data, to IWC-SORP and the wider Committee

24.2.1 Workplan

The work plan for issues related to IWC-SORP is given in Table 28.

Table 28

Workplan for the Southern Ocean Research Partnership.

Topic	Intersessional 2018/19	2019 Annual Meeting (SC/68a)	Intersessional 2019/20	2020 Annual meeting
Analyses	Continued analysis of data/samples from previous IWC-SORP voyages/fieldwork	Report	Continued analysis of data/samples from previous IWC-SORP voyages/fieldwork	Report
Voyages	Argentine coastguard '*Tango'* voyage along Western Antarctic Pensinsula (early 2019)	Cruise report		
	Almirante Maximiano voyage along Western Antarctic Pensinsula (early 2019)	Cruise report		
	Australian-led *RV Investigator* voyage to Ross Sea (early 2019)	Cruise report		
	New Zealand-led *RV Tangaroa* voyage to Ross Sea (early 2019)	Cruise report		
	German-led *RV Polarstern* voyage to Scotia Sea (early 2019)	Cruise report		
	Baleen whale and krill research voyages along Western Antarctic Peninsula	Reports	Baleen whale and krill research voyages along Western Antarctic Peninsula	Reports
Ships of opportunity	Continued use of ships of opportunity to conduct cetacean research	Reports	Continued use of ships of opportunity to conduct cetacean research	Reports
Acoustics	Retrieval and redeployment of passive acoustic recorders	Report	Retrieval and redeployment of passive acoustic recorders	Report
	Completion of annotated library of acoustic detections	Report		

24.3 National cruises that require IWC oversight

The Committee welcomed plans for national research cruises to be conducted in the intersessional period of 2018-2019. Details on the cruise plans and cruise reports are presented in Annex Q, item 4.2.

Attention: SC, C-A

The Committee ***recognises*** *the great value to its work provided by data from national cruises. The Committee:*

(1) ***endorses*** *the proposed sighting survey plans for cruises to be conducted with IWC oversight in the southwestern Okhotsk Sea by Russia, and in the North Pacific and the Antarctic by Japan; and*
(2) ***encourages*** *submission of abundance estimates from these studies the future.*

24.4 Review of cruise reports from national programs with IWC oversight

The Committee considered a process to optimise the review of cruise reports from national research programs with IWC oversight. Details are given in Annex Q, item 2.7

Attention: SC, CG-R

*The Committee **recognises** the value of information provided by national cruises with IWC oversight. The Committee noted that a process to optimise the review of national cruise reports is needed and*

*(1) **recommends** contracting governments to submit reports of multi-year cruises with IWC oversight biennially, in years between Commission meetings (e.g., SC "A" years);*
*(2) **agrees** that cruise reports will be summarised in a table;*
*(3) **notes** that that in certain circumstances, cruise reports may require additional evaluation; and*
*(4) **agrees** that the 'Requirements and Guidelines for Conducting Surveys and Analysing Data within the Revised Management Scheme' should be modified at next year's meeting to accommodate procedural changes with respect to the submission and review of national cruise reports.*

24.5 Work Plan

The Committee's work plan for continuing the IWC-POWER programme in 2019 and 2020 is provided below in Table 29.

Table 29

Workplan for issues related to IWC-POWER.

Item	Intersessional 2018-19	SC68a	Intersessional 2019-20	SC68b
IWC-POWER Cruise	Conduct 2018 survey and planning meeting for the 2019 Cruise (Bering Sea)	Review cruise report, report from the planning meeting and new abundance estimates from IWC-POWER cruises.	Conduct 2019 survey and planning meeting for the 2020 Cruise	Review cruise report, report from the planning meeting and new abundance estimates from IWC-POWER cruises.

25. SCIENTIFIC COMMITTEE BUDGET FOR THE CURRENT BIENNUM

25.1 Status of previously funded research, workshop proposals, data processing and computing needs

25.1.1 Funded proposals for the current biennium 2017-2018

Table 30summarises the status of the work funded by the Committee last year. The majority have been completed, but several remain ongoing. The projects all contributed considerably to the work of the Committee and the Committee thanked all of those involved.

25.1.2 Funded proposals in previous years still ongoing

A number of projects from previous years are still ongoing (see Table 30). These are all still of great value to the Committee and should be completed before the next meeting. Details of all ongoing projects can be found in SC/67B/01 Rev1.

25.1.3 Report on funds reallocations and contingencies for the Research Fund, Voluntary Fund for Small Cetaceans and SORP Voluntary Fund

SC/67b/01Rev1 provides information on the actual position against budget for the Research fund for 2017 as well as the position to 31st March for the 2018 financial year. The paper gives summary level and detailed information for the Research fund as well as the expected level of contingency available, which remains static at around 10% of the Research budget, or £32k. The document also provides details of the reallocations of budget amongst budget headings for 2017 and the 2018 year-to-date. Annex 1 gives a detailed position along with a status report for each budget line. Section 3 also provides details of voluntary funds which relate to Scientific Committee business – the Gray Whale Tagging Fund, the Small Cetaceans Fund and the SORP fund. For each there is an update of 2017 expenditure and 2018 to-date information along with details of commitments to future work in these funds.

Table 30

Summary of progress on proposals funded at SC67a

SC/67a RP no.	Title	Status
SC01	Invited Participants - SC/67b	Completed
IA01(67a)	Workshop for an in-depth assessment of North Pacific humpback whales	Ongoing (Annex F)
EM01	Two joint SC-CAMLR and IWC-SC Workshops	Ongoing (Annex L)
AWMP01	AWMP first intersessional Workshop and genetic work	Completed (SC/67b/Rep06)
AWMP02	AWMP second intersessional Workshop	Completed (SC/67b/Rep06)
CMP01(67a)	5th Workshop on the rangewide review of population structure and status of North Pacific gray whales	Completed (SC/67b/Rep07rev1)
BRG04	Satellite tagging best practices Workshop	Ongoing, Item 21
WW01	Intersessional Workshop: data gaps and modelling requirements for assessing the impacts of whale watching	Completed (SC/67b/Rep03rev1)
RMP01	Intersessional Workshop: *Implementation Review* of North Pacific Bryde's whales	Completed (SC/67b/Rep02)
RMP01(67a)	Intersessional Workshop: *Implementation Review* for Western North Pacific minke whales	Completed (SC/67b/Rep05)
WW01(67a)	Review CC Strategic plan on whalewatching pre-meeting on intersessional workshop	Completed (Annex N)
E05/E01(67a)	Cumulative impacts - pre-meeting or intersessional meeting	Completed (Annex K)
SM01	Intersessional Workshop: resolving *Tursiops* taxonomy	Completed (SC/67b/SM18rev1)
SM01(67a)	Intersessional Workshop: boto mortality	Completed (SC/67b/Rep01)
SH07	Defining blue whale population boundaries and estimating associated historical catches, using catch data in the Southern Hemisphere and northern Indian Ocean	Completed (SC/67b/SH23)
AWMP02	AWMP developers fund	Completed (Annex D)
IA02	Assessment modelling for an in-depth assessment of North Pacific sei whales	Ongoing (SC/67b/IA01)
RMP02	Essential computing support to the Secretariat for RMP	Completed (Annex D)
Research		
BRG01	Aerial photographic survey of southern right whales on the South Africa Cape nursery ground	Completed (SC/67b/SH01)
BRG03	Passive acoustic monitoring of the eastern South Pacific southern right whales, improving CMP outputs	Completed (SC/67b/CMP18)
SH03a	Northern Indian Ocean humpback subspecies determination-genetics	Ongoing (Annex H)
IA03	IWC-POWER cruise	Completed (SC/67b/Rep04)
SH01(67a)	Coding for Australian blue whale photo catalogue	Ongoing (Annex PH)
E02(67a)	Mercury in cetaceans (requested by the Commission)	Ongoing (SC/67a/E08)
SH02	Southern Hemisphere Blue Whale Catalogue	Completed (SC/67a/PH04)
SH08	Development of a permanent blue whale song reference library	Completed (SC/67a/SH11Rev1)
HIM01	Ship Strike Database Coordinator	Completed (SC/67a/HIM11)
E01	Cetacean Diseases of Concern	Ongoing (Annex K)
E03(67a)	IWC strandings initiative	Ongoing (Annex K)
E04	SOCER (State of the Cetacean Environment Report)	Completed (SC/67a/E01)

The Committee received a brief report on the IWC-SORP Research Fund. Following an open, competitive Call for Proposals (26 July to 17 August 2016) a total of £144,058 GBP was allocated from the IWC-SORP Research Fund to 10 research projects, ahead of the 2016-2017 austral summer survey season. Progress on these projects is detailed in SC/67b/SH18.

The Committee also noted that since SC67a, substantial vessel time has also been secured by IWC-SORP researchers for the 2019 and 2020 austral field seasons.

Attention: C, F&A, S

A full report on the new Call for Proposals, opened in September 2017 and closed in January 2018, was also received. A total of 19 proposals were received and evaluated by the Assessment Panel under the coordination of the Chair of the Scientific Committee. The Committee thanks Fortuna for convening the Assessment Panel and expressed its gratitude to the Panel members who all provided valuable and thoughtful input into the assessment process. The Committee welcomes the outcome of the Assessment Group and agrees with the allocation of a total of £493,544 GBP from the IWC-SORP Fund to 15 projects (Table 31).

The Committee agrees on these recommended allocations and requests the Secretariat to submit them to the Finance and Administration Committee, as soon as feasible, for it consideration. Should the Commission endorse these financial recommendations, the Committee requests the Secretariat to inform successful and unsuccessful proponent immediately after the next Commission's meeting.

Table 31
List of the funding allocations by project recommended by the IWC-SORP Assessment Panel

ID	Chief Investigator	Title	Requested amount (£)	Recommended amount (£)	Level of funding (Partial/Full)
1	Baker & Steel	Is migratory connectivity of humpback whales in the Central and Eastern South Pacific changing? A decadal comparison by DNA profiling	27,598	26,375 (deducted in house instrument expenses)	P
2	Charrassin	Application of satellite telemetry data to better understand the breeding strategies of humpback whales in the Southern Hemisphere	21,200	21,200	F
3	Branch	Modelling somatic growth and sex ratios to predict population-level impacts of whaling on Antarctic blue whales	32,594	32,594	F
4	Friedlaender & Constantine	Pregnancy rates in Southern Ocean humpback whales: implications for population recovery and health across multiple populations	29,334	19,984 (equipment deducted and some analytical costs)	P
5	Herr	Recovery status and ecology of Southern Hemisphere fin whales (*Balaenoptera physalus*)	82,300	81,900 (equipment deducted)	P
6	Friedlaender & Constantine	A circumpolar analysis of foraging behaviour of baleen whales in Antarctica: Using state-space models to quantify the influence of oceanographic regimes on behaviour and movement patterns	34,711	34,711	F
7	Buchan & Miller	A standardized analytical framework for robustly detecting trends in passive acoustic data: A long-term, circumpolar comparison of call-densities of Antarctic blue and fin whales	43,369	41,369 (publication costs)	P
8	Lang & Archer	Inferring the demographic history of blue and fin whales in the Antarctic using mitogenomic sequences generated from historical baleen	22,710	22,710	F
9	Zerbini & Clapham	Assessing blubber thickness to inform satellite tag development and deployment on Southern Ocean whales	22,646	22,426 (supply costs deducted)	P
10	Širović & Stafford	Acoustic ecology of foraging Antarctic blue whales in the vicinity of Antarctic krill studied during AAD interdisciplinary voyage aboard the *RV Investigator*	34,183	30,107 (airfares deducted)	P
12	Kelly &Maire	Development of statistical and technical methods to support the use of long-range UAVs to assess and monitor cetacean populations in the Southern Ocean	30,576	30,576	F
13	Reisinger & de Bruyn	An integrative assessment of the ecology and connectivity of killer whale populations in the southern Atlantic and Indian Oceans	33,650	33,650	F
14	Bengston Nash	Implementation of humpback whales for Antarctic sea-ice ecosystem monitoring; Inter-program methodology transfer for effective circumpolar surveillance	91,202	51,555 (equipment costs deducted)	P
17	Carroll, Torres, Graham	Circumpolar foraging ecology of southern right whales: past and present	21,290	21,290	F
18	Iñíguez Bessega	Habitat use, seasonality and population structure of baleen and toothed whales in the Scotia sea and the western Antarctic Peninsula using visual and passive acoustic methods and genetics	26,579	23,097 (equipment costs reduced, communication & network costs deducted)	P
		TOTAL	693,195	493,544	

Finally, the Committee was informed that the next Call should open prior to SC/68b (i.e. late 2019/early 2020) in readiness for IWC68 (2020). This timing would allow strategic prioritisation of the research toward which the Call is directed in order to meet IWC-SORP and IWC/SC priorities; allow knowledge gaps to be identified; and allow the IWC-SORP SSC to seek additional funding to augment the funds available in the IWC-SORP Research Fund.

26. COMMITTEE PRIORITIES AND INITIAL AGENDA FOR THE BIENNUM 2019-2020

The Committee's priorities and work plan by broad subject matter are provided in Tables under the relevant agenda items.

The Committee ***agrees*** *that the Chair, Vice-Chair and Head of Science, in co-operation with the Convenors, should examine the individual work plans by topic and develop an overall Committee biennial workplan and priorities taking into account the overall work load, meeting venues and efficiency. This should be submitted to the Commission meeting as an Annex to their two-year overview.*

27. SCIENTIFIC COMMITTEE BUDGET FOR THE BIENNUM 2019-2020

27.2 Budget for the next biennium

As in 2016, the Committee has developed a two-year budget, based on the proposed work plans. The process given in Annex S IWC, 2016) was applied, with extensive discussion carried out in each of the sub-committees and Working Groups to establish priorities among the presented proposals. Funding was not approved for one project (*Gulf of Penas, Southern right whales*) as further information is needed before funding can be agreed. The savings from 2018, some self-reductions and adjustments between years allowed inclusion of all funding proposals for 2019 and 2020 in the new budget of £315,800 per year.

Table 32

Workshop proposals agreed during this meeting (TBD: to be decided).

Title	Relevance	Date	Venue
Western gray whale update of CMP and conservation issues within modelling framework	CMP		
Marine debris	E	December 2019	Barcelona, Spain
Noise pre-meeting	E	Pre-meeting 2020	TBD
Cetaceans & ecosystem functioning: a gap analysis*	EM	TBD	TBD
Joint IWC-IUCN workshop to evaluate how the data and process used to identify Important Marine Mammal Areas (IMMAs) can assist the IWC to identify areas of high risk for ship strike	HIM	April 2019	Greece
Comprehensive Assessment of North Pacific humpback whales	NH		
Comparative biology, health, status & future of NA right whales	NH	Late 2019	Boston, USA
Implementation Review: North Pacific minke whales	RMP		
Catch series: Southern right whales	SH	Pre-meeting 2020	TBD
Intersessional workshop of the task team on South Asian River dolphins	SM	Feb 2019	TBD
Guiana dolphin pre-assessment	SM	October 2019	Curitiba, Brazil
Modelling whale watching impacts (MAWI)	WW	December 2019	
POWER planning meeting	ASI	Oct 2018	Tokyo, Japan
Wildmeat workshop	SM	Late 2019/early 2020	Africa
Tagging best practices	ASI	Jun 2018	Seattle, USA

* Japan referred to its statement on the adoption of the Agenda (Annex Z) and considered that several of the items for the proposed workshop (Item 16.4.4) are outside the competence of IWC. Therefore, it cannot support the proposed workshop or associated funding from the Committee's budget.

Table 33 shows the Committee budget requests for the biennium for each of the proposed priority activities.

27.2.1 Invited Participants

INVITED PARTICIPANTS

Invited participants (IPs) are a vital component of the working of the IWC's Scientific Committee. IPs contribute in many ways including as sub-committees and Working Groups Convenors, co-Convenors and rapporteurs, subject area experts and Convenors of intersessional groups. All sub-committees and Working Groups benefit from this budget item. This year under this budget item, 62 scientists from Australia, Argentina, Belgium. Brazil, Canada, Chile, China, Colombia, France, Germany, Italy, Japan, Mexico, Netherlands, Norway, Oman, Peru, Slovenia, South Africa, Spain, UK, USA were supported.

27.2.2 Workshops

RP16 WESTERN GRAY WHALE UPDATE OF CMP AND CONSERVATION ISSUES WITHIN MODELLING FRAMEWORK

The CMP is over 10 years old and requires updating. Initial work has been undertaken but the results of the rangewide workshop need to be incorporated and conservation-related questions need to be developed that can be addressed within the new population modelling framework developed as a result of the Committee's work. This is primarily related to the CMP and AWMP groups, however, it is also of importance to the work of IA and ASI in terms of precedents for future assessments and the work of HIM in terms of examining scenarios that take into account bycatch and the uncertainty associated with estimating it.

RP06 MARINE DEBRIS WORKSHOP

There remains an urgent need to better understand and address the threats posed by marine debris to cetaceans. The most effective way to do this, building on earlier work by the IWC and taking into account the greatly expanded interest in this topic by many other international bodies, is to hold a workshop. It is proposed that the workshop is held in Barcelona in December 2019 just before the World Conference on Marine Mammalogy (the joint meeting of the SMM and ECS).

RP05 NOISE PRE-MEETING

The sub-committee on Environmental Concerns will address Anthropogenic Noise as a focus topic during the Scientific Committee meeting in 2020. A pre-meeting workshop is proposed for SC68b, to address emerging issues related to the management of underwater noise and its impacts on marine species.

RP08 CETACEANS & ECOSYSTEM FUNCTIONING: A GAP ANALYSIS

Experts on the role and impact of cetaceans on ecosystem functioning will participate in a workshop/pre-meeting to discuss the current state of knowledge on the ecosystem functioning provided by cetaceans as requested by the Commission in Resolution 2016-3. This Resolution directed 'the Scientific Committee to further incorporate the contribution made by live cetaceans to ecosystem functioning into [its] work' and asked 'the Scientific Committee to screen the existing research studies on the contribution of cetaceans to ecosystem functioning, to develop a gap analysis regarding research and to develop a plan for remaining research needs'.

RP17 JOINT IWC-IUCN WORKSHOP TO EVALUATE HOW THE DATA AND PROCESS USED TO IDENTIFY IMPORTANT MARINE MAMMAL AREAS (IMMAS) CAN ASSIST THE IWC TO IDENTIFY AREAS OF HIGH RISK FOR SHIP STRIKE

The identification of 'high risk areas' for ship strikes of cetaceans is a key step toward establishing mitigation actions, through scheduling, re-routing or speed reduction. IUCN's proposed initiative to identify Important Marine Mammal Areas (IMMAs), would likely assist this effort. The SC has encouraged cooperation with the IUCN Task Force on this. The IUCN TF has completed three regional IMMA workshops, including the Mediterranean Sea. This proposed joint workshop will focus on identifying overlap between shipping and the IMMAs identified in the Mediterranean Sea.

Table 33

Summary of budget requests for the 2019-20 period. For explanation and details of each project see text.

RP no.	Title	Sub-committee/ working group	2019 (£)	2020 (£)
Invited Participants				
	Invited Participants - SC/68a and SC/68b	SC	85,000	65,000
Meeting/Workshop				
RP16	Western gray whale update of CMP and conservation issues within modelling framework	CMP	10,500	0
RP06	Marine debris	E	0	20,000[1]
RP05	Noise pre-meeting	E	0	12,000
RP08	Cetaceans & ecosystem functioning: a gap analysis	EM	0[2]	0
RP17	Joint IWC-IUCN workshop to evaluate how the data and process used to identify Important Marine Mammal Areas (IMMAs) can assist the IWC to identify areas of high risk for ship strike	HIM	10,000	0
RP19	Comprehensive Assessment of North Pacific humpback whales	NH	1000[3]	0
RP37	Comparative biology, health, status & future of NA right whales	NH		20,000
RP21	*Implementation Review*: North Pacific minke whales	RMP	13,000[4]	15,000
RP29	Catch series: Southern right whales	SH	0	15,800
RP25	Intersessional workshop of the task team on South Asian River dolphins	SM	7,000[5]	0
RP26	Guiana dolphin pre-assessment	SM	0	9,990
RP27	Modelling whale watching impacts (MAWI)	WW	0	17,000[6]
Modelling/computing				
RP20	In Depth Assessment of North Pacific sei whales	ASI	5,000	0
RP22	Develop an age-structured emulator for the individual-based energetics model (IBEM)	RMP	7,000	0
RP23	Essential computing support	RMP	11,500	11,500
RP36	Simulating line transect data to investigate robustness of novel analysis methods	ASI	6,000	0
Research				
RP01	IWC-POWER cruise	ASI	22,500[7]	22,500[8]
RP11	Abundance estimates of the franciscana dolphin in Buenos Aires province, Argentina	CMP	7,100	0
RP09	Gulf of Penas, Southern right whales	CMP	0	0[9]
RP10	Population dynamics of southern right whales at Península Valdés, Argentina	CMP	19,130	0
RP12	ES Pacific Southern right whales acoustic monitoring	CMP	13,700	16,800
RP13	Sample holotype specimen of *Megaptera indica* at the Muséum National d'Histoire Naturelle (Paris)	CMP	0	1,975
RP14	Assessing isolation of Arabian Sea humpback whales and continuity across the Arabian Sea through geographic variation in song	CMP	16,400	0
RP15	Quantitative assessment of threats to Arabian Sea humpback whales using existing photographic and UAV data	CMP	9,500	0
RP24	Collaborative analysis of WNP minke whale stock structure	SD-DNA	6,247	0
RP28	Updated catch series and assessments of four pygmy blue whale populations	SH	0[10]	12,865
RP30	Multi-ocean analysis of southern right whale demographic parameters and environmental correlates	SH	13,600	13,600
RP31	Southern Hemisphere fin whale song	SH	0	12,000
RP34	Photo-Identification information placards for naturalists and citizen scientists	SH	1000	0
RP07	IWC strandings initiative – emergency response and investigations	E	4,500	4,500
Databases				
RP18	Ship strikes database coordinator	HIM	7,000[11]	7,000[12]
RP33	Antarctic Blue Whale Catalogue: comparison of new photographs from 2014-20	SH	3,000	800
RP32	Southern Hemisphere blue whale photo catalogue	SH	16,810	3,000[13]
RP38	Secretariat database management	SC	3,000	3,000
Reports				
RP03	Mercury in cetaceans	E	0[14]	0
RP04	State of the Cetacean Environment Report	E	3,000[15]	3,000[16]
RP02	Amendment of RMP Guidelines to incorporate spatial modelling approaches to estimate abundance	RMP	3,000	0
General items				
	Implementation: resolutions and instructions from Commission & follow up from previous years' recommendations	SC	10,313	28,470
Total request			£315,800	£315,800

Notes: [1]Budget was reduced from £22,200, [2]£20,300 was the expected financial need for 2019 but savings from 2018 allowed for the reduced budget of £0; [3]£11,400 was the expected financial need for 2019 but savings from 2018 allowed for the reduced budget of £1,000; [4]£15,000 was the expected financial need for 2019 but savings from 2018 allowed for the reduced budget of £13,000. [5]Budget was reduced from £8,958, [6]£20,000 was the expected financial need for 2020 but financial savings for 2018 allowed for the reduced budget of £17,000, [7]£32,500 was the expected need for 2019 but financial savings from 2017 allowed for the reduced budget of £22,500, [8]£32,500 was the expected need for 2020 but financial savings from 2018 allowed for the reduced budget of £22,500, [9]The requested budget was £15,000 but further information is required before funding can be considered. The project will be re-evaluated at the 2019 SC meeting, [10]£6,185 was the expected financial need for 2019 but financial savings from 2018 allowed for the reduced budget of £0, [11]budget was reduced from £10,000, [12]budget was reduced from £10,000, [13]funding of approximately £7,280 may be requested for 2020 next year depending on progress, [14]£4,000 was the expected financial need for 2019 but savings from 2018 allowed for the reduced budget of £0, [15]budget was reduced from £4,000, [16]budget was reduced from £4,000.

27.2.1 Invited Participants

INVITED PARTICIPANTS

Invited participants (IPs) are a vital component of the working of the IWC's Scientific Committee. IPs contribute in many ways including as sub-committees and Working Groups Convenors, co-Convenors and rapporteurs, subject area experts and Convenors of intersessional groups. All sub-committees and Working Groups benefit from this budget item. This year under this budget item, 62 scientists from Australia, Argentina, Belgium. Brazil, Canada, Chile, China, Colombia, France, Germany, Italy, Japan, Mexico, Netherlands, Norway, Oman, Peru, Slovenia, South Africa, Spain, UK, USA were supported.

RP19 COMPREHENSIVE ASSESSMENT OF NORTH PACIFIC HUMPBACK WHALES

At SC67a, following discussion of the results of an assessment workshop held in April 2017, a Steering Group was established to facilitate a second North Pacific humpback whale assessment workshop, and to coordinate work required for this meeting. This meeting was not held prior to SC67b and the workshop is now planned for prior to the 2019 meeting of the Scientific Committee, with a view to completing or significantly advancing the assessment.

RP37 BALAENID WORKSHOP: BIOLOGY, HEALTH, STATUS

The North Atlantic right whale's population rate of increase is much lower than that of all other well-studied balaenid populations. This workshop will compare reproductive biology, health and status of North Atlantic right whales with those of other balaenid populations with the goal of determining their potential for growth and assessing the role of anthropogenic mortality as a driver of current population decline. Possible causes of the NARW's lower reproductive rate need reassessment include: sub-lethal effects of entanglements; environmental contaminants or marine biotoxins; inadequate prey base; stress from noise; genetic factors; and infectious diseases. This review will also help understanding of population changes for other balaenid populations.

RP21 *IMPLEMENTATION REVIEW*: NORTH PACIFIC MINKE WHALES

These workshops are essential in order for the Committee to conduct a full *Implementation Review* for Western North Pacific common minke whales following the Committee's Requirements and Guidelines. Conducting *Implementation Reviews* are a required activity under the RMP.

RP29 CATCH SERIES: SOUTHERN RIGHT WHALES

A new review of available catch data for measuring regional takes of southern right whales is overdue and the availability of new sources suggests that it is timely to do this. The expected outcome of this workshop is updated regional estimates of southern right whale catches, which can be used to conduct regional assessments of southern right whale past exploitation and develop population trajectories to measure past abundance and current recovery levels.

RP25 INTERSESSIONAL MEETING OF THE TASK TEAM ON SOUTH ASIAN RIVER DOLPHINS

The South Asian river dolphin, *Platanista gangetica*, is listed as an endangered cetacean species by the IUCN Red List assessment. Across its range, in the countries of India, Pakistan, Nepal, and Bangladesh, the species remains highly threatened by a range of anthropogenic activities at multiple scales. These range from localised threats caused by hunting, fisheries bycatch, or local disturbances as well as from large-scale alterations of the rivers by dams, barrages, waterways and river-linking schemes. In particular, large-scale and rapidly accelerating water development in the Indo-Ganges-Brahmaputra floodplains make the outlook for the South Asian river dolphin conservation grim. In recognition of this situation, the Scientific Committee has established a Task Team for the species and the team of experts will meet in person and discuss how to go forward.

RP26 GUIANA DOLPHIN PRE-ASSESSMENT (*SOTALIA GUIANENSIS*)

An intersessional workshop will assess the geographic extent of Guiana dolphin threats and conservation measures needed in both national and international contexts. The outcomes of the workshop shall include: (1) a Comprehensive Assessment of the status of Guiana dolphins; (2) recommendations to potentially improve management actions and the monitoring efforts associated with the current conservation plans of actions; and (3) a consolidated report to be presented to the SC at next year's meeting for review.

RP27 MODELLING WHALE WATCHING IMPACTS (MAWI)

There is little research on the potential mid- and long-term impacts of whale watching on cetacean populations. This is due to the complexity of the required modelling approaches, lack of clarity regarding the data needed to inform them, and the need to identify locations suitable for data collection. Without addressing these issues understanding the potential mid- and long-term impacts of whale watching is not possible. The workshop will bring together modellers and field researchers to achieve the following outcomes: (1) identify existing modelling approaches that could be used to understand the potential mid- and long-term impacts of whale watching, and determine whether new approaches are required; (2) determine which data currently being collected are suitable for answering questions regarding the mid- and long-term impacts of whale watching, and what new data are required; and (3) determine the feasibility of data collection, and identify locations where this has already been done or could be achieved.

27.2.3 Modelling/computing

RP20 ASSESSMENT MODELING FOR AN IN-DEPTH ASSESSMENT-NORTH PACIFIC SEI WHALES

The IA sub-committee is currently conducting a Comprehensive Assessment for North Pacific sei whales. This involves evaluating the status of a population using a population dynamics model that is specific to the biological parameters and movement behaviour of that particular population and is fitted to monitoring data. During the intersessional periods after the 2018 SC meeting and possibly also after 2019 SC meeting, it is expected that population dynamics models will be finalised and run using the existing data. This will result in an assessment of the status of the population.

RP22 DEVELOP AN AGE-STRUCTURED EMULATOR FOR THE INDIVIDUAL-BASED ENERGETICS MODEL (IBEM)

An IBEM provides an alternative population dynamics model to the usual cohort models, particularly because density dependence in births, growth and age-specific mortality are emergent properties of a species in a given environment (which can be stochastic). The IBEM is computationally infeasible for conducting *IST*s; the proposal is to develop a computationally efficient cohort model (emulator) which uses demographic parameters and their covariances generated using the IBEM.

RP23 ESSENTIAL COMPUTING SUPPORT TO THE SECRETARIAT

Regular *Implementation Reviews* are required under the RMP and AWMP. Computing support is alos required for Comprehensive and in-depth assessments. The Committee is currently about to undertake an *Implementation Review* for the North Pacific common minke whales, and more will follow. The Committee has developed a complex trials structure for *Implementation Reviews*. A key task in this process is to develop and validate the code for the simulation trials that are the core component of this process. Experience has shown that the Secretariat staff alone cannot handle this complete process themselves, so computing support is needed.

RP36 SIMULATING LINE TRANSECT DATA TO INVESTIGATE ROBUSTNESS OF NOVEL ANALYSIS METHODS

The IWC SC has already invested time and money in developing simulated line transect data to evaluate the robustness of the Norwegian minke whale and Antarctic minke whale survey data. This project will update the old code for the simulator to make it more user-friendly so that it can be made available to all SC members and to produce some standard data sets in accordance to the specifications of the ASI sub-committee.

27.2.4 Databases/catalogues

RP01 IWC-POWER CRUISE

The Committee has strongly advocated the development of an international medium- to long-term research programme involving sighting surveys to provide information for assessment, conservation and management of cetaceans in the North Pacific, including areas that have not been surveyed for decades. This is one of the most important international collaborations undertaken by the IWC and the cost to the IWC is minimal given the generous contribution of a vessel by Japan and acoustic equipment by the USA . Committee objectives have been developed for the overall plan and requested funding will allow for the continuing work of the initial phase and progress on developing the medium-term phase. The IWC contribution is for: (1) IWC researchers and equipment; (2) to allow the Committee’s Technical Advisory Group to meet to review the multi-year results thus far and develop the plans for the next phase of POWER based on the results obtained from Phase I; and (3) to enable analyses to be completed prior to the 2020 Annual Meeting.

RP11 ABUNDANCE ESTIMATES OF THE FRANCISCANA DOLPHIN IN BUENOS AIRES PROVINCE, ARGENTINA

Abundance estimates of franciscanas will be based on a series of aerial surveys along the coast of Buenos Aires Province, with the same survey design of surveys carried out in 2003 and 2004 (Crespo *et al*., 2010). The new estimate will allow comparing density values with those obtained in the previous surveys. This item represents only one third of the funds required for the project, with the remainder being provided by the Government of Argentina.

RP09 GULF OF PENAS, SOUTHERN RIGHT WHALES

Eastern South Pacific (ESP) Southern right whales (SRW) are classified as critically endangered as there are no more than 50 SRW in this population and there is no information on the ESP SRW breeding and feeding grounds. Gulf of Penas is one of the most remote and exposed areas in Chile, with limited access and wild weather that have prevented its exploration. The largest baleen whale mass mortality of almost 400 sei whales occurred in this area and almost remained unnoticed. Recently, a local living nearby the Gulf of Penas recorded the presence of SRWs, including several calves. The Gulf might be the unknown breeding ground of the ESP SRW. This area will be explored during the austral winter breeding season with a group of researchers and government officers to confirm this finding and if so, start immediately working towards the protection and management of the species and the area.

RP10 POPULATION DYNAMICS OF SOUTHERN RIGHT WHALES AT PENÍNSULA VALDÉS, ARGENTINA: THE INFLUENCE OF KELP GULL LESIONS ON THE HEALTH, CHANGES IN INCREASE AND MORTALITY RATES IN THE CONTEXT OF A DENSITY-DEPENDENT PROCESS

The recent mortality of southern right whales at Península Valdés, Argentina is the highest ever recorded for the species. Understanding the causes is critical to propose management and mitigation actions. Preliminary results from glucocorticoids in baleen from stranded calves show that stress from injuries due to Kelp Gull attacks negatively affects their physiological homeostasis, potentially leading to death. Also, aerial counts show an important reduction in population rate of increase as a whole (from 7% in the past to 0.5% at present), and changes in distribution (mainly of adults) and density along the Argentinian coast.

RP12 PASSIVE ACOUSTIC MONITORING OF THE EASTERN SOUTH PACIFIC SOUTHERN RIGHT WHALE

The Eastern South Pacific southern right whale population is Critically Endangered and in 2012 the IWC adopted a Conservation Management Plan (CMP). Over the years, few opportunistic sightings have been recorded and no breeding area has yet been identified. Until a breeding ground is found many CMP priority actions cannot be implemented. Thus, in 2016 the IWC Scientific Committee decided to support this passive acoustic monitoring (PAM) project to facilitate the identification of potential breeding areas along the coast of Chile and Peru. This project seeks to obtain temporal coverage over a complete annual cycle and spatial coverage depending on the number of sites. The PAM project is likely the most cost-effective way to investigate the seasonal and temporal distribution of southern right whales along the coast of Chile and Peru. The information will be crucial to identify aggregation areas and facilitate the implementation of CMP for this population.

RP13 SAMPLE THE HOLOTYPE SPECIMEN OF *MEGAPTERA INDICA* (GERVAIS, 1883) AT THE MUSÉUM NATIONAL D'HISTOIRE NATURELLE (PARIS)

Several lines of evidence suggest that humpback whales in the Arabian Sea/Northern Indian Ocean comprise a discrete, isolated and non-migratory population that merits a taxonomic revision. Genetic analyses of available samples are now underway in order to determine whether sub-species/species designation is merited. The resultant nomenclature will necessarily draw on a description of the type specimen of *Megaptera indica*, which is held at the Muséum National d'Histoire Naturelle in Paris. This work will develop an approach for examining and sampling this specimen so that the taxonomy of Arabian Sea humpback whales can be accurately defined, better informing regional conservation efforts, highly relevant to the IWC's stated interest in the establishment of a Conservation Management Plan for Arabian Sea humpback whales.

RP14 ASSESSING ISOLATION OF THE ARABIAN SEA HUMPBACK WHALE POPULATION AND CONTINUITY ACROSS THE ARABIAN SEA THROUGH GEOGRAPHIC VARIATION IN SONG

A study of geographic variation in humpback whale song indicates that the Arabian Sea song from Oman is distinct from the Southwest Indian Ocean (SWIO) song, and evidence from a small Indian sample suggesting continuity in song between the western and eastern Arabian Sea. This work will be followed up on with a detailed comparison of song across the Arabian Sea and continued assessment of song differences with the SWIO: The project will (1) assess the connectivity of Arabian Sea humpback whales from Oman to India by comparing existing samples of song between the two regions from several different years; and (2) assess and re-examine the differences in song exhibited between Oman and the SWIO with more recent data, particularly in light of evidence that SWIO singers were found off Oman during the Boreal summer of 2012.

RP15 A QUANTITATIVE ASSESSMENT OF THREATS TO ARABIAN SEA HUMPBACK WHALES USING EXISTING PHOTOGRAPHIC AND UAV DATA

The research will assess the prevalence of anthropogenic and natural threats to Arabian Sea humpback whales through a robust and quantitative assessment of available photographic data. These data include the entire Oman photo-ID catalogue, imagery recently acquired using UAVs (drones) and images provided by third parties. The latter include several images from elsewhere in the populations range. The project will provide an assessment of the relative prevalence of a suite of indices typically associated with major threats (fisheries entanglements, ship-strikes, other scars) as well as scars associated with natural sources (barnacles, cyamids, Penella sp., killer whales). Project outcomes will include assessment of the risks posed by each threat, as well as the development of a set of metrics with which further changes can be monitored. Project results will be reported to the IWC SC in 2019 and will contribute to the development of a draft Conservation Management Plan for this population.

RP24 COLLABORATIVE ANALYSIS OF WNP MINKE WHALE STOCK STRUCTURE USING JAPANESE MICROSATELLITE DNA DATABASE AND SPATIALLY EXPLICIT POPULATION STRUCTURE ANALYSES.

This item will help address the recommended 'analysis 2' from the report of the workshop on Western North Pacific common minke whale stock structure (SC/67b/Rep05) in support of the next intersessional meeting on WNP common minke whale stock structure. This specific aspect of the work will apply spatially explicit population structure analyses that provide greater power than the program STRUCTURE together with geographic context. The data will be analysed as a total dataset (not based on any assignment in STRUCTURE), but also include temporal subdivision to assess possible seasonal changes in patterns of connectivity. The latter aspect may be critical to understanding the true pattern of structure, but it will also be the most time-consuming, requiring extensive replication of the analyses. The results of these analyses will provide an assessment of structure in the context of biogeography using methods that have considerably more power than the program STRUCTURE and using an approach that will consider temporal patterns of movement.

RP28 UPDATED CATCH SERIES AND ASSESSMENTS OF FOUR PYGMY BLUE WHALE POPULATIONS

The SH sub-committee is conducting in-depth assessments of populations of Southern Hemisphere blue whales. Assessments have previously been conducted for two of the six populations (Antarctic blue whales, and Chilean blue whales), but not for the four pygmy blue whale populations addressed by this research. This project will provide crucial catch separation data and associated uncertainty needed to conduct stock assessments and provide the first stock assessments for each of the four populations. Such data are critical inputs for the assessments planned by the SC.

RP30 MULTI-OCEAN ANALYSIS OF SOUTHERN RIGHT WHALE DEMOGRAPHIC PARAMETERS AND ENVIRONMENTAL CORRELATES

This study aims to compare population demographics of southern right whales in Southern Hemisphere wintering grounds and investigate correlations between reproductive success and abundance trends, and environmental variables. This study is a component of the proposed SORP project - The right sentinel for climate change: linking foraging ground variability to population recovery in the southern right whale.

RP 31 ANALYSIS OF FIN WHALE SONG VARIABILITY ACROSS SOUTHERN HEMISPHERE

Fin whale songs consist of short pulses repeated at regular interpulse intervals (IPIs). These songs have been suggested as a tool to distinguish populations. Features that have be used for fin whale song separation include: spectral structure of individual pulses; their patterning; the IPIs; and presence of a higher frequency component of the pulses. Based on this higher frequency component, there appear to be two fin whale song types in the Southern Ocean. We propose to use a combination of song feature measurements to identify whether fin whale songs in the Southern Hemisphere could be indicative of population structure. Data to be used include recorders deployed in the Western Antarctic Peninsula, Weddell Sea, and Eastern Antarctica (Kerguelen and Casey) from 2014-16. Additional SH lower-latitude recordings are available in southeastern Pacific and South Indian Ocean. Overall, the analysis will enable a comprehensive review of fin whale song variability across the SH.

RP34 PHOTO-IDENTIFICATION INFORMATION PLACARDS FOR NATURALISTS AND CITIZEN SCIENTISTS

Pre-cruise training and reference placards describing examples of photo-identification subjects (large whales) will be developed for distribution to the tourist vessel industry in the South Georgia and Antarctic Peninsula region. Information will include primary ID features used for seven species likely to be encountered; right, blue, sei, fin, humpback, sperm and killer whales (key species). A Powerpoint presentation will be developed for distribution to naturalists working on tourist vessels, to orient them and their clients to the basics of whale identification photography. Minimal training is required for a considerable improvement to the quality of identification photographs that are collected by naturalists and citizen scientists and ultimately provided to the established photo-ID catalogues from the region. A formal collaboration with the global photo-ID platform, HappyWhale will be established.

RP07 IWC STRANDINGS INITIATIVE – EMERGENCY RESPONSE AND INVESTIGATIONS

Over the next two years, the Emergency Response and Investigations fund will support response, collection of data to determine the cause(s) or contributing factors for the event and/or to fill critical data gaps identified by the SC or Commission. The Initiative will be evaluated annually and policies and procedures adapted according to feedback from responses and through Steering Group/Expert Panel advice.

27.2.5 Databases and catalogues

RP18 SHIP STRIKE DATABASE COORDINATOR

The ongoing development of the IWC ship strike database requires data gathering, communication with potential data providers and data/database management. This project will provide support for expanding and maintaining the database.

RP33 ANTARCTIC BLUE WHALE CATALOGUE: COMPARISON OF NEW PHOTOGRAPHS FROM 2014-2020

In year one (2019) this project will compare the identification photographs of an estimated 45 individual Antarctic blue whales collected during ICR cruises 2014-17, to the Antarctic Blue Whale Catalogue. These identifications would increase the size of the catalogue (458 individuals) by almost 10%. In year two (2020) additional photos representing approximately 12 IDs are expected from collaborating scientists and citizen scientists that will be compared to the catalogue. The expected outcome is an expanded dataset that may improve estimates of population abundance and reveal new information on movement patterns.

RP32 SOUTHERN HEMISPHERE BLUE WHALE PHOTO CATALOGUE

The Southern Hemisphere Blue Whale Catalogue (SHBWC) is an international collaborative effort to facilitate cross-regional comparison of blue whale photo-identifications catalogues. To date more than 1,500 individual blue whales have been contributed to the SHBWC from researchers groups working on areas off Antarctica, Chile, Peru, Ecuador-Galapagos, Eastern Tropical Pacific, Australia, Timor Leste, New Zealand, Madagascar and Sri Lanka. Therefore, the SHBWC has become the largest repository of Southern Hemisphere blue whale photo-identifications. Results of comparisons among different regions will improve the understanding of basic questions relating to blue whale populations in the Southern Hemisphere such as defining population boundaries, migratory routes, visual health assessments, and to model abundance estimates. The results will contribute primarily to the IWC Southern Hemisphere blue whale assessments.

RP38 DATABASE MANAGEMENT

The IWC Secretariat hosts several databases for the SC. These have annual service costs associated with them including, web/database servers, storage, backups, software licences and other associated infrastructure or costs.

27.5.6 Reports

RP03 MERCURY IN CETACEANS: BIOGEOCHEMICAL CYCLING, TOXICOLOGICAL IMPACTS

In response to the Commission resolution on mercury, the objective of the work is to comple the global review of mercury in cetaceans, resulting in the documentation and mapping of decadal trends. The Scientific Committee will also invite experts in mercury in the environment and its cycling and in mercury and selenium cetacean toxicology to participate to provide further detail and interpretation of the current status and potential impact of mercury on cetacean populations at an ocean basin scale.

RP04 PRODUCTION OF ANNUAL STATE OF THE CETACEAN ENVIRONMENT REPORT (SOCER) FOR THE SCIENTIFIC COMMITTEE AND COMMISSION (2019 AND 2020)

SOCER is a long-standing effort to provide information to Commissioners and Committee members on key current global developments that are affecting the cetacean environment. Focus will be on the Atlantic Ocean (2019) and the Pacific Ocean (2020). It will, in both years, also present key current global developments that are affecting the cetacean environment. It will also contain a glossary of technical terms used and species names. A 5-year compendium spanning all regions is also being produced.

RP02 AMENDMENT OF THE RMP GUIDELINES TO INCORPORATE SPATIAL MODELLING APPROACHES TO ESTIMATE ABUNDANCE

The ‘Requirements and Guidelines for Conducting Surveys and Analysing Data within the Revised Management Scheme’, referred to as the ‘RMP Guidelines’ (IWC, 2012) constitutes a document prepared by the Scientific Committee to state the requirements and to guide the collection and analysis of survey data to compute abundance estimates for use in the Revised Management Procedure (RMP). Currently this document provides detailed guidance for developing estimates using design-based line transect shipboard and aerial surveys. Amendments are required to consider other methods, for example, model-based analysis of survey data and mark-recapture models. This project will update the RMP Guidelines as required by the Scientific Committee. This update will be completed in consultation with the project’s steering committee and presented for consideration of the SC by SC68b. The expected outcome is a new, revised document of with the ‘RMP Guidelines’.

27.5.7 General items

***IMPLEMENTATION*: RESOLUTIONS AND INSTRUCTIONS FROM COMMISSION & FOLLOW UP FROM PREVIOUS YEARS’ RECOMMENDATIONS**

This line is required to accommodate additional work requested by the Commission at IWC67 and work generated by meetings, workshops and projects funded and concluded in the first year (2019). This line can also accommodate new project proposals generated during the 2019 Scientific Committee meeting.

28. WORKING METHODS OF THE COMMITTEE

28.1 Rules of Procedure of the Scientific Committee

Attention: C, S

As per usual practice in the last biennium the Committee has been reviewing its working methods to improve transparency and align its processes with the biennial pace of the Commission. These changes and a number of changes that were made in previous years and approved by the Commission (i.e. SORP Voluntary Fund, new process to allocate and manage the Research Fund and the Small Cetacean Voluntary Fund Rules of Procedure) require a number of adjustments and additions to the Commission Rules of Procedure, Financial Regulations and Scientific Committee Rules of Procedure. The Committee ***agrees*** *to submit all proposed amendments to the Commission for its consideration (Annex W).*

The updated Rules also refer to the online ‘Scientific Committee Handbook’ that has been updated at this meeting. The Committee ***requests*** *the Secretariat to post the updated version online as soon as feasible. The Committee also* ***agrees*** *to that a pdf version of the Handbook be made available as a document for the Commission meeting.*

28.2 Biennial reporting and related matters

At its 2015 meeting, the Joint Conservation Committee and Scientific Committee Working Group (Joint CC/SC WG) agreed to undertake a collation and analysis of conservation-relevant recommendations from the Scientific Committee and organise these recommendations into key issues/areas highlighting those that feature regularly, including the creation of a pilot database. Double, Convenor of the Global Databases and Repositories Steering Group (GDR), presented an update on the development of this database. The Scientific Committee is fully engaged in this process and, this year, a standing agenda item was added to all sub-committee agendas to ensure a regular, more formal review of progress in delivering recommendations than was the case in the past.

Attention: SC, CC

The Committee ***welcomes*** *the development of the IWC Database of Recommendations, noting that this tool will give recommendations more prominence and improve the ability to measure progress. The Committee* ***agrees*** *to:*

(1) continue to improve its standardised way to present recommendations to include core information[13] *to facilitate input into the database; and*
(2) to work closely with the Secretariat to assist with the overall process of data entry.

28.3 Additional proposals for revisions to ‘Annex P’

The Committee continued this year the work begun last year to update Annex P in response to Commission Resolution 2016-2 and recommendations by previous Expert Panels.

Attention: C-R, SC,

The Committee ***recommends*** *the revisions to the previous Annex P reported in Annex P in response to Resolution 2016-2 and recommendations made by Expert.*

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[13] IWC/MAY18/CCSC/01

28.4 Succession plan for key Scientific Committee experts

Last year, the Committee had identified the need to consider 'succession planning' for key participants, particularly in relation to the *Implementation Reviews* and assessment processes. Informal discussions continued informally during the intersessional period and invitations were issued to three modellers to evaluate their interest in becoming active members of the IWC Scientific Committee, but only one could attend. Concern regarding succession planning of these other key positions on the Committee still remains and an intersessional group has been re-established to look at this and report back to the Committee next year (Annex Y).

The Committee also refers to its discussion related to a Deputy Head of Science in its review if the governance report (see Item 28.6.2).

28.5 Update on Data Availability requests

Suydam provided a summary of requests received under the Data Availability Agreement shown in Table 34.

Table 34

Summary of requests under the Data Availability Agreement.

Date	Requested by	Objective/Subject	Outcome
June 2015	de la Mare Australia) – Procedure B	(a) Consistent with recent advice of the Scientific Committee with particular respect to minke whale nutritive condition analyses, to develop a set of models that best capture the Committee's previous recommendations, taking into account the structure of the underlying processes giving rise to the data; and (b)To provide analyses relevant to the determination of sample sizes for detecting specified trends in the age at sexual maturity (ASM).	SC/66B/EM/02, SC/67A/EM/01, SC/67A/EM/02, SC/67A/EM/03, SC/67A/EM/04, SC/67A/EM/07, SC/67A/EM/08, SC/67B/EM/01 Rev1, SC/67B/EM/02, SC/67B/EM/03, SC/67B/EM/08, See EM Annexes, 2016 to 2018. Differing results between research groups about changes in body condition of Antarctic minke whales
January 2018	Baker (USA	The intent of the request is to examine plausible stock hypotheses. Analyses will rely primarily on tests of Hardy-Weinberg expectations, exact tests of differentiation, randomized Chi-squared tests (contingency tables), Analyses of Molecular Variance (AMOVA), as well as mixed-stock analyses, clustering methods and kinship (parent offspring pairs), to investigate dispersal and differences in haplotype frequencies, genotypes and sex for various geographic and temporal strata.	On-going

28.6 Any other matters

28.6.1 Welfare Assessment Tool

Since our last discussion in 2015 on animal welfare related matters relevant to the Committee (IWC, 2016, p.86), Dr. Nicol (Professor of the Royal Veterinary College, London) developed a 'Welfare Assessment Tool' following the recommendations of the Workshop to 'Develop Practical Guidance for the Handling of Cetacean Stranding Events' (South Africa, 2016) on this matter. This year, the Committee received a report from Nicol on the latest phase of the development of such a tool, that is being developed to help assess non-hunting related threats in the context of the IWC's Welfare Action Plan and in a joint project between the RVC and Humane Society International, supported by the UK Department for Environment, Food and Rural Affairs (Defra). The approach is based on application of the 'five domains model' (Beausoleil and Mellor, 2015; Mellor *et al*., 2015) and two hypothetical case studies have been explored, one related to marine debris and the other to whale-watching.

Trial assessments were presented and the Scientific Committee was asked for assistance and advice in the development of real examples for consideration. The Committee welcomed the information provided and further discussions were held informally. The Tool was also considered by the Whale Watching Subcommittee (see Annex N) and will be presented for consideration by the Commission at the next meeting of the Working Group on Whale Killing Methods and Associated Welfare Issues.

28.6.2 Review of the IWC review report

The final report from the Governance Review was released on the 16th April 2018 (downloadable here: https://archive.iwc.int/?r=6890). The Independent Review Panel report represents the view of the three panellists, based on a survey, in-person interviews and analysis of documents. It represents only the first step of the Governance Review process. The Chair of the Operational Effectiveness Working Group of the Finance and Administration Committee asked the Scientific Committee to provide a voluntary feedback to the Commission on recommendations related to the Committee.

The Scientific Committee formed an *ad hoc* Working Group to develop an initial response, which was then discussed in Plenary. The initial WG membership was restricted to the Scientific Committee Chair and Vice Chair, all Heads of Delegations present at the meeting, sub-groups Convenors that are also delegates, and former Scientific Committee Chair present at the meeting. This subset represented the view of Committee members that, given their roles, had a strong knowledge on the current and past structure and procedures of the Committee. More delegates and invited participants joined the discussion in Plenary. The final version of this preliminary feedback, which has the support of all 32 delegations attending the meeting and additional members of the Scientific Committee is provided in Annex X.

The Scientific Committee organised its discussion and feedback on Review Panel's recommendations and comments around five mutually exclusive subject areas (pre-eminence of the Scientific Committee, IWC strategic planning, communication, Scientific Committee function in relation to Commission and other subsidiary bodies, Secretariat function in relation to the Scientific Committee). Within each subject area, those recommendations of perceived importance to the WG were identified. Where feasible, a timeline for developing a response was proposed.

Attention: C, SC

Given the fact that both the Chair of the Commission (Morishita) and the Chair of the F&A Working Group on Operational Effectiveness (Phelps) reminded the Committee that the Commission has not yet decided the fate of the 'IWC review report', nor has yet requested a full engagement by the Committee, the Committee ***agrees*** *to submit the preliminary feedback on the report (Annex X) for the Commission's consideration.*

In addition, given the productive exchange of opinions and ideas on several aspects of the Committee working methods that occurred in during its discussions, the Committee ***agrees*** *to establish an Intersessional Correspondence Group on 'Improving on-going working practices of the IWC Scientific Committee' under DeMaster (see Annex Y). The ICG will provide a written summary of its proposals to the Scientific Committee 60 days prior to the start of the annual meeting of the Scientific Committee in 2019. This ICG will also be in charge dealing with the preparation of a draft document for the follow-up on Governance Review, should the Commission instruct the Committee to do so at its next biennial meeting.*

28.6.3 Additional discussion on other issue related to the Committee working procedures

A number of suggestion for improving the ability to follow a topic during the Scientific Committee meeting were discussed by the Committee and the Convenors group. In order to facilitate the full participation of members of the Committee to various sub-groups and, especially, to the discussion of cross-cutting issues relevant to different groups, the Committee **agrees** that next years the Convenors should: (a) organise joint-sessions early in the meeting and release draft reports of those discussion, as soon as feasible; (b) adopt a simple coding system for 'hot topics' (e.g. North Pacific common minke whales: NPMW, Antarctic minke whales: AMW; biopsy sampling; etc.), which will be included in the daily timetable together or instead of the Agenda item. The Convenors group will carefully consider these issues intersessionally.

29. PUBLICATIONS

The Secretariat reported on the excellent progress made with the *Journal* this year, and in particular that the previously noted backlog has now been dealt with. This has been particularly assisted by the excellent work of the new Associate Editors including Fortuna, Leaper, New, Jackson, Punt, Tiedemann, Zerbini. The Committee **thanked** the Publications Team for its dedication and hard work and **reiterated** the importance of the *Journal* and *Supplements* to its work.

30. ELECTION OF OFFICERS

This was the final year of office for the Chair (Fortuna) and the Vice-Chair (Suydam). In accordance with its Rules of Procedure, the Vice-Chair becomes the new Chair for the next three years. The Committee elects Zerbini (Brazil) to be the new Vice-Chair by consensus. The outgoing Chair will provide the formal report to IWC67 in Florianopolis, Brazil of the SC Reports from the 67a and 67b SC meetings.

The Committee rose in appreciation to thank the outgoing Chair. It wished to formally record its immense gratitude for her excellent leadership over the past three years. Dr. Fortuna's scientific and organizational skills provided a lasting legacy to the Committee. She adeptly faced the many complex and challenging issues during her term and tremendous progress has been made for the benefit of the entire Commission in meeting its science and stewardship objectives. The Chair, Head of Science, and Executive Secretary of the Commission added their thanks and congratulations to the many participants expressing their appreciation to Dr. Fortuna.

The Committee also welcomed with enthusiasm the new team of Suydam and Zerbini and looked forward to working with them over the next three years.

31. ADOPTION OF REPORT

The Committee adopted the report at 17:45 hrs on 6 May 2018, apart from the final items discussed during the last session. As is customary, these items were agreed by the Chair, rapporteurs and convenors. The Chair thanked the participants for their scientific contributions as well as their constructive dialogue. Given the sensitivity of several agenda items, this positive approach helped ensure that all views could be presented and rigorously discussed for a productive outcome. The Chair especially thanked the convenors, rapporteurs, Head of Science, and Vice-Chair for their excellent assistance. Finally, she reiterated her thanks to the government of Slovenia and the hotel staff for the facilities and great service, which contributed greatly to the success of the meeting.

Fortuna concluded that it had been an honour to serve as the IWC Scientific Committee Chair over the past three years. She expressed her gratitude for all the support provided by so many as she led this effort. She voiced her thanks for the Secretariat, and in particular her deep appreciation for the guidance provided by the Head of Science (Donovan) without whom she could not have accomplished her work.

Suydam congratulated Fortuna for having expertly led the Scientific Committee as their Chair over the past three years. He noted that the praise and applause from the participants in the room were well very much deserved given her outstanding leadership. Suydam noted that it will be a particular challenge to follow the incredible example set by Fortuna and thanked her for her mentorship. The Executive Secretary (Lent) added to these words of gratitude and commendation on behalf of the Secretariat and wished her all the best. She also offered the full support of the Secretariat to the incoming SC Chair Suydam.

Echoing the sentiments raised under Item 30, participants thanked the Chair for her adept, fair and efficient handling of the meeting, her unflagging dedication and her great contribution to the effective working of the Committee.

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Estimates of Eastern North Pacific Gray Whale Calf Production 1994-2016

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INTERNATIONAL
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ABSTRACT

Shore based surveys of northbound eastern North Pacific gray whale calves were conducted between March and June from the Piedras Blancas Light Station on the central California coast each year from 1994-2016. Estimates of the total number of northbound calves displayed a high degree of inter-annual variability, ranging from 254 calves in 2010 to 1528 calves in 2004. Calf production has been particularly high during the past 5 years (2012-2016) with a total of >6,500 calves estimated during this period, including four of the highest years of calf production (>1,000 calves per year) since our calf counts began in 1994. The 2016 estimate of calf production (1,351) is about 5% of the reported total abundance (26,960) for the eastern North Pacific population. A trend in median migration dates was observed, indicating that the midpoint of the migration is now occurring about a week later than it did in the mid-1990s. The 23-year data set described herein serves as an excellent foundation upon which to examine the inter-play between changing environmental conditions and gray whale population dynamics.

INTRODUCTION

The majority of Eastern North Pacific gray whales *(Eschrichtius robustus)* annually migrate southward from summer feeding grounds in the Pacific Arctic to wintering areas off Baja California, Mexico (Rice and Wolman 1971, Perryman and Lynn 2002). Both the southward and northward migration is segregated, to a large extent, by age, sex and reproductive condition. During the northward migration, females with their calves of the year are the last to depart the Baja wintering areas. These mother-calf pairs are observed on the migration route between March and May and typically arrive to the summer feeding grounds between May and June.

Shore-based counts of northbound gray whale calves have been conducted off central California each spring from 1994 to 2016. This report presents an overview of results from this 23-year time series of estimates of gray whale calf production.

METHODS

Shore-based counts of northbound gray whale calves have been conducted from the Piedras Blancas Light Station (north of San Simeon, California) each spring from 1994 to 2016. Data collection methods and analytical techniques have remained consistent each year and follow those reported elsewhere (see Perryman *et al*. 2002, 2011). Briefly, counts were conducted by four observers, with two on effort at any one time, rotating through the following schedule: (a) 90-min on effort as the offshore search area observer, (b) 90-min on effort as the inshore search area observer, (c) 3-hr off effort. Weather permitting, this work was carried out for 12 hours per day; 6 days per week in 1994-2003 and 2005 and 5 days per week in 2004 and 2006-2016. Primary search effort was carried out with unaided eye but 7x50 and 25x150 binoculars were also used when needed.

Based on night/day migration rate data derived from thermal sensors (1994-1996) and aerial surveys (1994-1995) to determine offshore distribution (Perryman *et al*. 2002), we assumed that: (1) the number of gray whale calves passing the survey site far enough offshore to be undetectable by visual observers was negligible, and (2) day and night passage rates were equivalent. We also assumed that detection probabilities were the same across acceptable sighting conditions (see Reilly *et al*. 1983; Reilly 1992). To correct for imperfect probability of detection of calves by the visual observers, we corrected the observer estimates of northbound calves by the average detection probability estimates from seven consecutive years (1994-2000) of replicate counts (mean = 0.889; SE = 0.06375).

Each day of survey effort was divided into four 3-hr periods and passage rates during these periods were calculated from the observed counts multiplied by the inverse of the detection function. To correct for periods when observers were not on watch (e.g. poor weather, night time, days off), we embedded the estimators in a finite population model that was stratified by week to account for varying passage rates (Cochran 1977). A Taylor series expansion (Seber 1982) was used to calculate the variance of the estimates.

RESULTS

Estimates of the total number of northbound calves showed a high degree of inter-annual variability, ranging from 254 calves in 2010 to 1528 calves in 2004 (Table 1). Calf production has been particularly high during the past 5 years (2012-2016) with a total of >6,500 calves estimated during this period, including four of the highest years of calf production (>1,000 calves per year) since our calf counts began in 1994 (Fig. 1). The 2016 estimate of calf production (1,351) is about 5% of the reported total abundance (26,960; Durban et al. SC/67a) for the eastern North Pacific population in 2016.

A trend in median migration dates was observed in the time series, indicating that the midpoint of the migration is now occurring about a week later than it did in the mid-1990s. The slope of the migration timing is significant (F = 6.030, p = 0.023) if the outlier from 1999, the first year of an unusual mortality event for the eastern North Pacific population, is deleted from the data set (Fig. 2).

DISCUSSION

During the 23-year time series reported here, estimates of gray whale calves displayed a high degree of inter-annual variability. Based on data from 1994 to 2000, Perryman *et al*. (2002) suggested that the reliance of female gray whales on stored fat resources during pregnancy combined with sea ice regulated access to food during the beginning of a feeding season may impact their ability to carry existing pregnancies to term. When these calf estimates were examined in the context of environmental data from the northern Bering Sea, a relationship was found between the timing of seasonal ice melt and estimates of northbound gray whale calves counted the following spring. In heavy ice years, when ice extends far to the south, the temporary lack of access to foraging areas appears to have a negative impact on calf production.

The particularly high calf production observed during the past 5 years (2012-2016), including four years of the highest calf production recorded (>1,000 calves per year) since our counts began in 1994 suggests that gray whales have been experiencing a period of favorable feeding conditions in the Arctic, possibly related due to the combination of expanding ice-free habitat (Moore 2016), increased primary production (Arrigo and Dijken 2015) and increased flow of nutrient-rich waters through the Bering Strait (Woodgate *et al*. 2012). This hypothesis is further supported by the recent (2014/2015 and 2015/2016) increase in abundance of the eastern North Pacific gray whale population (Durban et al. SC/67a)

The trend in median migration dates reported here, indicating that the midpoint of the migration is now occurring about a week later than it did in the mid-1990s, is analogous to the finding of a one week delay in annual mean sighting dates of southbound whales migrating past Granite Canyon, California (Rugh *et al*. 2001). While the impacts of climate change in the Arctic environment are far from being understood, this change in migratory timing of gray whales may reflect a response to shifting habitat parameters on the summer feeding grounds. In the short term, changes in the Arctic environment may represent “boom time” for baleen whales as suggested by Moore (2016).

ACKNOWLEDGEMENTS

Our shore-based surveys of gray whales conducted from the Piedras Blancas Light Station would not be possible without the support and hospitality provided by U.S. Department of Interior, Bureau of Land Management. We are particularly indebted to the support provided by John Bogacki, Jim Boucher and Ryan Cooper. A long list of talented field biologists contributed to this study but the contribution of Richard Rowlett, Susan Chivers and Morgan Lynn stand out as exceptional. The support of NOAA Fisheries and the International Whaling Commission has been a critical component of this research.

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Table 1. Survey summary information and annual estimates of calves 1994-2016.

Year	Effort (hrs)	Calf Count	Calf Estimate	SE
1994	671	325	945	68.21
1995	610	194	619	37.19
1996	694	407	1146	70.67
1997	709	501	1431	82.02
1998	554	440	1388	94.84
1999	737	141	427	41.10
2000	704	96	279	34.79
2001	722	87	256	28.56
2002	711	302	842	78.60
2003	686	269	774	73.56
2004	562	456	1528	96.00
2005	669	343	945	86.90
2006	531	285	1020	103.30
2007	469	117	404	51.20
2008	498	171	553	53.11
2009	476	86	312	41.93
2010	487	71	254	33.94
2011	500	246	858	86.17
2012	435	330	1167	120.29
2013	483	311	1122	104.14
2014	529	429	1487	133.35
2015	522	404	1436	131.01
2016	436	367	1351	121.38

Figure 1. Estimates of Eastern North Pacific gray whale calf production 1994-2016.

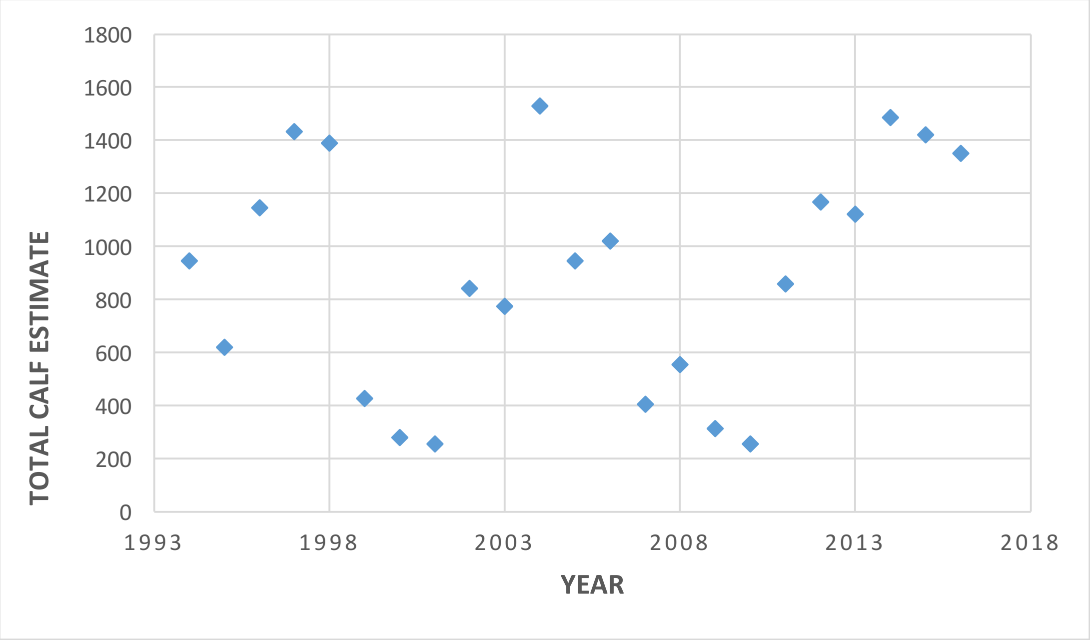
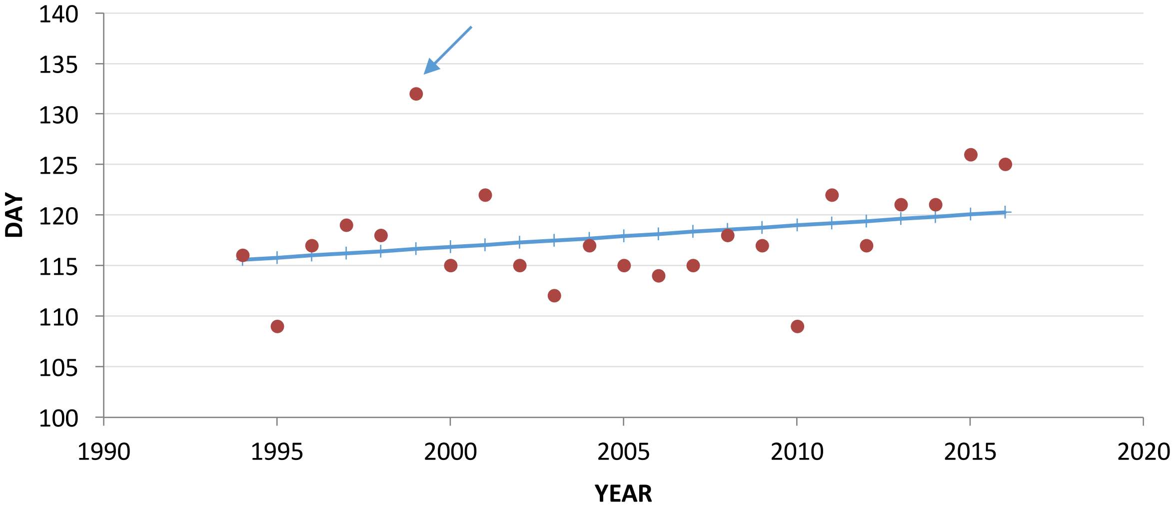


Figure 2. Annual median migration dates of northbound gray whale calves 1994-2016. Slope of linear regression is significant if 1999 point deleted (see arrow).



MARINE MAMMAL SCIENCE, 18(1):121–144 (January 2002)

GRAY WHALE CALF PRODUCTION 1994–2000: ARE OBSERVED FLUCTUATIONS RELATED TO CHANGES IN SEASONAL ICE COVER?

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ABSTRACT

We conducted shore-based sighting surveys to estimate the number of northbound migrating gray whale calves passing Piedras Blancas, California, for seven consecutive years (1994–2000). In addition, we conducted aerial surveys to determine offshore distribution of the migration in 1994 and 1995, measured day/night migration rates with thermal sensors in 1994–1996, and maintained concurrent replicate watches near the peak of each migration to estimate the proportion of the cow/calf pairs missed by the standard watch team. During good weather, we counted 325, 194, 407, 501, 440, 141, and 96 calves during 1994–2000, respectively. Correcting these counts for periods not on watch and for calves missed, produced final estimates of 945 calves (SE = 68.21) for 1994, 619 calves (SE = 67.19) for 1995, 1,146 calves (SE = 70.67) for 1996, 1,431 calves (SE = 82.02) for 1997, 1,388 calves (SE = 91.84) for 1998, 427 calves (SE = 41.10) for 1999, and 279 calves (SE = 34.79) for 2000. Calf production indices (calf estimate/total population estimate) are 4.2%, 2.7%, 4.8%, 5.8%, 5.5%, 1.7%, and 1.1% for the years 1994–2000, respectively. Fluctuations in calf production over this time period were positively correlated with the length of time that primary feeding habitat was free of seasonal ice during the previous year.

Key words: gray whales, *Eschrichtius robustus,* reproduction, calf production, surveys, arctic ice.

During the spring of each year, gray whale (*Eschrichtius robustus*) cows and calves migrate northward from the nursery lagoons of Baja California, Mexico, to their feeding grounds in the Bering and Chukchi Seas. Along the central California coast and in some areas to the north, this migration passes very close to shore. In the late 1970s and early 1980s, counts of northbound cow/calf pairs were made from sites in Alaska, Oregon, and California to estimate calf production for this stock (Hessing 1981, Herzing and Mate 1984, Poole 1984*a,b*). Hessing (1981) reported that calves represented 4.6% of the total count of gray whales migrating northward through Unimak Pass, Alaska. Herzing and Mate (1984) estimated that calves represented 4.6% of the population based on their 1980 survey of southbound and the northbound whales from Yaquina Head, Oregon. Poole (1984*a,b*) conducted the most intensive of these surveys in 1980 and 1981 from Pt. Piedras Blancas, California. From these surveys, Poole estimated calves passing this site comprised 4.7% to 5.2% of the population.

Since these surveys, the gray whale population has continued to increase at an estimated rate of about 2.5% per year reaching approximately 22,263 whales in 1995/1996 (Buckland and Breiwick, in press; Hobbs *et al.,* in press). During this same period, data collected from specimens taken in the Soviet aboriginal hunt suggested a steep decline in gray whale pregnancy rates (Zimushko and Ivashin 1980; Blokhin 1984, 1989, in press *a,b*). Reilly (1992) noted, however, that potential sampling biases in this hunt should be explored before conclusions were drawn from these data. In addition, benthic sampling in the Chirikov Basin from 1986 to 1988 revealed a 30% drop in biomass and a shift in the size structure of the amphipod community, which researchers suggested could indicate that gray whales were approaching the carrying capacity of this benthic resource (Highsmith and Coyle 1992; Coyle and Highsmith 1994; Stoker, in press).

In light of these studies, the National Marine Fisheries Service (NMFS) included a study of gray whale recruitment as part of the monitoring program associated with the removal of this stock from the List of Endangered and Threatened Wildlife and Plants (Rugh *et al.* 1999). In this paper we report the results of seven consecutive gray whale cow/calf surveys at Pt. Piedras Blancas between 1994 and 2000. Our primary objective was to determine whether the proportion of calves in the population (indexed here as the estimate of the number of calves passing Piedras Blancas divided by the population size estimated from surveys of southbound gray whales conducted by NMFS) had declined since the 1980 and 1981 calf surveys by Poole (1984*b*). We report estimates of the number of calves passing our research site during each survey year, the results of experiments conducted to estimate the proportion of calves missed by observers, and the results of day versus night migration rate experiments. We also explored the relationship between the duration of seasonal ice cover over primary feeding grounds and calf production for this population.

METHODS

Survey Site

We conducted the surveys from Pt. Piedras Blancas, San Luis Obispo County, California (35°40′N, 121°17′W) (Fig. 1a, b). Pt. Piedras Blancas is approximately 160 km south of Monterey and 240 km north of Santa Barbara.

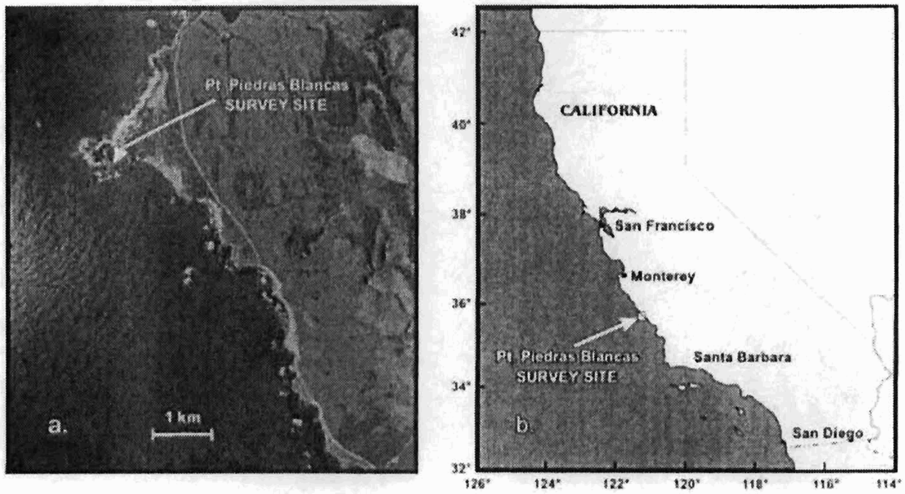

Figure 1. Aerial photograph of survey site at Pt. Piedras Blancas (a) and illustration showing location of site along the California coast (b).

Poole (1984*a,b*) selected this site for his 1980 and 1981 cow/calf surveys and noted it is the only point to intersect a straight-line course from Pt. Buchon to Pt. Sur along 160 km of the central California coast. A protected cove extends to the south and east of Pt. Piedras Blancas through which more than 90% of the cow/calf pairs passed during Poole's surveys.

Shore-based Surveys

We designed the surveys to encompass the entire duration of the northbound cow/calf phase of the migration as reported by Poole (1984*a*). The surveys began in March of each year and extended until late May or early June. Watches were maintained for 12 h/d, 6 d/wk. Two observers divided their effort between inshore and offshore watch areas (Fig. 2a). The offshore observer often assisted the inshore observer in determining the number of cow/calf pairs present and confirming their distance offshore as they rounded the point. Observers stood two, three-hour watches per day (3 h on watch followed by 3 h off watch), rotating from the offshore position to the inshore position after 1.5 h.

The primary searching technique was scans with the naked eye, but handheld binoculars (7×) and tripod-mounted 25× binoculars were used for confirming the presence of a calf and for searching far offshore. The offshore observer used 25× binoculars mounted on an adjustable tripod to scan the distant offshore area for approximately five minutes every half hour. Offshore search effort with the 25× binoculars totaled two hours per day. As pods exited the viewing area, observers measured the distance offshore using the reticle scale in the 25× binoculars if the whales were beyond 400 m, the minimum distance measurable on the reticle scale. We used the formulae

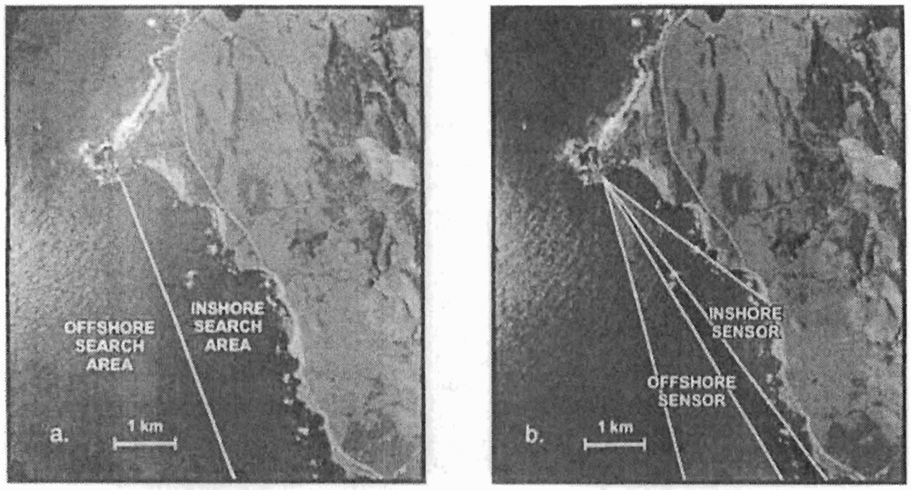

Figure 2. Approximate areas searched by inshore and offshore observers (a) and areas covered by two infrared sensors (b).

developed by Lerczak and Hobbs (1998) to determine offshore distance from reticle measurements. When cow/calf pairs passed too close to the shore to use the reticle scale, observers visually estimated the distance in meters. Observers recorded sea state (Beaufort scale) and visibility at the beginning of each watch and when conditions changed. We used the same visibility codes as Reilly *et al.* (1983), which range from a visibility code of 1 for excellent conditions to a code of 6 for unacceptable conditions. We chose, as did Poole (1984*b*), to exclude effort and sightings from periods when visibility conditions were poor (code 5, visibility <0.8 km).

Gray whale calves were identified by their small size, dark color, and lack of mature barnacle patches. Calves passed the survey site swimming in close association with an adult gray whale. We assumed that the large whale was the mother of the calf and refer to the two animals as a cow/calf pair. Our goal in these surveys was to count calves, but the presence of the cow with each calf greatly increased our probability of detecting the calves. Often the blow of a small calf was not visible to the observers even at a distance of 200 m, while the blows of adult gray whales were generally visible to the unaided eye beyond 4 km. Thus, we refer to cow/calf pairs when dealing with the topics related to detection of the passing calves and then to calves alone in sections concerning estimates of total calf numbers.

The probability of detection for a given cow/calf pair was not known in advance. To estimate the total number of whales that passed, we first needed to estimate these probabilities. For instance, whales that pass far offshore are less likely to be detected than those passing close to the survey team. In addition, no pairs which passed during off-watch hours (*e.g.,* at night or on Sundays) were recorded, and differing rates of passage during off-watch hours could bias estimates based on assumptions of equal rates. Finally, to account for imperfect nearshore detection, we used a replicate watch scheme to estimate nearshore detection probability. Methods for addressing each of these sources of bias in our total calf estimate are discussed below.

Aerial Survey

To estimate the fraction of pairs that were unlikely to be detected because of their distance offshore, we conducted a series of aerial surveys (seven between 27 April and 8 May 1994 and eight between 20 April and 2 May 1995) of the area from Piedras Blancas to a point of land about 35 km to the southeast. Each survey consisted of seven parallel transects spaced 2 km apart with the final transect about 12.3 km offshore. The leg nearest the shore followed the contour of the coast about 30 m outside the surfline. We alternated the starting point of the surveys between southern end and the northern end of the nearshore leg to avoid visibility bias caused by glare on southbound legs. Survey speed was maintained at 185 km/h at an altitude of 305 m.

The surveys were flown in a twin-engine, high-wing Partenavia aircraft. The forward section of this aircraft is made of clear plexiglass, which provided excellent visibility below and ahead of the plane. Large bubble windows were installed in each side of the cabin. Three observers, one in the forward section and one at each bubble window, searched for gray whales along the trackline and out to a distance of about 1 km on each side of the trackline. Distances to whales were determined by measuring vertical angles with hand-held inclinometers. The observer in the nose of the aircraft also operated the data-acquisition system which automatically recorded time and aircraft position for each sighting.

Infrared Sensor Sampling

To determine if our calf estimate required correction for diel variation in migration rate, we collected data during the 1994–1996 surveys with two forward-looking infrared (FLIR) sensors developed by the U.S. Navy (model AN/KAS-1A). These sensors sample in the far infrared region of the spectrum (wavelengths 8–12 μm) and can detect differences in temperature of 0.1°C. Our previous experience with these sensors has indicated that they can detect the blow of a gray whale in a temperate environment up to 8 km away (Perryman *et al.* 1999). The instrument can be selected to operate in either a narrow (1.1° × 2.2°, magnification 9×) or wide (3.4° × 6.8°, magnification 3×) field of view. We sampled using only the wide field of view.

The instruments were mounted on tripods positioned on a knoll (about 20m above sea level) that was adjacent to the visual survey site. From this position, the infrared sensors captured roughly two-thirds of the area monitored by the survey team (Fig. 2b). Weather permitting (no fog or rain, light winds), we operated these sensors for four hours each day and night during the peak of the migration (mid-April to mid-May).

Output from these instruments is standard composite RS-170 video. We recorded this output on 120-min VHS video tapes. Data titlers inserted between the instruments and the video recorders displayed time and date on the video record. We screened the tapes for blows at high speed and then reviewed sections with whales several times at normal speed. We identified cow/calf pairs by the relative sizes and frequencies of the blows and the relative position of the two whales. We used a paired *t*-test to test the null hypothesis of no difference in migration rates between our day (0700–1900) and night (1900–0700) strata. Counts from video tapes were paired for comparison with the most recent tape from the other stratum. Counts were not paired if the interval between day and night samples exceeded 24 h.

Replicate Watch Effort and Detection Probabilities

We conducted independent, concurrent replicate watches during part of each survey to estimate the fraction of calves passing near shore that are undetected by the primary observers (*e.g.,* Rugh *et al.* 1993). An experienced observer stood replicate watches at a site approximately 200 m from the primary observers. A small knoll located between the two locations prevented actions by observers at either location from cueing the other team to the presence of whales. Replicate observers stood watch for 6 h/d but the duration of each watch varied from two to three hours based on environmental conditions and personal preference.

To estimate the detection probabilities, we fit a heterogeneous mark-recapture model (Huggins 1989, Alho 1990, see also Appendix) to the paired standard/replicate watch data. This model is a "paired" logistic regression, and allows detection probability to depend on both environmental covariates (*e.g.,* sighting conditions) and sighting-specific covariates (*e.g.,* whale behavior), *via* a linear predictor and logistic link function. The model assumes independence in detections not only among different cow/calf pairs, but also between watch stations. No communication between watch teams is a necessary condition for between-station independence, but if detection probability varies among cow/calf pairs, it is not sufficient. Specifically, if one or more random factors that affect detection probability act on both watch stations simultaneously (*e.g.,* glare off the water), then detection will be correlated between watches unless these factors are included in the model through appropriate covariates. The correlation between stations can be either positive or negative, depending on the specific dependence on each random factor, but in either case it will create a bias in the estimated detection probabilities. Similarly, if random factors that affect detection probability are correlated among cow/calf pairs (*e.g.,* pod size), then detection will be correlated among cow/calf pairs unless these factors are included in the model, leading to overestimation of precision. Problems with non-independence are well-known in the context of mark-recapture models (*e.g.,* Seber 1982) and are not detectable in the data unless appropriate covariates are considered.

The detection probability covariates that we tested for significance were year (1994–2000), watch station (standard/replicate), pod size (1–4 pairs), glare (present/absent), visibility code (1–4), number of other pairs being tracked (0–7), and migration path (inshore/offshore). We used conditional maximum likelihood (ML) (Huggins 1989, Alho 1990) to fit coefficients for these covariates and asymptotic normal approximations to estimate their covariance matrix. We selected covariates using approximate chi-squared tests for the difference in deviance between nested models, along with residual analysis using partial residual plots and simulated half-normal plots (*e.g.*, Collett 1991). Finally, we used a Taylor series approximation (*i.e.*, the delta method) to estimate the covariance matrix for the fitted detection probabilities themselves. Simulations indicated that the analytic approximations used to estimate precision were sufficiently accurate, particularly because the estimated probabilities were not the largest source of uncertainty in the final abundance estimates.

Conditional on the n cow/calf pairs that were sighted by one or both watch stations, the likelihood in the paired observer model is given by

$$l_c(\beta; y) = \prod_{i=1}^{n} \frac{p_{i,std}{}^{y_{i,std}}(1 - p_{i,std})^{1-y_{i,std}} p_{i,rep}{}^{y_{i,rep}}(1 - p_{i,rep})^{1-y_{i,rep}}}{1 - (1 - p_{i,std})(1 - p_{i,rep})}$$

where

$$p_{i,s} = e^{x_{i,s}'\beta}/(1 + e^{x_{i,s}'\beta})$$

is the unconditional probability of detection at watch station s for the ith sighting, $x_{i,s}$ is a vector of covariates for that station/sighting, β is the vector of coefficients to be estimated, and

$$y_{i,s} = \begin{cases} 1, & \text{if the } i^{\text{th}} \text{ sighting was detected at station } s \\ 0, & \text{otherwise} \end{cases}$$

are binary indicator variables for station-specific detections.

Given estimates of the detection probabilities, we could then estimate the number of whales that passed by undetected during watch periods. The usual method in a mark-recapture model would be to use counts from both watches to estimate the number of undetected animals. However, the replicate watch was only on station during part of the survey period. Therefore, we used a somewhat simpler (see Discussion) estimator which was similar to the "Horvitz-Thompson-like" estimators used by Huggins (1989) and Alho (1990), but used sighting counts only from the standard watch. With this, we estimated the total number of whales passing during each 3-h period that observers from the standard team were on watch:

$$\hat{N}_j = \sum_{i=1}^{n_j} \frac{1}{\hat{p}_{i,std}}$$

$$\hat{\sigma}_j{}^2 \equiv \widehat{\text{var}}\, \hat{N}_j = \sum_{i=1}^{n_j} \frac{1 - \hat{p}_{i,std}}{\hat{p}_{i,std}}\left(1 + \frac{\hat{\sigma}_i{}^2}{\hat{p}_{i,std}{}^2}\right) + \sum_{i=1}^{n_j} \sum_{i'=1}^{n_{j'}} \frac{\hat{\sigma}_{i,i'}{}^2}{\hat{p}_{i,std}\hat{p}_{i',std}}$$

$$\hat{\sigma}_{j,j'}{}^2 \equiv \widehat{\text{cov}}(\hat{N}_j, \hat{N}_{j'}) = \sum_{i=1}^{n_j} \sum_{i'=1}^{n_{j'}} \frac{\hat{\sigma}_{i,i'}{}^2}{\hat{p}_{i,std}\hat{p}_{i',std}} \qquad (1)$$

where j indexes three-hour periods, i indexes sightings within each period, n_j is the number of sightings during three-hour period j, and the quantities

$$\hat{p}_{i,std},\ \hat{\sigma}_i^2, \text{ and } \hat{\sigma}_{i,i'}^2$$

are the conditional ML estimated probabilities and their estimated variances and covariances.

With the assumptions (1) that the number of whales that were completely undetectable because they passed too far offshore was negligible (see Results, Aerial Survey), and (2) that the estimated inverse detection probabilities ($1/\hat{p}_{i,std}$) were unbiased, these estimated three-hourly totals are unbiased. The assumption of no bias in the estimated inverse detection probabilities was based on simulations that indicated that their estimation bias was small with respect to their sampling variance, at least for the range of detection probabilities and sample sizes considered here.

To correct for periods when no observers were on watch, we embedded the above estimators in a finite population model. This model used 3-h periods as the sampling units, and we stratified by week to account for varying passage rates over time. The sample of observed hours was not taken at random: it comprised only daylight hours during acceptable observing conditions. However, with the assumption that whale passage rates did not depend on time of day or on weather (see Results, Infrared Sensor Sampling), the sample can be considered random with respect to the cow/calf pairs.

The actual number of whales passing during each 3-h period was not observed directly, but rather was estimated from the observed counts using the estimated detection probabilities. Thus, we used a finite population model that accounted for measurement errors (Cochran 1977) in the three-hourly totals. Specifically, from above, we assumed that the estimated three-hourly totals were unbiased and had uncertainty due both to random detection and from using estimated (*i.e.,* random) detection probabilities. Further, although individual detections were assumed independent, the estimated three-hourly totals were not independent because the estimated detection probabilities were used across all 3-h periods. With the assumption of no bias in the estimated three-hourly totals, the effect of correlated measurement errors is to inflate the true variance of the estimator of total abundance. Thus, we added appropriate terms to the usual finite population estimator of variance:

$$\hat{N} = \sum_k \frac{T_k}{t_k} \sum_j \hat{N}_j$$

$$\widehat{\text{var}}\ \hat{N} = \sum_k \frac{T_k}{t_k}\left(1 - \frac{t_k}{T_k}\right) s_k^2 + \sum_k T_k \hat{\sigma}_k^2 (1 - \hat{\rho}_k) + \sum_k \sum_{k'} T_k T_{k'} \hat{\sigma}_k \hat{\sigma}_{k'} \hat{\rho}_{k,k'}$$

where k indexes weeks, T_k and t_k are the total number and the observed number of three-hour periods during week k, s_k^2 is the usual sample variance of estimated three-hour counts during week k, and the sums are over all weeks observed. The quantities

$$\hat{\sigma}_k{}^2 = \frac{1}{T_k}\sum_j \hat{\sigma}_j{}^2 \quad \text{and} \quad \hat{\rho}_{k,k'} = \begin{cases} \dfrac{1}{T_k T_{k'}} \displaystyle\sum_j \sum_{j'} \dfrac{\hat{\sigma}_{j,j'}{}^2}{\hat{\sigma}_k \hat{\sigma}_{k'}} & \text{when } k' \neq k \\ \dfrac{1}{T_k(T_k - 1)} \displaystyle\sum_j \sum_{j' \neq j} \dfrac{\hat{\sigma}_{j,j'}{}^2}{\hat{\sigma}_k{}^2} & \text{when } k' = k \end{cases}$$

are stratified versions of quantities defined by Cochran (1977), where j indexes three-hour periods within week, and the sums are over all watch periods in week k.

To develop indices of calf production from our surveys and those conducted by Poole (1984*b*) from the same site, we divided the calf estimate for each year by abundance estimates derived from an unweighted GLM model fit to point estimates from counts of southbound gray whales passing Granite Canyon, California (Buckland and Breiwick, in press). Annual estimates of abundance from this model for the years 1980, 1981, and 1994–2000 were 15,954, 16,360, 22,702, 23,281, 23,875, 24,484, 25,109, 25,750, and 26,407, respectively.[1] A Taylor series expansion (Seber 1982) was used to calculate the variance of the indices.

Ice Conditions in the Northern Bering Sea

In a typical year, ice spreads rapidly southward through the Bering Straits in December, January, and February, driven by prevailing northerly winds. Ice continues to advance across the Bering Sea until late March and early April when melting and interactions with currents at the shelf edge stop its progress, and the ice slowly recedes. The temporal and spatial pattern of seasonal ice cover in the Bering Sea varies on both a seasonal and decadal scale. Several climatic features, including the position and intensity of the Aleutian Low, the sign and scale of the Pacific Decadal Oscillation (PDO), and El Niño-Southern Oscillation events probably all interact to drive the scale and timing of ice events (Cavalieri and Parkinson 1987, Francis and Hare 1994, Trenberth and Hurrell 1995, Maslanik *et al.* 1996, Mantua *et al.* 1997, Parkinson 2000). We selected sea ice as a factor to explore in our analysis of calf production because summer feeding in gray whales is restricted to specific shallow water areas that are ice-free only part of the year (Pike 1962, Moore and DeMaster 1997, Moore *et al.* 2000). Newly pregnant females are the first to return to these feeding grounds and they must store adequate fat to fast through the upcoming winter migration during which they give birth and lactate for a calf. Environmental effects that shorten the feeding season may affect the nutritive condition of these females and subsequently impact recruitment to the population.

We used a technique devised by Wyllie-Echeverria and Wooster (1998) to develop an ice index for comparison with our estimates of calf production. We obtained weekly ice charts for the Bering and Chukchi Seas from the National

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[1] Personal communication from Jeff Breiwick, NMML, 7600 Sand Pt. Way, NE, Seattle, WA 98115, February 2001.

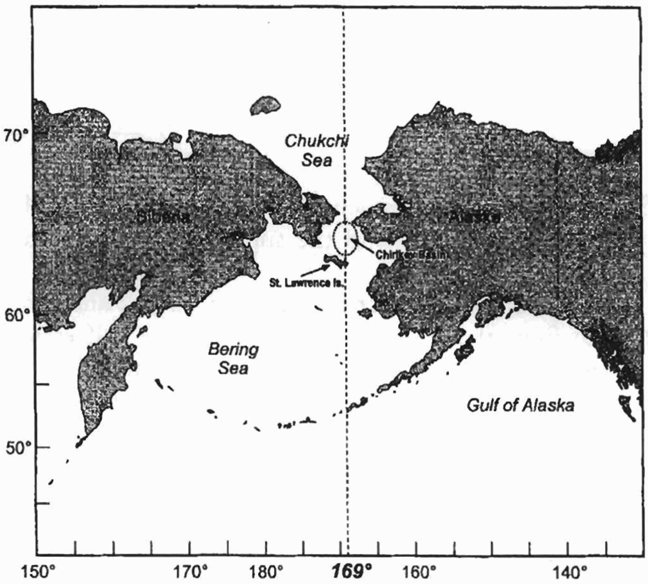

Figure 3. Location of 169°W longitude as it passes through the Bering Sea, across the Chirikov Basin feeding grounds and into the Chukchi Sea.

Snow and Ice Data Center (NSIDC) in Boulder, Colorado, for the years 1993–1999. From each chart, we determined the position of the ice edge along 169°W longitude. This meridian runs through St. Lawrence Island, across the primary gray whale feeding grounds of Chirikov Basin (Nerini 1984, Moore *et al.* 1986, Moore and DeMaster 1997), and then through the Bering Straits into the Chukchi Sea (Fig. 3). For each year, we developed a plot of the weekly locations of the ice edge along the selected meridian and then determined the length of time that a point near the center of the Chirikov feeding grounds (64°00′N, 169°00′W) was free of pack ice. We tested for correlations between the lengths of the feedings season (the ice-free periods) and our estimates of calf production for the following spring seasons. We also tested for such correlations with a one-year lag. If a reduction in feeding time impacts the probability that a pregnant female gray whale will carry a fetus to term, then a reduction in calf production should occur in the season immediately following the ice event. If a reduction in the feeding season impacts recruitment through suppression of ovulation or failure to conceive, there would be a one-year lag between the ice event and an observed reduction in the number of calves.

RESULTS

Raw Survey Data

During the seven years of this study our observers spent over 4,679 h searching from the Piedras Blancas field station and sighted 2,106 gray whale calves (Table 1). Each year we began the survey in mid- to late March and

Table 1. A summary of effort and counts for gray whale cow/calf surveys conducted between 1994 and 2000 from Piedras Blancas, California.

Survey year	Begin date	End date	Hours searched	Total calf count	Median migration date
1994	17 March	4 June	671	325	26 April
1995	20 March	26 May	610	194	20 April
1996	20 March	31 May	694	407	27 April
1997	10 March	28 May	709	501	29 April
1998	23 March	22 May	554	440	18 April
1999	22 March	10 June	737	141	11 May
2000	13 March	2 June	704	96	15 April

continued until sightings of gray whale cows and calves dwindled to insignificant numbers in late May or early June (Fig. 4). Because the timing of the northbound migration proved to be less predictable than the southbound gray whale migration, we adjusted timing and duration of our surveys to adapt to the passage rates of the northbound whales. The median migration dates ranged from 15 April to 11 May, and there was no statistical correlation between median date and total calf count ($r = 0.403$, $P = 0.460$). There was a 5.2-fold difference between our low count of 96 calves in 2000 and the high count of 501 calves in 1997.

Most of the northbound cows and calves (87.4% of pods) passed the survey site at a distance offshore that was too close to measure with the reticulated 25× binoculars (<400 m), so these distances were estimated by the survey team (Fig. 5). The two most distant detections were of two pairs that passed the point just over 1 km offshore, a distance at which gray whales can still be easily detected with the unaided eye.

Cows and calves generally remained close together, swimming side by side, as they approached and passed the survey site. On a few occasions, the calf was seen turning back into the protected cove when its mother rounded the point heading northward. On all these occasions, the mother turned back into the cove and retrieved the calf. Associations between cow/calf pairs and other northbound cows with calves or the occasional adult or juvenile were very ephemeral in nature, and most sightings (86%) were of single pairs. The largest aggregation of cows with calves that we recorded consisted of three pairs.

Aerial Surveys

In 1994 we flew nine complete replicates of the seven track lines extending from Pt. Estero to Pt. Piedras Blancas. Of the 34 cow/calf pairs sighted during the aerial surveys, all except two were found during flights along the most inshore tracking (Fig. 6a). Both of the offshore pairs were swimming toward the shore rather than parallel to the survey track lines. During the 1995 survey, we completed eight replicates of the same seven transects. All of the 41 cow/

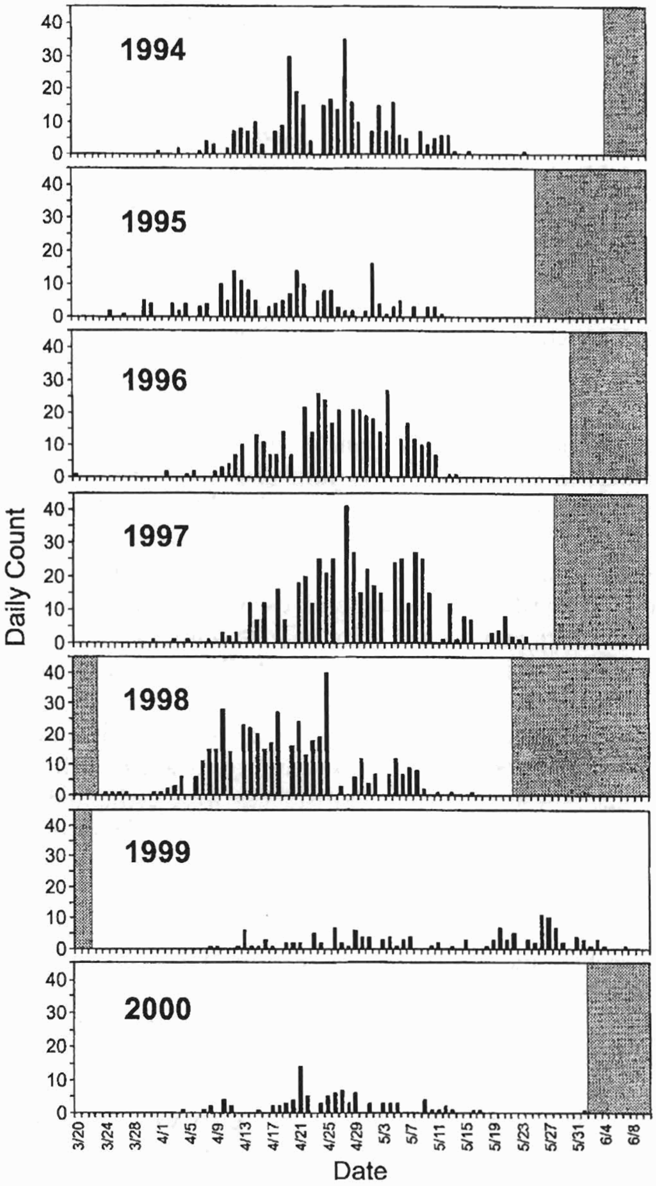

Figure 4. Daily counts of northbound gray whale calves from surveys conducted from Piedras Blancas, California. Shaded areas indicate days before and after survey period for that year.

calf pairs sighted were on the leg closest to shore (Fig. 6b). Our surveys indicated that most cow/calf pairs were found very close to shore and that the few found offshore were heading inshore. These results were consistent with the seven years of survey effort which indicated that cow/calf pairs are occasionally sighted offshore, south of Pt. Piedras Blancas, but that these pairs

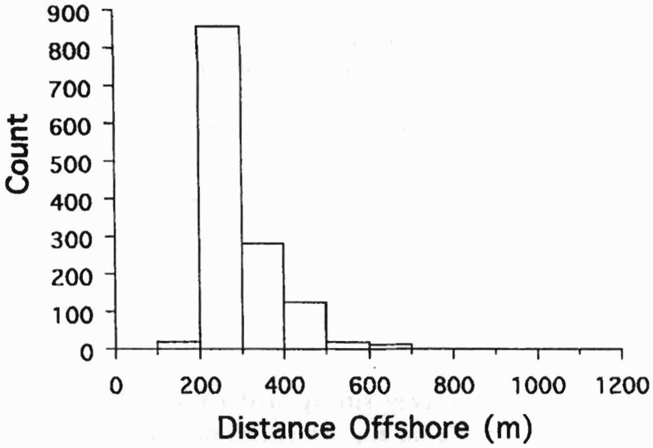

Figure 5. Distribution of offshore distances for gray whale calves passing Piedras Blancas during the surveys. Distances <400 m were estimated and those >400 m were calculated from measurements using 25× binoculars.

consistently pass the point <1 km offshore. Based on these results we did not adjust our estimates for calves passing far offshore.

Infrared Sensor Sampling

We compared day and night migration rates for northbound cow/calf pairs with data collected simultaneously by the two FLIR sensors (paired *t*-test) and found no evidence of diel differences in migration rates (Table 2). To increase the power of this test, we lumped the data from all three years and again tested for differences in counts between the day and night strata. This test also supported the hypothesis of no difference in day-night migration rates for

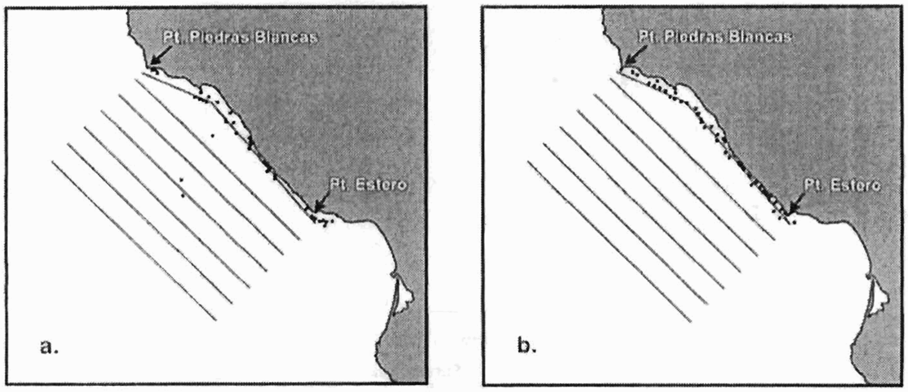

Figure 6. Aerial survey transects and gray whale calf sightings for 1994 (a) and 1995 (b). In 1994, nine surveys were flown and 34 calves were sighted. During eight surveys flown in 1995, 41 calves were sighted.

Table 2. Results of analysis of paired day and night counts of northbound gray whale calves on 2-h video tapes recorded from thermal sensors. Mean differences are absolute values for differences between all pairs of 2-h tapes in that test, and tapes averaged about 2 cow/pairs each.

Survey year	Paired samples	Mean differences	Paired *t*	*P*
1994	26	0.0	0.33	0.74
1995	32	0	0	1
1996	30	0.3	0.57	0.57
All years	88	0.2	0.19	0.85

cow/calf pairs passing the survey site (paired *t*-test, $P = 0.847$, df = 87). Given these results, we made no adjustment to our final calf estimate for diel differences in migration rate.

Replicate Watch

Of the covariates considered (year, watch station, pod size, glare, visibility code, number of other pairs being tracked, and migration path), only the main effects for year, pod size, and glare were significant at the 5% level (Table 3a). The significance of a yearly effect was due to the difference between a relatively large estimated detection probability for 1997 and a relatively small estimated detection probability for 1998 (Fig. 7). The result for 1997 may reflect the fact that the watch teams for that year were the most experienced, whereas the result for 1998 may reflect a learning curve for new observers. Because the object of this analysis was to compare yearly estimates of calf production, we chose to fully stratify by year so that differences in annual estimated numbers of calves would be less likely the result of differences in annual detection

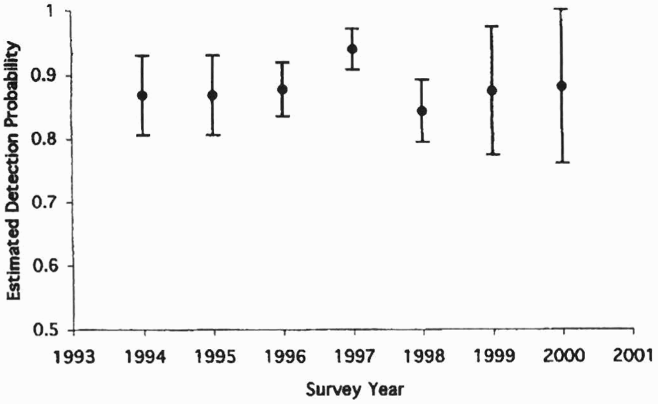

Figure 7. Annual estimates of detection probabilities for northbound gray whale cow/calf pairs. The 2000 estimate is pooled estimate for all previous years. Error bars are for ±1.96 SE.

Table 3a. Significance of adding main effects to the constant model. Change in deviance in each row of table represents the improvement in fit of model where detection probabilities p_{ij} depend on corresponding covariate, over model where the p_{ij} are constant. The P-value is from asymptotic χ^2 approximation to change in deviance.

Base model	Added covariate	Change in deviance	Change in df	P
Intercept only	—	(775.8)	(583)	—
	pod size: 1 *vs.* 2+	4.6	1	0.031
	Glare	3.7	1	0.056
	Year	11.2	5	0.047
	# Other pairs 0–3 *vs.* 4+	1.7	1	0.19
	Vis. code 1–2 *vs.* 3–4	1.7	1	0.19
	Path	0.82	1	0.36
	Watch station	0.29	1	0.59

probabilities. Stratifying fully by year did increase estimated standard errors over a partially stratified model, but it had little effect on estimated precision for the final calf abundance estimates. This was because most of the uncertainty in those final estimates was due to extrapolation to periods when the watch teams were off effort, *i.e.*, night and poor weather conditions.

After including year, the main effects for pod size and glare were no longer significant at the 5% level, although they were nearly so (Table 3b), and no other main effects or interactions were significant. It would have been possible to include terms for pod size and glare in the model, but we chose not to do so. One reason for this choice was that neither covariate could be measured precisely. Specifically, pod associations were often short-lived, and pairs along the same line of sight were sometimes recorded as groupings even though they were not. In addition, glare was defined by time of day, rather than being recorded directly by observers. There are two possible negative consequences of using a simpler model without terms for pod size and glare. First, ignoring covariates can introduce statistical dependence between watch stations and

Table 3b. Significance of adding main effects to year-stratified model. Change in deviance in each row of table represents improvement in fit of model where detection probabilities p_{ij} depend on both corresponding covariate and on year, over model where the p_{ij} depend only on year. The P-value is from the asymptotic χ^2 approximation to the change in deviance.

Base model	Added covariate	Change in deviance	Change in df	P
Intercept + Year	—	(764.6)	(578)	—
	Pod size: 1 *vs.* 2+	3.3	1	0.067
	Glare	2.5	1	0.11
	# Other pairs 0–3 *vs.* 4+	0.34	1	0.56
	Vis. code 1–2 *vs.* 3–4	1.8	1	0.18
	Path	1.2	1	0.28
	Watch station	0.29	1	0.59

Table 4. Estimates of detection probabilities p_{ij} as function of pod size and glare. Year-specific estimates were made, however estimates presented here are averaged over all years for simplicity of presentation. Final estimates used in our analysis depended only on year, and not pod size or glare; see text.

Factor	Level	Estimated average detection probability	Estimated SE
Pod size	1 pair	0.866	0.014
	2 or more pair	0.914	0.014
Glare	present	0.835	0.033
	absent	0.891	0.011

thus lead to biased estimates of detection probability. The effects of pod size and glare (Table 4), though practically significant for individual detections, were of a small enough magnitude that any bias in an estimated detection probability that ignores those factors was not important. This was confirmed by Monte Carlo simulation using a range of possible models, including ones with effects of larger magnitude than those actually estimated for pod size and glare. Second, the estimated detection probabilities come from data collected during the replicate watch period, but are applied to data from the remaining portion of the survey period as well. If covariates that were ignored have values that are, on average, different between the two periods, then the estimated average probabilities from the former period would not be applicable to the latter. There is no reason to expect that this is the case for either pod size or glare.

It is worth noting that partial residual plots for all of the covariates tested other than watch station showed a systematic pattern that, while not statistically significant, was consistent with what would be expected for those factors. For example, residuals plotted against visibility code showed that detection was somewhat less likely for higher codes (poorer visibility). The magnitude of the estimated coefficients for covariates whose main effects were not declared significant was of the same order as those for pod size and glare. In light of the residual plots, their lack of statistical significance may be caused by a difficulty, as with pod size and glare, in determining precise values for these covariates. For example, the path taken by a given cow/calf pair can include what would be considered both inshore and offshore areas. In any case, as with pod size and glare, their effects are of a small enough magnitude that any bias in estimating detection probabilities averaged over those factors would be small. Larger sample sizes (*i.e.,* more replicate watch effort) or a more objective or precise means of measuring those covariates might lead to smaller standard errors and statistically significant effects.

Calf Estimates

Our estimates of the total number of calves passing the survey site are based on counts from the standard watch, which were corrected for imperfect prob-

Table 5. Total calf estimates, estimates of detection probability, and indices of calf production for each survey years.

Survey year	Calf count	Detection probability	Total calf estimate	SE	Abundance estimate	Calf production index	SE
1994	325	0.868	945	68.21	22,710	4.2%	0.003
1995	194	0.868	619	67.19	23,281	2.7%	0.003
1996	407	0.878	1,146	70.67	23,875	4.8%	0.003
1997	501	0.894	1,431	82.02	24,484	5.8%	0.003
1998	440	0.844	1,388	94.84	25,109	5.5%	0.004
1999	141	0.875	427	41.10	25,750	1.7%	0.002
2000	96	0.889	279	34.79	26,407	1.1%	0.001

ability of detection estimated by analysis of the concurrent replicate watch data (Table 5). Although there were obvious and statistically significant (ANOVA, $F = 45.85$, $P < 0.001$, df = 6, 58) differences in total calf estimates between years, no predictable pattern or trend in gray whale reproduction is apparent from these results (Fig. 8).

Calf Production Indices

We divided our annual calf estimates by the corresponding fitted gray whale abundance estimates (Buckland and Breiwick, in press) to produce yearly indices of calf production (Table 5). We compared our indices of calf production with those derived by dividing the calf estimates from Poole (1984*a*) by the modeled abundance estimates for those years (Fig. 9) and again found significant differences between indices for some years (ANOVA, $F = 36.15$, $P < 0.01$, df = 8, 80). Pairwise comparisons (SNK) between yearly indices showed that the 1980 and 1981 indices were not significantly different ($P > 0.05$)

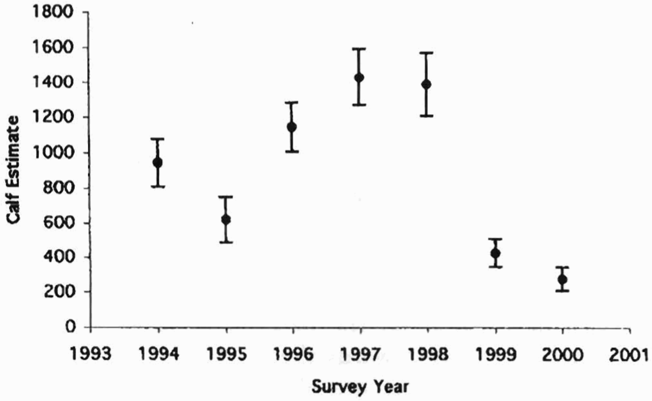

Figure 8. Estimates of the total number of gray whale calves passing Piedras Blancas during each survey year. Error bars are ±1.96 SE.

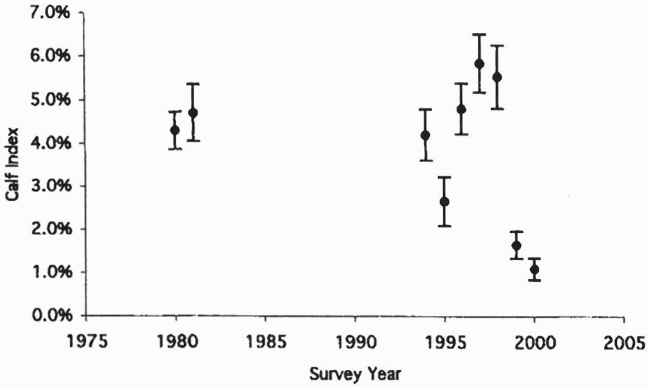

Figure 9. Indices of gray whale calf production derived from counts of northbound calves divided by modeled abundance estimates provided by Jeff Breiwick (AFSC, National Marine Mammal Laboratory). Calf estimates for 1980 and 1981 taken from Poole (1984*a*).

from those of 1994, 1996, and 1998. The clear outliers of the group of indices, 1995, 1999, and 2000, differed significantly from all other annual indices ($P < 0.05$). There was no evidence of a trend or detectable pattern in calf production over the period from 1980 to 2000.

Arctic Ice and Recruitment

The number of days that the selected reference point over the Chirikov Basin was free of seasonal ice varied from a high of 190 d (in 1993 and 1995) to a low of 147 d in 1999. We found a significant positive correlation between the ice (or feeding season) index and our estimates of calf production for the following spring ($r = 0.860$, $P = 0.010$). Thus, shorter ice-free seasons were followed by low estimated calf production, and longer ice-free periods were followed by higher estimated calf production (Fig. 10). When we introduced a one-year lag in our tests, we found no significant correlation between the ice index and calf production ($r = 0.289$, $P = 0.607$).

DISCUSSION

Like Poole (1984*a,b*), we found that the northbound migration of gray whale cows with calves closely followed the coastline in the vicinity of Piedras Blancas, with pairs often swimming just outside the surf line. This phase of the gray whale migration generally extends from late March to late May, with a median date around the last week of April. Cows with calves were most often sighted as single pairs. As the pairs approached the point from the southeast, they swam directly towards the survey site providing an excellent perspective for detecting the presence of a calf alongside the associated cow, even when the whales were still over 4 km from the survey team.

Although the cows with calves passed so close to the survey site that they

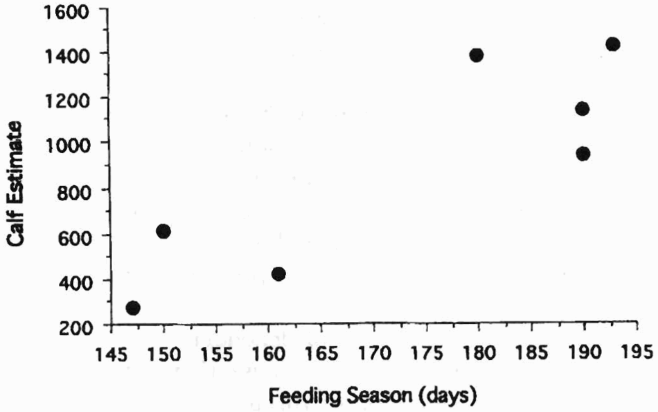

Figure 10. Number of days that gray whale feeding grounds on the Chirikov Basin were free of seasonal ice ("Feeding Season") and number of calves estimated from our surveys in subsequent spring.

could sometimes be heard as well as seen, we attempted to address each of the potential sources of bias raised from the much more difficult shore-based abundance surveys of southbound gray whales conducted from Granite Canyon, California (Reilly 1984). We scheduled the surveys to encompass the entire migration to avoid extrapolating the tails of the migration from whales counted during the core period. We conducted aerial surveys well offshore from the survey site and determined that correcting shorebased counts for whales passing far offshore was unnecessary. We excluded sightings and effort with poor visibility, codes >4, and our analysis of the replicate watch data revealed that the effect of visibility on sighting probabilities within the range of codes 1–4 was negligible. We estimated day and night migration rates from counts of whales detected with thermal sensors and found that the rates were not significantly different. We conducted concurrent replicate-watch effort each year and estimated the probability that gray whale cows and calves passing nearshore would be detected by the standard watch. Finally, as part of a complementary photogrammetric study, we used an aircraft to search for cows with calves among the adults and juveniles that constitute the first phase of the northbound migration and found none (Perryman, unpublished data). Based on these results, we assumed that passage rates measured during on-effort periods were representative of those during off-effort periods and only corrected our estimates for whales that passed nearshore but were missed by the survey team.

It would have been possible to include the replicate watch sighting counts directly in our estimates of three-hourly totals, as well as including them indirectly through the estimated detection probabilities. In fact, because the probability of detection by both watches together $(1 - (1 - p_{i,std})(1 - p_{i,rep}))$ was higher than that for the standard watch alone $(p_{i,std})$, the uncertainty due to random detection would have been somewhat smaller in our estimates of abundance. However, simulations indicated that because detection probability was already high, the decrease in standard error by including replicate sightings was only a few percent, and we did not use this more complicated estimator.

Although our results are inconsistent with the negative trend in pregnancy rates suggested by data from the Russian hunt (Reilly 1992), we found significant fluctuations in calf production for this population (over five-fold between some years). We suggest that years with low calf production were associated with feeding seasons effectively shortened by extensive seasonal ice and that suboptimal nutritive condition in pregnant females was the link in this apparent biophysical connection.

There is a continuum in the degree of dependency animals place on stored fats for reproduction (Thomas 1990). Because they rely almost entirely on stored fats and other tissues for support through the final stages of pregnancy and most of the lactation period, gray whales are an example of one extreme of this relationship. Recognizing the physiologically demanding nature of this life history, Rice and Wolman (1971) suggested that selective pressure for suppression of ovulation at times when a female is incapable of carrying a pregnancy to term might exist. Lockyer (1986) reported a link between prey abundance and subsequent ovulation rates for eastern North Atlantic fin whales (*Balaenoptera physalus*). Because we have observed lower calf production in the spring immediately following ice-shortened feeding seasons (1994, 1998, 1999), we attribute the lower levels of calf production to a failure to carry existing pregnancies to term. This suggests that in this case it was existing pregnancies, rather than ovulations or conceptions, that were impacted.

In addition to the very low calf numbers reported here, unusually large numbers of dead gray whales were found along the North American coast in 1999 and 2000 (Moore *et al.,* in press). Le Boeuf *et al.* (2000) reviewed the strandings data and other unusual aspects of gray whale demographics and behaviors and suggested that gray whales were undernourished when they began their long two-way migration in 1999. We agree that the symptoms observed in this population in 1999 and 2000 are likely related to an overall reduction in nutritive condition of individuals within this population. We suspect that the dramatic nature of these events are the result of a synergistic interaction of lower overall food availability (Highsmith and Coyle 1992, Grebmeier and Dunton 2000) and reduced access to this already depleted resource caused by extensive seasonal ice. It is still unclear, however, whether the observed changes in productivity and mortality indicate that this population has exceeded the carrying capacity of its environment or whether they reflect reactions to shorter term environmental events.

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APPENDIX

COMPARISON OF METHODS WITH BUCKLAND *ET AL.* (1993)

Much of the work described here was based on methods developed by Buckland *et al.* (1993) to estimate gray whale abundance. However, our statistical analysis differs in three ways.

First, whereas we accounted for unobserved periods using a finite population model, they estimated the number of whales passing during those periods by fitting a smooth function to the time series of estimated daily totals. An advantage of smoothing the time series is that, with appropriate assumptions on the form of the smoothed data, passage rates can be extrapolated before and after the range of days when observers are present. Because observers in this study were present over the entire duration of the northbound migration, such extrapolation was not needed.

Second, we used conditional ML to estimate detection probabilities from paired watch data, by maximizing the likelihood (Equation 1) derived by Huggins (1989) and Alho (1990) directly. In contrast, Buckland *et al.* (1993) developed a conditional ML algorithm that uses iterative maximization of a simpler likelihood (denoted by L, their page 239), in much the same spirit as the E-M algorithm (*e.g.,* Tanner 1996). However, their description inadvertently implies that their algorithm ultimately maximizes the simpler likelihood, when in fact that likelihood is used only as an intermediary. While not obvious, it can be shown that Buckland *et al.*'s iterative logistic regression algorithm does indeed maximize the correct conditional likelihood for the paired observer model (Equation 1). However, as with the E-M algorithm, using the simpler likelihood to derive the usual asymptotic variance estimators from ML theory leads to estimates of standard error that are too large, particularly with detection probabilities less than about 40.

Finally, the variance estimator given by Buckland *et al.* (1993, p. 240) accounts for variation in the estimate of abundance due to random detections of whales but does not account for variation due to using estimated (*i.e.,* random) detection probabilities. This component may or may not be a large portion of the total variance depending on the actual detection probabilities, which determine the magnitude of the first component of variance, and the sample size, which primarily determines the magnitude of the second component of variance. Our variance estimator for the hourly totals included components due to both sources of variance.

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Is it 'boom times' for baleen whales in the Pacific Arctic region?

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The marine ecosystem in the Pacific Arctic region has experienced dramatic transformation, most obvious by the loss of sea ice volume (75%), late-summer areal extent (50%) and change in phenology (four to six weeks longer open-water period). This alteration has resulted in an opening of habitat for subarctic species of baleen whales, many of which are recovering in number from severe depletions from commercial whaling in the nineteenth and twentieth centuries. Specifically, humpback, fin and minke whales (*Megaptera novaeangliae*, *Balaenoptera physalus* and *Balaenoptera acutorostrata*) are now regularly reported during summer and autumn in the southern Chukchi Sea. These predators of zooplankton and forage fishes join the seasonally resident grey whale (*Eschrichtius robustus*) and the arctic-endemic bowhead whale (*Balaena mysticetus*) in the expanding open-ocean habitat of the Pacific Arctic. Questions arising include: (i) what changes in whale-prey production and delivery mechanisms have accompanied the loss of sea ice, and (ii) how are these five baleen whale species partitioning the expanding ice-free habitat? While there has been no programme of research specifically focused on these questions, an examination of seasonal occurrence, foraging plasticity and (for bowhead whales) body condition suggests that the current state of Pacific Arctic marine ecosystem may be 'boom times' for baleen whales. These favourable conditions may be moderated, however, by future shifts in ecosystem structure and/or negative impacts to cetaceans related to increased commercial activities in the region.

1. Introduction

A 'new normal' climate is emerging in the Pacific Arctic marine ecosystem [1], coincident with the dramatic loss of sea ice at a rate which accelerated after 2000 [2]. Overall, the region has lost 75% of sea ice by volume and 50% in late-summer surface cover, coincident with the extension of the open-water period by four to six weeks. The marine ecosystem north of the Bering Strait is warmer, fresher and stormier than in the past, with annual inflow of Pacific waters roughly 50% higher now than prior to 2001 [3]. Satellite data suggest that this biophysical transformation supports increased rates of phytoplankton net primary production (NPP) by 42% in the Chukchi Sea and 53.1% in the Beaufort Sea, probably in response to reduced sea ice thickness and extension of the open-water period [4]. However, satellites cannot sample subsurface peaks in NPP, which are common throughout the Arctic Ocean [5]. Thus, a full accounting of changes to regional primary productivity remains elusive.

Whether owing to habitat expansion, increasing whale numbers, or both, subarctic species of baleen (mysticete) whales are now commonly reported in the Chukchi Sea. Specifically, humpback, fin and minke whales were seen between Bering Strait and 69° N latitude during aerial surveys conducted from July through to September 2009–2012, where none were seen during surveys conducted from 1982 to 1991 [6]. These three species appear to have expanded their range in late summer to now join the Arctic-endemic bowhead whale and

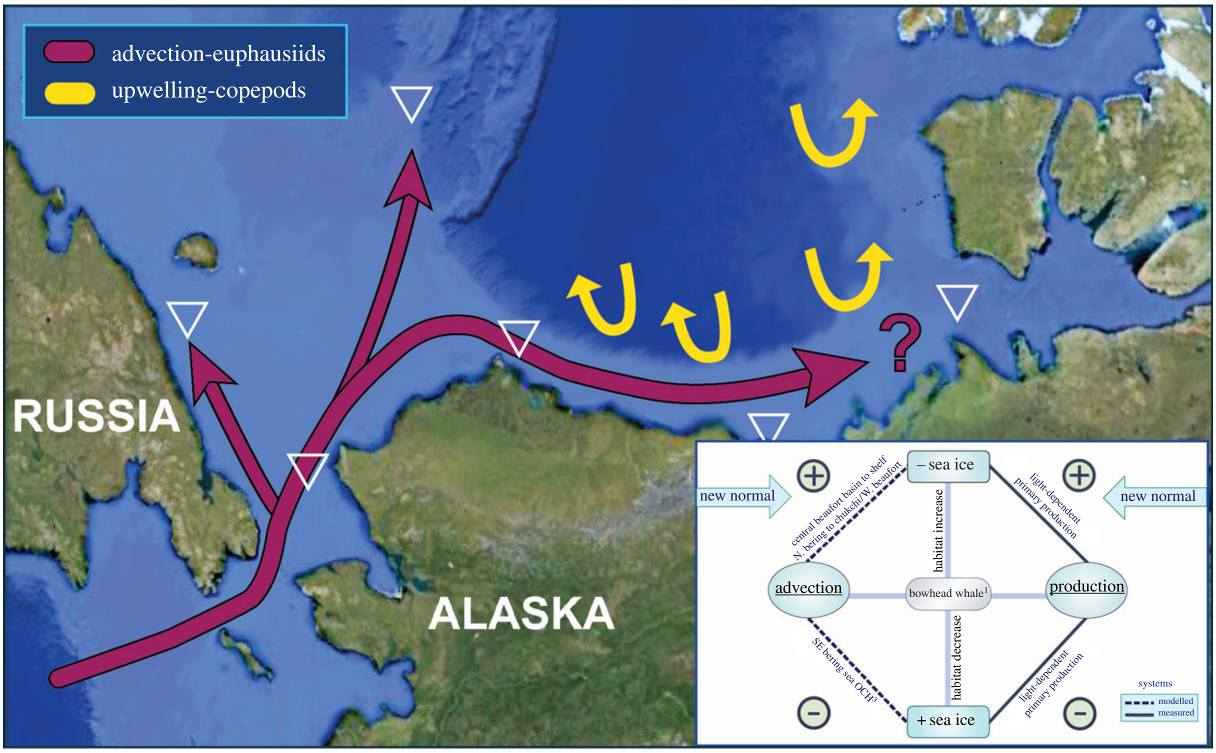

Figure 1. Advection of euphausiids (red) into the Chukchi Sea and upwelling of copepods (yellow) from the basin to the continental shelf in the Beaufort Sea are prey-delivery pathways that are probably enhanced by increased transport through the Bering Strait and wind-forcing combined with the loss of sea ice. Both enhanced production and increased advection common in the 'new normal' Pacific Arctic marine ecosystem deliver food to bowhead whales (inset). This graphic is a composite of revised figures [14,15]; triangles indicate areas where whale-prey associations have been reported [14]. (Online version in colour.)

the seasonally resident grey whale [7] in the rapidly changing marine ecosystem of the Pacific Arctic. Detections of whale calls at an autonomous recorder deployed from 2009 to 2012 revealed that humpback and fin whales remain in southern Chukchi waters through October and in some years into November [3]. Of note, detections of humpback and fin whale calls ceased near the onset of sea ice formation each year, coincident with the onset of bowhead whale call detections. In other words, the subarctic species departed as the Arctic-endemic species arrived, along with seasonal sea ice.

The pan-Arctic reduction in sea ice evident early in the twenty-first century triggered a number of reviews regarding the impact of this loss of habitat on marine mammals [8–10]. Polar bears (*Ursus maritimus*), walruses (*Odobenus rosmarus*) and ice seals appear to be particularly vulnerable because they rely on sea ice as a platform for key life-history functions such as birthing, nursing young, hunting and resting. Conversely, with the loss of sea ice, ocean habitat for cetaceans has expanded both spatially and temporally. This expansion of habitat coincides with the ongoing recovery of most populations of baleen whales from decades of commercial harvest in the nineteenth and twentieth centuries [11,12]. It also facilitates offshore commercial activities, including shipping and oil and gas development, which can have significant negative impacts on cetaceans [13].

In this opinion piece, I summarize observations and offer plausible explanations regarding changes to baleen whale-prey production and delivery coincident with the dramatic loss of sea ice, increased transport through the Bering Strait and amplified upwelling along the Beaufort Sea slope. This synoptic description, coupled with an overview of recent baleen whale seasonal occurrence in the Pacific Arctic, underpins a schematic of habitat partitioning among the five species. The diagram is intended as a first-step in recognizing the current status and role of baleen whales in the changing ecology of the Pacific Arctic.

2. Changes to baleen whale-prey production and delivery

Two well-documented alterations to the Pacific Arctic ecosystem that probably have changed production and delivery of baleen whale-prey in the twenty-first century are the aforementioned loss of sea ice and the increased inflow of Pacific water through the Bering Strait (figure 1). The thinning and extensive seasonal retreat of sea ice has fostered increased NPP, which probably supports higher rates of secondary production, including the mesozooplankton and forage fish prey of baleen whales. This suggested link between sea ice loss and increased prey production is supported by limited observations in the Chukchi Sea [16], where the abundance and biomass of mesozooplankton was higher in reduced-ice years (2007/2008) compared with years with extensive sea ice (1991/1992). The delivery of mesozooplankton prey from the northern Bering to the Chukchi Sea has also probably increased with the more robust northward transport at the Bering Strait since 2001 [3]. Corroborating evidence that prey are advected through the Strait includes the report of grey whales feeding on euphausiids in the southern Chukchi Sea in 2003 [17], and the description of large copepods and euphausiids abundant in the cold, nutrient-rich Bering Sea Anadyr Water advected into the southern and central Chukchi Sea in 2007 [18]. Humpback, fin and minke whales are efficient predators of these mesozooplankton as well as of forage fishes that may follow this plankton stream.

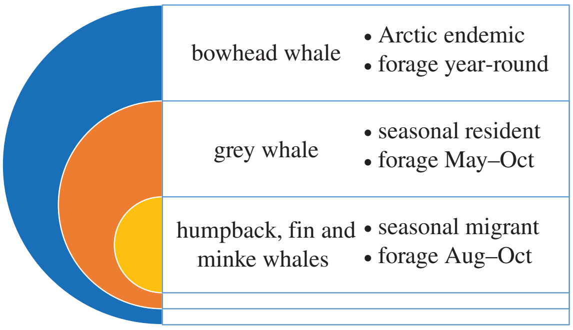

Figure 2. Schematic of habitat partitioning for five species of baleen whales in the Pacific Arctic. Bowhead whales feed on pelagic and epibenthic zooplankton from the northern Bering to Beaufort Sea (blue); grey whales feed on pelagic, epibenthic and benthic prey from the northern Bering through the Chukchi Sea (orange); humpback, fin and minke whales feed on zooplankton and forage fishes primarily in the Bering and southern Chukchi seas (yellow). (Online version in colour.)

The extreme retreat of sea ice combined with upwelling-favourable winds has also probably increased localized abundance of copepods and other mesozooplankton upwelled onto the Beaufort Sea shelf. Notably, the number and strength of upwelling events in the Alaskan Beaufort Sea has increased over the past 25 years [19]. In the western Beaufort, a sudden cessation of upwelling-favourable winds can spring a ‘prey trap’, which concentrates zooplankton for efficient foraging by bowhead whales [20]. Combined, the recent ‘new normal’ conditions in the Pacific Arctic seemingly provide Arctic-endemic bowhead whales with optimal foraging opportunities, both from increased upwelling of copepod prey in the Beaufort Sea and robust advection of copepod and euphausiids prey through the Bering Strait into the Chukchi and western Beaufort Sea (figure 1: inset). A suite of observations, including the seasonal ecology of bowhead whale core-use areas [21] and improved whale body condition coincident with sea ice loss [22], support this assertion.

3. Habitat partitioning among baleen whales in the Pacific Arctic

Habitat partitioning among the five baleen whale species is accomplished largely through temporal separation, underpinned by species-specific migration cycles and dissimilar prey preferences (figure 2). Bowhead whales occupy Bering Sea waters in winter, migrating though the Bering Strait in spring and feeding in the Beaufort and then Chukchi seas from late spring through to autumn [7,21]. Grey whales arrive in the northern Bering Sea in late spring and feed there and in the Chukchi Sea through to autumn [7]. Sightings and acoustic detections of humpback, fin and minke whales over the past decade suggest that they occupy the southern Chukchi Sea roughly from August through to October [3,6].

Foraging capability and prey selection can amplify habitat partitioning among the five species. The long, finely fringed baleen of bowhead whales are specialized for filtering zooplankton, while the coarse and short baleen of grey whales provide the means to filter out benthic prey from sediments sucked up from the seafloor—a capability unique to this species. Humpback, fin and minke whales are lunge feeders, adapted with variable length baleen and throat pleats for gulping both mesozooplankton and forage fishes. It is important to note that all five species can and do consume euphausiids or krill. While the role of krill as a key trophic-link in the Pacific Arctic is poorly understood, its importance as prey for baleen whales is well established in Atlantic Arctic and Antarctic marine ecosystems (e.g. [23,24]).

At present, conditions in the Pacific Arctic appear to be favourable (i.e. ‘boom times’) for all five species of baleen whales. Although the seasonal influx of subarctic species may result in some resource competition with bowhead and grey whales, migration timing and species-specific foraging capabilities will probably curtail inter-specific prey competition. More important is the capability of these species to act as sentinels to alterations in the marine ecosystem [25]. Specifically, baleen whales can provide clues as to the nature, direction and mechanisms of ecosystem shifts, such as where, when and how ‘new’ NPP is cycled. Whether new production is channelled to pelagic or benthic trophic pathways will restructure the ecosystem in ways that will be reflected in the distribution and relative abundance of these large consumers. Baleen whales also act as ecosystem engineers and their recovering numbers may actually buffer the marine ecosystem from destabilizing stresses associated with rapid change [26]. With more baleen whales recycling nutrients vertically and horizontally and, with increasing numbers of bowhead and grey whales re-suspending sediments during epibenthic and benthic foraging, the Pacific Arctic marine ecosystem will probably continue to change in ways now difficult to predict. A much needed circumpolar assessment of Arctic marine ecosystems (e.g. [14]) could be achieved by comparing changes in the Pacific Arctic to those in other regions, especially where sea ice loss has been quantified (e.g. [10]).

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Update on the use of a simulation-based approach to evaluate plausible levels of recruitment into the Pacific Coast Feeding Group of gray whales

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ABSTRACT

Previous genetic comparisons of the Pacific Coast Feeding Group (PCFG) of gray whales with whales feeding north of the Aleutians have shown significant levels of mitochondrial differentiation. The magnitude of the differentiation, along with the relatively high levels of genetic diversity identified within the PCFG, have raised questions about how much immigration into the group could occur before the signal of mtDNA differentiation is erased. Here we use a simulation-based approach to evaluate the range of plausible levels of immigration into the PCFG that could be occurring. The simulations incorporate annual immigration ranging from between 0 and 16 animals per year (once the larger ENP population reaches K), and simulations both with and without a pulse of +20 immigrants over two years are included. Results suggest that under the scenarios tested, current immigration into the PCFG of one migrant per year or less would produce levels of genetic diversity and differentiation that are inconsistent with the empirical data. The simulations were less informative with regard to placing an upper limit on the number of animals per year which could be immigrating into the PCFG, although comparison of F_{ST} and χ^2 (per degree of freedom) values between the simulated and empirical data suggests that immigration higher than 8 animals per year is unlikely. Comparisons between the observed and simulated values for the number of haplotypes, F_{ST}, and χ^2 (per df), which were the most informative measures, suggest that immigration of approximately 4 animals per year is most plausible.

INTRODUCTION

Genetic comparisons of samples collected from gray whales considered to be part of the Pacific Coast Feeding Group (PCFG) with those from animals that feed north of the Aleutians have revealed small but significant levels of mtDNA differentiation but no nuclear differentiation (Lang *et al.* 2011). In addition, a relatively large number of mtDNA haplotypes were identified within the PCFG (n=23 haplotypes, Lang *et al.* 2011), which is estimated to contain ~200 animals (IWC 2011). Analysis of photo-identification data indicates that on average, 10 animals per year were recruited[1] into the PCFG between 2004 and 2008, with larger numbers of recruits identified between 2000 and 2002 (IWC 2011). These recruits could be internal (i.e., calves born to PCFG mothers) or external (animals that previously fed north of the Aleutians and subsequently immigrated into the PCFG). An average of three calves per year were identified in the PCFG between 1998 and 2008 (Calambokidis *et al.* 2010), and it is presumed that at least half of the calves born each year may not have been identified as such (IWC 2011). Based on those assumptions, an estimated four animals per year may have recruited into the PCFG from northern feeding area(s) between 2004 and 2008, and a pulse of higher immigration may have occurred between 1999 and 2002, potentially in response to the increase in gray whale mortality that occurred in 1999 and 2000.

The results of these genetic and photo-id studies of the PCFG have raised questions about how much external recruitment into the PCFG could occur while still maintaining the observed level of mtDNA differentiation between the PCFG and animals feeding north of the Aleutians. The use of a simulation-based approach has the potential to provide information relevant to this question. As part of a previous IWC exercise (the Testing of Spatial Structure Methods, or TOSSM, project), simulated genetic datasets representing different population structure archetypes were created for performance testing of different analytical methods (Martien *et al.* 2009). The demographic parameters underlying the dataset generation model were based on the vital rates of

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[1] Here a 'recruit' is defined as an individual first photographed in the PCFG seasonal range (within the area spanning 41-52°N and between June 1 and November 30) in a given year and resighted within the seasonal PCFG range in at least one subsequent year.

eastern gray whales (Martien *et al*. 2004, Martien 2006). In discussions with the IWC Stock Definition subcommittee, it was agreed that the TOSSM dataset generation model could be useful in creating simulated datasets that would allow the plausibility of different hypotheses (e.g., different immigration rates into the PCFG) to be evaluated.

METHODS

Rmetasim

Simulated datasets were produced using the *rmetasim* package (version 1.1.05, Strand 2002) as run in the R statistical environment (R 2.14.1). *Rmetasim* performs individual-based population genetic simulations utilizing stage-based matrix population models. The transition probabilities in the matrices are used to randomly assign births, stage transitions, and deaths of individuals over time. Density dependent growth is implemented by the linear interpolation between matrices representing survival and reproduction rates at carrying capacity (K) and at zero population density (ZPD). A pre-birth pulse model is used, such that at the end of each simulation year, the youngest animals in the population are one year old.

Stage-based matrices

As previously mentioned, vital rate estimates for eastern Pacific gray whales (as described in Martien *et al.* 2004, Martien 2006) were used to parameterize stage-based matrices for the TOSSM exercise. Since the construction of these matrices, additional information has become available on the life history of gray whales. This new information was utilized to update the stage-based matrices from TOSSM, and when possible the vital rates used in constructing the new matrices were chosen to be the same as those utilized in the IWC's Implementation Review of gray whales. The following changes were made:

1) Adult survival rate was increased to the median estimate from Punt & Wade 2010 (S_A=0.982)
2) A separate term for calf survival rate (set to S_c=0.732, the median estimate in Punt & Wade 2010) was utilized. In the previous matrices, calf survival was the same as juvenile survival.
3) The median estimate from Punt & Wade 2010 was utilized for the rate of increase at ZPD (λ =1.063)
4) The age of first reproduction (AFR) was increased to 7 years at ZPD based on the Bradford *et al.* 2010 review.
5) A third juvenile stage was added to provide better control of AFR.

In addition, three identical adult stages for each sex were included in the new matrices. In contrast, the matrices used in the TOSSM project included a single adult male stage and separate fertile and lactating stages for adult females. This change was implemented for two reasons. First, it allowed for better control of generation time and greatly reduced the proportion of individuals in the simulations that lived to unrealistic ages under the increased adult survival rate. Secondly, it reduced the number of multiple births by the same female in a given year. In *rmetasim*, the fertility term represents the mean number of calves produced per female based on a Poisson distribution (Strand 2002). This results in some females producing more than one calf per year. Eliminating the separate fertile and lactating stages allowed us to reduce the fertility term (since it was applied to all adult females, not just a subset in the lactating stage), thereby reducing the number of multiple births (Table 1). However, this change also eliminated the minimum two-year calving interval that had been enforced in the TOSSM matrices. As such, under the new matrices some females in the simulation will give birth in consecutive years (Table 2).

Given the number of changes implemented in the new matrices, we ran the simulations using both the updated nine-stage matrices as well as the original five-stage matrices (as described in Martien 2006) utilized in the TOSSM exercise. The vital rates used to construct the original matrices and those utilized in the updated 9-stage matrices are detailed in Table 3. The parameter for juvenile survival rate was not derived from the literature but was calculated from the matrices to produce the desired value of lambda. The

Maximum Sustainable Yield Rate (MSYR) calculated from the 9-stage matrices is ~3.3%, while MSYR for the 5-stage TOSSM matrices is ~3.6%.

These vital rates were used to construct stage-based matrices representing the demography of the population near carrying capacity (K) and near zero population density (ZPD). Transition probabilities were calculated according to Caswell (2001) and the resulting matrices are shown in Table 4.

Population Trajectories

Dataset generation followed the steps outlined in Martien 2006, with the exception that coalescent datasets were generated using FastSimcoal (Excoffier and Foll, 2011) rather than SimCoal 2.1.2 (Laval and Excoffier 2004) to establish the effective size (Ne). In all scenarios, a single population was simulated in *rmetasim* for 4000 years to provide datasets representing the equilibrium population. This time period was shown to be sufficient for reaching equilibrium in a similar exercise for bowhead whales (Archer *et al.* 2010), that have a markedly longer generation time.

The mutation parameter incorporated in the simulations was adjusted to produce genetic diversity levels (as measured by the number of haplotypes and the haplotypic diversity) that are similar to the values observed for the "North" strata in the Lang *et al.* 2011 study. A range of mutation parameters were explored before setting the mutation parameter to 3.8×10^{-3} per generation, which produced measures of genetic diversity that were the most consistent with the observed data.

Carrying capacity (K) for the larger ENP population of gray whales was set to 20,000 animals, similar to the most recent abundance estimate (19,126 animals in 2006/2007; Laake *et al.* 2009). Carrying capacity for the PCFG was set to 200 in accordance with the estimated abundance of 194 animals in 2008 (Annex F, IWC 2011).

For all population trajectories, depletion due to commercial whaling was simulated as having occurred between 1846 and 1930. Attempts were made to utilize the catch history (Annex E, IWC 2011) with a multiplier to produce the desired level of depletion in 1930 (10% of K). However, when this modification was incorporated it resulted in a high number of simulation runs that failed due to the simulated population(s) going extinct. As such, the depletion per year was set to a constant proportion of K, such that the population was depleted by 7.1% of K in each year for the duration of the simulated whaling period. This level of depletion allowed the population to reach the desired level (0.10 of K, or ~2000 animals) by 1930. Examples of the population trajectories produced are shown in Figure 5.

Given that little is known about the origin of the PCFG, two different population histories were simulated. The first scenario ("post-whaling split") assumes that the PCFG split from the larger ENP population following depletion. After reaching equilibrium a single population was projected forward through the 1846-1930 whaling period with depletion occurring as described above. In 1930, 20 animals (10% of K_{PCFG}) were split from the larger population to represent the PCFG. The two populations were then allowed to increase until reaching K. *Rmetasim* employs a "hard ceiling" to restrict population growth to K, such that individuals are killed off randomly after reaching levels >10% higher than K.

The second scenario ("pre-whaling split") assumes that the PCFG split from the larger ENP gray whale population prior to the depletion of gray whales due to commercial whaling. In this scenario, the equilibrium population was split into two feeding groups to represent the northern feeding ground (K_{ENP}=20,000) and the PCFG (K_{PCFG} = 200). The split was presumed to occur at the start of the Little Ice Age (considered here to be at 1540), a period in which it seems plausible that ice conditions would have been favorable for gray whales to begin using more southern feeding grounds. Both populations were projected forward until 1846, when the depletion due to commercial whaling was simulated as described above. After reaching 1930, the simulated depletion ceased and the two populations were allowed to grow until reaching K.

Immigration rates ranging from 0 to 0.0008 were simulated. These migration rates correspond to the immigration of between 0 and 16 animals per year into the PCFG from the larger ENP population once it has reached K (Figure 6). In addition, each population history and migration rate combination was also simulated with a migration "pulse" of 20 individuals over two years. This pulse is reflected in the abundance of the PCFG in 2000 and in 2001. Examples of abundance trajectories for the PCFG under the different immigration scenarios are shown in Figure 7.

Additional simulations were performed in which the value of K_{PCFG} was increased from 200 to between 500 and 5000. These simulations incorporated a post-whaling split of the PCFG from the larger ENP, with the pulse migration of +20 animals over two years but no annual immigration into the PCFG. As in the "post-whaling split" scenarios described above, the split of the PCFG from the larger ENP was modeled such that the number of animals colonizing the PCFG in 1930 was 10% of K.

A final set of simulations were performed that incorporated a more recent split (between 1940 and 1990) of the PCFG from the larger ENP population. The number of animals splitting off to form the PCFG in a given year was derived by taking an average (over ten replicates) of the simulated abundance of the PCFG in each year when the abundance trajectories were modeled under the scenario of a post-whaling split of the PCFG in 1930 with no annual immigration.

A list of scenarios that have been simulated to date is included in Table 7. Of note, the simulations incorporating a pre-whaling split of the PCFG from the larger ENP are in progress and have not yet been completed.

Sampling and Genetic Analyses:

To generate the simulated dataset, the number of simulated animals sampled per year was set to match the number of animals sampled per year and per stratum in the Lang *et al*. (2011) study (Table 8). In the empirical study, some animals were sampled multiple times, and only one sample per individual was retained for the data analysis. For the simulated sampling, the year of sampling for such individuals was assigned as the first year that the animal was sampled. A total of 103 samples were collected from simulated ENP individuals and 71 samples were collected from simulated PCFG individuals.

These sampled individuals were used to generate summary statistics for each group. Genetic diversity was characterized by the number of mtDNA haplotypes, the mtDNA haplotype diversity, and the mtDNA nucleotide diversity. Differentiation between the two simulated groups was measured using F_{ST}, χ^2 (per degree of freedom), and ϕ_{ST}. The summary statistics generated from the simulated datasets were then compared to the observed summary statistics generated for the PCFG and the North strata in Lang *et al.* 2011.

To further evaluate how well the shape of the haplotype frequency distribution for the simulated ENP population matched the shape of the distribution for the North stratum in the empirical data, a χ^2 test was used to compare the two haplotype frequency distributions, and the number of significant tests ($p<0.05$) was calculated. In addition, the frequency of the most common haplotype in each replicate simulation was calculated and compared to the frequency of the most common haplotype in the empirical data for the North stratum. Given that the mtDNA summary statistics produced for the simulated ENP population under all scenarios was similar, these tests were only conducted using the data for the simulated ENP population produced under the model with a post-whaling split with pulse migration but no annual immigration.

In addition to showing the proportion of simulations that had higher and lower values for each statistic than the values generated from the empirical data, we used interpolation to calculate the "crossover point" at which the 50% probability (median) was reached (i.e. the point at which the proportion of simulated runs had values higher than the observed reached 50%). For the number of haplotypes, the crossover point was calculated as the point at which the lines representing the proportion greater than and the proportion less than crossed (as for the other statistics), but because some simulation replicates had values equal to (rather than less than or greater than) the observed value, this point was slightly lower than the 50% probability.

RESULTS

Although the goal is to produce 500 replicates of each scenario, currently only 100 replicates of each scenario are complete and are utilized in the results shown here.

Comparison of simulated and observed data for ENP

Table 9 includes a summary of the number of haplotypes, haplotypic diversity and nucleotide diversity for the simulated ENP population for the model incorporating the 9-stage matrices with a post-whaling split and pulse immigration. Results were similar under all scenarios tested (data not shown). Overall, median values for both the haplotypic diversity and the number of haplotypes were similar among the simulated and empirical datasets. The haplotypic diversity values generated in the simulated data were slightly lower than that in the observed data, with median values for the simulated data ranging from 0.948 to 0.950 (as compared to the observed haplotypic diversity of 0.952) and with 52-64% of replicates under the different immigration scenarios having lower haplotypic diversity than found in the empirical data. In contrast, the median number of haplotypes generated in the simulated datasets (33 to 34 haplotypes) was slightly higher than that found in the observed data (32 haplotypes). Between 62 and 75% of replicates for the different immigration scenarios generated values higher than the number identified in the empirical dataset. Although the nucleotide diversity calculated from the empirical data fell within the 90% range of the simulated values, nucleotide diversity in the simulated data was higher than that found in the observed data.

To evaluate whether the shape of our simulated haplotype distributions matched the shape of the observed distribution, we used a χ^2 test to compare the observed (North stratum) versus the simulated haplotype frequency distributions for the ENP population. The χ^2 test evaluates whether the haplotype distributions representing the empirical and simulated data could have been generated by random sampling of a single population. The χ^2 test is particularly sensitive to the frequencies of the most common haplotypes, as those haplotypes are the most likely to be represented in the random draws that represent immigration events. In our comparison, 12% of tests showed significant ($p<0.05$) differences (Figure 10), suggesting that the shape of the observed and simulated distributions were similar in most cases. We also compared the frequency of the most common haplotype in the empirical data with the frequency of the most common haplotype in the simulations. We found that the frequency of the most common haplotype was higher than that found in the empirical data for 47% of the simulation replicates. This finding is consistent with the expectation that if two samples are drawn from the same distribution, the frequency of most common haplotype would be expected to be greater in one sample than the other 50% of the time.

Comparison of simulated and observed data for the PCFG

Figure 11 shows a graphical representation of the proportion of simulated values for each statistic that are lower (shown in black) or higher (shown in gray) than the observed value generated from the empirical data for one of the scenarios tested (post-whaling split with pulse immigration, nine-stage matrices). Summaries of the number of mtDNA haplotypes (Table 12), mtDNA haplotype diversity (Table 13), mtDNA nucleotide diversity (Table 14), F_{ST} (Table 15), ϕ_{ST} (Table 16), and χ^2/df (Table 17) produced by the simulations under all completed scenarios are shown below.

With regard to comparisons between the observed and simulated data, the statistics based on haplotype frequencies (haplotypic diversity, F_{ST}, and χ^2/df) and haplotype numbers were the most informative. For all four of these statistics, scenarios based on annual immigration of one animal or less per year (at K) produced values that were inconsistent with the empirical data. The comparisons were less informative with regard to the highest level of immigration that could be occurring, although comparison of F_{ST} and χ^2/df values suggested that levels of immigration including > 8 animals/year (along with the pulse immigration) would produce values inconsistent with those produced by the empirical data.

Similar to the pattern seen in comparison of the observed and simulated data for the larger ENP population, the nucleotide diversity identified among the simulated datasets was higher than that seen in the empirical data. In the ϕ_{ST} comparisons, the value generated in the empirical comparison was more consistent with the lower range of values for annual immigration and indicated that more than 8 immigrants per year into the PCFG would produce values of ϕ_{ST} lower than that observed. Caution should be applied when interpreting this pattern, however, given the lower nucleotide diversities identified in the observed data when compared to the simulated datasets.

Table 18 shows the results of simulations evaluating scenarios in which the PCFG splits from the larger ENP population between 1940 and 1990. The results shown suggest that for no annual immigration into the PCFG to be plausible, the PCFG would have had to split from the larger population after 1950.

Table 19 shows the results of simulations evaluating scenarios in which the carrying capacity for the PCFG was set to between 500 and 5000. The results indicate that the carrying capacity for the PCFG would need to be higher than 500 animals for the simulated results to be consistent with the empirical data under a scenario of no annual immigration. Examples of the abundance trajectory of the PCFG for the K values tested are shown in Table 20. For all K values simulated, the abundance of the PCFG was close to carrying capacity by 2010 (Table 21).

DISCUSSION:

Comparison of the simulated and empirical datasets for the larger ENP population suggests that the simulations represent the empirical data reasonably well with regard to the number of haplotypes and their distribution. Although the simulations predict that we would find slightly higher number of haplotypes and a slightly lower haplotypic diversity than is present in the empirical data, the differences are small and the χ^2 test suggests that the two samples would be interpreted as being drawn from the same population in the majority (88%) of cases. The results of these comparisons suggest that similar frequency-based comparisons of the simulated and empirical data representing the PCFG should be informative.

The level of nucleotide diversity in the simulated data representing the larger ENP population is higher than that found in the empirical data, indicating that there are some aspects of the population's history that are not being captured by the simulations. It is likely that the gray whales in the North Pacific have experienced numerous fluctuations in abundance due to changing ice conditions in the past, and historic K may have been substantially larger than we have simulated here (e.g., Alter *et al*. 2007). Our simulations incorporate only a simplified version of the recent history of gray whales, and our results suggest that the statistics relying on nucleotide differences (e.g., nucleotide diversity and ϕ_{ST}) may be more sensitive to violations of our assumptions about past (pre-commercial whaling) population size and equilibrium. As such, the results derived from the comparisons of nucleotide diversity and ϕ_{ST} warrant further investigation and should be interpreted with caution.

The comparison of frequency-based statistics between the simulated and empirical datasets representing the PCFG suggests that annual immigration into the PCFG is likely to be higher than 1 immigrant per year under the scenarios tested. The simulations were less informative with regard to the upper bound on annual immigration that could be occurring. Although the F_{ST} and χ^2/df comparisons indicated that immigration of >8 animals/year would be inconsistent with the empirical data, the proportion of simulations with higher than the observed values for the number of haplotypes and the haplotypic diversity never exceeded 84% and 63%, respectively. For all four statistics, the proportion of simulations with higher (for the number of haplotypes and haplotypic diversity) or lower (for F_{ST} and χ^2/df) values than the observed appears to level off at the higher (8 -10 or more per year) levels of immigration. This pattern is particularly evident in the comparisons utilizing haplotypic diversity, where the proportion of simulations with higher or lower values than the observed levels off at ~50% for immigration of 8 or more animals per year. Haplotypic diversity is calculated based on the sum of squared allele frequencies. Given that relationship, as the number of haplotypes in a population increases, the addition of another haplotype, particularly one found in low frequencies as would be expected to be brought in by an immigrant, has little impact on diversity. As such, this statistic, and to a lesser extent the others, appear to have limited power to differentiate between the higher levels of immigration.

Although these statistics were limited in their ability to distinguish an absolute upper bound on how much immigration could be occurring, the calculation of the number of immigrants per year which corresponds to the “crossing point” provides some information on what the most plausible values of immigration could be (Table 22). The estimated number of migrants ranged from ~2 to 8 for the scenarios with pulse immigration under the updated matrices. For the reasons discussed above, the calculations based on ϕ_{ST} and haplotypic diversity may not provide the best estimates. Comparisons between the observed and simulated values for the number of haplotypes, F_{ST}, and χ^2/df, suggest that immigration of approximately 4 animals per year is most plausible. If the current abundance of the PCFG is approximately 200 animals, this represents immigration of ~ 2% per year. Of note, this estimate does not include the +20 animals which were simulated to immigrate into the PCFG in 2000 and 2001.

Although the simulation results could be sensitive to other parameters incorporated in the models, a limited evaluation of the effects of increased carrying capacity for the PCFG or a more recent founding time was conducted. These simulations suggested that to obtain the empirical results presented in Lang *et al.* 2011 under a scenario of no annual immigration, the abundance of the PCFG would have to be larger (>500 animals) than currently estimated. Gray whales have been observed feeding off of Kodiak Island, Alaska since at least 1999, with ~350-400 individuals counted during a single day in July 2000 (Moore *et al.* 2007). Approximately 20% of the animals photographically identified in this area between 2002 and 2005 are known to be animals that have also been photographed in the Pacific Northwest from northern California to southeast Alaska (Gosho *et al.* 2011). However, the median “crossing point” calculated from these comparisons suggest that values of K between 2000 (based on F_{ST}) and 3000 (based on the number of haplotypes) animals produce values that are most consistent with the empirical data, indicating that additional explanation may be needed.

The simulations exploring more recent founding times suggest that under a scenario with no annual immigration, the PCFG would have to have been founded after 1950, and more plausibly between the mid-1960s to mid-1970s, to produce simulated results that are consistent with the empirical data. Small numbers of gray whales have been sighted within the seasonal range of the PCFG since at least 1926 (Howell & Huey 1930, Gilmore 1960, Pike and MacAskie 1969, additional references in Rice & Wolman 1971), but photo-identification studies did not start until the 1970s, when the repeated return of individuals to the area was first documented (Hatler & Darling 1974, Darling 1984). Our simulations model an instantaneous colonization of the PCFG, such that for the scenarios modeling colonization in 1960 or later at least 60 whales become part of the PCFG in a given year. This aspect of our simulations is clearly an oversimplification. Given both the limited information available on use of the PCFG seasonal range prior to the 1970s and the limitations of our model, it is difficult to evaluate how the simulation results fit in with past records.

The simulations incorporating a pre-whaling split of the PCFG from the larger ENP population are in progress and are expected to be completed by the 2012 SC meeting. Future work will also include integrating the genetic data representing ENP gray whales in LeDuc *et al*. 2002 and Lang 2010 with the data represented in Lang *et al.* 2011 to ensure that the diversity values utilized here are as representative as possible of the larger ENP population. Simulations will also be performed to explore the effect of incorporating lower MSYR rates for the PCFG into the life history matrices underlying the models.

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Table 1. The proportion of birth events in the simulated data that resulted in multiple offspring for the same female in a given year.

	5-stage TOSSM matrices	9-stage matrices
Proportion of single offspring births:	64%	92%
Proportion of multiple offspring births:	36%	8%
Range of multiple offspring births:	2-7	2-3

Table 2. Calving intervals in the simulated datasets.

Measure	5-stage TOSSM matrices	9-stage matrices
Median	3	2
Mean	5.1	3.2
Variance	27.08	16.50
stdev	5.20	4.06
Min	2	1
Max	35	38

Table 3. Vital rates for gray whales. Generation time shown here is calculated based on a maximum age of 40 years (as in previous work).

	5-stage TOSSM matrices		9-stage matrices	
Vital Rate	At K	Near ZPD	At K	Near ZPD
Juvenile survival	0.925	0.94	0.905	0.935
Adult female survival	0.946	0.946	0.982	0.982
Adult male survival	0.954	0.954	0.982	0.982
Calf survival	0.925	0.94	0.732	0.732
Age of first reproduction	10	5	10	7
Rate of increase (λ)	1.003	1.072	1.000	1.064
Generation Time*	19.5	16.9	21.10	20.60

Table 4. The updated stage-based matrices for use at a) zero population density and b) carrying capacity are shown below.

a) Nine-stage matrices at ZPD:

	juv1	juv2	juv3	F1	F2	F3	M1	M2	M3
juv1	0.497	0.000	0.000	0.366	0.366	0.366	0.000	0.000	0.000
juv2	0.438	0.497	0.000	0.000	0.000	0.000	0.000	0.000	0.000
juv3	0.000	0.438	0.497	0.000	0.000	0.000	0.000	0.000	0.000
F1	0.000	0.000	0.219	0.942	0.000	0.000	0.000	0.000	0.000
F2	0.000	0.000	0.000	0.040	0.942	0.000	0.000	0.000	0.000
F3	0.000	0.000	0.000	0.000	0.040	0.942	0.000	0.000	0.000
M1	0.000	0.000	0.219	0.000	0.000	0.040	0.942	0.000	0.000
M2	0.000	0.000	0.000	0.000	0.000	0.000	0.040	0.942	0.000
M3	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.040	0.942

b) Nine-stage matrices at K:

	juv1	juv2	juv3	F1	F2	F3	M1	M2	M3
juv1	0.633	0.000	0.000	0.176	0.176	0.176	0.000	0.000	0.000
juv2	0.272	0.633	0.000	0.000	0.000	0.000	0.000	0.000	0.000
juv3	0.000	0.272	0.633	0.000	0.000	0.000	0.000	0.000	0.000
F1	0.000	0.000	0.136	0.914	0.000	0.000	0.000	0.000	0.000
F2	0.000	0.000	0.000	0.068	0.914	0.000	0.000	0.000	0.000
F3	0.000	0.000	0.000	0.000	0.068	0.914	0.000	0.000	0.000
M1	0.000	0.000	0.136	0.000	0.000	0.068	0.914	0.000	0.000
M2	0.000	0.000	0.000	0.000	0.000	0.000	0.068	0.914	0.000
M3	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.068	0.914

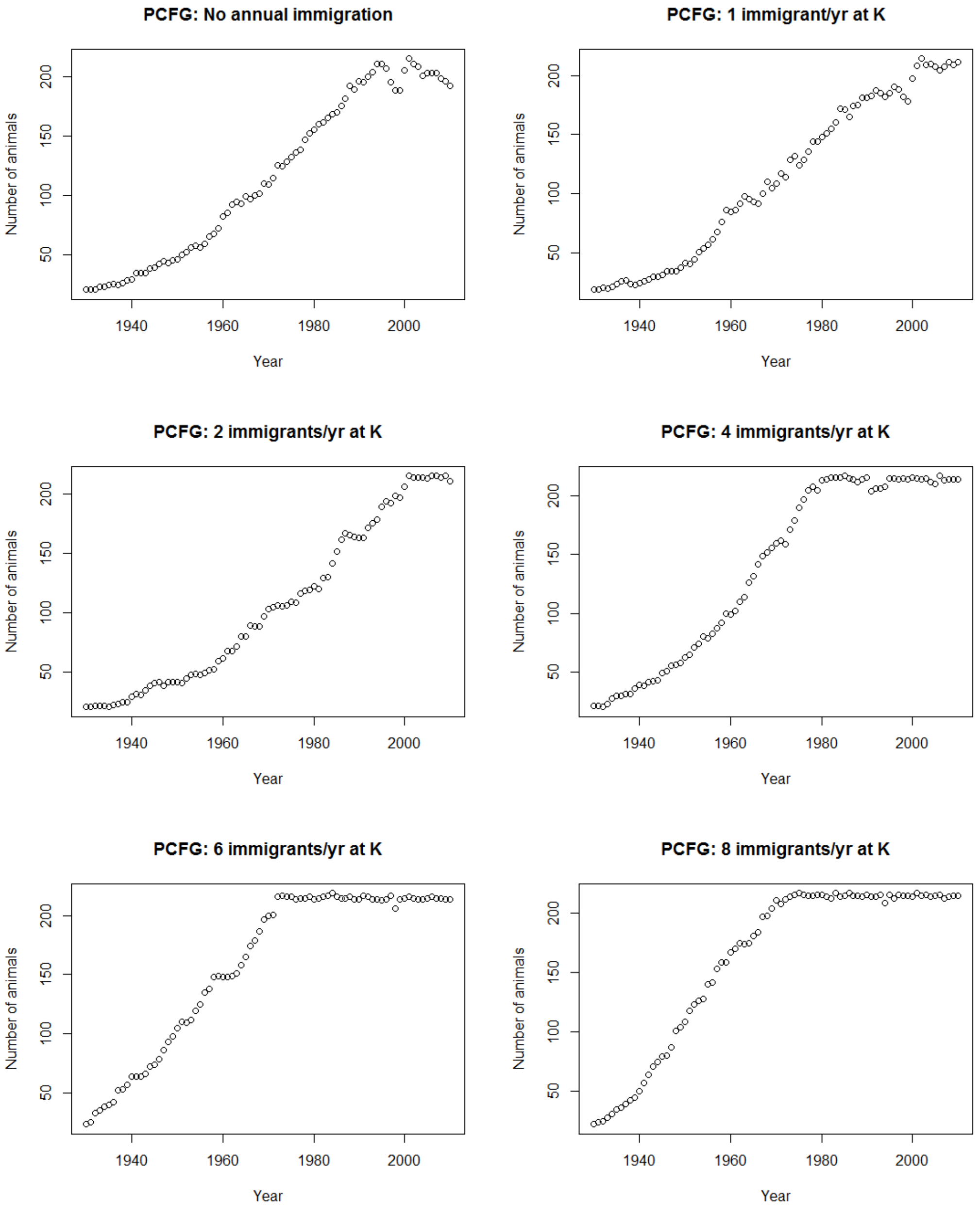
c) Five-stage(TOSSM) matrices at ZPD:

	juv1	juv2	fert	lact	male
juv1	0.730	0.000	0.000	0.940	0.000
juv2	0.210	0.000	0.000	0.000	0.000
fert	0.000	0.470	0.000	0.946	0.000
lact	0.000	0.000	0.946	0.000	0.000
male	0.000	0.470	0.000	0.000	0.954

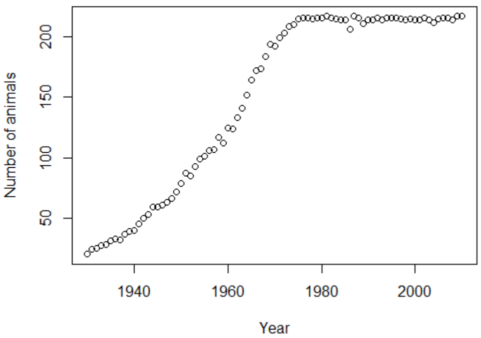
d) Five-stage (TOSSM) matrices at K:

	juv1	juv2	fert	lact	male
juv1	0.768	0.000	0.000	0.925	0.000
juv2	0.157	0.720	0.000	0.000	0.000
fert	0.000	0.102	0.648	0.946	0.000
lact	0.000	0.000	0.298	0.000	0.000
male	0.000	0.102	0.000	0.000	0.954

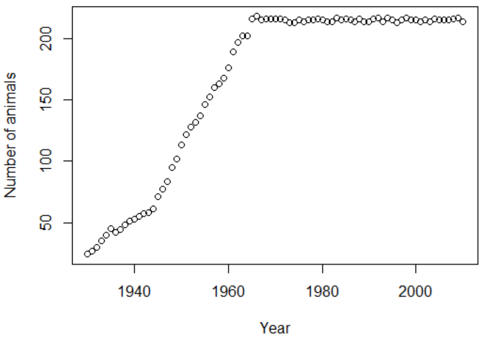
Figure 5. Examples of trajectories for PCFG, under a model incorporating a post-whaling split with pulse immigration. Plots for the abundance of the PCFG whales span 1930 to 2010, while the plot showing the abundance of the larger ENP population spans 1846 to 2010 to show the simulated depletion due to commercial whaling.



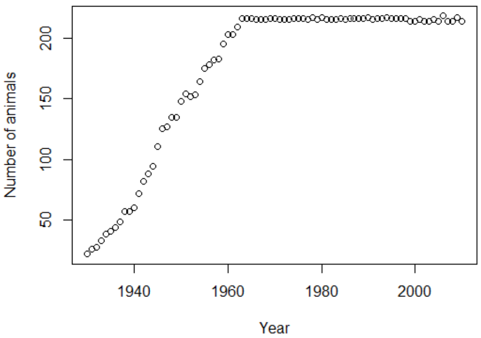
PCFG: 10 immigrants/yr at K



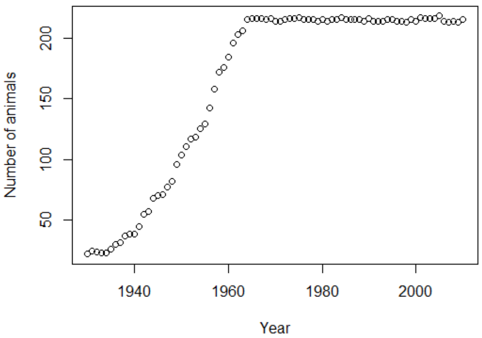
PCFG: 12 immigrants/yr at K



PCFG: 14 immigrants/yr at K



PCFG: 16 immigrants/yr at K



ENP

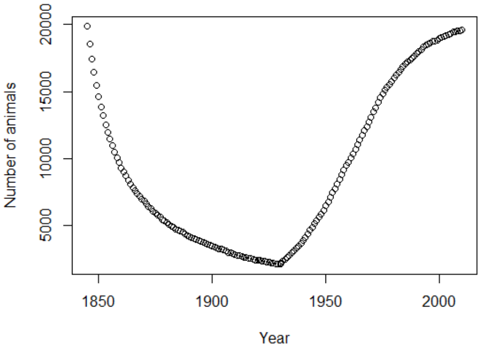
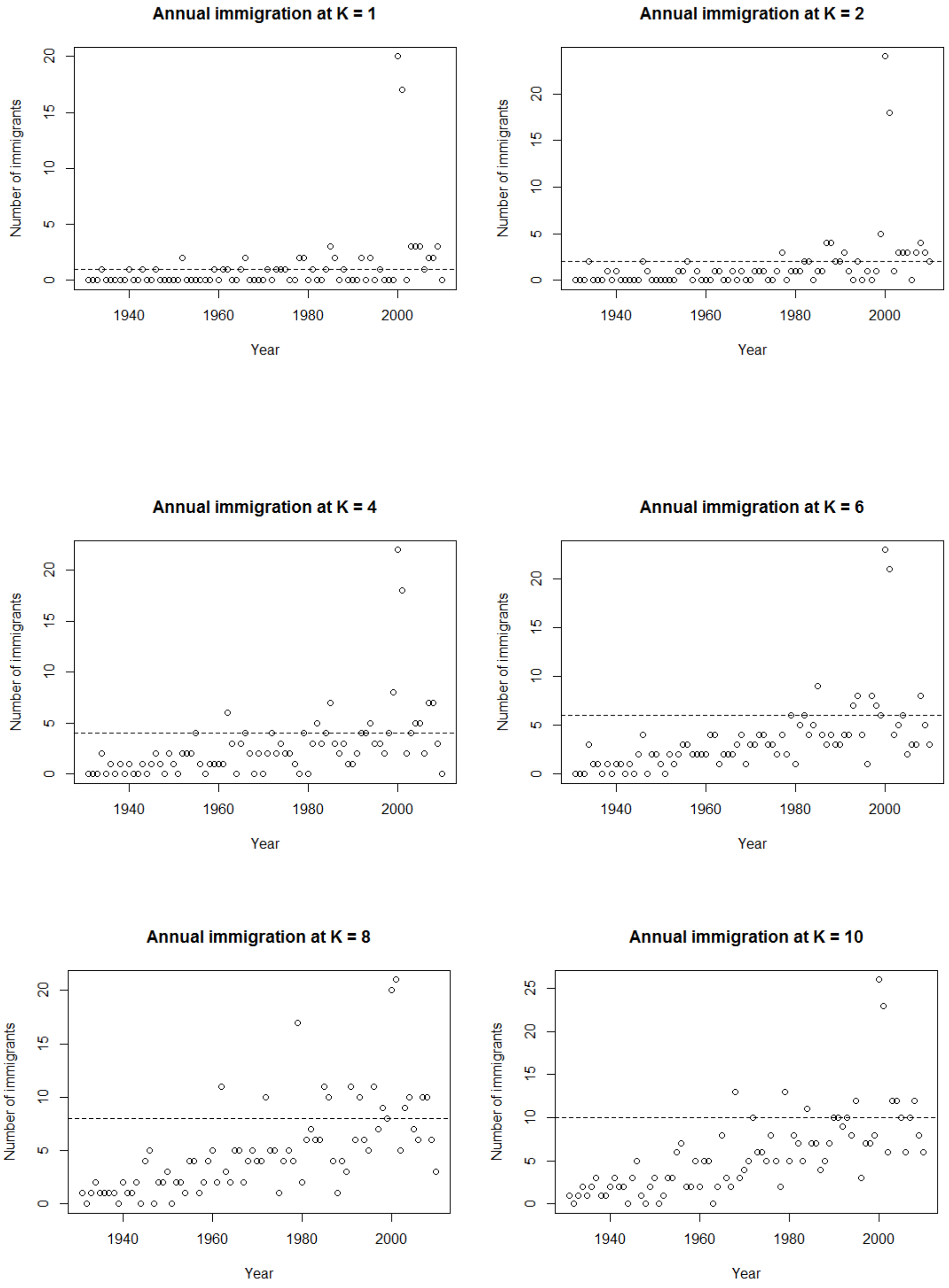
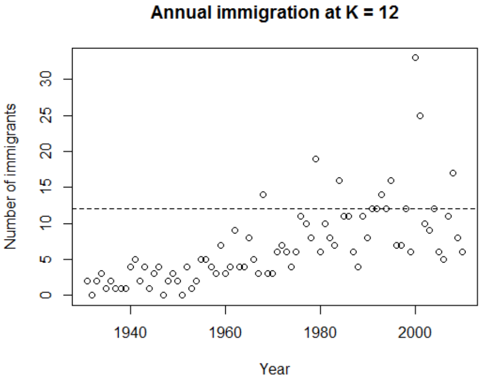
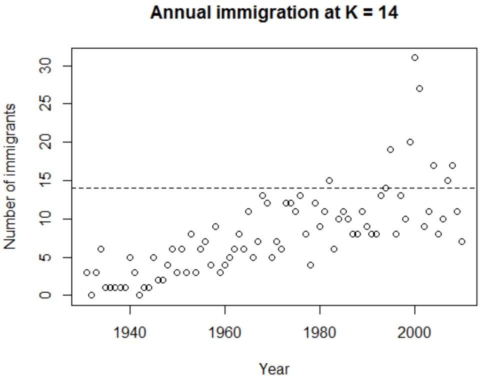


Figure 6. Example of the number of immigrants per year generated for one replicate (9-stage matrices with pulse immigration). The dotted line represents the number of immigrants per year that would be expected when the ENP population reaches K.

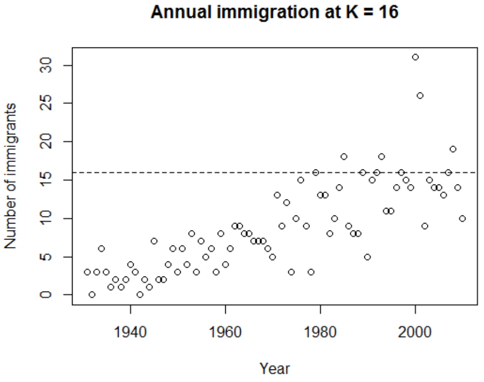




Annual immigration at K = 12



Annual immigration at K = 14



Annual immigration at K = 16

Table 7. List of scenarios that have been completed for 100 replications.

Index	Matrices	Timing of split	Year of split	PCFG Carrying Capacity (K)	Immigrants/yr into the PCFG (at K)	Pulse immigration
1	9-stage	Post-whaling split	1930	200	0	Y
2	9-stage	Post-whaling split	1930	200	1	Y
3	9-stage	Post-whaling split	1930	200	2	Y
4	9-stage	Post-whaling split	1930	200	4	Y
5	9-stage	Post-whaling split	1930	200	6	Y
6	9-stage	Post-whaling split	1930	200	8	Y
7	9-stage	Post-whaling split	1930	200	10	Y
8	9-stage	Post-whaling split	1930	200	12	Y
9	9-stage	Post-whaling split	1930	200	14	Y
10	9-stage	Post-whaling split	1930	200	16	Y
11	9-stage	Post-whaling split	1930	200	0	N
12	9-stage	Post-whaling split	1930	200	1	N
13	9-stage	Post-whaling split	1930	200	2	N
14	9-stage	Post-whaling split	1930	200	4	N
15	9-stage	Post-whaling split	1930	200	6	N
16	9-stage	Post-whaling split	1930	200	8	N
17	9-stage	Post-whaling split	1930	200	10	N
18	9-stage	Post-whaling split	1930	200	12	N
19	9-stage	Post-whaling split	1930	200	14	N
20	9-stage	Post-whaling split	1930	200	16	N
21	5-stage	Post-whaling split	1930	200	0	Y
22	5-stage	Post-whaling split	1930	200	1	Y
23	5-stage	Post-whaling split	1930	200	2	Y
24	5-stage	Post-whaling split	1930	200	4	Y
25	5-stage	Post-whaling split	1930	200	6	Y
26	5-stage	Post-whaling split	1930	200	8	Y
27	5-stage	Post-whaling split	1930	200	10	Y
28	5-stage	Post-whaling split	1930	200	12	Y
29	5-stage	Post-whaling split	1930	200	14	Y
30	5-stage	Post-whaling split	1930	200	16	Y
31	9-stage	Post-whaling split	1940	200	0	Y
32	9-stage	Post-whaling split	1950	200	0	Y
33	9-stage	Post-whaling split	1960	200	0	Y
34	9-stage	Post-whaling split	1970	200	0	Y
35	9-stage	Post-whaling split	1980	200	0	Y
36	9-stage	Post-whaling split	1990	200	0	Y
37	9-stage	Post-whaling split	1930	500	0	Y
38	9-stage	Post-whaling split	1930	1000	0	Y
39	9-stage	Post-whaling split	1930	1500	0	Y
40	9-stage	Post-whaling split	1930	2000	0	Y
41	9-stage	Post-whaling split	1930	3000	0	Y
42	9-stage	Post-whaling split	1930	5000	0	Y

* Pulse immigration consists of +20 animals in per year as reflected in the abundance in 2000 and 2001

Table 8. The number of samples collected per year from each stratum in the Lang *et al*. 2011 study.

Year	North	PCFG
1994	11	0
1995	0	0
1996	0	3
1997	1	3
1998	0	7
1999	1	0
2000	1	2
2001	27	0
2002	0	1
2003	12	3
2004	12	3
2005	10	1
2006	0	0
2007	0	0
2008	0	0
2009	0	13
2010	28	35
Total	103	71

Table 9. Summary of the haplotypic diversity, number of mtDNA haplotypes, and nucleotide diversity generated in the simulated ENP population. Only the results from the post-whaling split with immigration pulse models are shown as results were similar under all other models.

Haplotypic diversity:
ENP: H_{obs} =0.952

Matrices	Scenario	Immigration (Inds/Yr at K)	With pulse?	Median_ENP	Min_ENP	Max_ENP	Prop < than ENP	Prop > than ENP
9-stage	Post-whaling split	0	Y	0.948	0.883	0.973	61	39
9-stage	Post-whaling split	1	Y	0.951	0.869	0.973	52	48
9-stage	Post-whaling split	2	Y	0.950	0.878	0.974	56	44
9-stage	Post-whaling split	4	Y	0.950	0.874	0.974	57	43
9-stage	Post-whaling split	6	Y	0.950	0.890	0.972	56	44
9-stage	Post-whaling split	8	Y	0.948	0.869	0.973	64	36
9-stage	Post-whaling split	10	Y	0.949	0.878	0.977	62	38
9-stage	Post-whaling split	12	Y	0.950	0.786	0.971	54	46
9-stage	Post-whaling split	14	Y	0.948	0.862	0.973	61	39
9-stage	Post-whaling split	16	Y	0.950	0.877	0.977	52	48
Number of haplotypes: ENP: Nb_haps$_{obs}$=32								
9-stage	Post-whaling split	0	Y	33	25	47	36	52
9-stage	Post-whaling split	1	Y	33	24	44	33	57
9-stage	Post-whaling split	2	Y	33	23	46	40	54
9-stage	Post-whaling split	4	Y	33	22	44	37	54
9-stage	Post-whaling split	6	Y	34	24	42	25	62
9-stage	Post-whaling split	8	Y	33	22	45	38	55
9-stage	Post-whaling split	10	Y	33	20	45	38	54
9-stage	Post-whaling split	12	Y	33	20	43	37	57
9-stage	Post-whaling split	14	Y	33	23	44	38	52
9-stage	Post-whaling split	16	Y	33	25	45	31	56
Nucleotide diversity: ENP: $\prod_{obs}$ = 0.0142								
9-stage	Post-whaling split	0	Y	0.026	0.012	0.065	7	93
9-stage	Post-whaling split	1	Y	0.025	0.011	0.060	10	90
9-stage	Post-whaling split	2	Y	0.024	0.012	0.056	9	91
9-stage	Post-whaling split	4	Y	0.025	0.011	0.059	9	91
9-stage	Post-whaling split	6	Y	0.025	0.011	0.060	10	90
9-stage	Post-whaling split	8	Y	0.025	0.011	0.067	8	92
9-stage	Post-whaling split	10	Y	0.024	0.011	0.059	8	92
9-stage	Post-whaling split	12	Y	0.025	0.010	0.057	9	91
9-stage	Post-whaling split	14	Y	0.025	0.011	0.071	7	93
9-stage	Post-whaling split	16	Y	0.025	0.011	0.066	9	91

Figure 10. Histogram showing the distribution of p-values for a χ^2 test comparing the observed to the simulated haplotype distributions for the larger ENP population.

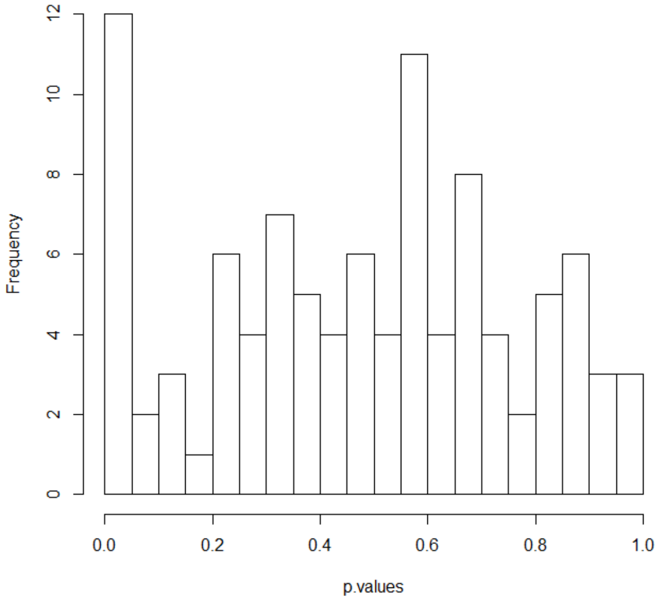
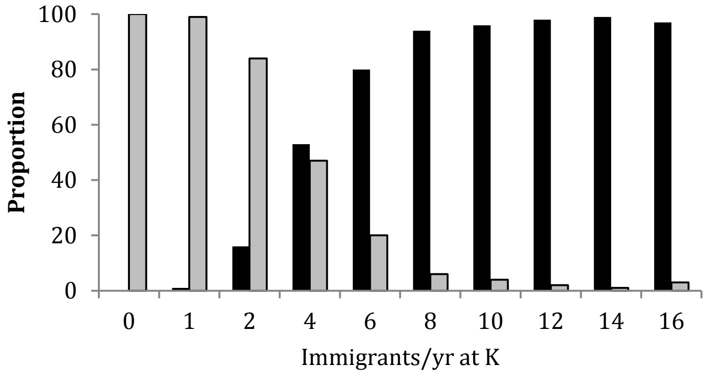
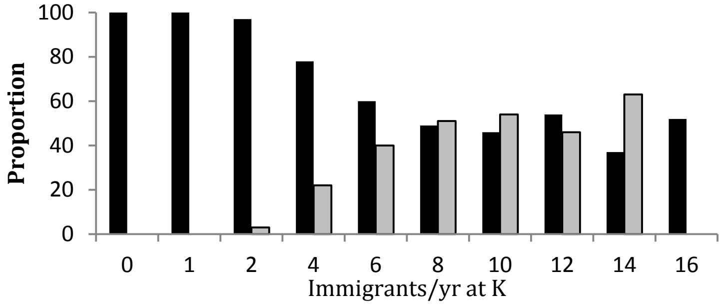


Figure 11. Graphical representation of the proportion of simulated values that are lower (shown in black) or higher (shown in gray) than the observed value generated from the empirical data. Simulated values are derived from the model incorporating a post-whaling split with pulse migration under the nine-stage matrices.

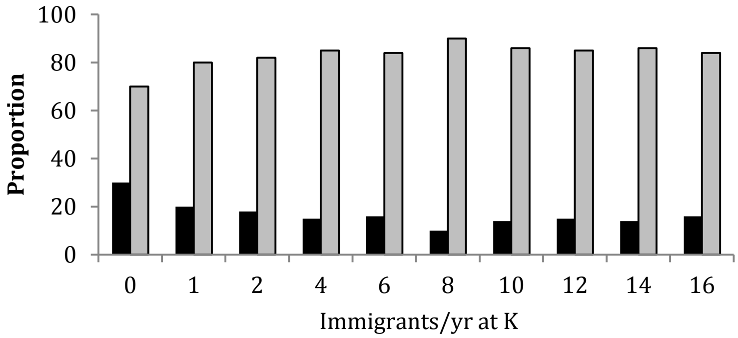
a.) Number of haplotypes:



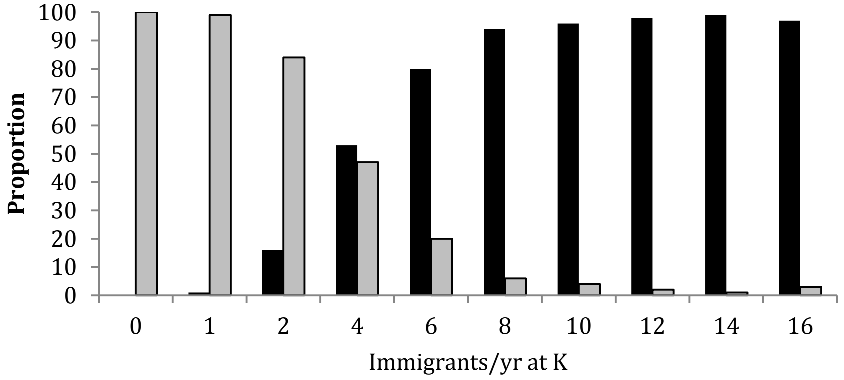
b.) Haplotypic diversity:



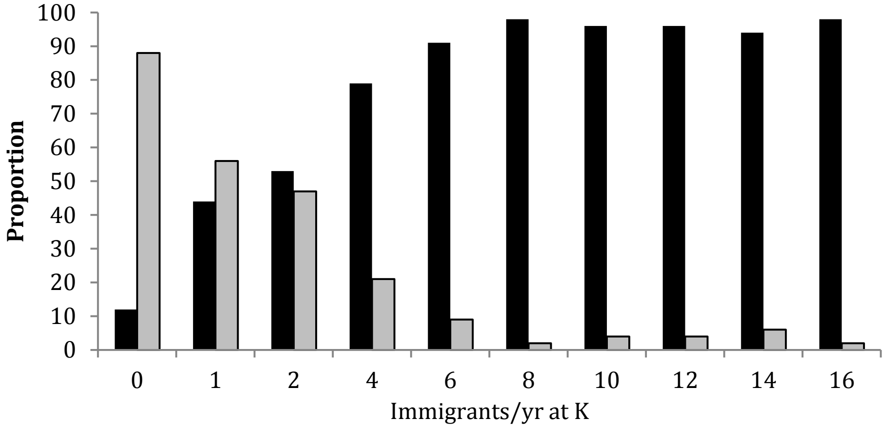
c.) Nucleotide diversity:



d.) F_{ST}:



e.) ϕ_{ST}:



f.) χ^2/df:

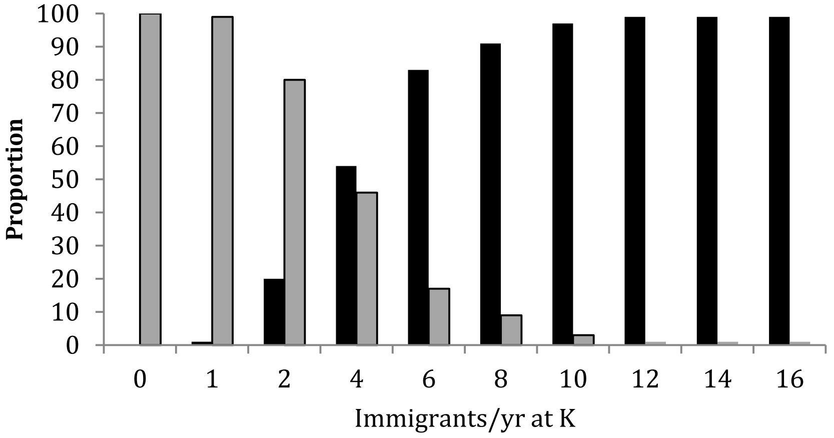


Table 12. Summary of number of mtDNA haplotypes in the simulated data for the PCFG. Scenarios highlighted in bold type produced results which were not consistent with those based on the empirical data.

PCFG: Nb_haps_{obs}=23

Matrices	Scenario	Immigrants/yr (at K)	With pulse?	Median_PCFG	Min_PCFG	Max_PCFG	Prop < PCFG	Prop > than obs
9-stage	**Post-whaling split**	**0**	**Y**	**12.0**	**6**	**19**	**100**	**0**
9-stage	**Post-whaling split**	**1**	**Y**	**16.6**	**11**	**26**	**96**	**2**
9-stage	Post-whaling split	2	Y	19.8	11	30	78	12
9-stage	Post-whaling split	4	Y	23.1	14	32	41	48
9-stage	Post-whaling split	6	Y	25.0	14	36	22	71
9-stage	Post-whaling split	8	Y	25.7	16	33	15	75
9-stage	Post-whaling split	10	Y	27.2	18	35	9	84
9-stage	Post-whaling split	12	Y	26.3	16	34	14	80
9-stage	Post-whaling split	14	Y	27.5	21	36	10	83
9-stage	Post-whaling split	16	Y	27.1	16	38	11	83
9-stage	**Post-whaling split**	**0**	**N**	**6.4**	**3**	**12**	**100**	**0**
9-stage	**Post-whaling split**	**1**	**N**	**12.5**	**6**	**20**	**100**	**0**
9-stage	**Post-whaling split**	**2**	**N**	**17.1**	**8**	**24**	**97**	**1**
9-stage	Post-whaling split	4	N	22.5	15	40	49	38
9-stage	Post-whaling split	6	N	23.9	12	32	36	52
9-stage	Post-whaling split	8	N	25.4	14	38	22	73
9-stage	Post-whaling split	10	N	25.8	17	37	27	66
9-stage	Post-whaling split	12	N	26.6	17	33	11	86
9-stage	Post-whaling split	14	N	27.0	17	36	11	84
9-stage	Post-whaling split	16	N	26.7	18	38	16	76
5-stage	**Post-whaling split**	**0**	**Y**	**10.4**	**6**	**16**	**100**	**0**
5-stage	**Post-whaling split**	**1**	**Y**	**15.0**	**7**	**23**	**99**	**0**
5-stage	Post-whaling split	2	Y	18.1	9	26	88	8
5-stage	Post-whaling split	4	Y	21.5	15	30	60	29
5-stage	Post-whaling split	6	Y	22.9	15	30	49	38
5-stage	Post-whaling split	8	Y	24.1	18	35	33	56
5-stage	Post-whaling split	10	Y	24.6	17	37	29	61
5-stage	Post-whaling split	12	Y	25.0	17	35	28	65
5-stage	Post-whaling split	14	Y	24.8	18	34	30	63
5-stage	Post-whaling split	16	Y	25.4	17	37	21	67

Table 13. Summary of haplotypic diversity in the simulated data for the PCFG. Scenarios highlighted in bold type produced results which were not consistent with those based on the empirical data.

PCFG: Hobs = 0.945

Matrices	Scenario	Immigration (Inds/Yr at K)	With pulse?	Median_ PCFG	Min_PCFG	Max_PCFG	Prop < than PCFG	Prop > than PCFG
9-stage	**Post-whaling split**	**0**	**Y**	**0.804**	**0.137**	**0.896**	**100**	**0**
9-stage	**Post-whaling split**	**1**	**Y**	**0.869**	**0.334**	**0.940**	**100**	**0**
9-stage	**Post-whaling split**	**2**	**Y**	**0.907**	**0.722**	**0.949**	**97**	**3**
9-stage	Post-whaling split	4	Y	0.933	0.699	0.970	78	22
9-stage	Post-whaling split	6	Y	0.939	0.810	0.971	60	40
9-stage	Post-whaling split	8	Y	0.945	0.848	0.972	49	51
9-stage	Post-whaling split	10	Y	0.948	0.857	0.974	46	54
9-stage	Post-whaling split	12	Y	0.943	0.825	0.969	54	46
9-stage	Post-whaling split	14	Y	0.951	0.842	0.972	37	63
9-stage	Post-whaling split	16	Y	0.944	0.866	0.979	52	48
9-stage	**Post-whaling split**	**0**	**N**	**0.754**	**0.344**	**0.867**	**100**	**0**
9-stage	**Post-whaling split**	**1**	**N**	**0.841**	**0.608**	**0.928**	**100**	**0**
9-stage	**Post-whaling split**	**2**	**N**	**0.888**	**0.748**	**0.946**	**99**	**1**
9-stage	Post-whaling split	4	N	0.932	0.788	0.974	84	16
9-stage	Post-whaling split	6	N	0.936	0.840	0.965	67	33
9-stage	Post-whaling split	8	N	0.941	0.835	0.974	59	41
9-stage	Post-whaling split	10	N	0.944	0.842	0.977	51	49
9-stage	Post-whaling split	12	N	0.946	0.870	0.971	45	55
9-stage	Post-whaling split	14	N	0.946	0.878	0.976	43	57
9-stage	Post-whaling split	16	N	0.947	0.841	0.976	48	52
5-stage	**Post-whaling split**	**0**	**Y**	**0.734**	**0.259**	**0.883**	**100**	**0**
5-stage	**Post-whaling split**	**1**	**Y**	**0.854**	**0.600**	**0.930**	**100**	**0**
5-stage	**Post-whaling split**	**2**	**Y**	**0.890**	**0.717**	**0.949**	**97**	**3**
5-stage	Post-whaling split	4	Y	0.915	0.752	0.958	92	8
5-stage	Post-whaling split	6	Y	0.929	0.768	0.963	79	21
5-stage	Post-whaling split	8	Y	0.931	0.796	0.965	74	26
5-stage	Post-whaling split	10	Y	0.934	0.720	0.973	78	22
5-stage	Post-whaling split	12	Y	0.935	0.747	0.968	64	36
5-stage	Post-whaling split	14	Y	0.937	0.823	0.965	67	33
5-stage	Post-whaling split	16	Y	0.934	0.834	0.971	68	32

Table 14. Summary of the mtDNA nucleotide diversity in the simulated data for the PCFG. Scenarios highlighted in bold type produced results which were not consistent with those based on the empirical data.

PCFG: ∏ obs = 0.0148

Matrices	Scenario	Immigration (Inds/Yr at K)	With pulse?	Median_PCFG	Min_PCFG	Max_PCFG	Prop < than PCFG	Prop > than PCFG
9-stage	Post-whaling split	0	Y	0.021	0.004	0.059	30	70
9-stage	Post-whaling split	1	Y	0.022	0.005	0.056	20	80
9-stage	Post-whaling split	2	Y	0.022	0.010	0.063	18	82
9-stage	Post-whaling split	4	Y	0.025	0.010	0.062	15	85
9-stage	Post-whaling split	6	Y	0.025	0.010	0.062	16	84
9-stage	Post-whaling split	8	Y	0.025	0.012	0.066	10	90
9-stage	Post-whaling split	10	Y	0.025	0.010	0.058	14	86
9-stage	Post-whaling split	12	Y	0.025	0.011	0.059	15	85
9-stage	Post-whaling split	14	Y	0.025	0.011	0.059	14	86
9-stage	Post-whaling split	16	Y	0.024	0.010	0.067	16	84
9-stage	Post-whaling split	0	N	0.020	0.002	0.080	32	68
9-stage	Post-whaling split	1	N	0.022	0.007	0.051	27	73
9-stage	Post-whaling split	2	N	0.023	0.007	0.064	18	82
9-stage	Post-whaling split	4	N	0.024	0.008	0.062	15	85
9-stage	Post-whaling split	6	N	0.025	0.010	0.064	13	87
9-stage	Post-whaling split	8	N	0.024	0.010	0.060	11	89
9-stage	Post-whaling split	10	N	0.026	0.010	0.074	14	86
9-stage	Post-whaling split	12	N	0.025	0.010	0.065	12	88
9-stage	Post-whaling split	14	N	0.025	0.011	0.059	12	88
9-stage	Post-whaling split	16	N	0.025	0.010	0.058	12	88
5-stage	Post-whaling split	0	Y	0.015	0.004	0.042	51	49
5-stage	Post-whaling split	1	Y	0.018	0.003	0.046	44	56
5-stage	Post-whaling split	2	Y	0.018	0.005	0.048	37	63
5-stage	Post-whaling split	4	Y	0.017	0.005	0.051	27	73
5-stage	Post-whaling split	6	Y	0.019	0.005	0.054	27	73
5-stage	Post-whaling split	8	Y	0.020	0.006	0.048	31	69
5-stage	Post-whaling split	10	Y	0.020	0.004	0.053	31	69
5-stage	Post-whaling split	12	Y	0.020	0.005	0.052	27	73
5-stage	Post-whaling split	14	Y	0.021	0.005	0.052	29	71
5-stage	Post-whaling split	16	Y	0.020	0.006	0.050	25	75

Table 15. Summary of F_{ST} values generated in the comparison of simulated data representing the PCFG and the larger ENP population. Scenarios highlighted in bold type produced results which were not consistent with those based on the empirical data.

$F_{ST\ obs} = 0.012$

Matrices	Scenario	Immigration (Inds/Yr at K)	With pulse?	Median	Min	Max	Prop > than obseved	Prop > than observed
9-stage	**post-whaling split**	**0**	**Y**	**0.069**	**0.019**	**0.254**	**0**	**100**
9-stage	**post-whaling split**	**1**	**Y**	**0.040**	**0.005**	**0.189**	**1**	**99**
9-stage	post-whaling split	2	Y	0.023	0.002	0.096	16	84
9-stage	post-whaling split	4	Y	0.011	-0.004	0.033	53	47
9-stage	post-whaling split	6	Y	0.005	-0.005	0.030	80	20
9-stage	post-whaling split	8	Y	0.002	-0.004	0.017	94	6
9-stage	**post-whaling split**	**10**	**Y**	**0.002**	**-0.007**	**0.021**	**96**	**4**
9-stage	**post-whaling split**	**12**	**Y**	**0.001**	**-0.006**	**0.019**	**98**	**2**
9-stage	**post-whaling split**	**14**	**Y**	**0.001**	**-0.007**	**0.013**	**99**	**1**
9-stage	**post-whaling split**	**16**	**Y**	**0.001**	**-0.007**	**0.020**	**97**	**3**
9-stage	**post-whaling split**	**0**	**N**	**0.099**	**0.029**	**0.295**	**0**	**100**
9-stage	**post-whaling split**	**1**	**N**	**0.051**	**0.020**	**0.146**	**0**	**100**
9-stage	post-whaling split	2	N	0.032	0.006	0.098	9	91
9-stage	post-whaling split	4	N	0.012	-0.004	0.058	47	53
9-stage	post-whaling split	6	N	0.008	-0.003	0.035	71	29
9-stage	post-whaling split	8	N	0.003	-0.004	0.025	91	9
9-stage	post-whaling split	10	N	0.003	-0.006	0.022	93	7
9-stage	**post-whaling split**	**12**	**N**	**0.001**	**-0.007**	**0.015**	**98**	**2**
9-stage	**post-whaling split**	**14**	**N**	**0.002**	**-0.007**	**0.016**	**98**	**2**
9-stage	**post-whaling split**	**16**	**N**	**0.001**	**-0.006**	**0.048**	**92**	**8**
5-stage	**post-whaling split**	**0**	**Y**	**0.101**	**0.018**	**0.323**	**0**	**100**
5-stage	post-whaling split	1	Y	0.044	0.007	0.150	6	94
5-stage	post-whaling split	2	Y	0.025	-0.002	0.097	18	82
5-stage	post-whaling split	4	Y	0.009	-0.004	0.045	64	36
5-stage	post-whaling split	6	Y	0.004	-0.008	0.040	87	13
5-stage	post-whaling split	8	Y	0.002	-0.004	0.021	90	10
5-stage	post-whaling split	10	Y	0.003	-0.005	0.025	94	6
5-stage	**post-whaling split**	**12**	**Y**	**0.001**	**-0.007**	**0.014**	**96**	**4**
5-stage	**post-whaling split**	**14**	**Y**	**0.001**	**-0.006**	**0.016**	**98**	**2**
5-stage	**post-whaling split**	**16**	**Y**	**0.000**	**-0.006**	**0.019**	**97**	**3**

Table 16. Summary of ϕ_{ST} values generated in the comparison of simulated data representing the PCFG and the larger ENP population. Scenarios highlighted in bold type produced results which were not consistent with those based on the empirical data.

ϕ_{STobs}=0.023

Matrices	Scenario	Immigration (Inds/Yr at K)	With pulse?	Median	Min	Max	Prop > than observed	Prop < than observed
9-stage	Arch1_sc1	0	Y	0.065	0.000	0.332	12	88
9-stage	Arch1_sc2	1	Y	0.030	-0.002	0.240	44	56
9-stage	Arch1_sc3	2	Y	0.021	-0.004	0.080	53	47
9-stage	Arch1_sc4	4	Y	0.007	-0.009	0.074	79	21
9-stage	Arch1_sc5	6	Y	0.000	-0.011	0.062	91	9
9-stage	**Arch1_sc6**	**8**	**Y**	**-0.001**	**-0.011**	**0.036**	**98**	**2**
9-stage	**Arch1_sc7**	**10**	**Y**	**0.000**	**-0.011**	**0.028**	**96**	**4**
9-stage	**Arch1_sc8**	**12**	**Y**	**-0.003**	**-0.011**	**0.055**	**96**	**4**
9-stage	Arch1_sc9	14	Y	0.000	-0.011	0.044	94	6
9-stage	**Arch1_sc9**	**16**	**Y**	**-0.001**	**-0.010**	**0.032**	**98**	**2**
9-stage	Arch1_sc1	0	N	0.090	0.005	0.439	7	93
9-stage	Arch1_sc2	1	N	0.043	0.002	0.237	23	77
9-stage	Arch1_sc3	2	N	0.026	-0.008	0.187	48	52
9-stage	Arch1_sc4	4	N	0.009	-0.010	0.064	84	16
9-stage	Arch1_sc5	6	N	0.007	-0.009	0.087	86	14
9-stage	Arch1_sc6	8	N	0.001	-0.011	0.071	87	13
9-stage	Arch1_sc7	10	N	-0.002	-0.011	0.051	93	7
9-stage	Arch1_sc8	12	N	-0.002	-0.011	0.037	93	7
9-stage	Arch1_sc9	14	N	-0.001	-0.010	0.040	93	7
9-stage	Arch1_sc10	16	N	-0.002	-0.010	0.092	94	6
5-stage	Arch1_sc1	0	Y	0.099	0.007	0.501	7	93
5-stage	Arch1_sc2	1	Y	0.032	-0.004	0.321	40	60
5-stage	Arch1_sc3	2	Y	0.014	-0.008	0.181	67	33
5-stage	Arch1_sc4	4	Y	0.005	-0.007	0.068	83	17
5-stage	Arch1_sc5	6	Y	0.002	-0.010	0.044	95	5
5-stage	Arch1_sc6	8	Y	0.000	-0.010	0.108	88	12
5-stage	**Arch1_sc7**	**10**	**Y**	**0.001**	**-0.010**	**0.051**	**95**	**5**
5-stage	**Arch1_sc8**	**12**	**Y**	**-0.003**	**-0.011**	**0.045**	**99**	**1**
5-stage	Arch1_sc9	14	Y	-0.002	-0.010	0.044	94	6
5-stage	Arch1_sc9	16	Y	-0.002	-0.011	0.042	94	6

Table 17. Summary of χ^2/df values generated in the comparison of simulated data representing the PCFG and the larger ENP population. Scenarios highlighted in bold type produced results which were not consistent with those based on the empirical data.

$\chi^2/\mathrm{df}_{\mathrm{obs}} = 1.42$

Matrices	Scenario	Immigration (Inds/Yr at K)	With pulse?	Median	Min	Max	Prop.< than observed	Prop.> than observed
9-stage	**Arch1_sc1**	**0**	**Y**	**2.65**	**1.57**	**3.66**	**0**	**100**
9-stage	**Arch1_sc2**	**1**	**Y**	**2.05**	**1.41**	**3.49**	**1**	**99**
9-stage	Arch1_sc3	2	Y	1.70	1.00	2.87	20	80
9-stage	Arch1_sc4	4	Y	1.41	0.85	2.13	54	46
9-stage	Arch1_sc5	6	Y	1.19	0.74	1.71	83	17
9-stage	Arch1_sc6	8	Y	1.11	0.77	1.69	91	9
9-stage	**Arch1_sc7**	**10**	**Y**	**1.07**	**0.66**	**1.51**	**97**	**3**
9-stage	**Arch1_sc8**	**12**	**Y**	**1.05**	**0.63**	**1.53**	**99**	**1**
9-stage	**Arch1_sc9**	**14**	**Y**	**1.06**	**0.59**	**1.43**	**99**	**1**
9-stage	**Arch1_sc9**	**16**	**Y**	**1.03**	**0.74**	**1.55**	**99**	**1**
9-stage	**Arch1_sc1**	**0**	**N**	**3.23**	**1.87**	**4.73**	**0**	**100**
9-stage	**Arch1_sc2**	**1**	**N**	**2.38**	**1.52**	**3.74**	**0**	**100**
9-stage	Arch1_sc3	2	N	1.93	1.25	3.21	9	91
9-stage	Arch1_sc4	4	N	1.47	0.94	2.12	43	57
9-stage	Arch1_sc5	6	N	1.30	0.81	2.02	73	27
9-stage	Arch1_sc6	8	N	1.16	0.71	1.76	84	16
9-stage	Arch1_sc7	10	N	1.14	0.71	1.62	91	9
9-stage	**Arch1_sc8**	**12**	**N**	**1.07**	**0.70**	**1.80**	**95**	**5**
9-stage	**Arch1_sc9**	**14**	**N**	**1.08**	**0.76**	**1.58**	**96**	**4**
9-stage	**Arch1_sc10**	**16**	**N**	**1.04**	**0.71**	**1.77**	**95**	**5**
5-stage	**Arch1_sc1**	**0**	**Y**	**2.87**	**1.50**	**4.41**	**0**	**100**
5-stage	**Arch1_sc2**	**1**	**Y**	**2.16**	**1.07**	**3.90**	**5**	**95**
5-stage	Arch1_sc3	2	Y	1.71	0.92	2.62	18	82
5-stage	Arch1_sc4	4	Y	1.32	0.82	1.89	64	36
5-stage	Arch1_sc5	6	Y	1.20	0.55	1.64	93	7
5-stage	Arch1_sc6	8	Y	1.12	0.68	1.67	94	6
5-stage	Arch1_sc7	10	Y	1.12	0.71	1.67	92	8
5-stage	**Arch1_sc8**	**12**	**Y**	**1.04**	**0.69**	**1.59**	**97**	**3**
5-stage	**Arch1_sc9**	**14**	**Y**	**1.02**	**0.64**	**1.47**	**98**	**2**
5-stage	**Arch1_sc9**	**16**	**Y**	**1.01**	**0.70**	**1.48**	**99**	**1**

Table 18. Measures of haplotypic diversity, number of haplotypes, and F_{ST} values produced in simulations incorporating a split of the PCFG between 1940 and 1990. These simulations utilized a model incorporating pulse migration and no annual immigration into the PCFG. Scenarios highlighted in bold type produced results which were not consistent with those based on the empirical data.

Haplotypic diversity:
PCFG: H_{obs} = 0.945

Year of split	Median_PCFG	Min_PCFG	Max_PCFG	Prop < than PCFG	Prop > than PCFG
1940	**0.863**	**0.591**	**0.925**	**100**	**0**
1950	**0.884**	**0.721**	**0.932**	**100**	**0**
1960	**0.905**	**0.766**	**0.950**	**98**	**2**
1970	0.927	0.821	0.963	80	20
1980	0.939	0.804	0.969	68	32
1990	0.942	0.883	0.969	55	45
Number of haplotypes PCFG: Nb_{obs}=23					
1940	**14**	**7**	**20**	**100**	**0**
1950	**16**	**10**	**23**	**99**	**0**
1960	**17**	**11**	**23**	**96**	**0**
1970	21.5	12	28	65	22
1980	24	15	33	33	57
1990	25	17	34	25	68
F_{ST} $F_{ST\ obs}$ = 0.012					
1940	**0.046**	**0.008**	**0.177**	**1**	**99**
1950	**0.036**	**0.011**	**0.104**	**1**	**99**
1960	0.022	0.003	0.077	16	84
1970	0.009	-0.005	0.029	64	36
1980	0.006	-0.003	0.035	84	16
1990	**0.003**	**-0.005**	**0.015**	**97**	**3**

Table 19. Measures of haplotypic diversity, number of haplotypes, and F_{ST} values produced in simulations incorporating a carrying capacity for the PCFG ranging from 500 to 5000 animals. These simulations utilized a model incorporating pulse migration and no annual immigration into the PCFG. Scenarios highlighted in bold type produced results which were not consistent with those based on the empirical data.

Haplotypic diversity:
PCFG: H_{obs} = 0.945

K-PCFG	Median_PCFG	Min_PCFG	Max_PCFG	Prop < than PCFG	Prop > than PCFG
500	**0.876**	**0.714**	**0.937**	**100**	**0**
1000	**0.911**	**0.808**	**0.949**	**96**	**4**
1500	0.922	0.818	0.959	90	10
2000	0.932	0.765	0.966	72	28
3000	0.934	0.841	0.965	73	27
5000	0.945	0.849	0.967	47	53

Number of haplotypes
PCFG: Nb_{obs}=23

K-PCFG	Median_PCFG	Min_PCFG	Max_PCFG	Prop < than PCFG	Prop > than PCFG
500	**14**	**7**	**24**	**99**	**1**
1000	**17**	**9**	**23**	**98**	**0**
1500	20	12	27	90	5
2000	20.5	15	28	69	21
3000	22	15	32	51	40
5000	26	16	34	20	73

F_{ST}
F_{ST}obs = 0.012

K-PCFG	Median_PCFG	Min_PCFG	Max_PCFG	Prop < than PCFG	Prop > than PCFG
500	**0.037**	**0.013**	**0.111**	**0**	**100**
1000	0.021	0.006	0.058	21	79
1500	0.015	0.002	0.044	39	61
2000	0.012	-0.002	0.041	52	48
3000	0.007	-0.003	0.025	74	26
5000	0.006	-0.004	0.019	91	9

Table 20. Example trajectories for simulations with K_{PCFG} set between 500 and 5000. Note that scale of y-axis differs across figures.

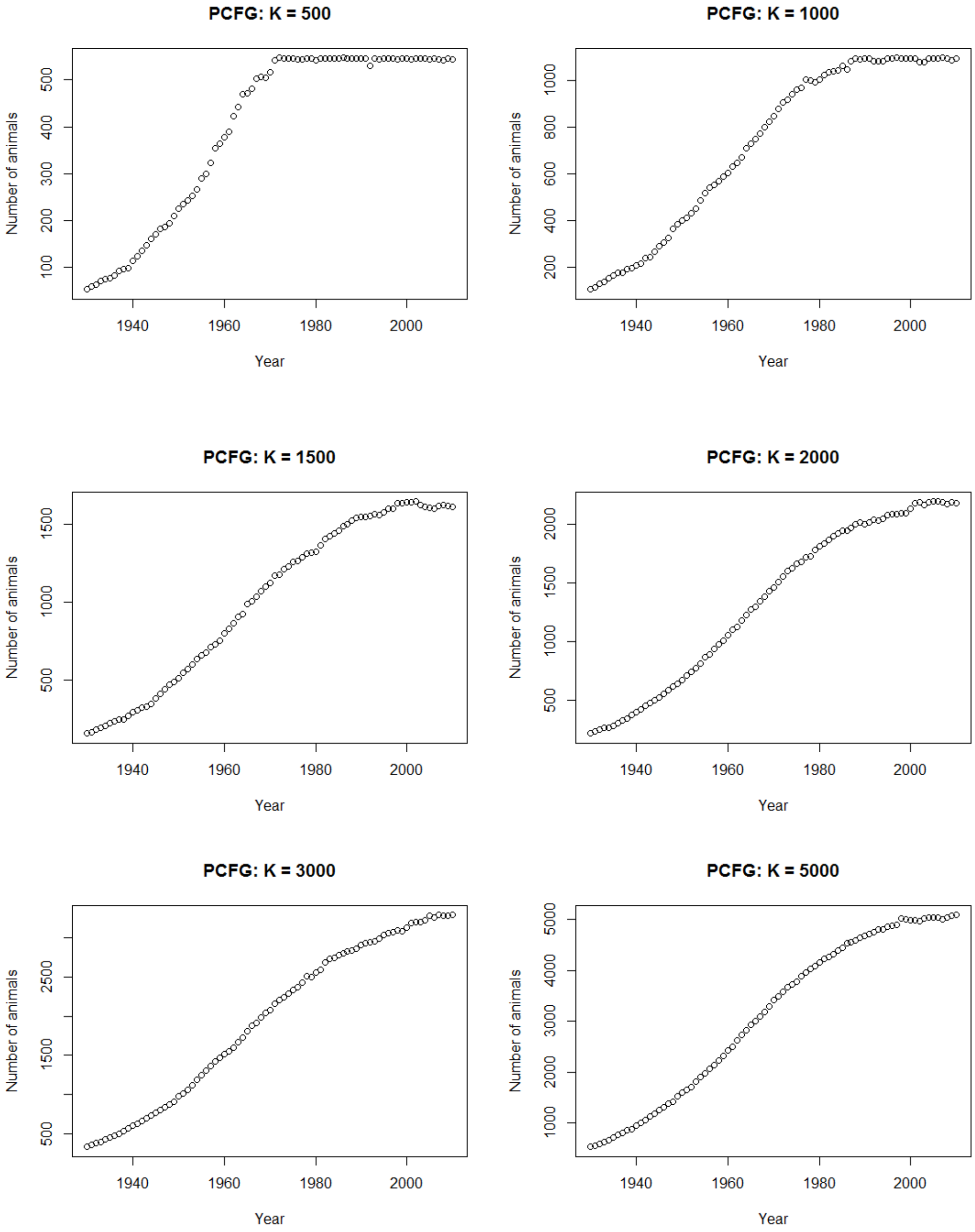


Table 21. Median PCFG abundance in 2010 for scenarios with K_{PCFG} set between 500 and 5000.

K_{PCFG}	N_{2010} (median and 90% range)
500	501 (466 – 542)
1000	998 (923-1063)
1500	1496 (1391-1588)
2000	1994(1864-2080)
3000	3002(2831-3128)
5000	4945 (4790-5095)

Table 22. The expected number of immigrants/year at the cross-over point under the scenarios with and without pulse immigration. The cross-over is derived by calculating the point at which 50% of the simulation replicates produce values for each summary statistic that are higher than that for the empirical data.

Matrices	Timing of split	Pulse migration	Number of haplotypes	Haplotypic diversity	F_{ST}	Φ_{ST}	χ^2/df
9-stage	Post-whaling split	Y	3.77	7.82	3.84	1.67	3.76
9-stage	Post-whaling split	N	4.35	10.25	4.25	2.11	4.47
5-stage	Post-whaling split	Y	6.76	-----	3.39	1.37	3.39

Appendix:

This appendix includes additional tables and figures aimed at understanding how well the model underlying our simulations is mimicking reality and/or the IR trial structure.

Table A1. Generation time estimates as calculated using different maximum ages for both 5-stage TOSSM and 9-stage matrices.

	5-stage matrices		9-stage matrices	
Max Age	K	ZPD	K	ZPD
40	19.52	16.92	21.05	20.59
50	21.68	18.74	23.65	23.86
100	26.04	22.25	28.29	32.87
150	26.64	22.69	28.61	34.93
1000	26.71	22.74	28.63	35.27

Table A2. The number of calves produced per year in simulated datasets at K as compared to data derived from photo-identification studies

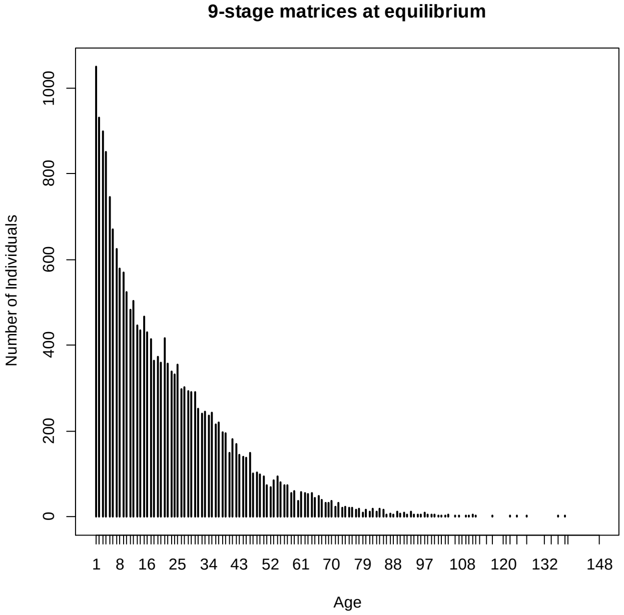
Source	Abundance (median with range):	Number of calves/yr	% Calves
5-stage matrices:	197(156-218)	11 (2-31)	6%
9-stage matrices:	195 (161-217)	10 (2-23)	5%
Photo-identification estimates	194 †	3 (0-9)††	2%

†Annex F, IWC 2011

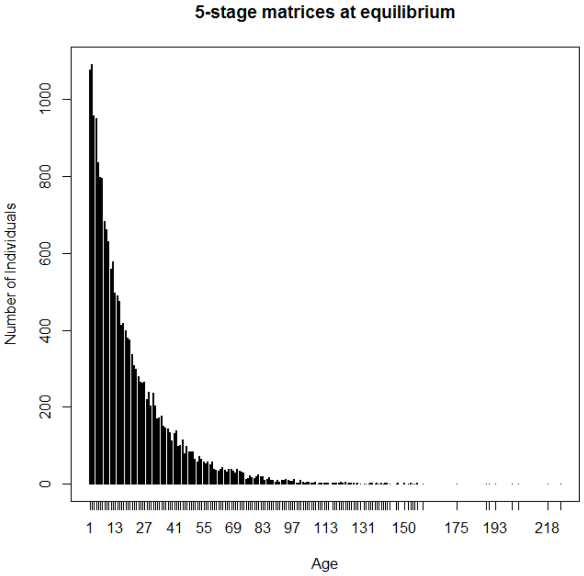
†† Calambokidis *et al.* 2008 (data from 1998-2008)

Figure A1. Age distribution in simulated datasets (note different x-axis scales):

a) Nine-stage matrices:



a.) Five-stage matrices:



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The western gray whale: a review of past exploitation, current status and potential threats

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The western gray whale: a review of past exploitation, current status and potential threats

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ABSTRACT

Gray whales (*Eschrichtius robustus*) occur along the eastern and western coastlines of the North Pacific as two geographically isolated populations and have traditionally been divided into the eastern (California-Chukchi) and western (Korean-Okhotsk) populations. Recent molecular comparisons confirm, based on differences in haplotypic frequencies, that these populations are genetically separated at the population-level. Both populations were commercially hunted, but only the eastern gray whale has returned to near pre-exploitation numbers. In contrast, the western population remains highly depleted, shows no apparent signs of recovery and its future survival remains uncertain. Research off Sakhalin Island, Russia between 1995 and 1999 has produced important new information on the present day conservation status of western gray whales and provided the basis for the World Conservation Union (IUCN) to list the population as 'Critically Endangered' in 2000. The information presented here, in combination with potential impacts from anthropogenic threats throughout the range of this population, raises strong concerns about the recovery and continued survival of the western gray whale.

KEYWORDS: GRAY WHALE; PACIFIC OCEAN; NORTHERN HEMISPHERE; CONSERVATION; OKHOTSK SEA; EXPLOITATION; POPULATION STATUS

INTRODUCTION

Gray whales (*Eschrichtius robustus*) are known to occur along the eastern and western margins of the North Pacific (Andrews, 1914; Rice and Wolman, 1971); they have been extinct in the North Atlantic for several hundred years (Mead and Mitchell, 1984). Recent genetic studies show that animals from the eastern (California-Chukchi) and the western (Korean-Okhotsk) Pacific should be recognised as geographically and genetically separated at the population level (LeDuc *et al.*, 2002). Although both populations were greatly reduced by commercial whaling, only the eastern gray whale has returned to numbers approaching the suspected pre-exploitation population size (IWC, 1998). In contrast, the western gray whale was thought to be extinct as recently as the early 1970s (Bowen, 1974), but later published reports confirmed that the population was extant (Berzin, 1974; Brownell and Chun, 1977). Today, the western gray whale population remains highly depleted and shows no apparent signs of recovery (e.g. Weller *et al.*, 1999; IWC, 2002b). Information regarding the life history and biology of the western population is sparse (Andrews, 1914; Rice and Wolman, 1971) and only recently has it come under concerted study (e.g. Brownell *et al.*, 1997; Weller *et al.*, 1999).

Historic records and recent data suggest that summer feeding grounds for the western population are in the Okhotsk Sea, but the location(s) of the winter breeding grounds, suspected to be along the coast of southern China, remain unknown (Wang, 1984; Henderson, 1990). Contemporary findings from an ongoing US-Russia mark-recapture photo-identification project between 1995 and 2001 suggest that the total population size is <100 individuals (e.g. Weller *et al.*, 1999; IWC, 2002b). Low-level human-related mortality south of the Okhotsk Sea (Brownell and Kasuya, 1999; Baker *et al.*, 2002), and the onset of large-scale multinational oil and gas development programmes within Okhotsk waters, pose potential new threats to the continued survival of this population.

Serious concern over the status of this population has been expressed by the World Conservation Union (by assigning it 'Critically Endangered' - Hilton-Taylor, 2000) and by the International Whaling Commission (IWC, 2002b).

RANGE AND DISTRIBUTION

Western gray whales occur off Russia, Japan, the Democratic People's Republic of Korea (North Korea), Republic of Korea (South Korea) and People's Republic of China (China). Although historic sighting and whaling records indicate that gray whales occurred in areas north of the presently described Okhotsk Sea feeding ground, the present day population range appears to be largely confined to the region between the west central Okhotsk Sea off the northeastern coast of Sakhalin Island (summer-autumn) and the South China Sea (winter). Individuals remain in shallow, mainly nearshore waters, year-round; except when crossing the La Perouse and Tartarskiy Straits off the southern end of Sakhalin Island or during north-south migrations in the Sea of Japan, and the Yellow and East China Seas. Although few records of gray whales are available south of Hong Kong (Wang, 1984; Zhu, 1998), it is presumed that they maintain a nearshore affinity throughout the southern portion of their range.

Main habitat

Gray whales are known for their long-distance migrations between sub-tropical calving and mating grounds near continental coasts and high-latitude feeding grounds in the Arctic and sub-Arctic (e.g. Rice and Wolman, 1971; Swartz, 1986). As bottom-feeding specialists, gray whales aggregate during summer and autumn in shallow shelf waters and offshore banks where benthic and epibenthic invertebrate communities are concentrated (Nerini, 1984; Oliver *et al.*, 1984; Kim and Oliver, 1989). Traditional nearshore migratory routes connect high-latitude feeding areas with warm-water coastal and inshore wintering grounds. Today, the primary summer-autumn feeding habitat for western

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gray whales is located off the northeastern coast of Sakhalin Island (Weller *et al.*, 1999; 2002). The calving and mating grounds for this population are unknown, but records from sightings, strandings and whaling catches from 1933-1996 indicate that at least some western gray whales occur in coastal waters off China in the South China Sea (Wang, 1984; Zhu, 1998).

Distribution

Key areas of distribution include the summer feeding grounds off northeastern Sakhalin Island (~52°50'N 143°20'E). Known portions of the north-south migratory route include regions off the eastern shore of Sakhalin Island in the Okhotsk Sea and along the eastern shores of mainland Russia near Peter the Great Bay and along the Korean peninsula in the Sea of Japan (Andrews, 1914; Brownell and Chun, 1977; Berzin, 1990). It is thought that prior to the 20th century, two groups of gray whales may have migrated to coastal waters off Japan (Omura, 1984). One of these groups was thought to travel along the eastern (Pacific) shore of Honshu during their southbound migration while en route for a supposed calving ground in the Seto Inland Sea (Omura, 1984). The other group was suspected to migrate along the eastern shore of Korea, cross the Korean Strait near Ulsan, and ultimately arrive at southwest Honshu and northwest Kyushu (Omura, 1984). Although gray whales were once hunted by net fishermen off the eastern shore of Honshu (Omura, 1984), present-day sightings of the species off Japan are very rare (Kato and Tokuhiro, 1997).

The winter distribution of this population is unknown. Whaling records indicate that peak gray whale numbers off southern Korea occurred in two seasonal pulses, one during the southward migration between December and January, and the other between March and April during the northward migration (Andrews, 1914; Kato and Kasuya, 2002). Whalers working off Ulsan, South Korea found that a majority of adult females taken between December-January were carrying near-term foetuses and were thought to be within two to three weeks of parturition (Andrews, 1914). Based on these observations, and his own measurement of one 4.76m foetus, Andrews suggested that calves were probably born somewhere off the southern end of the Korean Peninsula, and that this region represented the probable southern terminus of the winter migration (Andrews, 1914).

The idea that western gray whales overwinter off the southern coast of Korea, as suggested by Andrews (1914), was largely speculative (Rice, 1998). Several lines of evidence suggest that Andrews miscalculated the true position of the wintering grounds. Rice and Wolman (1971) reported an average near-term foetus size of 4.62m for eastern gray whales taken off central California between December and January. Thus, the observed foetus size, seasonal timing and latitudinal position (about 34°N) reported for Korea and central California closely corresponded. However, eastern gray whales migrate to breeding areas as far south as 20°-27°N off Baja California (Rice and Wolman, 1971; Swartz, 1986). Although Andrews suspected that western gray whales terminated their southern migration off southern Korea, a location approximately 7°-14° north of the eastern gray whale wintering grounds, historical records indicate that they occur as far south as the Yellow Sea, East China Sea and South China Sea (Henderson, 1972; 1984; 1990; Wang, 1978; 1984; Omura, 1988; Zhu, 1998; Kato and Kasuya, In press). Some evidence is available that western gray whales range at least as far south as 20°N off Hainan Island in southeastern China (Wang, 1984; Zhu, 1998). In addition, several unverified sighting reports led Omura (1974) to suggest that an alternative or additional calving and mating area was in the Seto Inland Sea (34°-35°N) off southern Japan, but little direct evidence is available to support this idea.

EXPLOITATION

Groups of Koryak natives (Kamentsy, Parentsy and Itkantsy) living along the northeastern shores of the Okhotsk Sea hunted whales, although the particular species killed by these aboriginal whalers were not well documented (Krupnik, 1984); the author, however, believed that gray whales were hunted until the early 20th century. Whaling by Japanese hand-harpoon whalers was underway by at least the 16th century and Japanese net-whalers continued to take whales during the 17th-19th centuries (Omura, 1984). European and American whalers operating in the western North Pacific (mainly in the Okhotsk Sea) took gray whales from the late 1840s to perhaps the start of the 20th century (Henderson, 1984; 1990). Russian steam whalers took gray whales in the coastal waters of the Far East at the end of the 19th century (Andrews, 1914; Brownell, unpublished data). Japanese and Korean whalers continued to hunt gray whales until as recently as 1966 (Kasahara, 1950; Mizue, 1951; Brownell and Chun, 1977; Omura, 1984).

The reduction in the western Pacific gray whale population can be attributed largely to modern commercial whaling off Korea and Japan between the 1890s and 1960s. The population has been protected from commercial whaling since 1946, under the International Convention for the Regulation of Whaling. The Soviet Union and Japan joined the International Whaling Commission (IWC) in 1948 and 1951, respectively. The Republic of Korea and China, however, did not join until 1978 and 1980, respectively. Prior to their IWC membership, at least 67 gray whales were killed in the period 1948-1966 off the Republic of Korea (Brownell and Chun, 1977). Although no capture records are available from 1967 to the time that either the Republic of Korea or China joined the IWC, it cannot be assumed that gray whale catches did not occur during this period. Kasahara (1950) summarised whaling operations off northern Korea prior to 1945. Today, the Democratic People's Republic of Korea is not a member of the IWC and nothing is known about whaling in its waters since the end of World War II.

Western gray whales were probably never as numerous as their eastern counterparts. While pre-exploitation numbers for the western population are unknown, it has been speculated that they once may have numbered between 1,500-10,000 individuals (Yablokov and Bogoslovskaya, 1984). Berzin and Vladimirov (1981) estimated that only 1,000-1,500 gray whales remained in the population by 1910, after some commercial exploitation had already occurred. However, details of how these pre-exploitation and 1910 estimates were derived are not provided.

Kato and Kasuya (In press) estimated that some 1,800-2,000 whales (including 44 individuals killed by net whaling in the 1890s) were taken in the period 1891-1966, mostly off Korea and Japan. Peak annual catches of 100-200 whales began as early as 1907, but occurred primarily between 1911 and 1919 (no data were available for 1910) during which time at least 1,034 whales were killed, with a mean annual take of 115 whales. In the period 1920-1929, 289 whales were killed, with a mean annual take of 29 whales. By the 1930s, gray whale captures had greatly declined, with only 48 whales killed between 1930 and 1934 for a mean annual take of 10. No known additional catches occurred until 1942. Based on these catch data, it is apparent that by the early 1930s gray whales were far less abundant off the coasts of Korea and Japan and had likely reached commercial extinction. Continued low-level hunting between the 1940s and 1966, including the 67 whales captured in waters off South Korea, resulted in at least 71 whales killed. Kato and Kasuya (In press) hypothesise that the continued, albeit low-level, whaling pressure during this time is responsible for hindering the recovery of the western population. If the projected population size in 1910 was between 1,000-1,500, as estimated by Berzin and Vladimirov (1981), the removal of at least 1,442 whales recorded in the period 1911-1966 lends support to the above hypothesis offered by Kato and Kasuya (In press).

By the 1930s, the western gray whale was considered by many to be extinct (Mizue, 1951; Bowen, 1974). Nishiwaki and Kasuya (1970), believing the western population to be extinct and unaware of the Korean catches and sightings in the 1960s, suggested that sightings of two gray whales, one in about 1959 and one in 1968 off the coast of Japan, represented strays from the eastern population. However, Brownell and Chun (1977) described the probable existence of the western population based on catch records from the Korean coast during a nearly 20-year period between 1948 and 1966. These catch records, combined with the observation of four gray whales in the western Okhotsk Sea in 1967 (Berzin, 1974) and the sighting of a female gray whale and her calf in Korean waters in May 1968 (Brownell and Chun, 1977) indicated that western gray whales continued to survive in small numbers and that the observations reported by Nishiwaki and Kasuya (1970) were likely to be of western rather than eastern gray whales.

CURRENT POPULATION STATUS

The western gray whale population survives as a small remnant population (Blokhin *et al.*, 1985; Weller *et al.*, 1999). Aerial and ship-based sighting records in the Okhotsk Sea between 1979 and 1989 indicated that gray whales aggregated predominantly along the shallow-water shelf of northeastern Sakhalin Island and were most common offshore of the southern portion of Piltun Lagoon (Blokhin *et al.*, 1985; Berzin *et al.*, 1988; 1990; 1991; Berzin, 1990; Blokhin, 1996). Two non-quantitative population estimates have been reported in the Russian literature (Vladimirov, 1994; Blokhin, 1996). An estimate of 250 by Vladimirov (1994) was derived from cetacean sighting records collected between 1979 and 1992 in the Okhotsk Sea; these records were collected from a variety of observation platforms, during different seasons, and employed mostly non-systematic sampling strategies. Although counts may be inflated by repeated observations of the same individuals, the highest number reported by Vladimirov (1994) during any sampling period was 34 gray whales observed in 1989 off northeastern Sakhalin Island. The author does not explain the origin of the estimate 250. An estimate of 100 by Blokhin (1996) was based on eight shore counts and one helicopter survey conducted between July and August of 1995 along the northeastern Sakhalin Island coast. The highest number of whales counted on any one day during that period was 42 but again, the author did not explain the origin of the estimate of 100. Therefore, both of these estimates must be considered unreliable.

Recent photo-identification studies conducted between 1994 and 1999 on the primary feeding ground off northeastern Sakhalin Island (Weller *et al.*, 1999; 2000; Würsig *et al.*, 1999; 2000) have identified a total of 88 individual whales (Table 1). These photo-identification data indicate high levels of annual return and pronounced seasonal site fidelity for most whales (Table 2). While new individuals continue to be identified annually, the rate at which this is occurring is low. Only 18 previously unidentified whales (excluding calves) were photographed during 91 days of effort between 1998 and 1999. This finding suggests that a majority of the population had been identified in the period 1994-1997 (Weller *et al.*, 2000). Between 1995 and 1999, 11 reproductive females and their

Table 1

Annual survey effort, number of groups encountered and whales identified in the period 1994-1999.

Year	Sampling period	No. of surveys	Hours of direct observation	Rolls of film used	Groups encountered	Whales identified
1994	7 Sep. - 12 Sep.					10
1995	15 Aug. - 19 Aug.	5	10.1	15	23	27
1997	9 Jul. - 8 Sep.	22	33.4	72	114	47
1998	6 Jul. - 29 Sep.	35	50.5	91	125	54
1999	29 Jun. - 13 Oct.	56	122.0	160	434	70
Overall		118	216.0	338	696	88*

*The number of whales identified annually includes resightings of individuals from previous years, resulting in a total of 88.

Table 2

Annual sighting trends and resighting percentages of whales photo-identified in the period 1994-1999.

Year	Whales identified	Calves/non-calves identified (crude birth rate)	New non-calves	Non-calves identified from previous years
1994	10		10	
1995	27	2/25*	20	20.0% ($n=5$)
1997	47	2/45 (4.3%)	25	44.4% ($n=20$)
1998	54	8/46 (14.8%)	5	89.1% ($n=41$)
1999	70	3/67 (4.3%)	13	80.6% ($n=54$)

* Insufficient data available to calculate crude birth rate.

15 calves were observed (Weller *et al.*, 2000). Two calves were observed in each of 1995 and 1997, eight in 1998 and three in 1999. Crude birth rates ranged between a low of 4.3% in 1997 and 1999, to a high of 14.8% in 1998. Of the 12 calves identified between 1995-1998, seven (58.3%) have not been resighted on the Sakhalin feeding grounds subsequent to their birth year.

Mature population size[1]

Estimating the number of whales inferred to be capable of reproduction or 'number mature' is problematic for western gray whales because there are limited direct data, and demographic estimates depend on the population growth rate, which is currently unknown. Two approaches are used here to estimate plausible, albeit conservative, numbers mature. The first uses information from Rice and Wolman (1971), who found that 24% of the eastern gray whales in their sample were sexually immature and from this suggested that the total proportion of immature animals in the population was more likely to be 44%-61%. Using the minimum estimate of 88 western gray whales (Weller *et al.*, 1999; 2000) and using the estimated proportion immature from Rice and Wolman (1971), the number of mature whales in the western population ranges between 34 and 49.

However, the eastern gray whale population was growing at the time Rice and Wolman conducted their study and would therefore be expected to consist primarily of immature animals; this would not be the case for a stable population. The second method used here is based on the premise that the proportion mature for a stable population can be estimated using age-specific birth and mortality rates. Rice and Wolman (1971) reported the mean age of sexual maturity for eastern gray whales to be eight years (range = 5-11 years). Reilly (1992) estimated adult survival to be 0.95. Although there are no data for first year survival in gray whales, it is assumed here that survival does not differ strongly from that for humpback whales (*Megaptera novaeangliae*), which is 0.875 (Barlow and Clapham, 1997). For a stable population, therefore, the estimated proportion mature is 63%, which for the estimate of 88 whales in the present case results in 55 mature animals.

In addition to the uncertainty surrounding the estimated values of the population parameters, this estimate assumes that all mature adults are capable of reproduction. If, as suspected, the western population is not growing, then it is plausible that reproduction has been compromised because the population is so small. Data from another small population that has failed to recover provide a pessimistic comparative scenario. Only 70% of North Atlantic right whale (*Eubalaena glacialis*) females known to be mature are reproductively active (IWC, 2001). If it is assumed that all males reproduce but only 70% of the females do, then 85% of the sexually mature animals are capable of reproduction. Thus, of the 55 mature western gray whales estimated using this approach, only 47 would meet the IUCN definition of mature (see below).

Clearly, both these approaches are somewhat crude and are based on assumptions that may not be valid. However, both suggest a mature population size of less than 50 mature individuals, including only 11 known calf-bearing females documented between 1995 and 1999.

Potential threats to the population

Although there is some evidence that an undetermined level of hunting may occur (e.g. Brownell and Kasuya, 1999; Baker *et al.*, 2002), it seems likely that the major threats for this population may stem from indirect mortality (e.g. bycatches and ship strikes) and habitat pollution and degredation.

Gray whales are known to be vulnerable to incidental catches in fisheries (e.g. IWC, 1994) and there are extensive coastal net fisheries off southern China, Korea and Japan (Zhou and Wang, 1994; Kato, 1998; Kim, 2000). The substantial nearshore industrialisation and shipping congestion throughout the migratory corridor(s) of this population also represent potential threats by increasing the likelihood of exposure to chemical pollution and ship strikes. Present and planned large-scale offshore gas and oil development in the South China Sea and in close proximity to the only known feeding ground for western gray whales off northeast Sakhalin Island in the Okhotsk Sea is of particular concern (e.g. see Brownell *et al.*, 1997; Brownell and Yablokov, 2001; IWC, 2002b). Activities related to oil and gas exploration, including high-intensity geophysical seismic surveying, drilling operations, increased ship and air traffic, and oil spills all pose potential threats to gray whales (e.g. Moore and Clarke, 2002). Disturbance from underwater industrial noise may displace whales from critical feeding, migratory and breeding habitat (e.g. Bryant *et al.*, 1984; Richardson *et al.*, 1995; Brownell and Yablokov, 2001). Physical habitat damage from drilling and dredging operations, combined with possible impacts of oil and chemical spills on benthic prey communities, also warrant concern.

A recent concern is the deterioration in physical condition of numerous individuals; during 1999, 2000 and 2001 whales have been observed that appeared to be unusually thin ('skinny') while on the summer feeding grounds (Weller *et al.*, 2000; authors' data). Morphological attributes correlated with this description varied among individuals, but consisted of at least one of the following: (1) an obvious sub-dermal protrusion of the top edge of the scapula from the body with associated thoracic depressions at the anterior and posterior insertion points of the flipper; (2) the presence of depressions near and posterior to the blowholes and head; and (3) a pronounced depression along the neural/dorsal spine of the lumbar and caudal vertebrae resulting in the appearance of a 'bulge' along the lateral flank.

While the causal mechanism(s) for the observed deterioration in physical condition and apparent health status of some whales is unknown, any of the following alone or in combination may be contributing factors: (1) natural or human produced changes in prey availability or habitat quality; (2) physiological changes related to stress; or (3) disease. Regardless of the cause, the loss of even a few whales (especially reproductive females) due to this deterioration in physical condition will greatly hinder population growth and ultimately prevent its recovery. Therefore, it is essential that this situation is carefully monitored and that all anthropogenic activities be reduced to an absolute minimum.

Although a natural occurrence, predation by killer whales (*Orcinus orca*) may also pose an additional threat to the recovery of this population at its currently reduced number. Killer whales are known to kill eastern gray whales, especially calves, off central and northern California (Rice and Wolman, 1971; Baldridge, 1972). Andrews (1914) found killer whale tooth raking on the flukes and flippers of a majority of the gray whales killed off Korea and

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[1] In terms of evaluating the western gray whale population under 'Criterion D' (population estimated to number less than 50 mature individuals) of the World Conservation Union (IUCN), the definition of 'mature individuals' in this context is defined as 'the number of individuals known, estimated or inferred to be capable of reproduction' – see section on 'International concern and conservation measures'.

documented numerous accounts of killer whales attacking both living and already captured gray whales. Although killer whales are somewhat common off the Sakhalin Island gray whale feeding ground, no aggressive interactions between the two species have been observed (Weller *et al.*, 2000). However, of 69 gray whales photographically identified between 1997 and 1998 on the feeding ground off Sakhalin, over 33% had tooth rakes from killer whales on their flukes, flippers or bodies (authors' data). This finding suggests that killer whales are at least threatening, and perhaps killing, western gray whales somewhere within their range but any associated mortality related to these observations is currently unknown.

Other factors, for which the cause is unknown but which give rise to concern for this population include low calf survival estimates ($<42\%$) between 1995 and 1998; a male bias (59.4% males, 40.6% females; $n=64$) in the [biopsy] sampled population and a more pronounced male bias (77.8% males, 22.2% females; $n=9$) in sampled calves.

INTERNATIONAL CONCERN AND CONSERVATION MEASURES

Largely on the basis of the recent information provided by the joint USA-Russia research programme (1995-2001) initiative and summarised here, the World Conservation Union (IUCN) listed the western gray whale population as 'Critically Endangered' in 2000 (Hilton-Taylor, 2000). In particular, this was due to the criterion that the population is estimated to have less than 50 mature individuals.

Serious concern over the status of the population has also been expressed by the Scientific Committee of the International Whaling Commission (IWC, 2002b). As a result of this, the Commission itself passed a Resolution in 2001 calling for concerted action by range states and others to pursue actions to eliminate anthropogenic mortality and disturbances on this population (IWC, 2002a). The IWC also strongly endorsed a continuation and expansion of the current research programme.

CONCLUSION

It is apparent that long-term research and monitoring efforts of the western gray whale population need to be continued and expanded. The extensive past exploitation of this population, in combination with potential new threats from anthropogenic activities throughout its range, raises questions about the potential recovery and continued survival of the western gray whale. Future measures to protect this population will require international research collaboration between all range state countries and development of effective conservation measures and dedicated cooperation between science, industry and government.

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Наблюдения за серыми китами (*Eschrichtius robustus*) юго-востока Камчатки

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Sightings of grey whale (Eschrichtius robustus) near southeastern Kamchatka

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В последние годы в прибрежных водах Камчатки и Командорских островов участились случаи встреч серых китов (*Eschrichtius robustus*). На полуострове они наблюдаются от мыса Рубикон на севере до мыса Лопатка на юге. Основываясь на данных мониторинга, проводимого в отдельных местах со стационарных постов, можно утверждать, что в настоящее время появление серых китов носит регулярный характер.

О встречах одиночных и небольших групп серых китов в камчатской акватории неоднократно упоминалось многими авторами (Слепцов 1955, Votrogov, Bogoslovskaya 1980), но все встречи были характерны для севера Камчатки до м. Олюторский в приграничных с Чукоткой районах, куда заходят серые киты чукотско – калифорнийской популяции. При авиаучетных работах, выполненных в августе 1983 г. южнее м. Олюторского, встречаемость серых китов резко падает (Богословская 2002) и численность их не превышает 30 голов, причем в Карагинском заливе их насчитывалось всего 6 особей. Сдерживающим фактором продвижения чукотских серых китов на юг вдоль Камчатского побережья, возможно, является активная рыболовная деятельность. Например, от устья р. Ильпырь до устья р. Озерная (560 км) в летний период промысла лосося выставляется более 200 ставных неводов с обслуживающим маломерным флотом и крупнотоннажными приемщиками рыбы и эта обстановка является неблагоприятной для обитания китов.

В 1999-2000 гг. два серых кита отмечались в акватории о. Беринга (Командорские острова) в бухтах Лисинской и Никольской. Причем в бухте Никольской киты периодически наблюдались на протяжении более месяца.

Серые киты, наблюдаемые на самом юге Камчатки и Курильских островах, могут принадлежать к охотско-корейской популяции (Blokhin et al. 1985, Votrogov nad Bogoslovskaya 1986). По личному сообщению М.К. Маминова, при обследовании юго-востока Камчатки он наблюдал одиночных серых китов в акватории этого района еще в 1980-х гг.

В бухте Вестник серые киты отмечаются с 1994 г. Ежегодно от 3 до 6 китов проводят здесь 8-9 месяцев. В бухте Ольги киты встречаются с 1995 г. В настоящее время их численность достигает 10 особей (таблица). В устье р. Кроноцкой в 2000-2001 гг. наблюдались 3 серых кита, но позднее обследование данного района не

During the recent years, in the coastal waters of Kamchatka and Commander Islands gray whales (*Eschrichtius robustus*) have been sighted increasingly frequently. In Kamchatka, they have been sighted from Cape Rubikon in the north to Cape Lopatka in the south. Based on monitoring data, conducted in certain areas from stationary posts, there are grounds to conclude today, that gray whales occur regularly.

The sightings of single whales and small groups in the Kamchatka water area, has been repeatedly mentioned by numerous authors (Слепцов 1955, Votrogov, Bogoslovskaya 1980), but all the sightings were characteristic of northern Kamchatka to Cape Olyutorsky in areas bordering on Chukotka where gray whales of the Chukotka-Californian population enter. In the course of aerial surveys conducted in the August 1983 south of Cape Olyutorsky, the rate of occurrence of gray whales sharply declines (Богословская 2002), their number not exceeding 30 individuals, with only 6 individuals in Karaginsky Bay. A limiting factor for advance of Chukotka gray whales southward along Kamchatka shore may be active fishery. For instance, from the mouth of the Ilpyr River to the mouth of the Ozernaya River (560 km) during the summer season of salmon fishery over 200 trap nets serviced by small tonnage fleets and a large-tonnage fish receiver and this situation is unfavorable for whales.

In 1999-2000, two gray whales were recorded in the water area of Bering Island (Commander Islands) in the bays Lisinskaya and Nikolskaya. In Nikolskaya Bay, whales were repeatedly sighted for over a month.

Gray whales observed in the very south of Kamchatka and the Kurils can belong to the Okhotsk-Korean population (Blokhin et al. 1985, Votrogov nad Bogoslovskaya 1986). According to personal communication by A.K. Maminov who surveyed southeastern Kamchatka, he sighted gray whales in the water area of that region as early as the 1980s.

In Vestnik Bay, gray whales have been sighted since 1994. Each year from 3 to 6 whales spend 8-9 months there. In the Olga Bay, whales have been sighted since 1995. To date, their number reaches 10 individuals (table). In the mouth of the Kronotskaya River in 2000-2001 there were 3 gray whales, but subsequent survey of the region concerned was not conducted. During the проводилось. В конце 1990-х гг. в бухте Калыгирь отмечали 2 китов, из которых 1 был детенышем. В устье р. Налычева до 8 серых китов наблюдаются с 1996 г. Киты придерживаются предустьевых зон крупных и средних рек, где они имеют возможность кормиться на выносах ила на небольших глубинах.

Во второй декаде сентября 2002 г. напротив Халактырского Пляжа (район г. Петропавловска-Камчатского) было встречено 6 серых китов на изобатах 50-70 м. В конце сентября 2002 г. в районе бухты Русской был отмечен мигрирующий на юг одиночный серый кит, за которым было проведено наблюдение в течении 38 минут. Всего отмечено 9 серий фонтанов со средней продолжительностью заныриваний между ними 4 мин. 20 сек. (1:18 - 5:56). За период нахождения у поверхности кит делал в среднем 5-6 всплытий с фонтанами (2-9), средняя продолжительность между фонтанами составила 14,9 сек (11-20). Однажды кит занырнул, выставляя хвостовую лопасть, видимо проверяя место на пригодность кормежки (глубина 88 м). После сближения с судном, которое шло параллельным курсом со скоростью 6-5,2 узла и пересечением курса судна по носу и сокращением дистанции с 1,5 км до 200 м, кит стал вести себя осторожно, остановился, начал затаиваться и слегка выставлял дыхало на поверхность воды, практически не давая фонтаны. После ухода судна, кит стал вести себя обычно и сделал серию из 7 фонтанов. После чего наблюдение было прекращено.

Серые киты, обитающие на юго-востоке Камчатки, облюбовали акваторию Кроноцкого заповедника, Южно-Камчатского заказника и прилегающие к ним воды (таблица), где, согласно Правилам охраны и промысла морских млекопитающих, существует 3-х мильная охранная зона, в которой запрещена всякая хозяйственная деятельность, в том числе и судоходство.

Иногда отмечаются отдельные встречи китов в необычных местах. В августе 2000 г. наблюдался заход некрупного животного в реку Большую на западной Камчатке. Другая встреча одиночного кита отмечена в Авачинской бухте в декабре 2003 г. Взрослый зверь провел половину суток в небольшой полынье и спокойно кормился возле механического цеха судоремонтного завода в черте города Петропавловска-Камчатского и ушел вслед за рабочим буксиром. Общее количество китов в акватории полуострова достигает примерно 20-25 особей.

Таким образом, в последние годы серые киты неизвестного происхождения регулярно встречаются вдоль восточного побережья Камчатки и в акватории Командорских островов, хотя и в небольшом количестве. Можно предположить, что в северной части акватории полуострова и на Командорах обитают киты чукотско-калифорнийской популяции, а в южной части акватории Камчатки наблюдаются киты охотско-корейской популяции. Особый интерес представляют киты, встречающиеся в юго-восточной части Камчатки, которые, возможно, появились здесь из-за влияния нефтеразведки и добычи на шельфе о. Сахалин. Так, в 2000 г. серый кит, встреченный на о. Парамушир, был отмечен ранее на о. Сахалин (Трухин А.М., лич. сообщ.).

late 1990s in Kalagyr 2 whales were sighted, one being a calf. In the mouth of Nalycheva River up to 8 gray whales have been recorded since 1996. Whales stick to the pre-mouth zones of big and middle-sized rivers, where they feed at silt accumulations and at small depths.

During the second ten days of September 2002 against the Khalaktyrsky Beach (the region of Petropavlovsk-Kamchatkskу) 6 gray whales were sighted at isobaths of 50-70 m. In late September, 2002 in the Russkaya Bay regions, a gray whale migrating southward was sighted, which was monitored for 38 minutes. A total of 9 spout series with a mean length of diving duration of 4 minutes 20 seconds (1:18 - 5:56) were recorded. While it stayed near the surface, the whales surfaced 5-6 times with 2-9 spouts, the mean duration of the period between the spouts being 14.9 seconds (11-20). Once the whale dived its tail flukes above the surface: apparently it was testing the site for suitability for feeding (depth 88 m). Upon approaching the ship, which was sailing in a parallel direction at a speed of 6-5.2 knots and crossing the course on the bow side and reduction of the distance from 1.5 km to 200 m, the whale started behaving carefully, would protrude the blowhole onto the surface practically without making spouts. After the ship left, the whale behaved normally producing 7 spouts, whereupon the observation was discontinued.

Gray whales dwelling in southeastern Kamchatka prefer the water area of the Kronotsky Reserve, Southern Kamchatka Sanctuary and adjacent waters (table), where according to the Regulations for Protection and Harvest of Marine Mammals, there is a three-mile protection zone, where any economic activity, including navigation, is banned.

Occasionally, there are some individual sightings of whales in unusual places. In the August 2000, a big animal entered the river Bolshaya in western Kamchatka. Another sighting of a solitary whale was recorded in Avachinsky Bay in the December, 2003. An adult individual spent half a day in a small polynya and was quietly feeding near a mechanical shop in a shipyard within Petropavlovsk-Kamchatsky area and left after a tug. The total number of whales in the Kamchatka water area reaches roughly 20-25 individuals.

Thus, during the recent years gray whales of unknown origin regularly occur along the eastern coast of Kamchatka and in the water area of the Commander Islands although in small number. There are grounds to believe that in the northern part of the water area and in the Commander Islands, there dwell whales of the Chukotka-Californian population, and in the southern part of the water area of Kamchatka, whales of the Okhotsk-Korean population are observed. Of special interest are whales occurring in the southeastern Kamchatka, which, presumably, appeared there due to the effect of oil prospecting and oil extraction on the Sakhalin shelf. In fact in 2000, the gray whale that was sighted off Paramushir Island was previously recorded off Sakhalin (Трухин А.М., pers. com.).

Назрела необходимость полного и целенаправленного мониторинга серых китов у берегов Камчатки, выяснения их статуса, происхождения, сопоставления полученных по единой методике данных с материалами из других регионов.

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A need has arisen for complete and goal-oriented monitoring of gray whales off Kamchatka, revelation of their status, origin, comparison according to a single method of data available and materials from other regions.

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Табл. Встречи серых китов на Камчатке (1994-2003 гг.)
Table. Encounters of gray whales at Kamchatka (1994-2003)

Год *Year*	бх. Ольги / *Olga Bay*				бх. Вестник / *Vestnik Bay*			
	Встреч *Observations*	Китов *Whales*	Макс. числ-ть *Max number*		Встреч *Observations*	Китов *Whales*	Макс. числ-ть *Max number*	
			Месяц *Month*	кол-во *Number*			Месяц *Month*	кол-во *Number*
1994	-	-	-	-	46	101	4, 6	6
1995	2	2	6, 10	1	6	8	12	3
1996	1	1	9	1	62	98	8-10	5
1997	5	5	11, 12	1	9	11	6	3
1998	25	38	8, 10	3	111	182	10	4
1999	-	-	-	-	49	79	6, 10-12	3
2000	24	31	6-9	2	38	67	7, 8-11	4
2001	12	23	7, 9	3	56	78	6, 12	3
2002	30	88	7	11	48	56	9, 12	3
2003	16	82	6	10	27	54	12	5
Total	115	270			452	734		

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ECOLOGY

The Peculiarities of Foraging Migrations of the Korean–Okhotsk Gray Whale (*Eschrichtius robustus*) Population in Russian Waters of the Far Eastern Seas[1]

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Abstract—Photographic identification of the Korean–Okhotsk gray whale *Eschrichtius robustus* population has been conducted since 2002 by researchers of the Institute of Marine Biology at the Far East Branch of the Russian Academy of Sciences (IMB FEB RAS), with financial support provided by Exon Neftegas, Ltd. and Sakhalin Energy Investment Co., in order to study the migration features and biology of this species. In 2008, photo-ID studies were carried out in two areas, off the northeastern coast of Sakhalin Island and off the southeastern coast of Kamchatka. As a result of the studies, 122 whales known from the Sakhalin gray whale catalogue were photographed. Of them, 97 individuals were registered off Sakhalin, 24, off Kamchatka, and one whale was observed at both sites. In addition, 25 more gray whales that had not been sighted off Sakhalin Island before were found off the coast of Kamchatka. Based on these photographic materials, the whales physical and skin conditions were also analyzed. Cases of sightings of gray whales in areas that are remote from their traditional summer and fall feeding grounds in the Far Eastern seas of Russia are discussed.

Key words: gray whale, photo-ID, distribution, Sakhalin, Piltun, Kamchatka, oil-gas projects.

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Studies of the relatively small in number and endangered Korean–Okhotsk (or western) gray whale (*Eschrichtius robustus*) population have been conducted off northeastern Sakhalin Island, Russia since 2002 [4, 6, 10]. The work is performed as a part of the monitoring program financed within the oil and gas projects Sakhalin-1 (operated by Exon Neftegas, Ltd.) and Sakhalin-2 (operated by Sakhalin Energy Investment Co.). Observations generally covered the two traditional feeding areas visited by gray whales in the summer and fall: (1) Piltun area (52°40′–53°30′ N), which stretches along the shore opposite to Piltun Bay, where the whales forage mostly at depths of less than 20 m, and (2) the Offshore area located about 30–40 km off Chaivo Bay (51°50′–52°25′ N), with depths of 35–60 m [2, 12, 22]. Recently, gray whales were also observed off the southeastern coast of the Kamchatka Peninsula [1]. Gray whale sightings took place in the waters of Nalychev Bay with depths of around 30 m in 2004; the animals were also observed in Vestnik Bay at depths of about 15–24 m and in waters of Olga Bay at depths of 5–17 m in 2006–2007 [5, 19].

Observations of the gray whale distribution off Sakhalin Island and the Kamchatka Peninsula shows that the current migration pattern of this species along the Asian coastline needs farther investigation. For this reason, the necessity arose to analyze the peculiarities of the interrelations between Korean–Okhotsk and California–Chukchi (or eastern) gray whale populations with the use of additional data obtained through up-to-date techniques. International practice has shown that many questions about the spatial distribution and biology of marine mammals, particularly cetaceans, can be successfully answered by means of photographic identification [8, 13]. Use of this method for the study of the Korean–Okhotsk population of the Gray Whale (*E. robustus*) made it possible to compose the Sakhalin gray whale catalogue [15, 18], which is updated annually. In this paper, we present the results of our efforts on photoidentification of *E. robustus* individuals sighted offshore Sakhalin Island and the Kamchatka Peninsula in 2008.

MATERIAL AND METHODS

The primary data for the gray whale photo-IDs were collected in two areas off Sakhalin Island during expeditions on the R/V *Akademik Oparin* from June 25 to July 23 and from August 24 to October 10, 2008 (Fig. 1). Between these two periods, while the vessel operated under another program off the West Kamchatka shore and along the Kuril Islands, regular day-

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[1] The article was translated by the authors.

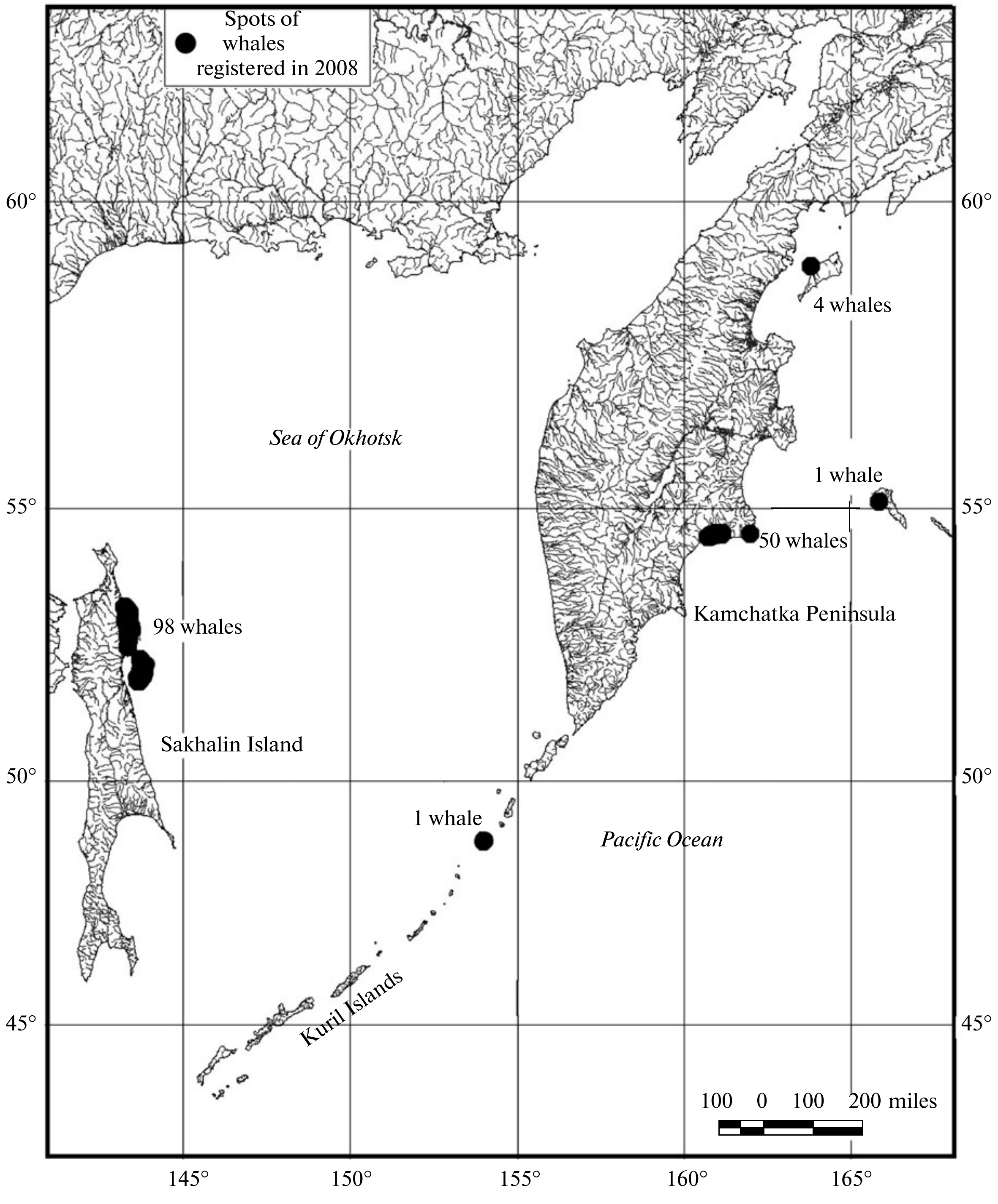

Fig. 1. Distribution of gray whales known from the Sakhalin and Kamchatkan catalogues in waters of Russian Far East in June–October 2008.

time observations of marine animal distributions were also conducted on board.

The material was obtained through the well-coordinated operations of an observer in the pilot house and a research team in a Zodiac boat. When the observer sighted a whale or a group of whales, he informed the team in the Zodiac about the location and distance to the animals, their number, and the behavior. At a distance of around 100 m from a whale, researchers began photo and video recording (with a Nikon D2X digital camera equipped with a telephoto lens Nikkor 80–400 mm and a Sony HDR-HC7 digital video camera). At the time of these operations, the position of the boat (and the whale) was fixed with a

Table 1. Number of whales identified off the northeastern coast of Sakhalin Isl. in 2002–2008

Year	Total per year	Number of whales registered earlier						Number of new whales per year	Number of whales from previous years and not sighted in the current year	Number of whales in the catalogue
		2002	2003	2004	2005	2006	2007			
A	B = C + D + E + F + G + H + I	C	D	E	F	G	H	I	J	K = B + J
2002	47	–	–	–	–	–	–	47	–	47
2003	82	35	–	–	–	–	–	47	10	92
2004	96	39	33	–	–	–	–	24	22	118
2005	117	41	40	18	–	–	–	18	19	136
2006	121(5)*	42	37	15	14	–	–	13(5)*	27	148(5)*
2007	125(4)*	40	39	16	10	7	–	13(4)*	35(5)*	160(9)*
2008	98	33	33	17	5	3	2	5	67(9)*	165(9)*

Note: * Whales in brackets have temporary ID Nos. This ID is assigned to an animal that does not have good photographs of its right side in the catalogue.

GPS receiver, and other characteristics of the environment, such as the depth, sea state, presence of other marine mammals or watercraft, the whales mud plumes, etc., were recorded.

The same type of information was collected during the studies in Olga Bay off the Kamchatka Peninsula shore (Fig. 1). Whales were photographed through a Canon 40D digital camera with a 75–300 mm telephoto lens.

Individual gray whales were identified by distinctive marks on their sides and flukes. For this, we used standard photo ID methods, which are described in Special Issue No. 12 of the International Whaling Commission [9]. Left to right side matches were recognized confidently provided all the following criteria were satisfied: (1) the whale was photographed as a solitary individual; (2) two photographic series of both sides of the whale with the same fluke were obtained during one sighting; (3) as a final check, the height, spacing and ratio of the distinctive knuckles in the ridge on the caudal peduncle were considered [7]. A whales body pigmentation was the primary feature used in identifying individuals, and scars and barnacle patches were considered as supplementary signs.

Upon being included into the Sakhalin catalogue, whales recorded off Sakhalin were assigned an ID number starting with KOGWno., and those observed in Kamchatkan waters received the code KamGW with an ID number in the Kamchatka catalogue. If known gray whales were sighted in both regions, then they were assigned dual numbers, for instance, KOGWno. = KamGWno., and included in both catalogues. Special attention was paid to finding whales with various abnormalities in physical condition of their bodies, obvious sloughing, or an anomalous skin condition.

Data obtained in previous years of studies [3, 11, 15, 17] and data from direct counts of gray whales [20] were also used when discussing the results of the photo-ID conducted in 2008.

RESULTS AND DISCUSSION

Number of Identified Gray Whales

The Sakhalin gray whale catalogue created in 2002 and updated annually now numbers 165 identified individuals (Table 1). Among the whales listed in the catalogue, some individuals have been regularly registered off Sakhalin Island for the past 6 years, other ones have not been seen for a long time, and a third group were found for the first time. In 2008, 97 gray whales from the Sakhalin catalogue were sighted on the shelf off Sakhalin Island, 24 individuals from the same catalogue were photographed in Olga Bay, Kamchatka Peninsula, and one whale was seen both off Sakhalin and Kamchatka. Thus, in 2008, we observed 122 whales known by the Sakhalin catalogue (Fig. 2).

Currently the Kamchatka catalogue, which was composed in 2004, numbers 78 gray whales; 39 of them are also included in the Sakhalin catalogue, which means they were sighted off Sakhalin previously. In 2008, among 50 gray whales registered off southeast Kamchatka, 25 individuals had never been observed previously off Sakhalin Island and therefore were not entered in the Sakhalin catalogue. It is now unclear if these whales belong to the Korean–Okhotsk

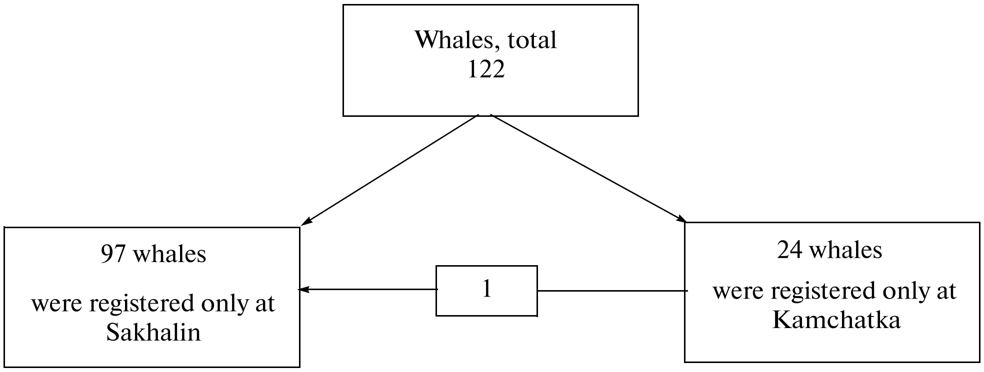

Fig. 2. The number of Gray whales that were registered, (i.e. photoidentified) in Sakhalin and in Olga Bay, Kamchatka, in 2008.

(western) or California–Chukchi (eastern) population.

In 2008, the total number of gray whales identified offshore Sakhalin Island was 98, which was fewer than in 2007 (125 individuals). This can be probably explained by the duration of the studies and the number of whale sightings. Thus, photo-ID studies offshore Sakhalin in 2008 lasted for 29 days and those in 2007 lasted for 62 days. Consequently, the number of registrations of animals in 2007 was about 2.5 times larger.

Gray Whale Movements between Feeding Areas

The data available show that gray whales not only perform seasonal migrations from their wintering sites to the areas where they forage in summer and fall, but also make significant spatial relocations in order to use resources of one or several feeding areas [3, 22]. The spatial relocations of this kind can be divided into intra-annual and inter-annual ones.

Intra-annual relocations of whales between feeding areas can be of various scales. An example of relatively small-scale relocations is whale movements between feeding areas off the northeastern Sakhalin coast. In 2008, of all the 98 whales identified in Sakhalin waters, 36 were sighted only in the Piltun feeding area, another 36, only in the Offshore feeding area, and 25 more whales were registered in both sites (Table 2). This fact indicates that some of whales use both feeding areas in the same season. Furthermore, one whale among those sighted in the Piltun and Offshore feeding areas was also found north of the Piltun area, in the nearshore waters not far from the town of Okha. Cases of intra-annual relocations like these were also recorded previously; in 2007, 38 whales were registered both in the Piltun and the Offshore feeding areas.

Table 2. Grey whale relocations between feeding areas on the northeastern shelf of Sakhalin Isl. in 2002–2008

Year	Number of whales identified in various areas						
	Piltun	Offshore	Piltun and Offshore	Chaivo	Chaivo/Piltun and Chaivo/Offshore	northern areas	Chaivo/Piltun/Offshore
2002	13(12)*	35(34)	1	–	–	–	–
2003	51(47)	35(31)	4	–	–	–	–
2004	95(89)	7(1)	6	–	–	–	–
2005	114(109)	7(2)	5	–	–	5(1)	–
2006	105(67)	33(14)	16	28(7)	19(1)	–	2
2007	93(48)	70(25)	38	20(0)	13(0)	–	7
2008	61(36)	61(36)	25	1(1)	–	1	–

Note: * Whales in brackets were registered only in the areas above.

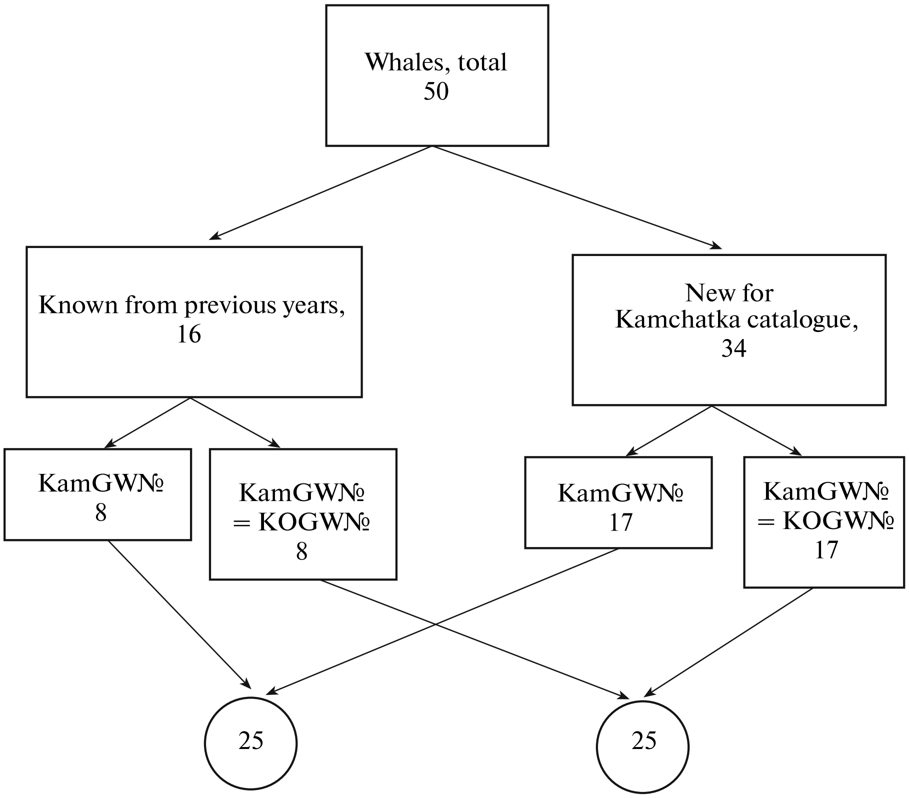

Fig. 3. Gray whales from the Sakhalin catalogue that were registered off the northeastern coast of Sakhalin Isl. (KOGWno.) and in Olga Bay, southeastern coast of the Kamchatka Peninsula, (KamGWno.) in 2008.

It was also established that whales may forage both in Sakhalin waters and off Kamchatka during the same season, which means they make large-scale intra-annual relocations. Two whales in 2006 and one whale in 2008 were first identified off Kamchatka, and later in the season they were found again in the Offshore feeding area off Sakhalin. In 2007, 13 whales sighted off Kamchatka were then observed in Sakhalin waters.

Inter-annual relocations are whale movements between feeding areas over consecutive years. Thus, some of the whales that were seen in 2008 only in the Piltun feeding area were recorded in the Offshore feeding area in previous years. Half of the whales registered in Olga Bay, Kamchatka Peninsula, in 2008 previously had been recorded off Sakhalin (Fig. 3). Those ten whales recorded off the Sakhalin shore in 2008 were also sighted off Kamchatka in 2007. In 2007, 20 of 37 whales identified on the southeastern shelf of Kamchatka had been sighted off Sakhalin in previous years. Similarly, 5 whales of the 13 sighted off Kamchatka in 2006 were also observed off Sakhalin Island both in previous and subsequent years.

It should be mentioned that, besides the previously known areas of whale aggregations that form off the northeastern coast of Sakhalin Island and off the Kamchatka Peninsula in the summer and fall, other areas in far eastern seas exist where representatives of the western gray whale population have been repeatedly observed. After the pictures of three whales photographed in Kekurny Bay on July 13, 2006 and Babushkin Bay on July 28, 2006 in the Northern Sea of Okhotsk, were analyzed the animals were included in the new catalogue under the ID code NOGW [19]. In 2007, one of these whales was sighted both in the Piltun feeding area and in Olga Bay and therefore assigned the ID number KOGW159/KamGW034/NOGW003 in the Sakhalin and Kamchatkan catalogues. Furthermore, one whale that was registered in Olga Bay, Kamchatka Peninsula, in 2007 was then photographed in Zakatny Bay off Shiashkotan Island, Kuril Ridge, in 2008. Later in 2008, this whale was sighted again in Olga Bay (Fig. 1). On June 6, 2008, one whale photographed near Medny Island, Commander Islands, had been encountered in Olga Bay, Kamchatka, in 2007, and then was sighted again in Olga Bay in August 2008. Four gray whales observed off Karaginsky Island, Northeast Kamchatka, on July 8, 2008, previously had not been sighted anywhere else (Fig 1). It is difficult to judge if the new locations of gray whale sightings given above are potential feeding areas for these animals, because data are scarce and no reliable evidence of their foraging there has been obtained. But we may suppose that these are cases of spatial relocations that gray whales make in search of sites with enough food resources.

Data on the movements of young whales are of great interest. A total of eight whales first recorded as calves off Sakhalin in 2007 were photographed in Olga Bay, Kamchatka Peninsula, in the following year. A whale identified as a suckling calf in the Piltun feeding area in 2004 was never seen there subsequently but was regularly registered off Kamchatka in 2006, 2007, and 2008. Similarly, two calves that were identified first in the Piltun area in 2003 were observed only off Kamchatka during the 3 years noted above. One whale that was identified as a calf off Sakhalin in 2005 was repeatedly sighted there in 2006 and 2007 and then photographed off Kamchatka in 2007 and 2008.

Mother–Calf Pairs

Unlike other categories of whales, mother-calf pairs were registered only in the Piltun feeding area until 2008. They were observed most frequently in shallow waters near the Piltun Bay opening, in the sites of higher concentrations of benthic organisms, where mothers teach their offspring to forage from July through mid September. In 2008, three cow–calf pairs and two independent young whales, possibly calves, were photographed in the Piltun feeding area.

In 2008, for the first time in the entire period of studies one cow–calf pair was recorded in Olga Bay, Kamchatka Peninsula. Previously, this mother was recorded offshore Sakhalin in 2002–2006 and in Olga Bay, Kamchatka, in 2007. In 2003, the female brought her calf to Sakhalin. The low occurrence of mother–calf pairs in Kamchatkan waters can be more probably explained by the smaller scale and shorter duration of gray whale observations, as compared to those conducted off Sakhalin.

The Physical Conditions of Whales

As we showed earlier in materials collected in 2005–2007, characteristics of the bodys physical condition (BPC) in the underfed and sometimes very emaciated whales that arrive to feed offshore Sakhalin Island in the spring greatly improve during summer [16].

In 2008, the BPC in 20 whales (including three nursing cows) photographed offshore Sakhalin in the beginning of the season was lower than the normal level. For the summer and fall season, the body condition of eight whales improved to the normal level. However the rest of the animals either did not restore their normal BPC or were not observed in the late season. Furthermore, five of the six nursing cows that had subnormal body conditions in 2007 were again photographed in 2008 when all five had regained their optimum physical state. As in previous years, the body condition of all the calves recorded in 2008 fitted the optimum.

The high-quality photographs also allowed evaluations of skin condition. In 2008, no whales were recorded with skin sloughing, as had been the case previously [21]. However, two individuals had noticeable white patches of an unknown nature on their skin; the same had been earlier observed in western grey whales [14].

CONCLUSIONS

Based on the results presented here, it can be concluded that adult individuals of the studied population of gray whales perform intra- and interannual relocations between the Piltun, Offshore, and Kamchatkan areas. One of the probable explanations of a behavior like this is changes in food abundance, although comprehensive monitoring studies of the composition and resources of benthos and nektobenthos in the newly discovered areas of whale sightings are needed to substantiate this statement.

Half of the gray whales listed in the Kamchatka catalogue (39 of 78 individuals) probably belong to the western population, while the affiliation of the other half remains unclear. The same can be said about the whales identified off the southeastern shore of Kamchatka in 2008; half of them (25 of 50) had been earlier included in the Sakhalin catalogue, and the population status of the remaining ones is undetermined. These results allow us to make two suppositions: (1) a substantial proportion of gray whales of unknown origination belong to the western population but they have not been sighted near Sakhalin Island to date; or (2) these gray whales belong to the eastern population. In the former case, it is necessary to ascertain why individuals of the western population have not been registered near Sakhalin Island. With the latter supposition, we can assume that gray whales of the eastern and western populations are not sufficiently isolated from one another geographically, and an overlap of their ranges exists in feeding areas.

The recent gray whale sightings in the Northern Sea of Okhotsk, off Shiashkotan Island, Kuril Ridge, and off Medny Island, Aleutian Ridge, indicate that these animals can be encountered in places other than off northeast Sakhalin Island or southeast Kamchatka. However, up to this time, encounters like these have remained sporadic and it is still poorly known why and how frequently these sites are visited by gray whales.

To better understand the degree to which western grey whales have fidelity to certain feeding areas, to reveal peculiarities in the movements made by animals between the feeding areas, to establish the frequency of their visits, and to find the causes of these movements, we need additional data that would cover the entire variety of gray whale habitats and the routes of their seasonal migrations.

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Observations of Western Gray Whales by Ship-based Whalers in the 19th Century

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Abstract

Animals belonging to the small, endangered population of western gray whales (*Echrichtius robustus*) are observed today primarily during the summer open-water season in feeding areas off the north-eastern coast of Sakhalin Island, Russia. The migration route(s) and wintering area(s) used by this population are largely unknown. Gray whales once had a fairly extensive distribution in the Sea of Okhotsk but little detailed information has been published on when and where they occurred. Open-boat, ship-based whalers from the United States and a few other countries conducted an intensive hunt for bowhead whales (*Balaena mysticetus*) and North Pacific right whales (*Eubalaena japonica*) in the Sea of Okhotsk from the 1840s to 1870s. According to entries in voyage logbooks, the American whalers regularly encountered (and sometimes hunted) gray whales in the far north-eastern corner of the Okhotsk Sea (Shelikhov Bay, Gizhiginskaya Bay and Penzhinskaya Gulf) between early May–late August. They also observed gray whales in summer along the northern coast of the sea (especially Tauskaya Bay), around the Shantar Islands, in Sakhalin Bay, off Cape Elizabeth at the northern tip of Sakhalin Island and along the west coast of the Kamchatka peninsula. No evidence was found in the logbooks studied of gray whales (and indeed of whaling effort) off north-eastern Sakhalin Island where most observations of gray whales occur in the present day.

Introduction

Recent and current interest in gray whales (*Eschrichtius robustus*) from the western Pacific (Korean-Okhotsk) population has centred on that population's endangered status and the ongoing threats to its survival and recovery. Specifically, there is concern about (a) the small number of whales in the population; (b) environmental degradation and disturbance from oil and gas development on the north-eastern Sakhalin Island shelf, the main area where the population is presently known to congregate in summer to feed; and (c) mortality of gray whales in Japanese waters, mainly in set nets.

The history of this population has been reviewed by Mizue (1951), Nishiwaki and Kasuya (1970), Brownell and Chun (1977), Omura (1988), Weller et al. (1999, 2002) and Kato and Kasuya (2002). In addition to those reviews, Henderson (1972, 1984, 1990) made reference to ship-based whaling on the western population during the 19th century, primarily by American and French whalers. In our recent studies of whaling history in the North Pacific, we have examined a sample of American voyage logbooks that contain substantial unpublished data on western gray whales. The present paper uses those data to describe where and when western gray whales were observed by ship-based whalers during the 19th century.

The data confirm that in the past gray whales used various parts of the Okhotsk Sea, likely as feeding grounds and as routes to and from such grounds. Given the rapid proliferation of offshore oil and gas operations around the perimeter of the Okhotsk Sea as well as on the entire Sakhalin Shelf, understanding the historical (and thus both current and potential) summer range is essential.

Background

Offshore or ship-based whaling for gray whales along the Asian coast from southern China to Japan and in the Sea of Okhotsk has been less well documented than shore-based whaling there. Among the reasons for this difference is the death in June 1999 of David Henderson, who authored classic studies of the American pre-modern, ship-based fishery for *eastern* Pacific gray whales (1972, 1984) and was working on a similarly exhaustive study of the Okhotsk fishery for *western* Pacific gray whales (e.g. see Henderson 1984, p. 176, note 14; Kugler 1984, p. 157, note 6). Henderson (1972) provided only limited information on western gray whales although on his Map I, he offered an intriguing sketch of their distribution (Fig. 1). Henderson's 1984 book chapter (pp. 176-177) indicates that gray whales were not hunted by the American whalers in the Sea of Okhotsk until sometime in the 1840s and that catches of 6-7 whales per ship were being made by the 1850s. He judged that the total kill of gray whales in the Okhotsk Sea by the American fleet was probably similar to that in the Bering Sea and Arctic Ocean, i.e. a few hundreds (his estimate of total kill in the latter areas between 1845-1874, adjusted for hunting loss, was 539; Henderson 1984, p. 169). Some American whaling for gray whales continued in the Sea of Okhotsk until at least the mid-1880s (Henderson 1984, p. 177), by which time most of the remaining Arctic fleet was committed to the 'hazardous, though profitable, whaling in the Arctic [i.e. Bering, Chukchi and Beaufort seas]' (Clark 1887, p. 19). The Sea of Okhotsk was also a frequent destination of French whalers from the mid 1840s until perhaps the mid 1860s (Du Pasquier 1982, pp. 183, 192, 245-249; Kugler 1984, p. 152) and they probably took at least some gray whales although we have not found any direct evidence for this (Du Pasquier 1986, p. 274). At least three Russian whaleships (all originating from Finland) also visited the Okhotsk Sea in the 1850s (Clark 1887, pp. 206-207).

The Okhotsk Sea fishery for balaenids was most intensive from 1847-1867, with nearly 1,400 vessel-seasons, 90% of them from the United States and the rest from France, Bremen, Russia, and the Hawaiian Islands, and occasionally Great Britain, Norway, and Chile (Kugler 1984, p. 153). As an example of the intensity of this fishery, one ship's logbook reported that 65 other whaling vessels were in sight on 27 August 1854 in Shantar Bay (*Good Return*). In that same month, Lindholm (1863) counted 82 ships in the bay and on one day 363 whaleboats were in sight from his ship (*Storfursten Constantin*). Bowhead whales (*Balaena mysticetus*) and North Pacific right whales (*Eubalaena japonica*) were the principal targets and, according to Henderson's preliminary analyses (as reported by Kugler, *op cit.)*, more than 15,000 bowheads and

2,400 right whales were killed and processed by the Okhotsk whalers in those first 20 years. The fishery continued until the 1890s.

Henderson's only publication containing data on western Pacific gray whales (apart from the few references to Okhotsk whaling in his 1972 book and his 1984 book chapter) was a short article on American whaling in southern China in the 1860s (Henderson 1990). There he recounted two voyages to the 'Chinese gray whale ground' in the winter of 1868-69 – by the New Bedford ships *Cornelius Howland* and *Onward*. Although they failed to strike any, the crews of these vessels sighted gray whales near the Chinese mainland coast at c. 25-26ºN off the island of 'Hatan Ho Tan' (Haitan, Pingtan Dao, or Tao on modern maps, according to Henderson), in the middle of Taiwan (Formosa) Strait, and off the northern coast of Taiwan.

Materials and Methods

In addition to a search of the literature, we sampled whaling voyage logbooks from the Kendall Whaling Museum and Old Dartmouth Historical Society collections, both available at the New Bedford Whaling Museum library in New Bedford, Massachusetts. Okhotsk Sea logbooks were identified using library finding aids, *Whaling Logbooks and Journals* (Sherman et al. 1986), and *The History of the American Whale Fishery* (Starbuck 1878), as well as through references in logbooks to other vessels sighted or 'spoken' on the grounds. Data from the logbooks, including date, position, details concerning whale observations, and other vessels spoken, were entered into an Access database and plotted using ArcMap.

Frequently, the exact location could not be determined from the logbook and therefore it was necessary to estimate positions by interpolation and reference to landmarks. A particular problem encountered while working with this material was that place names used by the American whalers did not always correspond to the Russian names. For that reason, we compiled a gazetteer in the course of our logbook reading as a research tool. Sketch maps prepared by the whalers themselves were useful in that regard (Fig. 2). A composite map of the region was developed from a variety of sources (Fig. 3). When places are mentioned throughout the text of this paper, alternative names have been indicated in brackets.

The American whalemen used several different terms to refer to gray whales, including ripsacks (rip sacks), musseldiggers (mussel diggers), devil fish, scrags, scamperdowns, California grays, graybacks and California whales.[1] They called bowheads polar whales, steepletops, bowheads (bow heads) or often just whales (in most but not all instances, the species can be inferred from the context). Blue whales (*Balaenoptera musculus*) were consistently called sulphur bottoms (or sulfur bottoms). Right whales, humpback whales (*Megaptera novaeangliae*) and 'finback' whales (probably mainly fin whales, *B.*

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[1] Henderson (1972, pp. 34-35; 1984, pp. 163-164) included mud digger, digger and hard head in the list of names used for the gray whale by American whalemen, but we did not encounter these terms in our limited sampling of logbooks.

physalus, though this name also may have been applied to sei whales, *B. borealis*) were referred to as such.

Results

Our sample of logbooks included 21 multiyear voyages that visited the Okhotsk Sea one or more times, for a total of 43 ‘vessel-seasons’ in the Okhotsk. The ships were in the region for more than 5000 days, and daily positions have been determined or estimated for most of those days (Fig. 4). The sampled voyages spanned the period from 1847-1885 though the majority of them took place in the 1850s and 1860s. Logbooks of 14 voyages, including 24 vessel-seasons in the Okhotsk, contained references to sightings of gray whales. There was a total of 152 daily entries with observations of gray whales, including sightings, chases, strikes and captures (Fig. 5).

Occurrence

Citing early Russian literature, Yablokov and Bogoslovskaya (1984) described gray whales (and humpback whales) as having been “very common and even abundant in the coastal waters of the northern part of the Okhotsk Sea and off the western shores of the Kamchatka Peninsula.” They surmised (as did Tomilin 1957, p. 314) that gray whales migrated into the Okhotsk Sea from the Sea of Japan via both Tatar Strait (Tatarskiy Proliv) and La Perouse Strait. Indeed, American logbook data imply that gray whales at least occurred in or near La Perouse Strait in mid-June (e.g. some were sighted and chased there by *Cicero*, 16 June 1859, c. 46ºN, 142ºE). Vladimirov (2004) questioned the feasibility of gray whales entering (or leaving) the Okhotsk Sea via Tatar Strait ‘due to the small depths of the Amur Firth (2-3 m) … which must be a natural obstacle for migrating animals’. In contrast, Rice and Wolman (1971, p. 20), citing Mizue (1951), suggested that all gray whales passed through Tatar Strait ‘as none was ever seen in La Perouse Strait’.[2]

Many voyages to the Okhotsk Sea originated in Hawaii and therefore the ships entered via the northern Kuriles (usually in the vicinity of Paramushir Island) and then worked northwards along the western shore of Kamchatka. According to Henderson (1972, p. 87, citing reports from *Fortune*, 6-8 June 1855, *Mary and Susan*, 19-30 August 1848 and *Montezuma*, 30 May and 29 September 1860), gray whales were observed mainly along the northern coast of the Sea of Okhotsk, and this is consistent with Yablokov and Bogoslovskaya (1984).

Gray whales were observed consistently by the American whalers in the southeastern portion of Shelikhov Bay (Zaliv Shelikhova) and in Penzhinskaya Gulf (Penzhinskaya

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[2] From Mizue (1951, p. 79): “… it is reported by Mr. Tago that they reach Hokkaido or the western coast of Sakhalin in May or June and then through the Mamiya [Tatar] Channel go to the northern part of the sea of Okhotsk, where they seem to spend their summer. On their southwards migration they seem to take the same course as they come up north. It is not probable that grey whales pass through the Soya [La Perouse] Channel to the farther north, for fin and hump-back whales are captured there from the landstation in Hokkaido but not grey whales.”

Guba) from early May (earliest record 6 May 1885; *Mary and Helen II*) to the end of August (approximately 43 observations in our sample; Fig. 5). They were seen in Gizhiginskaya Bay (North-east Gulf) between mid-May and late August (approx. 46 observations, including a report of ‘thousands of devilfish but no bowheads’ in the logbook of the *Benjamin Cummings* on 3 June 1869) and in the vicinity of Magadan along the north-central coast of the Sea of Okhotsk (i.e. in Tauskaya Gulf/Guba, generally called Tausk or Taousk Bay) from at least early June to early July and from mid-August to mid or late September (approx. 19 observations). Gray whales were seen occasionally just east of Okhotsk City in the north-western Sea of Okhotsk (*Lancaster*, 12 September 1860; *Oliver Crocker*, 29 August 1861). There is little evidence that they still occur in any of those northern areas (Maminov and Blokhin 2004) although it is unclear how much search effort has been expended there at the appropriate times.

Only a handful of references to gray whales in the vicinity of the Shantar Islands were found in the logbooks: ‘a few rip sacks’ northeast of Big Shantar Island on 5 June 1860 (*Oliver Crocker*), ‘muscle diggers’ somewhere in the Shantars on 7 September 1855 (*Nassau*) and ‘Devilfish or Ripsack whales’ in Taylor’s Bay, off Ulbansky Bay, on 13 August 1885 (*Mary and Helen II*). Another sighting was recorded about midway between Ayan and the Shantar Islands on 14 June 1860 (*Lancaster*). Tomilin (1957, p. 314) cited Russian observations in Akademii and Ulbanskii bays. Also, in recent years a few observations have been reported in September in Tugurskiy and Ulbanskiy bays (Maminov and Blokhin 2004).

The American whalers observed gray whales, sometimes in sizeable concentrations (e,g., 20-30 seen in a day, references to “plenty” being seen), in Sakhalin Bay (Sakhalinskiy Zaliv) and off Cape Elizabeth (Mys Yelizavety) at the northern tip of Sakhalin Island (*Mary and Susan*, various entries between 18 August – 9 September 1848). A sighting of two gray whales in summer 2005 in Severnyy Bay (just south-west of Cape Elizabeth) (Tyurneva et al. 2006) demonstrates the continued use of that area by the extant population. Also, gray whales were seen in southern Sakhalin Bay in August 2000 (Maminov and Blokhin 2004).

Finally, American whalers sighted gray whales at least occasionally near the northern (Cape Huntsville, 58º05'N, 157º06'W; *Europa*, 17 May 1869), central (vicinity of Moroshechnoye, 55º51'N, 155º52'E; *Mary and Susan*, 13 July 1849) and southern coasts of western Kamchatka (51°16'N, 155º23'W; *Europa*, 14 September 1868). Although Blokhin (1996) reported that gray whales had not been seen along the western coast of Kamchatka in many years, one was reported in August 2000 at the mouth of the Bolshaya River (Vertyankin et al. 2004). In that regard, the logbook of *Mary and Helen II* refers to arrival at the Bolshaya mouth on 12 September 1885, the vessel having departed the Shantar Islands on 23 August bearing east “for ‘Bolshaya River’ for Right Whales”. The 13 September logbook entry states: “I am bound back to the west end of the Sea north of the Shantar Islands for I am convinced there are no whales to be seen about this locality or where I have been expecting to find ‘Ripsack Whales’ off the mouth of the ‘Bolshaya River’.” Having found neither right nor gray whales off Kamchatka, the *Mary and Helen*

II relocated to Tauskaya Bay, with the top of the logbook page for 19-20 September declaring, “In ‘Tausk Bay’ among the ‘Ripsack Whales’.”

In recent years sightings of gray whales have become regular in Olga Bay (between Cape Seniavin and Cape Kozlov) and Vestnik Bay (just north of Cape Lopatke, c. 51º35'N) on the south-eastern coast of Kamchatka (Vertyankin et al. 2004) and at least some of the individuals seen there have been photographically matched to individuals observed off north-eastern Sakhalin (Yakovlev et al. 2007).

We found no evidence beyond that presented by Henderson (1990) that American whalers observed or took gray whales in Chinese waters where sightings and a few strandings and kills were reported in the 20th century (Wang 1984; 1993, 1999; Zhu 1998; Blokhin and Blokhin 2006). However, our logbook sample included little coverage of whaling in those waters.

Removals

Our reading of logbooks thus far has not revealed any major inconsistencies with Henderson’s (1984) findings as summarised above. Gray whales clearly were secondary targets and they were pursued mainly at times when the preferred bowheads and right whales were unavailable. For example, in 1859 the ship *Oliver Crocker* arrived in Tauskaya Bay at the end of May, with its first sighting of ‘mussel diggers’ reported on 3 June. Within a few days the boats were engaged in the pursuit of bowheads in the bay. Three were bomb-lanced and/or harpooned, but lost, between 6-10 June. By 15 June the run of bowheads had ended, and after a few more days the hunt for gray whales began. Between 19-30 June the *Crocker*’s boats were lowered daily and no fewer than nine gray whales were taken and processed. In addition at least two were lost when the harpoon drew or the line was cut. Two of the processed whales had sunk initially and, in both instances, were only recovered two days later. Three other ships were spoken in the bay during the second half of June – *L.C. Richmond*, *Robert Morrison* and *Cambria* – but it is unclear whether any of them took gray whales (the *Richmond* was seen taking a bowhead on 13 June; the *Cambria* reportedly had taken three bowheads that season as of 30 June). On 1 July the *Crocker* sailed towards the Shantar Islands where bowheads were plentiful and hunting for them resumed on 11 July. There is no further mention of gray whales that year in the *Crocker* logbook. Also, in the next two years, even though the *Crocker* followed a broadly similar itinerary, there is nothing in the logbook to suggest another episode of intensive gray whaling. Two were taken in North-east Gulf on 3 August 1861, the only day during the 1861 season when the logbook indicates the boats were lowered for ‘ripsacks’.

The ship *Europa* arrived in Gizhiginskaya Bay (North-east Gulf) early in the 1868 season, with its first bowhead sighting on 19 May. From then until 28 June, when the first bowhead was taken, only one more bowhead was seen by the crew (on 7 June), whereas gray whales (and ‘finbacks’) were seen often and the boats were lowered on at least three occasions with the explicit intention of hunting gray whales (none was taken by the *Europa* until 20 June). The logbook records that on 5 June 1868: “Lowered for Ripsacks for the purpose of trying our new whaling guns, tried four shots and the irons would not enter the blubber.” In 1869 the *Europa* followed the same itinerary but had more success finding and taking bowheads, and there was only one brief lull (11-12 June) when attempts were made to take both gray whales and a ‘finback’. Later that season (26 July), the *Europa* ‘picked up’ and processed a dead gray whale found floating in Penzhinskaya Gulf between Ship Rock and Big Grampus Island and the log refers frequently to ‘ripsacks’ being observed (e.g. 17 August near Ship Rock, ‘…not seeing anything but Ripsacks’) but with only one more desultory attempt made to hunt them (27 August).

In 1885 the *Mary and Helen II* reached the north-eastern part of the Okhotsk Sea by the end of April and gray whales were sighted on 6 May and again on 20 May, by which time no bowheads had yet been seen. In fact, only one brief sighting of a bowhead was made before mid-June. Even though gray whales were seen many more times, the boats were not lowered to chase them (except on 21 June and 11 July ‘by mistake’) until the brief and intense episode in Tauskaya Bay in mid-September mentioned above.

Before the present study is considered complete, we expect to produce a quantitative estimate of the American catch of western gray whales, adjusted appropriately to account for hunting loss. For the present, we note the following catch information: 9 (plus 2 struck/lost) by *Oliver Crocker* in 1859 and 2 in 1861 (see above); 1 by *Florida* (15 bbl) (Williams 1964, pp. 185) and 1 by *South Boston* in 1861 (Williams 1964, p. 186); 4 by *California* in 1863 (Henderson 1972, p. 87); 1 each by *Endeavour*, *Rainbow* and *Europa* in 1867 (*Europa* 1867); 1 by *Europa* (salvaged) in 1869; and 4 by *Mary and Helen II* in 1885.

The estimated total landed catch of western gray whales by modern whaling and Japanese net whaling between 1890-1966 was 1,800-2,000 (Kato and Kasuya 2002). No other catches are known to have taken place during that time or since 1966 although some unreported catches may have been made by catcher boats from the People’s Republic of China or the Republic of Korea, neither of which belonged to the International Whaling Commission until 1980 and 1978, respectively. It is also possible that some catches were made by whalers from the Democratic People’s Republic of Korea or from Taiwan.

Discussion

Occurrence

Mizue (1951) analysed catch dates and positions for 545 gray whales in the ‘East Sea Area’ of Korea. The catches all occurred between November and May with a strong peak in December (63%) and January (22%). The infrequency of catches in other months from September through March apparently was not related to effort because, as Mizue (p. 76) points out, the same area was an important whaling ground for fin whales and ‘many catcher-boats work during the season, from September to March next year’ and so the whalers ‘would have certainly caught grey whales if they had seen them in the months of October, November, February and March’.

The speculation by Mizue (1951) that gray whales migrated northwards from Korea through the Mamiya Channel (Tatar Strait) in May or June and thence to summering grounds in the northern Sea of Okhotsk is not inconsistent with some of the American whalers' observations. It is unclear, however, whether Mizue was correct in his belief (shared by Andrews 1916, p. 210) that gray whales calved and mated in Korean waters. There is no reason to doubt that at least some of the whales migrated to as far south as 25ºN along the Chinese mainland and moved though Taiwan (Formosa) Strait (Henderson 1990). Also, it is important to consider that Mizue's reasoning that gray whale females with large foetuses taken in mid-December off Korea were 'immediately before birth' and that 'delivery is made among the islands at the southern extremity of the Korean Peninsula' was without the benefit of Rice's (1983) analysis showing a 'prenatal diapause' in eastern Pacific gray whales such that foetal growth 'virtually ceases' during the final month of pregnancy and birth occurs between early January and mid-February (median 27 January). It is therefore plausible that the strong peak in occurrence of female gray whales in Korean waters from early December to early January (Mizue 1951, his Table 5) represents primarily a movement of migrating animals towards a destination farther south for parturition.

Based on the American whalers' observations summarised in this paper, gray whales were consistently observed in specific portions of the Sea of Okhotsk during the middle decades of the 19th century. Although most of the observations reported in the logbooks occurred on grounds where bowhead whales were the primary targets, some observations were also made on right whale grounds (e.g. on the Okhotsk side of Paramushir Island/Mys Lopatka, 51º16'N, 155º23'W, 14 September 1868, *Europa* 1867-1868). No sightings were reported on the north-eastern Sakhalin Shelf where western gray whales are observed most often today. However, none of the logbooks read for this study contained evidence that the American whalers visited that area (Fig. 4). The ship positions of whaling voyages into the Okhotsk Sea between 1844-1852 indicate some effort off the far northern, east-central and southern shores of Sakhalin but almost none along the north-eastern coast on or near the present-day feeding areas (Josephson et al. 2008). Lindholm (1863), a whaleman with much experience in the southern part of the Okhotsk Sea (particularly around the Shantar Islands), reported that gray whales were 'found in large numbers close to Cape Elizabeth [northern end of Sakhalin Island] and in the northern section of the sea during the summer'.

It is important to emphasize that the spatial and seasonal coverage of the Sea of Okhotsk represented by the logbooks was dictated primarily if not solely by the whalers' interest in catching bowhead whales and right whales though it was also influenced by the logistical constraints of sailing conditions, ice coverage and day length. It is fair to question whether the relative concentration of sightings of gray whales in the far north-eastern reaches of the sea (Gizhiginskaya Bay and Penzhinskaya Gulf ; Fig. 5) reflects relative density or is instead the result of a strong bias in search effort. It was not possible to address this issue rigorously given the biased nature of the effort data (the whalers went where they hoped to find bowhead whales and right whales) and the uncertainty about how consistently observations of non-target or secondary-target species like the gray whale were reported in the logbooks.

Removals

As indicated earlier, Henderson (1984) suggested that commercial ship-based whalers in the Sea of Okhotsk took about as many gray whales between the 1840s-1880s as were taken over roughly the same period in the Bering Sea and Arctic Ocean. Our findings are consistent with Henderson's suggestion. It is clear from the logbooks we read that gray whales were of little interest to the whalemen during the early years of the Okhotsk fishery when bowheads and right whales were available in good numbers. In the 1840s and early 1850s, few masters bothered to lower the boats when gray whales were observed on or en route to the bowhead or right whale grounds. This seems to have begun changing by the mid 1850s when logbooks record gray whales being chased more often (e.g. *Gov. Troup*, 9 July 1854 near the Jamskiye Rocks [Yamske Islands]; *Cicero*, 16 June 1859 in La Perouse Strait).

Within a given voyage, particularly from the 1860s onwards, it was not unusual for the crew to pursue *eastern* gray whales in the Mexican lagoons or alongshore Baja California and California in the winter, and *western* gray whales in the Sea of Okhotsk in the summer. Kugler (1984, p. 153-4) referred to these as 'loop voyages', with the southern and northern components separated by visits to Hawaii and perhaps the Sea of Japan in the spring. Charles M. Scammon, for example, on the San Francisco ship *William C. Nye* during his last year as a whaling captain, sailed to the Okhotsk Sea for bowhead whaling in summer 1862 and then to Magdalena Bay for gray whaling in the following winter (Henderson 1972, pp. 86, 271).

The gray whale's reputation as a 'devilfish' is borne out by occasional statements in the logbooks. For example, when boats from the ship *Europa* (1866-1867) attacked a 'ripsack' in North-east Gulf on 19 August 1867, the bow boat 'got stove' after making the first strike, and then the other boats made the kill.

Conclusions

In the sample of logbooks examined, there was no evidence that American 19th century whalers visited the north-eastern coast of Sakhalin Island where gray whales have been studied intensively over the past decade. However, gray whales were observed regularly in certain other parts of the Sea of Okhotsk where the ship-based whalers hunted bowhead whales during the summer. They observed and hunted gray whales relatively often in the north-eastern corner of the sea, especially in Gizhiginskaya Bay (North-east Gulf) and Penzhinskaya Gulf. Gray whales were present in Gizhiginskaya Bay as early as mid-May when (or at least very soon after) the whalers arrived and gray whales continued to be observed there through the end of August. Good numbers also were observed in early June and as late as the third week of September in Tauskaya Bay Magadan coast) and in late summer (mid-August to mid-September) in Sakhalin Bay off the north-western coast of Sakhalin Island.

The historical distribution of gray whales in the Sea of Okhotsk appears to have been much more extensive than it is at present although increased search effort at appropriate times in areas of historical occurrence is needed confirm their absence from such areas. Although not definitive, the information on western gray whales obtained from American 19th century whaling logbooks is of potential value in the following ways:

- To inform the timing and spatial coverage of modern survey effort.
- To support, in principle if not also in planning as to time and location, a satellite tagging and tracking programme to learn more about the movements of western gray whales.
- To contribute to an accurate reconstruction of catch history for input to population models.
- To provide a basis for formulating hypotheses regarding stock structure.

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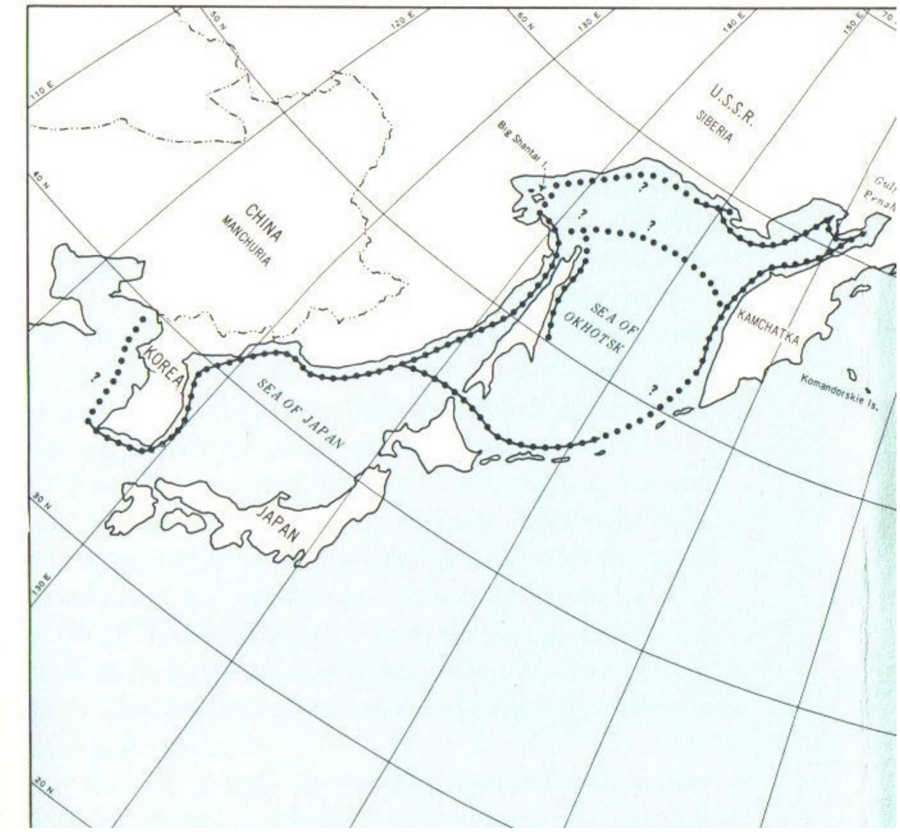

Figure 1. Excerpt from ‘Distribution, Migration Routes, and Calving Grounds of Pacific Gray Whales’ in Henderson (1972). Cited sources used by Henderson as the basis for this map include Mizue (1951), Tomilin (1957) and ‘Scammon’s and other historical records’.

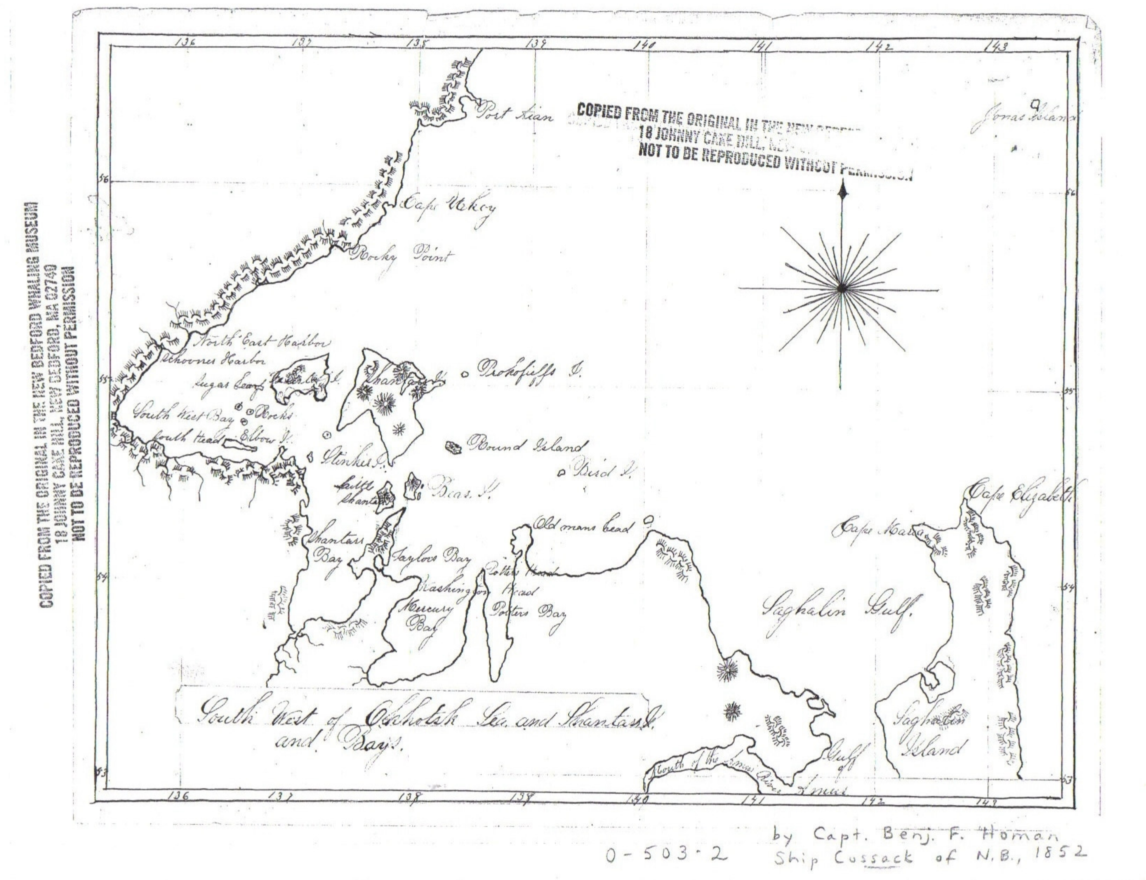

Figure 2. Sketch map from logbook of ship *Cossack* of New Bedford, 1852.

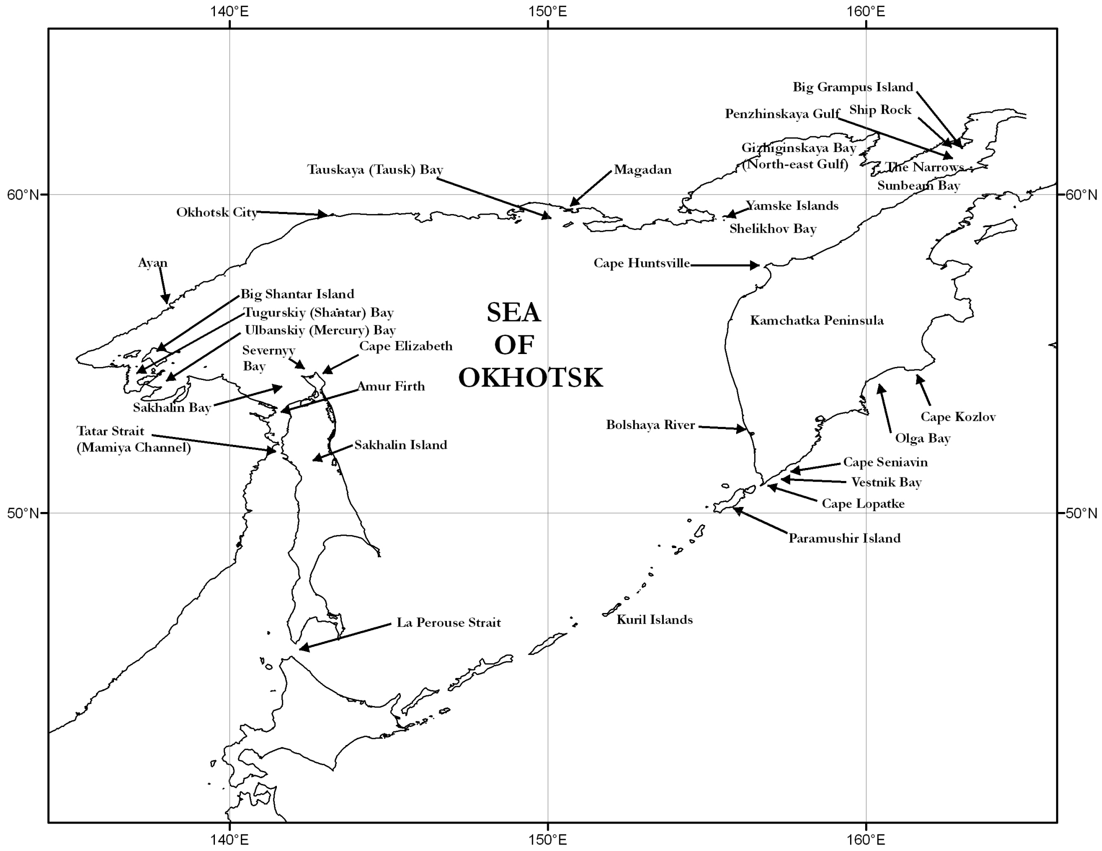

Figure 3. Places mentioned in text.

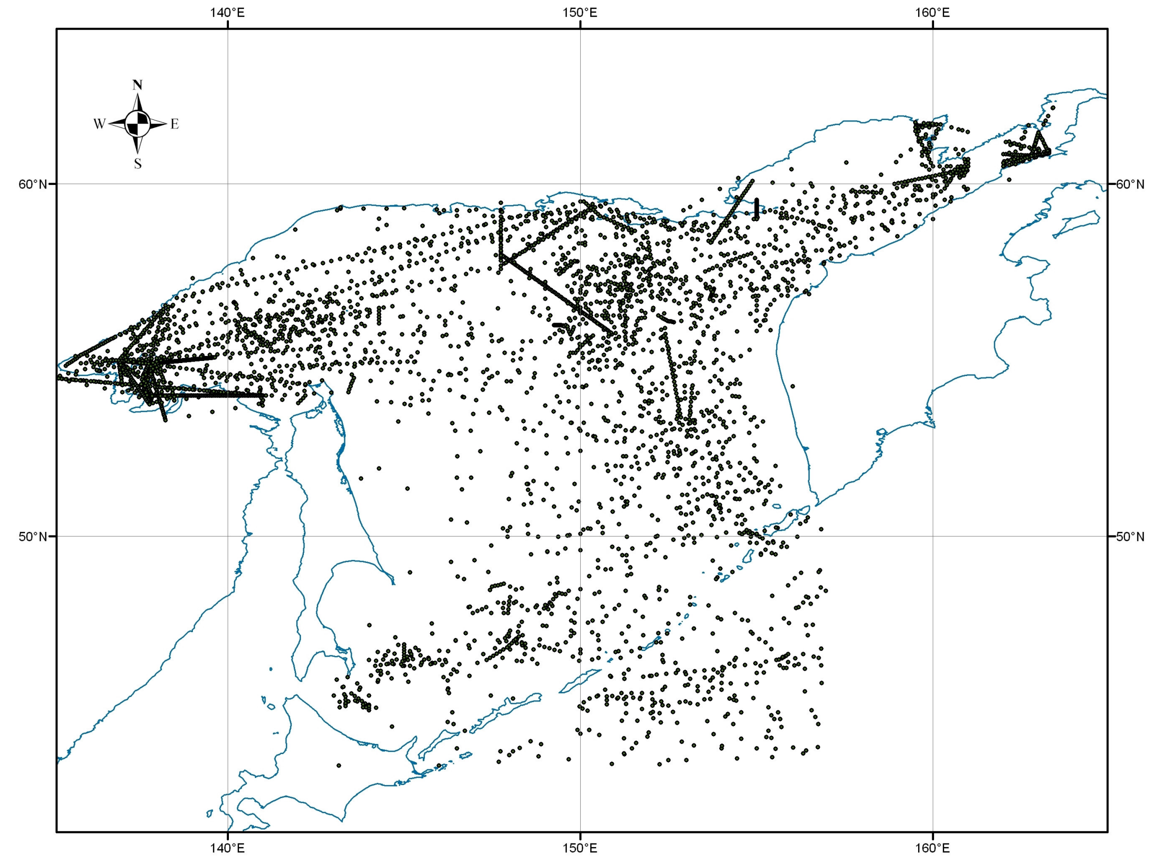

Figure 4. Approximate positions of whaling vessels in and immediately outside the Sea of Okhotsk based on logbook records of 21 voyages (43 vessel-seasons). Note the nearly complete absence of search effort along the north-eastern coast of Sakhalin Island.

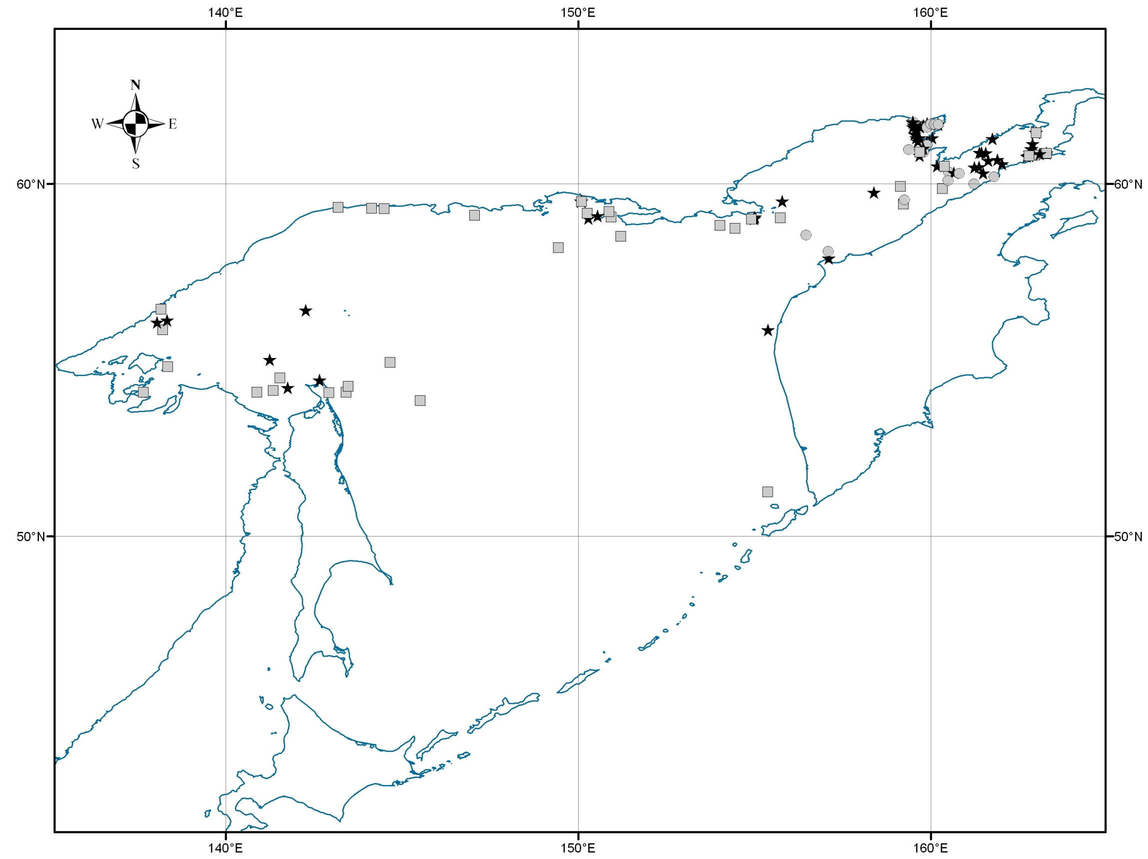

Figure 5. Approximate positions of 152 sightings (including kills) of gray whales in the Sea of Okhotsk by 19th century American whalers. Note that some symbols are overprinted in areas with many observations. Circles: April-May; stars: June-July; squares: August-September-October. Also note that many positions are based on extrapolation or interpolation from ship positions reported on days before or after that of the gray whale sighting. All data are from logbooks; see text.

NEW SERIES, VOLUME I, PART V.

MONOGRAPHS OF THE PACIFIC CETACEA.

I.—THE CALIFORNIA GRAY WHALE (*RHACHIANECTES GLAUCUS* COPE).

MEMOIRS

OF THE

AMERICAN MUSEUM OF NATURAL HISTORY.

THE CALIFORNIA GRAY WHALE (*RHACHIANECTES GLAUCUS* COPE).

ITS HISTORY, HABITS, EXTERNAL ANATOMY, OSTEOLOGY AND RELATIONSHIP.

BY ROY C. ANDREWS.

PLATES XIX–XXVII AND 22 TEXT FIGURES.

CONTENTS.

HISTORY, HABITS AND EXTERNAL ANATOMY

HISTORY, HABITS AND EXTERNAL ANATOMY.

FOREWORD.

The present paper is the first of a series of monographs which are in course of preparation upon the large Cetaceans of the Pacific Ocean. The collection of specimens and field studies upon this group began in 1908 upon the coasts of Vancouver Island and southeastern Alaska and has since been carried on along the shores of Japan and Korea.

It was originally intended to embody all the results of these investigations in a single volume but continued field work and many interruptions have so delayed the assembling of the vast amount of data secured that it has seemed advisable to bring out the material upon each genus or species as fast as it is prepared for publication.

ACKNOWLEDGMENTS.

It gives me the greatest pleasure to acknowledge the generosity and assistance of the President and Directors of the Toyo Hogei Kabushiki Kaisha (Oriental Whaling Co., Ltd.) of Osaka, Japan. Not only did these gentlemen freely extend the courtesies of their ships and stations but presented to the Museum the skeletons of the whale which forms the subject of the present paper. At all times the officers and employees of the Toyo Hogei Kaisha assisted me in every way possible, and it was entirely through their efforts that field studies and the collection of specimens was made possible.

To the untiring efforts of my friend Mr. D. Ogiwara, formerly an officer of the whaling company, much of the success of my two expeditions to Japan is due. Mr. Ogiwara, who is deeply interested in the advancement of science, not only rendered great practical assistance but always stood ready to give me the benefit of his sound advice and intimate knowledge of Japanese business methods.

Mr. T. Shibuya, Manager of the Shimonoseki branch of the Toyo Hogei Kaisha, was of the greatest assistance in many ways, especially in securing the two skeletons of *Rhachianectes* which were shipped to America.

Mr. Kondo, the station master at Ulsan, Korea, and Mr. T. Matsumoto, his assistant, deserve the greatest thanks not only for contributing materially to my study but also for making my stay in their home most enjoyable as well as profitable.

Thanks are also due to Messrs. Oto, Iku Kita, E. J. Kitson and S. Reed for assistance in various ways.

Captain H. G. Melsom of the S.S. 'Main' was my constant companion at Ulsan. Not only did he entertain me frequently upon his ship but contributed much information from his vast store of knowledge and long experience with Gray Whales. Captain Melsom was the first whaleman to learn to take "Devilfish" in Korean waters and it was he who laid the foundation for the winter fishery which has been so successfully prosecuted there by the Japanese for the last fifteen years. Captains Johnson and Hurum also entertained me frequently and gave me much valuable information.

Sincere thanks are due to Mr. Chas. L. Bernheimer of New York City for generous financial assistance during the field work upon which this paper is based.

During the years 1880–1882, Dr. J. A. Allen began work upon an extensive monograph of the Cetacea. A vast amount of material was examined and numerous plates were prepared by the well known artist, Mr. J. H. Blake. Because of ill health, however, this work was later abandoned and has remained in manuscript to the present day with the exception of the portion relative to *Eubalœna glacialis*, which was published in 1908.[1] Dr. Allen has very kindly offered me the use of this material and so far as possible it will be combined with the results of my own research. For the present paper the only available portion was that of the "general history" from the years 1868 to 1879. It is also a pleasure to acknowledge Dr. Allen's invaluable assistance and advice in preparing this paper for the press.

Dr. F. W. True has not only read portions of the manuscript but has devoted considerable time to an examination with me of the fossil genera of baleen whales in relation to *Rhachianectes*, and I was thus afforded the benefit of his thorough knowledge of this difficult material. For his never-failing kindness I wish to express my sincere appreciation. My thanks are also due to Dr. W. K. Gregory for much advice and many valuable suggestions.

My mother, Mrs. C. E. Andrews, kindly prepared the table of percentage measurements and assisted me in other ways, and to her my sincerest thanks are extended.

The photographs of the skull and skeleton were made by Mr. Julius Kirschner, the Museum photographer.

INTRODUCTION.

Knowledge of the habits and external anatomy of the California Gray Whale has rested almost exclusively upon the observations of Captain C. M. Scammon made nearly forty years ago. Shortly after the publication of his book 'The Marine Mammalia,' in 1874, the Gray Whale fishery began to decline and for several years was conducted only in a desultory manner by a number of Portuguese upon the shores of Lower California. During the past twenty years the species had been lost to science and many naturalists believed it to be extinct.

While studying Cetaceans upon the coast of Japan in 1910, the writer learned from the Japanese whaling company of the existence of an animal known as the *Koku kujira* or "Devil-fish," which formed the basis of their winter fishery upon the southeastern shore of Korea.

The descriptions indicated that the *Koku kujira* would prove to be none other than the lost California Gray Whale and I determined to investigate it at the earliest opportunity. Consequently, during the winter of 1911–12, I returned to the Orient and spent the months of January and February at the station of the Toyo Hogei Kaisha at Ulsan, a small village on the southeastern coast of Korea, forty miles north of Fusan.

During this time fifty or more Gray Whales were taken and it was possible to make a careful study of the habits and external characters of the species. Skeletons of two adult individuals were also secured, one of which was sent to the American Museum of Natural History in New York City and the other to the U. S. National Museum at Washington, D. C.

These are the first skeletons of this species to be preserved in any American Museum and are, moreover, the only *complete* specimens in the world.

The British Museum of Natural History, South Kensington, England, contains a skeleton and a second is to be found in the Imperial Museum of Tokyo, Japan. There is also one skull of the Gray Whale from California in the United States National Museum.

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[1] Bull. Amer. Mus. Nat. Hist., Vol. XXIV, Art. XVIII, pp. 277–329, pls. xix–xxiv.

The study of this animal has been especially interesting since it was almost an untouched field. The fact that the most diligent search of the literature of the subject discloses only 23 titles, and that the great majority of these papers are either short notices or compilations, indicates how little this whale, which is among the most remarkable of all large Cetaceans, has been studied.

General History.

"The California Gray whale was first introduced into scientific literature by Professor Cope in 1868 [1] under the name *Agaphelus glaucus*. For our first knowledge of its characters, however, we are indebted to Dr. W. H. Dall whose manuscript notes, outline figures and specimens of baleen transmitted by him to the Museum of the Essex Institute (now the Museum of the Peabody Academy of Science), Salem, Mass., formed the basis of Professor Cope's description. Dr. Dall's notes and figures were based upon an examination of two specimens, and though very incompletely indicating the characters of the species, were sufficient to show it to be one not previously described.

"Shortly afterward the external characters were quite fully given by Captain Scammon together with a detailed account of the habits, habitat and products, and of the California coast whaling of which it formed the chief basis. Captain Scammon's account was accompanied by two rough figures of the animal. At the same time the species was made the basis of a new genus (*Rhachianectes*) by Prof. Cope.[2] Captain Scammon's account was substantially republished in 1871 in the 'Overland Monthly' magazine,[3] and in 1874 was incorporated into his 'Marine Mammals' [4] with, however, much additional matter and new and creditable illustrations. In 1871 Pechuel-Losch gave a short account and figure of the animal in his 'Wale und Walfang' [5] but added nothing of importance to its history as given by Scammon in 1869. In 1870 Professor Van Beneden thus refers to the genus *Rhachianectes:* 'Si ce genre ne repose pas sur une balénoptère mutilée, c'est-à-dire qui a perdu sa nagoire dorsale, c'est une des plus belles découvertes qui aient été faites depuis bien longtemps en Cétotologie." [6]

"In view of Scammon's history of the species, the doubt here expressed has a strange aspect, but happily he later had abundant opportunity of satisfying himself that his doubt was groundless and it was also his good fortune to publish in 1877 the first description and figure [7] of the skull of the 'California Gray' from photographs, transmitted by Dr. O. Finsch." [8]

In 1879, Professor Cope examined at San Francisco, a "schooner-load of bones" of this species brought from Scammon's Lagoon, Lower California, to be ground up and sold as fertilizer and says: "Having examined a large number of the bones I can complete the characters of the genus *Rhachianectes*,[9] which have been but imperfectly known. The cervical vertebræ are all

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[1] Proc. Acad. Nat. Sci. Phila., 1868, pp. 225–227.

[2] *Ibid.*, 1869, pp. 15, 40–49, figs. 7, 8.

[3] Vol. VI, No. 2, Feb. 1871, pp. 118–125.

[4] The Marine Mammals of the North-western Coast of North America, by Charles M. Scammon, 1874.

[5] Das Ausland, 1871, pp. 1185–1186.

[6] Ostéographie des Cétacès, livr. 8, 1870, p. 235.

[7] Bull. de l'Acad. de Belgique, 2me Sér., T. XLIII, 1877, pp. 92–96, pl. 1.

[8] J. A. Allen, manuscript notes.

[9] Professor Cope's original reference to the genus, embraced in four lines, is as follows: "This genus is now first characterized. Its only known species I originally united with Agaphelus Cope, but the form of the scapula is so different that it must be distinguished. While that of Agaphelus is identical with that of Balænoptera, it is in the present genus quite like that of Balæna." — Proc. Acad. Nat. Sci. Phila., 1869, p. 15.

distinct, and the second and third at least enclose a vertebral canal. A first rib (the only one not broken up) has two heads; two other short ribs, perhaps first and second, are united distally into a broad sheet of bone. It is uncertain how far the union of these ribs is constant. The scapula has both coracoid and acromion. The orbital process of the frontal is of medium width, somewhat as in some species of *Megaptera*." [1]

A. W. Malm [2] described in 1883 fragments of the skeleton of *Rhachianectes* secured by the 'Vega' Expedition and figured parts of the skulls of several individuals.

In 1886 Charles H. Townsend published in the 'Bulletin of the United States Fish Commission' a brief report upon the condition of the Gray Whale fishery at that time along the coast of California and remarks: "Of the eleven whaling stations mentioned by Scammon as established along the coast ten or twelve years ago, only five remain. . . ." In commenting upon the numbers of the Gray Whale, he says: "At the San Simeon station in December, 1885, I could see whales blowing almost every hour during the day. From the elevated 'look-out,' or observation station, on shore an extensive stretch of ocean could be examined with the telescope. During my stay, and for a short time afterward, covering a period of fully a month, Mr. Clark counted forty whales passing southward. Many of these were too far off shore to be pursued by the three boats that were daily cruising outside during the season, and a few may have been other species than gray whales, but counting the forty whales actually seen in December and doubling that number to include those that passed at night during the same period, we have eighty whales per month easily accounted for. Doubling this number again to include those which pass within sight of the lookout station in January (for the 'down season' lasts two months), we have one hundred and sixty whales as the number that may readily be seen at the present time from one point alone during the 'down season.' What proportion this number bears to the number passing off shore would be hard to say, but it is certainly less than half, since the whales near the coast are mostly females seeking bays and lagoons in which to bring forth their young, which would leave the males and young whales unaccounted for.

"These safe and obviously low estimates, and the above table showing the actual catch during the past three seasons, afford a very fair showing for a species so scarce in 1880 that only one individual could be captured, and indicate a tendency towards its re-establishment while unmolested in its breeding resorts." [3]

In the 'American Naturalist' for 1888, John Dean Caton [4] gave a popular compiled account of the Gray Whale and its habits, and twelve years later F. E. Beddard [5] very briefly described a skeleton of this species in the British Museum.

The last contribution to our knowledge of this interesting animal was made by Dr. F. W. True [6] in 1904. Dr. True summarized the existing facts relative to the external and internal anatomy of *Rhachianectes glaucus* with enlightening critical comments and also presented detail measurements and photographs of the Monterey skull in the National Museum.

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[1] American Naturalist, Vol. XIII, Oct. 1879, p. 655.

[2] Bihang K. Sven. Vet. Akad. Handl., Vol. VIII, No. 4, 1883, pp. 17–37.

[3] Bull. U. S. Fish. Comm., Vol. VI, 1886, pp. 346–350, pls. vi, vii.

[4] American Naturalist, Vol. XXII, 1888, pp. 509–514.

[5] A Book of Whales, 1900, pp. 168–170.

[6] Smiths. Contrib. to Knowledge, Vol. XXXIII. The Whalebone Whales of the Western North Atlantic, 1904, pp. 287–292, pl. 47 and pl. 49, fig. 3.

LIFE HISTORY.

Migration.— The Gray Whales begin to appear at Ulsan, southeast Korea, about the end of November on their southward migration. Single pregnant females come first and a little later both males and females are seen but the latter considerably outnumber the former. About January 1, schools of from ten to fifteen males, with perhaps one or two females, appear, the female always leading. From the 7th to the 25th of January, when the migration is completed, only males are present, the females all having passed.

In November and December, when the females are taken, almost every individual will be found to be carrying young nearly ready for birth. As these would necessarily be delivered within two or three weeks after passing Ulsan, the birth must occur in the bays among the numerous small islands at the extreme southern end of the peninsula. Indeed Captain H. G. Melsom, who has hunted Gray Whales for fifteen years along the Korea coast, has often observed them in this vicinity, but because of the abundance of other and more valuable species, they are not killed at this time by the Japanese. When travelling southward the whales are always hurrying straight ahead as though anxious to arrive at the breeding grounds and are never accompanied by small calves; upon the northward migration, however, young have been seen following their parents.

The "Devilfish" again arrives at Ulsan, travelling north, about the middle of March and by the 15th of May they have all passed by. Although the greater portion of the herd goes straight northward, Captain Melsom reports that during the end of April and first week of May he has observed many Gray Whales in Broughton Bay, Korea; these animals seemed to be feeding and had apparently broken the migration by a sojourn in the bay.

A comparison of these observations upon the Korea whales and those made by Scammon on the California coast is interesting. It shows that the breeding grounds of the two herds are in very nearly the same latitude and that their migration dates correspond closely. In regard to this Scammon writes: "The California Gray whale is found only in north latitudes, and its migrations have never been known to extend lower than 20° north. It frequents the coast of California from November to May. During these months the cows enter the lagoons on the lower coast to bring forth their young, while the males remain outside along the seashore. The time of gestation is about one year. Occasionally a male is seen in the lagoons with the cows at the last of the season, and soon after both male and female, with their young, will be seen working their way northward, following the shore so near that they often pass through the kelp near the beach. It is seldom they are seen far out at sea. This habit of resorting to shoal bays is one in which they differ strikingly from other whales. In summer they congregate in the Arctic Ocean and Okhotsk Sea. It has been said that this species of whale has been found on the coast of China and about the shores of the island of Formosa, but the report needs confirmation.[1]

"In October and November the California Grays appear off the coast of Oregon and Upper California, on their way back to their tropical haunts, making a quick, low spout at long intervals; showing themselves but very little until they reach the smooth lagoons of the lower coast, where, if not disturbed, they gather in large numbers, passing and repassing into and out of the estuaries,

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[1] From personal observation and the statements of the whalers, I doubt if the Gray Whales migrate far south of the peninsula of Korea. During my own travels along the China and Formosa coasts, I have neither seen nor heard of Gray Whales. R. C. A.

or slowly raising their colossal forms midway above the surface, falling over on their sides as if by accident, and dashing the water into foam and spray about them. At times, in calm weather, they are seen lying on the water quite motionless, keeping one position for an hour or more. At such times the sea-gulls and cormorants frequently alight upon the huge beasts. The first season in Scammon's Lagoon, coast of Lower California, the boats were lowered several times for them, we thinking that the animals when in that position were dead or sleeping, but before the boats arrived within even shooting distance they were on the move again" (*l. c.*, pp. 22–24).

As yet it is impossible to state whether or not the Korea and California herds mingle in the north during the summer. Information gathered from the whalers tends to show that a large part of the former herd summers in the Okhotsk Sea and the latter in Bering Sea and further north. Individuals of the two herds may mingle and interbreed during their sojourn in the north, but it is probable that whales which have been born near either the Korea or California coasts will find mates among the members of their own herd during the southward migration and return annually to their birth place. It is quite conceivable that the case of the Gray Whale may be analogous to that of the Fur Seal where it has been shown conclusively that members of the American and Japanese herds do not mingle in the north although separated by comparatively few miles of water at certain times of the year.

Period of gestation and rate of growth.— Because of its regular annual migrations the period of gestation of this species can be more nearly determined than in the case of most other large whales, and appears to be about one year. Mating probably takes place in the south during December or early January, and the calf is ready for delivery the following year.

As stated above (see 'Migration'), the females which appear at Ulsan, Korea, travelling southward are nearly all bearing calves almost ready for birth. Upon the return journey the females are accompanied by young calves, and Capt. H. G. Melsom writes that he killed on March 13 and 14, 1912, at Chan Chien Dogo (near Broughton Bay), Korea, upon their northward migration, two females bearing fœtuses 7 and 10 inches long, respectively. These fœtuses were probably not more than 2½ months old, which would indicate that the mating had taken place late in the previous December and that the calves would be delivered the following December or January when the whales returned to the south. A female 1300 cm. (42′ 8″) in length taken at Ulsan, Korea, on January 8, 1912, contained a fœtus 476 cm. (15′ 7½″) long, and ready for birth; it would certainly not have been carried more than a week or ten days longer.

Whether or not the females again mate immediately after giving birth to their young it is impossible to state, but from Scammon's observations, quoted below, I believe it to be unlikely and that calves are born but once in two years.

Scammon says that the period of gestation is about one year, and remarks: "This statement is maintained upon the following observations: We have known of five embryos being taken from females between the latitudes of 31° and 37° north, on the California coast, when the animals were returning from their warm winter haunts to their cool summer resorts, and in every instance they were exceedingly fat, which is quite opposite to the cows which have produced and nutured a calf while in the lagoons; hence we conclude that the animals propagate only once in two years" (*l. c.*, p. 23, note).

Mr. C. H. Townsend, writing in 1886 of the San Simeon (Cal.) station, says: "Unlike Monterey, this station depends almost entirely for its business upon the gray whales, which pass southward with great regularity from December until February. The 'up season,' lasting until

April, is also profitable at San Simeon, but the catch there consists chiefly of males, the females keeping farther off shore when passing northward with their young. During the last ten years Captain Clark has seen but one female accompanied by young in the vicinity of his station. At San Simeon, and all the whaling establishments situated south of it, females exceed the other sex in numbers during the 'down run' and most of them contain well-developed young. At this place and at San Luis Obispo, the nearest neighboring station, I saw four young whales lying on the beach, which had been taken from females killed in the vicinity during that season (December, 1885). Their average length was about 12 feet; the largest, which I sketched, being 17 feet long, and from an adult nearly 40 feet in length. They were probably within two weeks of the time of birth when the parent animals were killed" (*l. c.*, pp. 347–348).

From the above data it may be safely affirmed that the length at birth of the majority of Gray Whales is between 12 and 17 feet. When the females go north in March on the Korea coast, the calves which have been born near the end of the previous December accompany them, and by the time they reach Ulsan are about twenty-five feet in length, This makes a growth of nine or ten feet during a little less than three months. This may seem extraordinary, but it is quite in accord with what apparently takes place in all baleen whales. Without doubt the rate of growth for the calf is very rapid during the first few months after birth and until sexual maturity is reached.

Thirty-two feet is the minimum length for Gray Whales taken at Ulsan, and individuals of this size must certainly have been born during the previous winter. Thus, accepting 14 feet as the average length at birth, we get a growth of 18 feet during a little less than one year.

How long the young nurse is problematical but it must be considerably less than one year because, so far as I am aware, nursing calves or females have not been taken at Ulsan on the southward migration, and some would certainly have been brought in if the suckling period was not over before the animals reached that point upon the coast.

Spouting and diving.— The height and form of the spout varies with conditions. Normally the vapor rises vertically ten or eleven feet in a thick column having the width at the summit about twice that at the base (Plate XXIV, Fig. 7). It may, however, reach a height of fifteen feet if the whale is large and has been submerged for a considerable period. The spout is single in the majority of cases, but Captain Melsom asserts positively that at times it is divided like that of a Right Whale. As in all Cetaceans the initial spout after a period of submergence is generally the highest and fullest.

The number of respirations between the dives is fairly regular. When the whale has been below for several minutes upon rising to the surface it will usually blow two or three times before again going down.

When cruising along the shore the animal generally remains submerged seven or eight minutes and blows three times when it reappears. Captain Melsom assures me that when a large female is taking a straight course it will remain below four or five minutes and rise to make three spouts very regularly; at other times a single whale will remain down ten minutes and a school between fifteen or twenty minutes, depending upon circumstances.

When travelling straight ahead and unmolested the Devilfish swim under water for a distance of 300 or 400 fathoms quite regularly and rise to spout three times.

Under normal conditions the animals 'sound' much as do Humpbacks. As soon as the spout has been delivered, the body begins to revolve and as the dive progresses the flukes are lifted out of the water and drawn slowly under. The flukes are not invariably shown, however, even when sounding; some animals will almost always 'fluke out' and others, not at all. Under no circumstances do the Gray Whales arch the back as strongly as do the Humpbacks nor do the animals raise themselves so far out of the water.

During the 'surface' or 'intermediate' dives only a small part of the back is shown, the motion is forward and downward, and the flukes are never exposed.

Speed.— The Gray Whales are slow swimmers and cannot exceed seven or eight knots per hour even when badly frightened and doing their best to get away. Ordinarily when 'travelling,' and unmolested, they make about three or four knots, and when cruising along the shore perhaps two or three knots per hour.

The Gray Whale is essentially a shore-loving species and on its annual migration always prefers to swim along close to the beach. At times the whales will go in so close to the shore that they are actually rolling in the surf and seem to enjoy being pounded by the breakers. Scammon has observed the same habit in the California animals and says: "About the shoals at the mouth of one of the lagoons, in 1860, we saw large numbers of the monsters. It was at the low stage of the tide, and the shoal places were plainly marked by the constantly foaming breakers. To our surprise we saw many of the whales going through the surf where the depth of water was barely sufficient to float them. We could discern in many places, by the white sand that came to the surface, that they must be near or touching the bottom. One in particular, lay for half an hour in the breakers, playing, as seals often do in a heavy surf; turning from side to side with half extended fins, and moved apparently by the heavy ground-swell which was breaking; at times making a playful spring with its bending flukes, throwing its body clear of the water, coming down with a heavy splash, then making two or three spouts, and again settling under water; perhaps the next moment its head would appear, and with the heavy swell the animal would roll over in a listless manner, to all appearance enjoying the sport intensely. We passed close to this sportive animal, and had only thirteen feet of water" (*l. c.*, p. 24).

Frequently when being hunted the Korea whales would escape by swimming into water so shallow that the ships could not follow them and remaining there until the men had given up the chase.

Food.— Although the stomachs of a great number of Gray Whales were examined carefully I could never discover what constitutes their food. In every case the stomach was more or less filled with dark green water in which the only solid materials were bits of kelp, a little sea weed, and small masses of a light green gelatinous material. The stomachs of two individuals contained a number of small water-worn pebbles and several masses, six to eight inches long, of what appeared to be finely shredded raw meat still connected by its fibers; this was certainly not fish. It is probable that the kelp and sea weed had been taken in with other material, as in the case of the pebbles. The excrement of all the whales had about the consistency of thick cream and was dark green like the water in the stomach.

All the gunners asserted that when the Gray Whales appear at Ulsan on their migrations they are invariably travelling straight ahead and apparently not stopping to feed. This information, combined with the fact that little except water could be found in the stomachs, lends strong support to the theory that upon their annual migrations the Devilfish feed but very little, if at all. If feeding is indulged in, it would seem extraordinary that no specimens have been brought to the station having food, or its remains, in their stomachs. The presence of fæces in the intestines may be due to the fact that these organs had not entirely emptied themselves since the last period of feeding in the north. The green color of the water in the stomach and of the excrement is probably due to bileary secretions.

It is possible that while upon their migrations the whales eat quantities of the jelly fish which are so frequently seen near the kelp fields just off shore. These animals, consisting largely of water, would be very quickly acted upon by the digestive fluids and the lack of solid material in the stomach be thus explained. Captain Melsom has seen Gray Whales in the Okhotsk Sea during the summer which were not travelling but were swimming slowly about.

It is interesting to note that neither Scammon nor Townsend could get any definite information as to the food of the Gray Whales of the California coast. Scammon remarks: "To our personal knowledge, but little or no food has been found in the animal's stomach. We have examined several taken in the lagoons, and in them we found what the whalers called 'sedge' or 'sea-moss' (a sort of sea-cabbage), which at certain seasons darkens the water in extensive patches both in and about the mouths of the estuaries. Whether this was taken into the stomach as food some naturalists doubt, giving as a reason that the whale, passing through the water mixed with this vegetable matter, on opening its mouth would of necessity receive more or less of it, which would be swallowed, there being no other way in which it could be disposed of. The quantity found in any one individual would not exceed a barrelful.

"From the testimony of several whaling-men whom we regard as interested and careful observers, together with our own investigations, we are convinced that mussels have been found in the maws of the California Grays; but as yet, from our own observations, we have not been able to establish the fact of what their principal sustenance consists" (*l. c.*, pp. 24, 25, note).

Townsend says in regard to the food: "The opinion of the men with whom I talked is that it does not feed to any great extent outside of its arctic habitat. It is certainly much thinner on the northward than on the southward run, a male that would yield 30 or more barrels of oil in the down season yielding less than 25 two months later. Whalers admit their ignorance of what constitutes the food of this animal, and can find nothing in its stomach during the breeding season" (*l. c.*, p. 349).

Affection.— The male Devilfish at all times shows strong affection for the female and Captain Melsom tells me that during the migration, when a school of males led by one or two females is found, if one of the latter is wounded, often the former will refuse to leave until she is dead. One day when hunting a pair he wounded the cow and the bull would not leave, keeping close alongside and pushing his head over her body. Later he struck the male with a harpoon but did not get fast and even then it returned and was finally killed. Captain Melsom assures me, however, that if the male is killed the female will seldom remain.

Scammon has recorded instances of the female's love for her young and it was because of her vigorous defense when attacked on the breeding grounds that the name "Devilfish" was gained. The whalemen in Korea, however, where the hunting is done from small ships by the Norwegian method, do not regard the animals as especially dangerous. They seldom lance one from the 'pram,' as is frequently done with Finbacks because the Gray Whales seem to be very sensitive to pain, and as soon as the iron penetrates the body the animal will raise itself in the water, throwing its head from side to side and sometimes lashing about with its flukes and fins.

Attacks by Killers (*Orca orca*).— The Gray Whales seem to be objects of continual persecution by the Killers; much more so than any of the other large whales. Among the first eight or nine Devilfish which I examined at Ulsan, three attracted my attention at once because the entire anterior part of the tongue had been torn away. Teeth marks plainly showed in the remaining portion and upon consulting the gunner, Captain Hans Hurum, who had killed them, he told me that it had been done by Killers at the time he shot the whales. Seven Gray Whales were in the school, and shortly after he began to hunt them fifteen Killers appeared. The whales became terrified at once and he had no difficulty in killing three of the seven. When the Orcas gathered about, the whales turned belly up and lay motionless, with fins outspread, apparently paralyzed by fright. A Killer would put its snout against the closed lips of the Devilfish and endeavor to force the mouth open and its own head inside. This extraordinary method of attack was corroborated by Capt. Johnson who had been hunting the same school of Gray Whales, and, moreover, by all the whalemen at the station who had witnessed it upon many other occasions.

Out of the thirty-five Gray Whales which I examined especially, seven had the tongues eaten to a greater or less extent and one had several large semicircular bites in the left lower lip. The Killers do not confine their attention entirely to the tongue for almost every whale which was brought in had the tips and posterior edges of the fins and flukes more or less torn; in several specimens fresh teeth marks were plainly visible where the fin had been 'shredded' as the whale drew it out of the Orca's mouth.

Although none of the Gray Whales exhibited teeth marks on other parts of the body undoubtedly some of them are killed by the Orcas. A female Killer which was brought to the station had several pieces of flesh in its stomach besides a strip of whalebone three inches long; I could not positively identify the latter but believe it to have been from a small Devilfish. A male Killer was taken at the same time by Captain Hurum who told me that in the animal's death flurry it had thrown up two great chunks of flesh.

Captain Melsom brought a Gray Whale to the station one day and I was interested to find the tongue almost gone. He said he had passed a school of Killers in the morning and later, after steaming about fifteen miles, had killed the Devilfish. A short time afterward, a long distance away, he saw the fins of a school of Killers which were coming at full speed straight for the ship. They circled about the vessel and one of them forced open the mouth of the dead whale to get at the tongue. When Captain Melsom fired at the Killer with his Krag rifle the animal lashed out with its flukes, smashing the ship's rail, and disappeared.

As soon as Orcas appear if the Gray Whales are not paralyzed by fright they head for shore and slide in as close as possible to the beach where sometimes the Killers will not follow them. The Devilfish will actually go into such shallow water as to roll in the wash and even try to hide behind rocks. The Orcas are not afraid of the ships and will not leave the whales they are chasing when the vessels arrive, thus giving much assistance to the human hunters.

Captain Johnson, of the 'Rex Maru,' brought to the station at Ulsan a Gray Whale which had been shot in the breast between the fins. He had first seen Killers circling about the whale which was lying at the surface, belly up, with the fins outspread, being absolutely paralyzed by fright. The vessel steamed up at half speed and Johnson shot at once, the iron striking the whale in the breast.

Such is the fear of the Gray Whale that when, as frequently happens, porpoises are playing about a single animal, it will sometimes become terrified, thinking that the Killers have appeared.

I have never personally witnessed it but the gunners tell me that a pod of Gray Whales can be stampeded much as can a herd of cattle. If three or four ships are near each other when a school of Devilfish are found, they draw together, each vessel going at full speed and making as much noise as possible. The whales at once sound, but as soon as they rise to spout the ships steam at them again. The Devilfish go down once more but do not stay under long, ascending at shorter intervals until finally they are ploughing along at the surface. The animals are 'scared up' as the gunners say, and become terrified to such a degree that everything is forgotten except the desire to get away. It is not always possible to stampede a herd, and often the whales will disappear at the first sound, not rising again until a long distance away. If Killers are about at the time a herd of Gray Whales are being hunted it is very easy for the ships to stampede them.

Even if the Devilfish do exhibit considerable stupidity when danger from Killers threatens, at other times they are the cleverest and most tricky of all large whales. One day the S. S. 'Main,' Captain Melsom, was hunting a Gray Whale in a perfectly smooth sea. The whale had been down for fifteen minutes when suddenly a slight sound was heard near the ship and a thin cloud of vapor was seen floating upward from a patch of ripples which might have been made by a duck leaving the surface. The whale had exposed only the blowholes, spouted, refilled the lungs and again sunk, doing it almost noiselessly. The gunners assert that this is quite a usual occurrence when a single Gray Whale is being hunted.

Diseases.— Most whales are subject to diseases of various kinds and the Devilfish is no exception. One specimen was brought to the station at Ulsan, with all the flesh on the left side of the head badly decomposed and in some places entirely gone, leaving the bone exposed; what remained hung in a soft, green, evil-smelling mass. The whale had evidently suffered considerably from the disease for it was very thin and the blubber dry.

A second specimen had a large swelling on the ventral ridge of the peduncle, which upon being opened, proved to be a large capsular tumor about one foot in depth and of a like diameter.

The skin upon the snout of a third individual was drawn into small circular patches leaving large sections of the blubber exposed.

SIZE.

The available material relating to the size of *Rhachianectes glaucus* consists of the following: From Korea, records of one hundred and twenty-two specimens taken by the whaling company during 1909–10, and of twenty-three measured by myself in 1912; from California, the measurements given by Scammon and Dall of two specimens taken in Monterey Bay, and the record by Pechuel of one from the Bay of San Simeon.

My own measurements of the total length were taken from the notch of the flukes to the tip of the snout, either along the side of the belly as the animal lay in the water or as each section was drawn upon the cutting wharf. Every whale was also measured by a representative of the company, and as the total length was secured by the Japanese in a way similar to mine it may be assumed that all the Korean specimens are directly comparable.

In the following tables measurements of both males and females are arranged according to size.

Table I. Measurements of 53 females.

Place	Date	Total Length Feet	Total Length Cm.	Place	Date	Total Length Feet	Total Length Cm.
Ulsan	Dec. 5, 1909	45	1371	Chan Chien Dogo	Dec. 8, 1909	41	1249
“	“ 9, “	“	“	“ “ “	“ 13, “	“	“
“	“ 17, “	“	“	“ “ “	“ 15, “	“	“
“	Jan. 9, “	“	“	“ “ “	“ “ “	“	“
“	“ 15, “	“	“	Ulsan	“ 21, “	“	“
“	Dec. 5, “	44	1340	“	“ 27, “	“	“
Chan Chien Dogo	“ 6, “	“	“	“	Jan. 6, 1910	“	“
Ulsan	“ 28, “	“	“	“	“ “ “	“	“
“	“ 18, “	43	1310	“	Dec. 26, 1909	40	1218
“	“ 23, “	“	“	“	“ 4, “	“	“
“	“ 25, “	“	“	Chan Chien Dogo	“ 7, “	“	“
“	Jan. 6, 1910	“	“	“ “ “	“ 11, “	“	“
“	“ “ “	“	“	“ “ “	“ 16, “	“	“
“	“ 15, “	“	“	Ulsan	“ 26, “	“	“
“	Dec. 1, 1909	42	1279	“	“ 28, “	39	1188
“	“ 2, “	“	“	“	Jan. 1, 1910	“	“
“	“ 7, “	“	“	“	“ “ “	“	“
Chan Chien Dogo	“ 10, “	“	“	Chan Chien Dogo	Dec. 17, 1909	38	1158
Ulsan	“ 11, “	“	“	“ “ “	“ 19, “	“	“
“	“ 18, “	“	“	Ulsan	“ 31, “	37	1127
“	“ 19, “	“	“	“	Jan. 3, 1910	34	1036
Hidokatsu,	Dec. 20, 1909	42	1279	“	“ 5, “	33	1005
Chan Chien Dogo	“ 22, “	“	“	“	“ 1, “	32	975
Ulsan	“ “ “	“	“	. . .	. . . . .	. .	.
“	“ 24, “	“	“	Ulsan, (R. C. A.)	Jan. 9, 1912	43'3"	1317
“	“ 26, “	“	“	“ “	“ 8, “	42'8"	1300
“	Jan. 6, 1910	“	“	“ “	“ 10, “	38'1"	1160

Table II.—Measurements of 95 males.

Place	Date	Total Length Feet	Total Length Cm.	Place	Date	Total Length Feet	Total Length Cm.
Ulsan	Dec. 9, 1909	43	1310	Chan Chien Dogo	Dec. 18, 1909	40	1218
“	“ 17, “	“	“	“ “ “	“ 18, “	“	“
“	“ 30, “	“	“	“ “ “	“ 19, “	“	“
“	Jan. 3, 1910	“	“	“ “ “	“ 20, “	“	“
“	Dec. 1, 1909	42	1297	Ulsan	“ 21, 1909	“	“
“	“ 18, “	“	“	“	“ 27, “	“	“
“	“ 27, “	“	“	“	“ 29, “	“	“
“	“ 27, “	“	“	“	“ “ “	“	“
“	“ 30, “	“	“	“	“ “ “	“	“
“	Jan. 9, 1910	“	“	“	“ 30, “	“	“
“	Dec. 1, 1909	41	1249	“	“ 31, “	“	“
“	“ 4, “	“	“	“	“ “ “	“	“
“	“ 22, “	“	“	“	“ “ “	“	“
“	“ 29, “	“	“	“	Jan. 1, 1910	“	“
“	“ “ “	“	“	“	“ 12, “	“	“
“	“ 3, “	40	1218	Oshima, Japan	Feb. 9, 1910	“	“
“	“ 4, “	“	“	Ulsan	“ 25, “	“	“
Chan Chien Dogo	“ 6, “	“	“	“	Dec. 9, 1909	39	1188
Ulsan	“ 8, “	“	“	“	“ 15, “	“	“
Chan Chien Dogo	“ 15, “	“	“	“	“ 16, “	“	“

Table II.— Continued.

Place	Date	Total Length Feet	Total Length Cm.
Ulsan	Dec. 17, 1909	39	1188
"	" 23, "	"	"
"	" 26, "	"	"
"	" " "	"	"
"	" 29, "	"	"
"	" 30, "	"	"
"	" 30, "	"	"
"	" 31, "	"	"
"	" " "	"	"
"	Jan. 6, 1910	"	"
"	" 9, "	"	"
"	" " "	"	"
"	" 12, "	"	"
"	Feb. 20, "	"	"
Chan Chien Dogo,	Mar. 14, "	"	"
Ulsan	Jan. 6, "	38	1158
"	" 8, "	"	"
"	" 9, "	"	"
"	" " "	"	"
"	" 21, "	"	"
"	Mar. 2, "	"	"
"	Dec. 15, 1909	37	1127
"	" 20, "	"	"
"	" 31, "	"	"
"	Jan. 3, 1910	"	"
"	" 4, "	"	"
"	" 7, "	"	"
"	Feb. 13, "	"	"
"	Dec. 17, "	36	1097

Place	Date	Total Length Feet	Total Length Cm.
Ulsan	Jan. 5, 1910	36	1097
"	" 7, "	"	"
"	" 7, "	"	"
. . . .	. . . .	. .	.
Ulsan (R. C. A.)	Jan. 13, 1912	41′½″	1250
" "	" 19, "	"	"
" "	" 8, "	40′8½″	1240
" "	" 10, "	"	"
" "	" 21, "	"	"
" "	" 24, "	40′6½″	1235
" "	" 20, "	40′2½″	"
" "	" 9, "	39′5½″	1202
" "	" 11, "	39′1″	1190
" "	" 17, "	"	"
" "	" 16, "	38′9″	1180
" "	" 17, "	"	"
" "	" 8, "	38′5″	1170
" "	" " "	38′1″	1160
" "	" 13, "	"	"
" "	" 9, "	37′6½″	1143
" "	" 14, "	35′7½″	1085
" "	" 10, "	35′3½″	1075
" "	" " "	34′5½″	1050
" "	" 16, "	32′2″	980
. . . .	. . . .	. .	.
Monterey, Cal. (Scammon)	1865	42	1280
" " (Dall)	——	48	1462
San Diego, Cal. (Pechuel)	——	32	975

Like all baleen whales, the female *Rhachianectes* is larger than the male. The maximum size of the 123 specimens measured by the whaling company was 1371 cm. (45′); this length was reached by four females. The maximum for males was 1310 cm. (43′). A female 1317 cm. (43′ 3″) long and two males each 1250 cm. (41″ ½′) were the largest of the 23 specimens which I measured in 1912. Dall has recorded an unsexed individual 1554 cm. (51′) and a male 1462 cm. (48′) in length. If these measurements are correct Dall's specimens must have been of unusual size for the whalers in Korea assured me that examples longer than 1371 cm. were extremely rare. Measurements of his 1462 cm. whale show such a remarkable disagreement with all other specimens that there must have been some error in either taking or recording the dimensions. My friend Capt. H. G. Melsom, who has spent nearly fifteen years hunting Gray Whales in Korea, tells me that he killed two female whales 49 and 47 feet long, respectively; these are the largest specimens he has ever known killed.

The average length for all females measured by the whaling company and by myself agrees closely and is respectively 1254 cm. (41′ 2″) and 1259 cm. (41′ 4″); for all males it is 1188 cm. (39′) and 1172 cm. (38′ 6″). There can be little doubt that specimens larger than 1371 cm. (45′) are exceedingly rare.

It is difficult to arrive at a satisfactory conclusion as to the length at which *Rhachianectes glaucus* becomes sexually mature, for at present there are few data relative to this subject. Townsend took a fœtus 518 cm. (17′) long from a female, "about forty feet long," and the only pregnant female which I examined was a specimen 1300 cm. (42′ 8″) in length. The condition of the skeleton proved this animal to be fully adult.

The measurements of length are arranged in tabular form in the following table (Table III).

Table III. Summary of Measurements.

Locality	Average for all specimens of both sexes		Average for all females		Average for all males		Maximum for females	Maximum for males	Minimum for females	Minimum for males
	No. of Whales	Length	No. of Whales	Length	No. of Whales	Length	Length	Length	Length	Length
Korea, measured by R. C. A.	23	cm. 1184 ft. 38′9½″	3	cm. 1259 ft. 41′4″	20	cm. 1172 ft. 38′6″	cm. 1317 ft. 43′3″	cm. 1250 ft. 41′1″	cm. 1160 ft. 38′1″	cm. 980 ft. 32′2″
Korea, measured by Whalers	123	cm. 1213 ft. 39′10″	50	cm. 1254 ft. 41′2″	73	cm. 1188 ft. 39′	cm. 1371 ft. 45′	cm. 1310 ft. 43′	cm. 975 ft. 32′	cm. 1097 ft. 35′5″
California, measured by Scammon, Dall, and Pechuel	4	cm. 1318 ft. 40′8″		—	3	cm. 1239 ft. 40′8″	—	cm. 1462 ft. 48′	—	cm. 975 ft. 32′

PROPORTIONS.

In the following tables detail measurements of Korea and California representatives of *Rhachianectes glaucus* will be found. It was possible to take a fairly complete series of measurements of some of the Korea specimens while of others only a few could be secured but all have been presented with the hope that they may be of aid to future students of this species.

In the second table certain of the most reliable measurements have been selected, and their ratios to the total length given, to ascertain the degree of individual variation and to facilitate comparison.

It will be seen upon examination of the table of ratios that there is a greater or less variation in almost all the proportions. The question at once arises as to whether or not this can be due wholly to individual differences or in part to inaccuracy of measurement. The lengths of all specimens were secured while the animals were lying in the water or else were the totals of the different sections as the whales were being "cut in." The length was never taken over the back but usually along the side or breast, and in most cases I believe it to be accurate. In Nos. 2, 9, and 11 there is a possibility of doubt, but none of the ratios of these specimens show unusual variation.

All the measurements, except the total length and the distance from the tip of the snout to the axilla, were secured without difficulty after the sections of the whale had been drawn upon the wharf.

I have included in the table, measurements of the fully grown fœtus No. 1*a*, for as these were taken at leisure with the greatest care there is no doubt as to their accuracy and they furnish a valuable standard for comparison with the adult individuals.

Table IV.—Detail Measurements of Korea and California specimens.

	ULSAN, KOREA																								CALIFORNIA		
	No. 1 Jan. 8 ♀	Foetus No. 1a Jan. 8 ♂	No. 2 Jan. 8 ♂	No. 3 Jan. 8 ♂	No. 4 Jan. 8 ♂	No. 5 Jan. 9 ♂	No. 6 Jan. 9 ♀	No. 7 Jan. 9 ♂	No. 8 Jan. 10 ♂	No. 9 Jan. 10 ♀	No. 10 Jan. 10 ♂	No. 11 Jan. 10 ♂	No. 12 Jan. 11 ♂	No. 13 Jan. 13 ♂	No. 14 Jan. 13 ♂	No. 15 Jan. 14 ♂	No. 16 Jan. 16 ♂	No. 17 Jan. 16 ♂	No. 18 Jan. 17 ♂	No. 19 Jan. 17 ♂	No. 20 Jan. 19 ♂	No. 21 Jan. 20 ♂	No. 22 Jan. 21 ♂	No. 23 Jan. 24 ♂	Scammon Monterey 1865 ♂	Dall Monterey Jan. 1860 ♂	Pechuel San Diego ♂
	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.
Total length snout to notch of flukes	1300	435	1160	1240	1170	1143	1317	1202	1240	1160	1050	1075	1190	1250	1160	1085	1180	980	1190	1180	1250	1225	1240	1235	1280	1462	975
Tip of snout to eye	250	81	220	227	222	218	244	250	240	....	200	220	225	245	210	220	220	175	232	232	230	230	240	225	229	315	....
" " " " blow hole (center)	224	74	....	220	210	205	220	....	207	....	....	210	205	232	196	208	215	165	....	210	220	210	235	210	183	145	244
" " " " axilla	....	152	....	....	....	366	390	....	390	365	320	380	....	440	....	350	....	310	....	400	....	415	410	....	335	....	....
Notch of flukes to anus	410	141	370	370	....	363	377	346	335	....	350	355	....	375	335	360	325	280	350	345	355	370	360	365	366	442	....
" " " " dorsal "hump"	485	177	....	450	....	413	....	....	405	373	425	375	350	....	....	....	....	350	....	....	405	....	....	....	....	....	....
Anus to clitoris or penis	....	45	....	....	....	....	....	....	120	....	125	....	....	....	....	....	....	....	....	....	....	....	....	....	142	61	....
" " umbilicus	....	75	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Flukes tip to tip	310	103.5	320	302	....	290	306	....	330	275	300	300	....	302	310	300	320	....	320	....	....	290	320	....	305	267	274
Length right lobe of flukes axially	150	62	....	....	....	155	....	....	....	....	....	175	....	....	....	....	....	....	....	....	....	150	....	....	....	....	....
" left " " " "	....	60	....	....	....	160	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Greatest thickness of flukes at insertion	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	22	23	....	....
" breadth " " ant. post	....	40	....	....	....	....	....	....	....	....	106	112	....	....	105	100	95	....	110	....	118	90	....	....	104	....	....
Depth of peduncle just ant. to flukes (on curve)	80	29	76	70	....	68	....	....	75	70	....	80	....	70	....	....	70	....	78	....	....	75	80	80	46	....	....
" " " midway between flukes and anus	....	49	110	....	....	140	....	....	127	135	126	....	....	126	115	114	135	....	130	....	....	150	....	150	....	....	....
Length of pectoral, tip to head of humerus	228	....	240	230	220	222	220	225	230	....	224	220	....	230	....	218	235	180	218	228	240	220	220	235	....	....	....
" " " " " " post. insertion	137	67	165	160	145	150	140	160	160	....	156	155	....	165	....	148	155	120	150	160	175	160	150	170	....	....	....
" " " " " " ant. "	205	94	....	190	....	190	190	185	180	....	....	....	....	....	....	....	190	....	....	....	....	....	....	....	198	183	153
Greatest breadth of pectoral	75	33	90	94	79	83	85	89	90	....	85	85	....	92	....	82	....	68	85	88	90	85	90	95	87	....	61
Distance from eye to ear	56	24	55	....	....	....	....	....	53	....	52	....	53	62	50	....	50	....	....	50	....	50	....	....	....	....	....
" eye above ear	2[1]	1[1]	....	....	....	....	....	....	5	....	5	....	5	6	5	....	5	....	....	5	....	2	....	....	....	....	....
Length of right blowhole (straight)	25	9	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	21	....	....
" " left " "	25	9	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Dist. apart of blowholes anteriorly	7	4.5	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
" " " " posteriorly	23	9	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....
Length of row of baleen (straight)	220	....	203	....	198	190	210	215	....	....	182	200	204	219	185	190	183	155	200	....	200	210	....	200	....	....	....
Longest plate baleen (inside)	40	....	48	....	....	40	46	40	....	....	....	45	....	....	38	36	45	32	45	....	40	38	....	42	46	36	31
Number plates of baleen (one side)	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	158	162	148	....	....	....	154	....	....	....	....	....
Number of throat furrows	2	2	2	3	3	2	2	2	2	....	2	2	....	2	3	2	3	2	2	2	4	2	2	2	....	....	....
Length of longest throat furrows	....	59	140	150	165	160	170	....	150	....	165	153	....	165	150	145	150	130	155	160	....	170	170	....	....	....	....
Distance apart anteriorly	15	6	22	....	32	....	....	....	....	....	....	....	....	....	....	19	....	....	....	....	....	20	....	....	....	....	....
" " posteriorly	....	16	47	....	50	....	....	....	....	....	....	....	....	....	....	55	....	....	....	....	....	50	....	....	....	....	....
Tip of mandible to ant. end of furrows	65	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	....	75	....	....	....	....	....

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[1] Nos. 1 and 1a had the ear *above* the eye.

It will be seen from the table that the greatest variation appears in the distance from the notch of the flukes to the dorsal "hump" amounting to 11%; this will be discussed later.

The variation of 5.3% in the width of the flukes from tip to tip may in great measure be accounted for by the fact that the tips of the flukes were very frequently injured. The same can be said of the measurement of the pectoral from the tip to the head of the humerus, but in a less degree, for usually one of the flippers, at least, was uninjured and the correct length could thus be secured.

The measurements of the California examples neither conform to each other nor to those from Korea. In Scammon's specimen the distance from the tip of the snout to the blowholes is 14.2% of the total length. This is much less than in any of the Korea whales and, moreover, gives a difference of 3.6% between the measurements from the tip of the snout to the eye and to the blowhole. This can hardly be correct. The same discrepancy is apparent in Dall's figures, but to a greater degree. The ratio to the total length of the tip of the snout to the eye is greater than in any of the Korea specimens, and that from the tip of the snout to the blowholes is much less, the difference between the two being 11.6%. One, or both, of these measurements is certainly incorrect.

Pechuel's figures give the distance from the snout to the blowhole as 25% of the total length, while the greatest in the Korea specimens is 19.5%. It is impossible to account for this discrepancy.

Scammon's measurements from the snout to the axilla, of the flukes from tip to tip, and of the depth of the peduncle just anterior to the flukes, are all at such variance with the Korea specimens that they must either be incorrect or have been taken in quite a different manner from my own. The same is true of Dall's measurements of the flukes from tip to tip and of the length of the fin. These data in reference to the California specimens are, therefore, of little value either for comparison with the Korea examples or with each other.

Table V.—Proportional Measurements of Korea and California specimens.

	ULSAN KOREA													
	No. 1 ♀	No. 1a Fœtus ♂	No. 2 ♂	No. 3 ♂	No. 4 ♂	No. 5 ♂	No. 6 ♀	No. 7 ♂	No. 8 ♂	No. 9 ♀	No. 10 ♂	No. 11 ♂	No. 12 ♂	No. 13 ♂
	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.
Total length, snout to notch of flukes	1300	435	1160	1240	1170	1143	1317	1202	1240	1160	1050	1075	1190	1250
	%	%	%	%	%	%	%	%	%	%	%	%	%	%
Tip of snout to eye	19.2	18.6	18.9	18.3	18.9	19.0	18.5	20.7	19.3	—	19.0	20.4	18.9	19.6
“ “ “ “ blowhole	17.2	17.0	—	17.7	17.9	17.9	16.7	—	16.6	—	—	19.5	17.2	18.5
“ “ “ “ axilla	—	34.9	—	—	—	32.0	29.6	—	31.4	31.4	30.4	35.3	—	35.2
Notch of flukes to anus	31.5	32.3	31.9	29.8	—	31.7	28.6	28.7	27.0	—	33.3	33.0	—	30.0
“ “ “ “ dorsal “hump”	37.3	40.6	—	36.2	—	36.1	—	—	32.6	32.1	40.4	34.8	29.4	—
Flukes, tip to tip	23.8	23.6	26.0	24.3	—	25.3	23.2	—	26.6	23.7	28.5	27.9	—	24.1
Depth of peduncle just anterior to flukes	6.1	6.6	6.5	5.6	—	5.9	—	—	6.0	6.0	7.6	7.4	—	5.6
“ “ “ midway between flukes and anus	—	11.2	9.4	—	—	12.2	—	—	10.2	11.6	—	—	—	10.0
Fin, tip to head of humerus	17.5	—	20.7	18.5	18.8	19.4	16.7	18.7	18.5	—	20.9	20.4	—	18.4
“ “ “ anterior insertion	15.8	21.6	—	15.3	—	16.6	14.4	15.3	14.5	—	—	—	—	—
“ greatest breadth	5.7	7.5	7.7	7.5	6.7	7.2	6.4	7.4	7.2	—	—	7.9	—	7.3

Table V. — Continued.

	ULSAN KOREA											CALIFORNIA		
	No. 14 ♂	No. 15 ♂	No. 16 ♂	No. 17 ♂	No. 18 ♂	No. 19 ♂	No. 20 ♂	No. 21 ♂	No. 22 ♂	No. 23 ♂	Amount of variation in ratios	Average of ratios	Scammon ♂	Dall ♂	Pechuel ♂
	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.	cm.
Total length, snout to notch of flukes	1160	1085	1180	980	1190	1180	1125	1125	1240	1235			1280	1462	975
	%	%	%	%	%	%	%	%	%	%	%[1]	%[1]	%	%	%
Tip of snout to eye	18.1	20.2	18.6	17.8	19.4	19.6	18.4	18.7	19.3	18.2	2.9	19.0	17.8	21.5	——
" " " " blowhole	16.8	19.1	18.2	16.8	——	17.7	17.6	17.1	18.9	17.0	2.8	17.6	14.2	9.9	25.0
" " " " axilla	——	32.2	——	31.6	——	33.8	——	33.8	33.0	——	5.7	32.4	26.1	——	——
Notch of flukes to anus	28.0	33.1	27.5	28.5	29.4	29.2	28.4	30.2	29.0	29.5	5.8	30.4	28.5	30.2	——
" " " " dorsal "hump"	——	——	——	35.7	——	——	32.4	——	——	——	11.0	34.7	——	——	——
Flukes, tip to tip	26.7	27.6	27.1	——	26.8	——	——	23.6	25.8	——	5.3	25.6	23.8	18.2	28.1
Depth of peduncle just anterior to flukes	——	——	5.9	——	6.5	——	——	6.1	6.4	6.4	2.0	6.3	3.5	——	——
" " " midway between flukes and anus	9.9	10.5	11.4	——	10.9	——	——	12.2	——	12.1	2.8	10.9	——	——	——
Fin, tip to head of humerus	——	20.0	19.9	18.3	18.3	19.3	19.2	17.9	17.7	19.0	4.2	18.9	——	——	——
" " " anterior insertion	——	——	16.1	——	——	——	——	——	——	——	1.3	15.4	15.4	12.5	15.6
" greatest breadth	——	7.5	——	6.9	7.1	7.4	7.2	6.9	7.2	7.6	2.2	7.1	6.7	——	6.2

Color.

Plates XIX and XX.

None of the published descriptions of the color of *Rhachianectes glaucus* which I have been able to find occupy more than three or four lines, or give other than the vaguest impression of the animal's appearance. Scammon says: "The California Gray is unlike other species of baleen whales in color, being of a mottled gray, very light in some individuals, while others, both male and female, are nearly black" (*l. c.*, p. 20). Scammon's figure (*l. c.*, plate ii, fig. 1) shows a rather slender whale, gray, and irregularly marked with white on the entire upper half of the body from the head to the flukes; the lower half is represented as almost plain.

This type of coloration is just the reverse of what was observed in Korea specimens. It is true that several examples were seen which had the back more or less heavily marked, but in every case where this occurred the lower half of the body was so thickly covered with white and gray patches that there was a great preponderance of the light color. Unless the California specimens are very different from those of Korea, which is highly improbable, Scammon's figure is incorrect. This view is strengthened when the drawing of *Balænoptera sulfurea* (*l. c.*, plate xiii) is examined for it is quite unlike a Pacific Sulphurbottom in coloration. Scammon's first figure of *Rhachianectes*, published in 1869,[2] although very crude, gives in the side view a really better suggestion of the color of the animal than does the plate in his 'Marine Mammalia.' In his first figure the markings are shown evenly distributed over the entire body from the head to the flukes and not confined to the dorsal surface as in the later drawing.

In Cope's article on the Gray Whale (1868), Mr. W. H. Dall's description of two specimens seen by him at Monterey, Cal., is quoted, as follows: "Color above and below, black, with a gray bloom like a plum. This distinguishes this species from the known Balænæ of the Pacific, which are more or less white on the belly and fin" (*l. c.*, p. 226).

Pechuel's figure of *Rhachianectes* is diagrammatic and there is little attempt at coloration.

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[1] This does not include fœtus No. 1a.

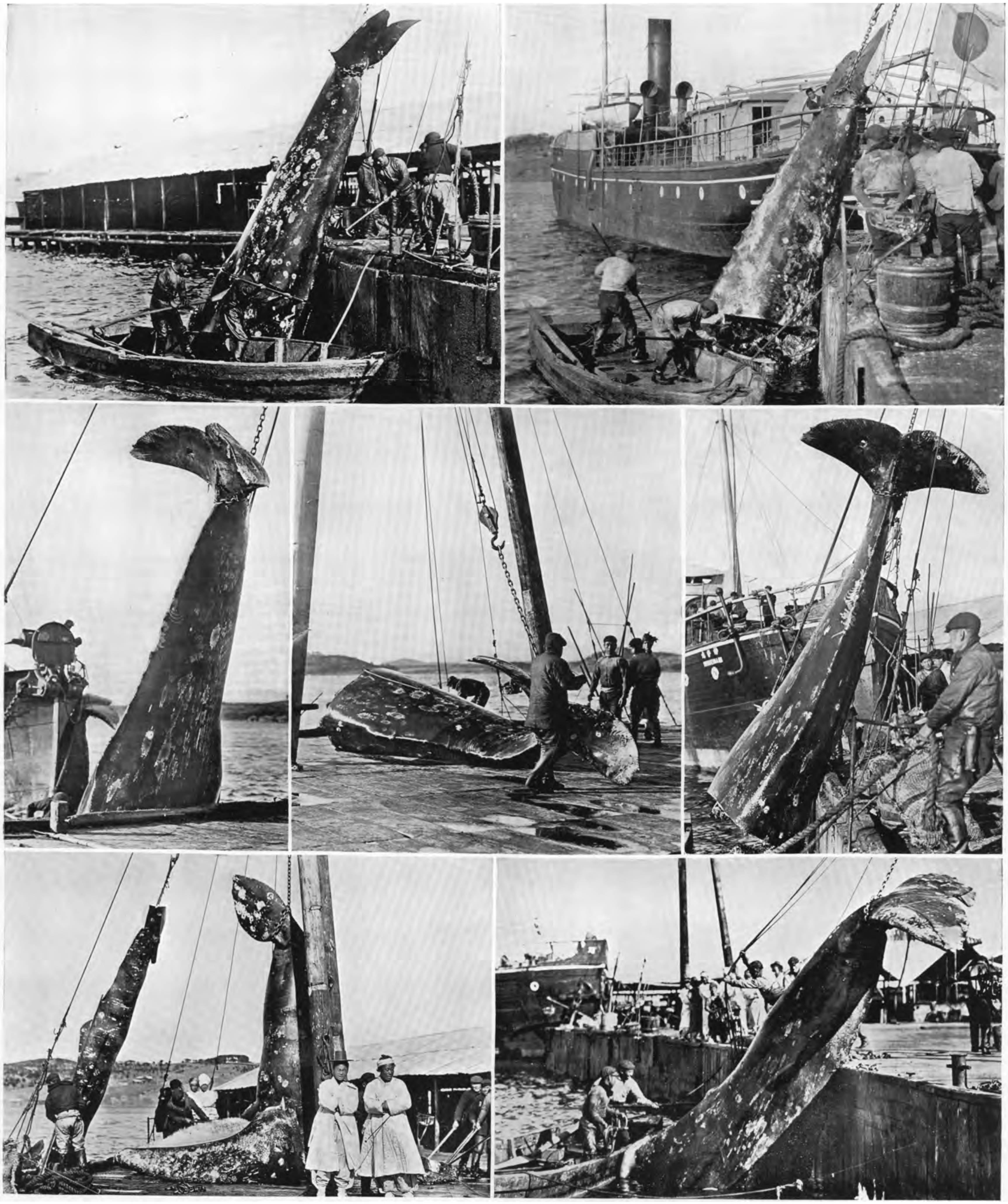
[2] Proc. Phil. Acad. Nat. Sci. Phil., 1869, fig. 8.

PLATE XIX.

PLATE XIX.

Rhachianectes glaucus.

Fig. 1. Lateral view of peduncle showing white markings, mostly cirriped scars.
Fig. 2. Lateral view of peduncle showing normal gray and white markings and total absence of cirriped scars.
Fig. 3. Head, pectoral fin and section of back blubber.
Fig. 4. Direct lateral view of peduncle showing dorsal crenulations.
Fig. 5. Dorsal view of peduncle showing normal gray markings and flukes.
Fig. 6. Peduncle lying upon the wharf.
Fig. 7. Posterior portion of body showing inferior outline.



Rhachianectes glaucus.

He says in regard to this: "Abweichend von allen anderen Walen ist seine Farbe ein melirtes grau, Manche sind ganz fleckig, selten sieht man gleichmässig dunkel gefärbte."[1]

The following description of Korea examples is, therefore, the only detailed account of the color of the Gray Whale that has thus far been published.

There seems to be quite as much individual color variation in *R. glaucus* as in other baleen whales, some examples being abnormally dark with but few gray markings while others are very light, the entire body being so thickly covered with blotches of white and gray that there is a preponderance of the light color. It is obvious, therefore, that no description which will apply to all individuals can be given, but between the light and dark extremes there was a certain type of coloration possessed by a majority of the examples which came under my observation. This may be described as follows: The head, throat, back, and the dorsal and ventral ridges of the peduncle are black, or very dark slate, and are usually unmarked. On the dorsal and lateral surfaces of the distal half of the rostrum there is considerable white and light gray in flecks and small spots; this is frequently true of the chin, lower lips, and both mandibular rami. On the under side of the rostrum just exterior to the bases of the baleen rows, there is a band of flesh pink, or white, about three inches wide. The amount of white on the rostrum and lips varies greatly with individuals but it is seldom entirely absent. The throat and sides to the pectorals are usually unmarked. From the fins to a point opposite the anus, on the sides, breast and belly, are many roughly elliptical and circular markings with irregular edges. These markings have gray centers shading to very light gray, or white, on the edges and are broken by small round, or oval, black spots (Plate XX, Fig. 6). They follow the long axis of the body and generally closely approximate each other.

On the sides of the peduncle the gray markings become scattered and are generally smaller and darker. The whole body from the head to the flukes has many white or light gray circular scars of varying sizes, apparently left by parasitic cirripeds; on some individuals these almost obscure all other markings.

The pectoral fins are dark slate like the body. Above, on the posterior half, there are a few scattered white circles and spots. Below, the white circles are more numerous and on the distal half are two more or less broken bands of white, or very light gray, about 8 cm. wide and 45 cm. long between the 2nd and 3rd and 3rd and 4th fingers; the band between the 2nd and 3rd fingers is usually the longer. The posterior edge of the fin is very frequently white.

The flukes are black or dark slate like the body, a few white circles and spots being scattered over both surfaces, generally more on the lower. Frequently the posterior edges and tips are white.

In connection with the preceding description it is interesting to refer to the color of fœtus No. 1*a*, described below. This specimen was almost ready for birth and gives an excellent idea of the disposition of the markings on the Gray Whale before the body has been scarred by parasites and by contact with rocks. The general color must become much darker after birth than it is during fœtal life.

Color Variations.— There are striking variations from the type of coloration described above. Three specimens out of the twenty-one on which color notes were taken were exceptionally light colored. One (No. 8, male) had the entire rostrum, lips and mandibular rami dotted and specked

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[1] Pechuel-Loesche, Wale and Walfang. Ausland, Vol. 44, 1871, p. 1186.

with gray and white. The sides of the breast and throat, from the fins forward, were streaked longitudinally with long gray lines, and the center of the throat thickly splashed with white. The back was heavily marked with oblong blotches of white. The only portion of the whale unmarked was the dorsal and ventral ridges of the peduncle.

A second whale (No. 11, male) had almost no white on the lips, rostrum or throat, but the sides of the body and peduncle, from the fins to the flukes, were so thickly washed, circled and blotched with gray and white that there was much more light than dark color.

No. 19, female, had the lower lips and distal portion of the mandible finely dotted and flecked with gray and white. The sides, belly, and the entire peduncle were so thickly covered with small light gray patches, that there was more light than dark color. The ground color of this whale was dark gray and not slate, or black, as usual.

No. 3 was a dark whale and No. 5 exceptionally so. The body was black and had only a few small and rather indistinct gray markings on the sides, back and lower half of the peduncle.

No. 6, female, was black. On the left side of the throat were a few long stripes of white, which seemed to be scars. The remainder of the throat, breast and belly was unmarked save for a single large, irregular, light-gray patch on the belly; the entire peduncle was plain except for a little white along the dorsal ridge. No. 14, male, was much like No. 6; No. 17, male, although a very dark individual, had the rostrum, lips and mandibular rami mixed white and gray, and the sides of the peduncle, body and back streaked with long, narrow gray lines.

There seems to be a tendency among the whalers to believe that all individuals which show a preponderance of light color are of the greatest age. Averages and comparisons of the lengths of the very dark, very light, and normal examples of *R. glaucus* shows but little difference between them and gives no basis for believing that the animals become lighter with increasing years. Only three of the whales which I examined were females, one of these being exceptionally dark and the other somewhat lighter than normal. The males presented both light and dark extremes and every variety of intermediate coloration. I believe, therefore, that the color differences have nothing whatever to do with sex or age, or that they are other than purely individual.

For reference the field descriptions of twenty-one individuals examined at Ulsan, Korea, are given below:

Field color descriptions of 23 Korea specimens.

No. 1. Female. Length, 1300 cm. General color dark slate. Much white on the distal half of the rostrum, snout and upper lips just above the bases of the baleen rows. Many fine, grayish lines on the back, and numbers of irregular white streaks over the entire body; the latter appeared to be scars from old wounds. Inferior half of peduncle from genitalia to flukes thickly marked with irregular elliptical patches of light gray.

Pectoral fins dark slate above, having both margins and tips whitish, the light color extending far up on the superior surface of the fin.

Flukes above dark slate with many white dashes and circles, the latter undoubtedly caused by parasitic cirripeds.

No. 1*a*. Fœtus. Male. Length, 476 cm. General color gray. The entire head and throat to the posterior insertion of the pectoral fins is light gray. A line of small, dark gray spots and dashes extends from the eye to a point a short distance above the pectoral. On the throat are a few small patches of very light gray, almost flesh white, and several large irregular markings of dark gray.

PLATE XX.

PLATE XX.

RHACH~~I~~ANECTES GLAUCUS.

Fig. 1. Direct lateral view of head showing few parasite scars.

Fig. 2. Three-quarters posterior view of head showing many parasite scars.

Fig. 3. Dorsal view of head and blowholes; note the barnacles *Cryptolepas rhachianecti* embedded in the skin, and the masses of *Cyamus scammoni*.

Fig. 4. Front view of head.

Fig. 5. Direct lateral view of head and mandible of fœtus No. 1*a*.

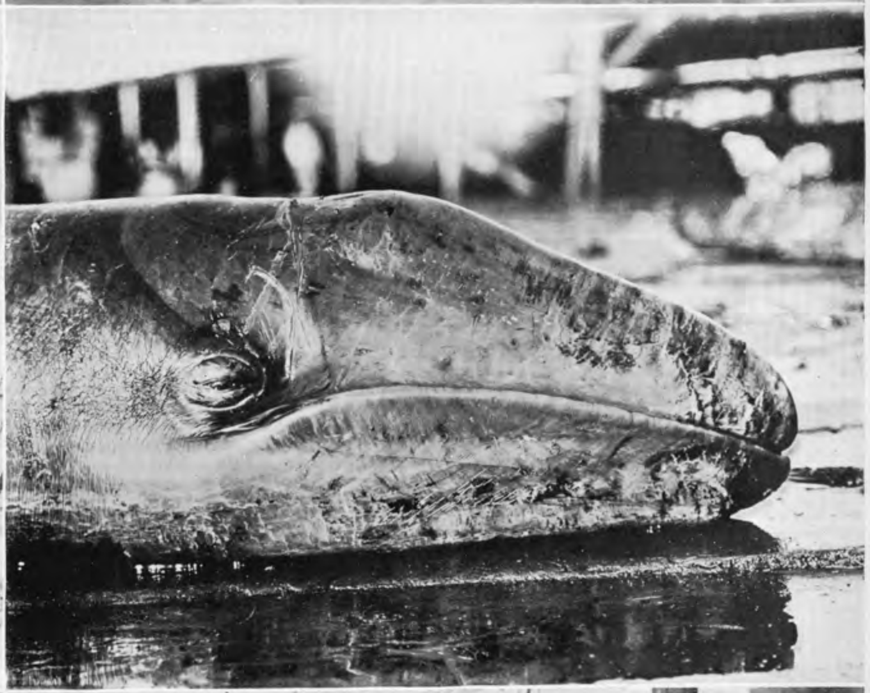
Fig. 6. Section of peduncle showing normal gray and white markings.

1

3

2

5



6

4

RHACHIANECTES GLAUCUS.

On the sides a slight ridge is formed by the ends of the vertebral transverse processes below which the lateral and ventral surfaces of the body, forward almost to the pectoral fins, bear many irregular oblong and elliptical patches of very light gray; the markings are longitudinal, follow the long axis of the body and are so thick that there is more of the light than of the dark color. The back, above the line of the transverse processes, is light gray thinly marked with irregular, dark gray oval and oblong patches. On the right side, just posterior to the tip of the pectoral laid back, is a circular, pure white spot about 4 centimeters in diameter and a second smaller one above the posterior insertion of the fin.

The pectorals are plain dark gray on both surfaces but have light posterior and anterior edges.

The flukes are plain light gray above with dark anterior and posterior margins. Below, the ground color is light gray but coarse, broken whitish lines run transversely across each fluke from the anterior edge and curve inward toward the notch; this gives more white than dark color to the inferior surface.

No. 2. Male. Length, 1160 cm. Many fine white spots and flecks on snout, symphysis of mandible, and on both rami, but the remainder of the head is plain dark gray. Posterior to the genitalia both sides of the body have many large irregular patches of light gray about thirty cm. long by twelve cm. wide, and numerous blotches, circles and spots of white. There is a large patch of light gray about 150 cm. long by 45 cm. wide on the right side of the back and a large white spot just posterior to the tip of the pectoral fin laid back. The mid-dorsal region has either very few gray markings or none at all. The lower half of the peduncle is covered with rather fine dashes and circles of white.

The pectoral fins are alike on both surfaces. On the distal two-thirds between the second and third and the third and fourth digits there are two broad parallel bands of white. The remainder of the fin is so dotted, barred and circled with white that there is more white than dark.

Both surfaces of the flukes are dark slate thickly covered with irregular bands, spots and dashes of white. The left lobe has the inferior surface of the distal end almost entirely white.

No. 3. Male. Length, 1240 cm. A dark individual. The general color is dark slate, almost black. On the dorsal and lateral surface of the rostrum there is considerable light gray, but except for numerous cirriped scars, especially on the sides of the peduncle, the body has comparatively few light markings.

On both surfaces of the pectoral fins there is a broad longitudinal band of white between the fingers, and a few circles and spots of white on other parts of the flipper. The posterior edges are also white.

No. 4. Male. Length, 1170 cm. General color of body dark slate. The entire rostrum is clear light gray, shading into darker on the head, but does not show much white; neither is there white on the lips or mandibular rami. The dorsal region of the peduncle and body forward to the pectoral fins is unmarked dark slate but the sides have many small spots, dashes, and circular scars of white.

The pectoral fins are dark slate above and have a whitish longitudinal band between the fingers; also a few large cirriped scars. The anterior edge of the fin is dark slate and the posterior edge white.

No. 5. Male. Length, 1143 cm. A very dark individual. Head, back, sides and upper half of peduncle, black. Lower half of peduncle has a few small, light gray markings and on the back and sides near the pectorals are several rather indistinct, gray patches; scattered over the body are a few large, white circular scars. Mucous membrane in the roof of the mouth light pink as are the lips just above the bases of the baleen rows.

The pectoral fins are black, above, except for two or three large white circles. Below, there is one large oblong patch of white between the fingers.

Both surfaces of the flukes are plain, unmarked black.

No. 6. Female. Length, 1317 cm. A very dark whale. Throat, breast and belly plain black except for a few long white stripes (apparently scars) just above the furrows and a large, irregular, light gray patch on the belly. The back and sides are black, almost unmarked, and on the peduncle *there are no gray patches* and only a few cirriped scars; along the dorsal ridge is a little white.

The superior surface of the pectoral fins is black with a few white circles; inferiorly both flippers are marbled and circled with white.

No. 7. Male. Length, 1202 cm. The entire distal third of the rostrum and the dorsal ridge to the blowholes is greatly roughened, or "cornified," thickly infested with parasitic *Cyamus*. There is no white on the rostrum.

The superior surface of each pectoral fin has but little white. On the inferior surface two broad bands of white run between the fingers to the tip of the fin and there is a large white patch near the base.

No. 8. Male. Length, 1240 cm. The lightest colored specimen which has been brought to the station. The dorsal ridge of the rostrum is almost entirely white having but few gray specks; the left side of the rostrum is like the dorsal surface but the right side is covered with fine gray and white flecks and dots giving a "pepper and salt" effect (apparently many small barnacles had fastened here). From chin to pectorals the sides of the throat and breast are streaked with long, longitudinal gray lines about five mm. wide and the center of the throat is thickly splashed with white. The rami of the mandible and the lower lips are mixed white and gray ("pepper and salt"). The entire back is thickly marked with small white circles and dots and the sides of the body, posterior to the fins, and of the peduncle are covered with blotches of white, fairly regular in size and about 25 cm. long by 10 wide; the edges of the blotches are irregular. The mid-dorsal and mid-ventral regions of the peduncle are plain black except for a circular patch of white about 30 cm. in diameter.

On the inferior surface the pectorals have two broad longitudinal bands between the digits, that nearest the posterior edge being the longest; there are also many smaller patches and scars on the lower surface. Above, the pectorals have much less white, only one band being present.

The flukes are black, above, thinly circled with white but below have much white.

No. 9. Female. Length, 1160 cm. Sides of body and of the peduncle blotched with light gray; the markings are heavier on the body. Ventral region almost plain.

No. 10. Male. Length, 1050 cm. A dark individual. Throat and lips plain dark slate with practically no lighter color. On the sides backward to a point opposite the anus are a good many large, gray, oval and oblong markings having irregular margins; the sides are also thickly studded with barnacles. The dorsal and ventral regions of the peduncle are plain but there are a few white circles and spots on the sides. The dorsal "hump" has patches of light gray, almost white, on either side and a large white spot on the right side; just anterior to the penis is a gray blotch.

Above, the pectoral is black with only one white spot.

The flukes are black on both surfaces save for a few white circles; the distal half of the posterior edge is all white.

No. 11. Male. Length, 1075 cm. A light individual. There is almost no white on the rostrum, lips, or throat. Sides of body and of peduncle so thickly washed, circled and marked with gray and white that there is much more light than dark color present.

No. 13. Male. Length, 1250 cm. Sides of body from the fins to a point opposite the anus, have many large gray and white markings and an extensive area of clear light gray. The peduncle has few gray markings on the sides but many white barnacle scars (many barnacles are still in position).

On the inferior surface, both fins are black but have a number of white spots joining to form a band about 60 cm. long between the second and third fingers. There are a good many other white spots and circles along the posterior edge, the remainder of the fin being unmarked. The superior surface is almost like the inferior but shows somewhat less white.

No. 14. Male. Length, 1160 cm. An exceptionally dark whale. The head is black showing practically no white or gray markings and but few parasites. On the chin and throat and on the breast between the fins there are many white flecks and circles but the remainder of the breast and belly is plain. On the left side from the fin to a point opposite the penis is an area of clear light gray about 60 cm. wide; on the right side its place is taken by a number of rather dark gray, roughly oblong, markings. The peduncle is almost entirely black but has a few gray patches on the inferior half.

No. 15. Male. Length, 1085 cm. The head shows a little white on the dorsal surface of the rostrum and on the sides a good many white barnacle scars. The sides of the body from the pectoral fins to a point opposite the anus have numerous light gray patches with white edges which almost join each other; these also cover the belly but do not extend on to the back. The superior half of the peduncle is plain black and the remainder thinly covered with rather small gray markings.

No. 16. Male. Length, 1180 cm. A light individual. The head, lips, throat and back are black except for a few gray patches just posterior to the blowholes and a white spot on the lips. The sides of the body from the fins to a point opposite the anus are covered with rather small gray patches which become larger and more numerous on the lateral surfaces of the peduncle. (These patches are gray in the center shading to white on the edges and broken by small black spots or dashes). The dorsal and ventral regions of the peduncle are unmarked.

The pectoral fins are black, above, circled with white. The inferior surface has fewer circles but is washed with white in several places. The flukes are black below with a few white circles. (In coloration the tail resembles that of *Megaptera*).

No. 17. Male. Length, 980 cm. A dark whale. The sides of the rostrum, lips and mandibular rami are mixed gray and white ("pepper and salt"). The back, sides of body and peduncle are marked with long gray lines which resemble scratches but seem to be normal.

The flukes are very light colored on the inferior surface and have whitish lines running transversely across each lobe and curving inward toward the notch.

No. 18. Male. Length 1190 cm. The dorsal and lateral surfaces of the rostrum are very light gray; the entire mandible is dark but shades into very light gray about 60 cm. from the symphysis. The sides of the body from the pectoral fins to a point opposite the anus has many, rather dark gray markings a few of which are present on the proximal half of the peduncle; the remainder of the peduncle is very dark slate. The back is unmarked save for a few small barnacle scars.

No. 19. Male. Length, 1180 cm. A very light whale. The ground color of the body is dark gray and not the usual slate, or black. Distal half of mandible gray and white mixed. The sides of the body, belly and entire peduncle are thickly covered with small gray patches, irregular in shape, but having their longitudinal axes following the axis of the body. The gray markings are about 15 cm. long by 8 cm. wide and coalesce so that there is more of the light gray and white than the darker ground color.

No. 20. Male. Length, 1215 cm. Ground color dark gray. Sides of rostrum and head to the eyes very light gray; just above the bases of the baleen rows is the usual narrow pinkish band. Sides of body to the fins have many gray markings, and the back, belly and, in fact, the entire body is thickly covered with white cirriped scars. The dorsal and ventral regions of the peduncle are unmarked, but the sides have a number of gray patches which become smaller posteriorly and cease about 120 cm. from the flukes.

The pectorals are dark on the superior surfaces with only a few white flecks. There is a considerable quantity of white flecks, spots and circles scattered over the inferior surfaces and the posterior edges are white.

The flukes are dark above and below showing but few white circles and spots.

No. 23. Male. Length, 1235 cm. A light individual. The head, lips and jaws are mostly light gray with flecks of white. There is much light gray on the sides of the body in small patches, bars, dashes and flecks. The sides of the peduncle show some light gray markings and the ventral surface a few irregular white lines resembling scratches.

EXTERNAL ANATOMY.

Plates XX–XXIV.

Outline of Body.— The rostrum is strongly convex, the highest point being just anterior to the blowholes. Directly behind the spiracles there is a shallow concavity about sixty cm. long, and from that point to the "hump" the dorsal outline is regularly convex. From the hump the upper ridge of the peduncle slants very gradually downward to the flukes. The throat is rather flat but opposite a point midway between the eye and the anterior insertion of the fin, the breast and belly swell outward in a gradual curve to the anus broken only by a slight bulge at the penis. At the anus there is an abrupt dip and from that point to the flukes the ventral outline of the peduncle is slightly convex; the greatest convexity is just anterior to a point midway between the anus and flukes. The body is deepest opposite the tip of the pectoral fin laid back.

The outline of the body in Scammon's figure of *Rhachianectes* needs some correction. From the blowholes to the end of the peduncle crenulations the back is straight when it should be convex and there is little indication of a hump. The breast and belly are hardly full enough, the prominent dip just posterior to the anus is not shown, and the ventral outline of the peduncle should be slightly convex.

Head.— The head of *Rhachianectes* is distinctly characteristic and differs strongly from that of all other baleen whales. Its shape, in some respects, is intermediate between that of the

PLATE XXI.

PLATE XXI.

Rhachianectes glaucus.

Fig. 1. Eye and ear.
Fig. 2. Inner view of baleen.
Fig. 3. Blowholes and *Cyamus scammoni.*
Fig. 4. Three-quarters view of tongue.
Fig. 5. Lateral view of anterior portion of snout showing cornified areas due to the action of parasites.
Fig. 6. Inferior view of anterior portion of snout.
Fig. 7. Fœtus No. 1*a*.

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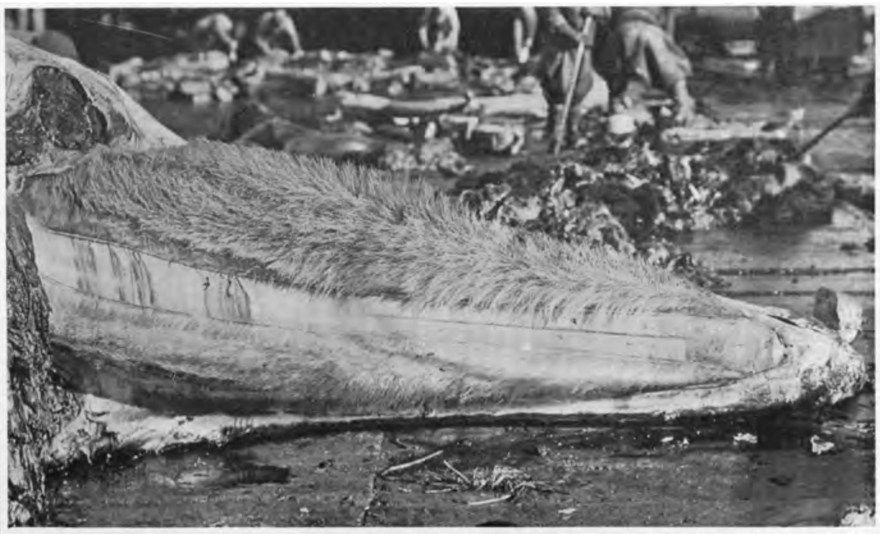

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RHACHIANECTES GLAUCUS.

Balæninæ and the Balænopterinæ. It is not so large proportionately, and the rostrum is neither as narrow nor as curved as in the former, but is much narrower and deeper than in the latter.

The rostrum is convex dorsally, narrow and very deep, especially so just anterior to the blowholes. On either side of the rostrum just anterior to, and below, the spiracles is a prominent swelling about forty-five cm. wide which runs forward, narrows, and gradually becomes lost. Immediately below this swelling is a shallow depression extending for the entire antero-posterior length of the rostrum.

The head is deep vertically and in whale No. 3, male, 1240 cm. in length, the distance from the eye to the summit of the head over the curve of the side was 94 cm.

The blowholes are situated in a slight depression just behind the highest point of the rostrum, the anterior ends being slightly higher than are the posterior. They appear as two slightly curved slits, the convexities inward, having a long and rather shallow furrow between them. In whale No. 1, 1300 cm. in length, the blowholes were 25 cm. long, the anterior ends being 7 cm. apart and the posterior ends 23 cm.

In Cope's description from Dr. W. H. Dall's note there is the following statement: ". . . . the blowholes are entirely concealed by four dermal plicæ, which accounts for the small misty spout peculiar to the species" (*l. c.*, 1868, p. 226). I am at a loss to know what is meant by the "four dermal plicæ," as the blowholes of all the specimens which I examined were open and did not differ greatly from those of other baleen whales.

The region immediately about the spiracles was usually thickly infested with parasitic *Cyamus scammoni*.

Eye.— The eye forms a rather prominent swelling above, and a little behind, the corner of the mouth and is surrounded by two furrows the anterior and posterior ends of which almost meet. In some cases the ends of the furrows actually join thus forming a complete circle about the eye but in the majority of individuals the ends stand a short distance apart. The upper lid is considerably fuller and more prominent than is the lower. On whale No. 21, male, 1225 cm. in length, the furrows about the eye were each 18 cm. long, and the eye opening itself 5 cm. from the anterior to the posterior commissure.

The eyeball from an adult male 1158 cm. in length had a circumference of 205 mm. after it had been trimmed of adhering fat. The iris was 26 mm. long and 17 mm. in vertical diameter. The pupil was 10 mm. long and 6 mm. in diameter, oval, with the superior edge somewhat flattened.

The iris was a clear, dark brown band 6 mm. wide, the outer edge of which shaded into a narrow whitish ring. Encircling the iris was a band of light gray, 4 mm. in width, which shaded off gradually into very dark gray.

Auricular orifice.— The ear opening varies in size, as in all large whales, but is usually about 18 mm. in longitudinal diameter and directed upward at an angle of nearly 30 degrees. The meatus is a little larger than a good sized pencil.

The position of the ear is somewhat variable. In whale No. 1, female, 1300 cm. in length, the ear was 56 cm. behind the eye and 20 cm. *above* it. In fœtus No. 1*a*, male, from the same whale, the ear was 24 cm. behind the eye and 1 cm. above it. In none of the other twenty-three specimens on which notes were taken was the ear above the eye, it usually being from 2 to 5 cm. below it.

Scammon remarks in this connection: "The ear, which appears externally like a mere slit in the skin two and one half inches in length, is about eighteen inches behind the eye, and a little above it" (*l. c.*, p. 20). In the table of measurements the distance from the eye to the ear of eleven specimens will be found.

Tongue.— The tongue of *Rhachianectes* is narrow, thick and solid, resembling that of a Right Whale much more strongly than it does the soft, shapeless tongue of *Megaptera* or any *Balænoptera.* The dorsal surface is regularly convex except at the distal end where it becomes concave, and the tip is upturned and deeply cleft. There is a narrow flattened strip on the top which runs from the proximal to the distal end. A cross-section of the tongue would be a semicircle with a slight dorsal compression. The color is usually flesh-pink becoming bluish gray at the tip.

Whale No. 17, male, 980 cm. in length, had a tongue 145 cm. long, 78 cm. wide over the curve and 50 cm. thick in the center. The tongue of No. 18, male, 1190 cm. in length, was 170 cm. long and 110 cm. wide over the curve.

Baleen.— The baleen plates of *Rhachianectes* differ from those of all other whales in being very thick and heavy, in the almost complete absence of transverse ridges, in having the outer edges thick and rounded instead of thin and sharp, and in the coarseness of the bristles. The baleen rows are not joined anteriorly by a narrow strip of small bristle-like plates as are those of the Balænopterinæ, in this respect resembling the Balæninæ.

The basal half of each plate is regularly concave, but in the distal half the concavity gradually disappears and the plate becomes flat. The color of the laminæ is yellowish white, or light yellow.

There are decidedly fewer baleen laminæ in each row than in any other large whale, the number varying from 138 to 174 on each side, the distance between the plates at the bases is from 5 to 10 mm. Following is a record of the number of baleen plates, *on one side only*, of different individuals, counting in every case the first and last lamina which was more than 50 mm. long and 5 mm. wide; the plates were all counted while *in situ:* 174, 168, 164, 162, 160, 158, 154, 148, 138.

The anterior ends of the baleen rows of whale No. 21, male, 1225 cm. in length were 35 cm. from the tip of the snout and 15 cm. apart; the posterior ends at the bases were 14 cm. apart and at the widest point the tips of the two rows diverged 65 cm.

The mucous membrane in the roof of the mouth between the bases of the baleen rows is white or flesh-pink.

The bristles of the proximal half of each plate are about 13 cm. in length but gradually elongate reaching a length of 25 cm. near the tips; they are round, very coarse and contrast strongly with the finer bristles of all other baleen whales. When seen *in situ* the bristles give the effect of a mat of thick, coarse fibers.

The baleen bristles are either entirely yellowish white like the plates themselves, or those of the posterior section may be gray, or dark gray, and the anterior portion yellowish white. The color of the bristles of twelve individuals was recorded showing that seven had some portion gray and five entirely yellowish white. Following is a list of the specimens in which the color of the bristles was noted:

PLATE XXII.

PLATE XXII.

RHACHIANECTES GLAUCUS.

Fig. 1. Throat showing two grooves.
Fig. 2. “ “ “ “
Fig. 3. “ “ three “
Fig. 4. “ “ “ “
Fig. 5. “ “ “ “
Fig. 6. Tongue in position.

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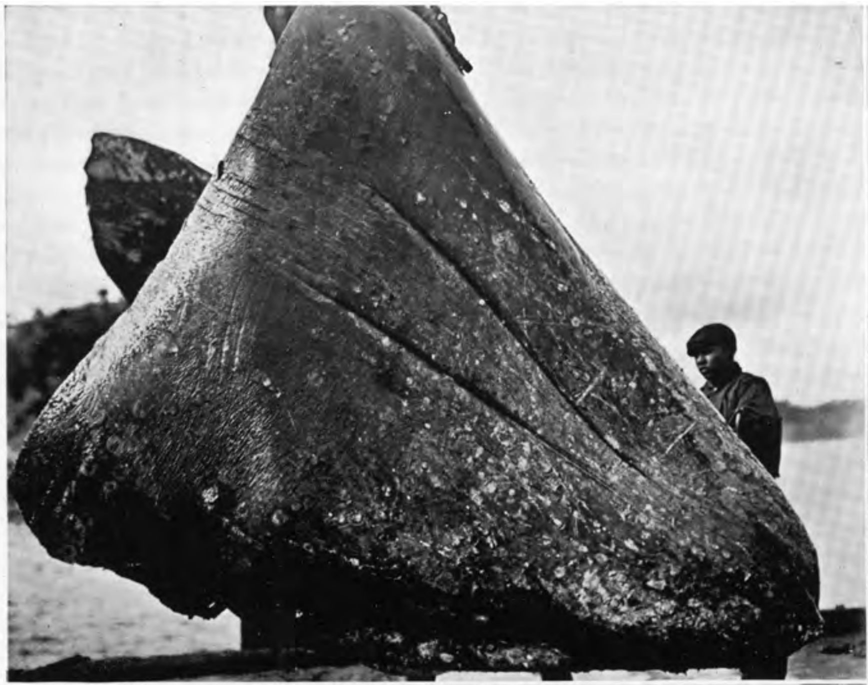

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Rhachianectes glaucus.

Color of bristles.

Capture Number	Sex	
4	♂	Posterior half gray, anterior half yellowish.
5	♂	" " " " " "
6	♀	All yellowish.
7	♂	Posterior half dark gray, anterior half yellowish.
8	♂	" two-thirds gray, anterior one-third yellowish.
11	♂	All yellowish.
13	♂	Posterior two-thirds gray, anterior one-third yellowish.
14	♂	All yellowish.
18	♂	" "
20	♂	Posterior three-fourths gray, anterior one-fourth yellowish.
21	♂	All yellowish.
23	♂	Posterior half gray, anterior half yellowish.

The descriptions given above of the baleen and bristles were written at the whaling station in Korea with fresh specimens at hand. I find upon examination of the set of baleen which was shipped to the Museum that both the bristles and laminæ are now very much darker than when fresh. This is due both to the drying of the plates and from soiling with dirt and grease. The bristles are now a strong brown and the plates yellowish-brown. I believe that in the great majority of cases any light colored baleen while being shipped from the field to a museum will be more or less soiled in transit and consequently the only reliable descriptions of such material are those that have been taken from fresh specimens.

Dall says that *Rhachianectes* has 145 laminæ of baleen on each side and that it is "light yellow," while Scammon describes it as "light brown or nearly white." Van Beneden speaks of the baleen in the Vienna Museum as being pale like that of *Balænoptera acuto-rostrata*. The baleen in the U. S. National Museum from San Luis Obispo, Cal., is stated by Dr. True to be yellowish-white except at one end of the series where for a distance of about eight inches the blades and bristles are dull chocolate-brown. He says: "The largest plates measure 18 in. in length without the bristles, and 6 in. at the base. The longest bristles measure 9½ in., and were perhaps originally a little longer" (*l. c.*, p. 290).

Throat furrows.— On either side of the median gular line *Rhachianectes glaucus* has two or more deep furrows. Their anterior ends closely approach each other and stand parallel for a short distance but gradually spread apart posteriorly. The furrows begin about 165 cm. from the tip of the mandible and end opposite a point half way between the eye and ear; the posterior ends are generally almost three times as far apart as are the anterior. Whale No. 24, male, 1225 cm. in length, had furrows 170 cm. long, the anterior ends being 20 cm. apart and the posterior ends 50 cm.; the anterior ends were 75 cm. from the tip of the lower jaw.

Although two furrows seem to be the usual number for *R. glaucus*, three are not infrequently present, and one individual which I examined possessed *four*. Whale No. 3, male, had three grooves, the left being 150 cm. long and the right 116 cm.; between their anterior ends was a shorter furrow 100 cm. in length. No. 4, male, also had three furrows, the two outer being 165 cm. long and the median 130 cm. The two outer furrows of No. 14, male, were 120 cm. in length and the one between them 154 cm. long; this was the only individual in which the median furrow was the longest of the three. In No. 16, male, the median furrow was 62 cm. in length while the two outer measured 150 cm.

No. 20, male, had *four* distinct furrows; the median and two outer ones were of about the same length and between the middle and left near the *posterior* end was a fourth short groove. Out of the twenty-one specimens in which the number of gular furrows were recorded fifteen had two, and six three, or more. Several whales were brought in which were not measured or described and among them were four or five individuals showing three throat furrows. The grooves are almost 5 cm. in depth and have rounded edges.

The gular furrows of *Rhachianectes* seem to be a specialization in the direction of the throat and breast grooves of the Balænopterinæ. Since in *Rhachianectes* they are presumably present to increase the throat capacity they throw light upon the origin of the folds in the Balænopterinæ and tend to substantiate Prof. Kükenthal's theory that their purpose is to allow the short-headed members of this subfamily to take into the mouth a greater quantity of water containing their food.

The grooves of the Balænopterinæ in their early development were probably few in number and confined to the gular region, as in the case of *Rhachianectes.* As specialization of the entire body continued the furrows increased in number and in length extending backward upon the abdomen to give the greater thoracic expansion made necessary by the extraordinary development of the lungs.

It is well known that the sternum in all baleen whales is reduced to a vestige, and that the proximal ends of the ribs articulate loosely with the vertebral column, the distal ends of all but the first pair being free. Thus the frame-work of the thoracic cavity is capable of great lateral movement. In conjunction with the skeletal changes the lungs become greatly enlarged and adapted to retain the air during a considerable period of submergence. The increased power of lung expansion called for external as well as internal modification of the breast and the furrows which had already developed upon the throat became more numerous and prolonged posteriorly. The greatest number of furrows and their most frequent branching is between the pectoral fins, as might be expected.

In the existing Balænopterinæ, when the lungs are filled with air the whole thorax expands laterally and with it the flexible skin between the folds. Thus the furrows, besides their original function of increasing the throat capacity during the feeding operation, are also of use during respiration. *Rhachianectes* being a shallow water whale and a relatively primitive form, has not as yet developed the furrows upon the breast and abdomen.

In the case of the Balæninæ extensive specialization of the entire head has taken place and it has become of such a proportionately great size that there has been no necessity for increasing the throat capacity by the development of furrows; like the head, the entire thorax has become enormously enlarged by the great thickening of the body and has thus accommodated itself to the processes of respiration.

The Odontoceti, because of the nature of their food and the manner of securing it, are not under the necessity of increasing their throat capacity by the development of furrows.[1] In this group, moreover, which are not as extensively specialized as are the baleen whales, the sternum is long and the "thoracic box" is relatively immobile.

Pectoral limb.— The pectoral fins of *Rhachianectes* are distinctly individual being intermediate in shape between those of the Balæninæ and the Balænopterinæ. They are much broader and thicker proportionately and not so pointed as the fins of the latter subfamily, but are more lanceolate, and not as heavy, as thick or as broad as the pectorals of the Balæninæ.

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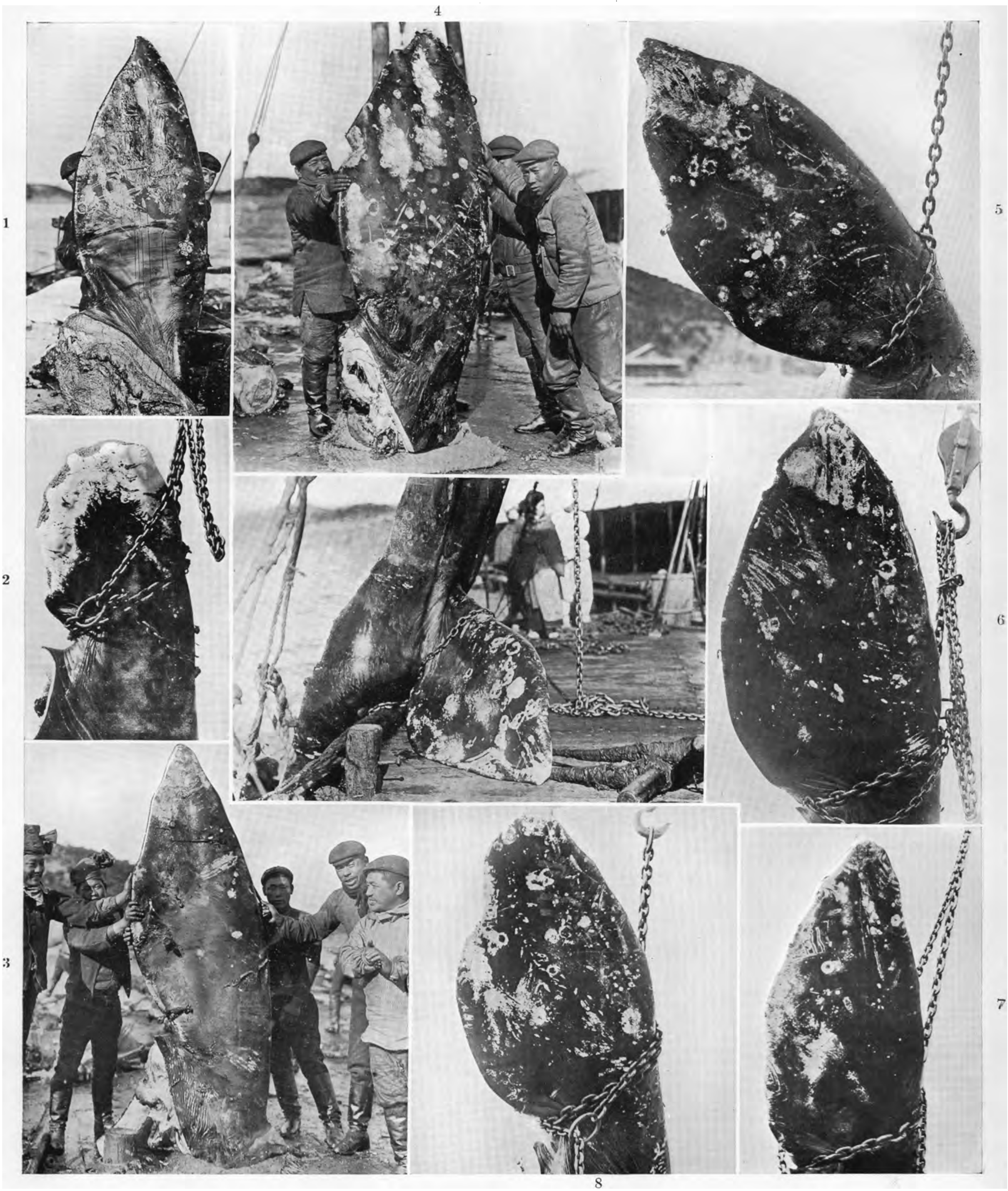
[1] This is not literally true since the Ziphioides have two throat furrows.

PLATE XXIII.

PLATE XXIII.

RHACHIANECTES GLAUCUS.

Fig. 1. Superior surface of uninjured pectoral fin.
Fig. 2. Pectoral fin injured and infested with parasitic *Cyamus scammoni*.
Fig. 3. Superior surface of slightly injured pectoral fin.
Fig. 4. Inferior surface of pectoral fin showing usual type of coloration (slightly injured).
Fig. 5. Inferior surface of pectoral fin.
Fig. 6. “ “ “ “ “
Fig. 7. “ “ “ “ “ (injured).
Fig. 8. “ “ “ “ “ “



Rhachianectes glaucus.

If photos of the pectoral of *Rhachianectes* are compared with those of a Right Whale or of any *Balænoptera* it will be seen at a glance that its shape is intermediate between the two types.

The flipper of *Rhachianectes* is broadly lanceolate. The posterior edge is about 3 cm. thick and strongly convex except just behind the rather blunt tip where a shallow concavity is formed; the anterior edge is regularly convex. The greatest breadth of the fin is at a point almost midway between the tip and the axilla, and the four digits are so prominently outlined that each may be traced for almost its full length before the fin has been stripped of blubber. There is considerable variation in the breadth of the pectoral among different individuals due to a greater or less convexity of the posterior border. Out of the twenty-three specimens on which notes were taken all but two had at least one of the flippers more or less injured on the posterior edges or tips. This, I believe, was mainly the work of Killers (*Orca orca*) which apparently keep the Gray Whales in a continual state of terror when upon their annual migrations. It may also be due, in some degree, to contact with rocks, as this species is generally to be found close in shore and frequently rolls about in the surf in very shallow water. Wherever the edges or tips of the fins were injured they were invariably thickly covered with parasitic crustaceans, *Cyamus scammoni*, and frequently the hard barnacle *Cryptolepas rhachianecti* was embedded on both surfaces.

Scammon's figure is hardly an accurate representation of the flipper of *Rhachianectes glaucus*. The outer edge is too straight, the tip is too blunt, and the fin is not broad enough.

In color, the pectorals are dark slate like the body. Above, on the posterior half, are a few scattered white circles, spots and flecks; below, the white circles and spots are more numerous and there are two, more or less broken, bands of white, or very light gray, about 8 cm. wide and 45 cm. long between the 2nd and 3rd, and 3rd and 4th fingers; the band between the 2nd and 3rd digits is usually the longer. The posterior edge of the fin is generally white.

There is much variation in the amount of white on the pectorals. Some individuals had the two bands between the fingers present on both surfaces and the entire fin thickly covered with spots, circles, dashes and flecks of white. Others had the distal third of the flipper washed with light gray, or white, while in still other cases white was practically absent on both surfaces. In almost all cases, however, there was more of the light markings on the lower surface than on the upper. A large proportion of the white circles and spots seemed to be scars left by parasitic cirripeds and were exactly similar to those on the flippers of *Megaptera*.

Flukes.— The flukes of *Rhachianectes glaucus* are quite unlike those of any other large whale. In shape they resemble most closely those of *Physeter macrocephalus* but both the anterior and posterior edges are more convex than in the latter species and the notch is more open and shallower. They are strikingly different from the slender, graceful flukes of *Balænoptera* and equally so from *Balæna* and *Eubalæna*. The resemblances to *Megaptera* are only superficial.

When either lobe of the flukes of *Rhachianectes glaucus* is viewed singly it is strongly suggestive of the pectoral fin in shape. The anterior margin is slightly convex becoming more so near the distal end. The posterior edge for the proximal two-thirds is strongly convex, but the distal third just behind the tip is slightly concave. Since the tips of the flukes in all adult specimens are more or less injured the concavity generally does not show and the posterior edge is evenly convex from the notch to the tip. The posterior edge, instead of being extremely thin as in *Balænoptera*, is almost three cm. in thickness and is broken by shallow, rounded emarginations. These crenulations must be normal as they were present in a fœtus (No. 1*a*) which was almost ready for birth, and in nearly all the adult specimens. They are analogous to the emarginations on the flukes of the *Megaptera* but are neither so numerous nor so deep and give a wavy effect rather than the scalloped appearance seen in the Humpback.

The entire posterior edge is frequently infested with *Cyamus*, which fasten themselves upon the slightest abrasion, and the posterior outline is often entirely changed by the attacks of these parasites or by other injuries. The notch is deep and usually open but varies considerably in this respect.

The flukes are black above and below like the body. A few circles, flecks and dashes of white are scattered over both surfaces, the lower usually being most heavily marked. As with the pectorals, the amount of white is extremely variable. The white circles and spots in many cases are the scars left by barnacles; two or three individuals had flukes exactly resembling those of a Humpback in color.

The flukes of a fœtus (No. 1*a*) on the inferior surface had wide, dark gray anterior and posterior borders and very light gray central portions. Many broken whitish lines curving inward toward the notch ran transversely across each lobe starting on the anterior edge. In a general way this was suggestive of the inferior surface of the flukes of *Balænoptera musculus*. One adult individual (No. 17) had flukes marked in exactly the same manner but as it was quite unlike all other specimens examined this must be considered to be an unusual type of coloration.

Dorsal crenulations of peduncle.— On the dorsal ridge of the peduncle, beginning about 100 cm. from the insertion of the flukes, is a series of low, rounded crenulations which end a short distance beyond a point opposite the anus in an evenly rounded bunch, or "hump," about 50 cm. long and 7 or 8 cm. high. The crenulations are about 30 cm. apart, those nearest the flukes being the least developed and those just posterior to the "hump" the most prominent. Their number and size are open to considerable variation, one individual having only 6 rather indistinct tubercles while another had 14, even the most posterior of the row being well developed; 9 or 10 is the usual number as shown by the following table:

Number of crenulations.

Capture Number	Sex	
5	♂	9
6	♀	6
8	♂	10
10	♂	10
11	♂	8
13	♂	10
14	♂	10
15	♂	7
20	♂	14
22	♂	9
23	♂	9

These crenulations are very similar to those on the dorsal ridge of the peduncle of the Humpback but are somewhat more prominent. They were noted by Dall, Scammon and Townsend. Dall says: "On the vertebral line, for fourteen feet from the caudal flukes, is a series of 18 ridges, like the teeth of a saw, which are altogether dermal in their character" (*l. c.*, 1868, p. 226). Out of some 30 individuals which I examined only one possessed as many as 14, the next highest being 10; it would appear, therefore, that 18 is rather an unusual number.

Scammon's statement that it "has a succession of ridges, crosswise along the back, from

PLATE XXIV.

PLATE XXIV.

RHACHIANECTES GLAUCUS.

Fig. 1. Flukes showing barnacle scars; posterior edges slightly injured.
Fig. 2. Flukes; posterior edges very slightly injured.
Fig. 3. Posterior edge of flukes.
Fig. 4. Peduncle of fœtus No. 1*a*.
Fig. 5. Section of blubber at end of peduncle crenulations ("hump").
Fig. 6. Gray Whale spouting blood.
Fig. 7. Normal spout of a Gray Whale.

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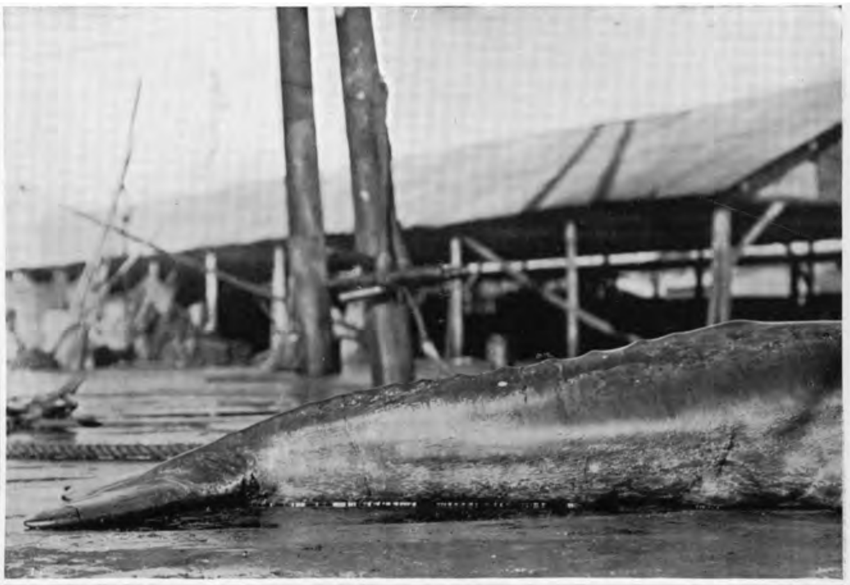

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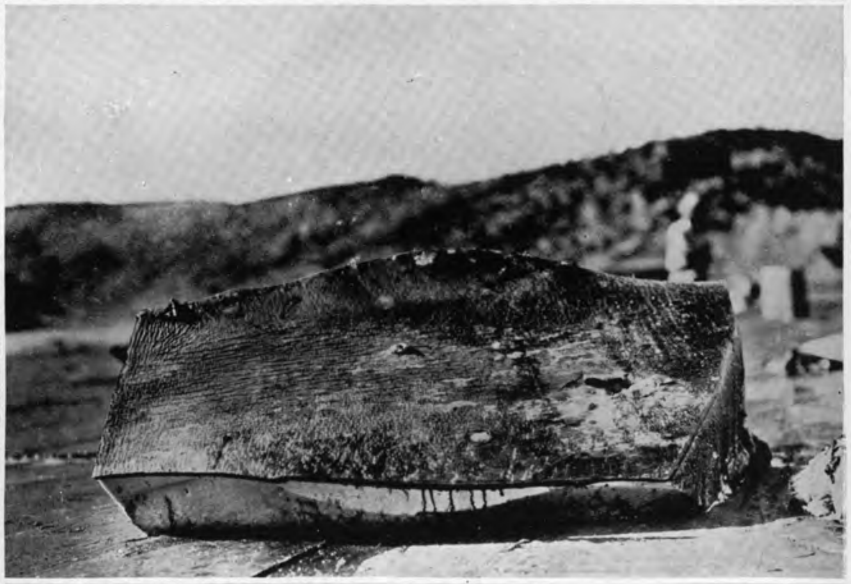

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Rhachianectes glaucus.

opposite the vent to the flukes" is misleading for the ridges are certainly never transverse; although he figures them in their proper position he does not show the hump at the anterior end of the series.

Townsend speaks of the crenate ridge as being present in a fœtus but says he did not observe it in the adult. He may have seen a specimen in which it was so slightly developed as to have escaped his notice for it is probably never entirely absent.

In a fœtus 476 cm. long which I examined it was fully developed and 12 crenulations could be distinguished. Townsend's figure shows the crenate ridge as an elevated phlange which gives a somewhat erroneous idea of its true character for the dorsal ridge of the peduncle is not itself extended.

It seems somewhat remarkable that the presence of the hump or bunch, which ends the series of crenulations anteriorly, has not been previously mentioned, for in nearly all the individuals examined it was prominent and attracted my attention at once. By referring to the table of proportional measurements it will be seen that the relative position of the hump is decidedly variable, there being a difference of 11% between the highest and lowest ratios to the total distance from the notch of the flukes to the hump. Its average position relative to the length of the animal is the same as in the *Megaptera*, and by but little modification a dorsal fin similar to that of a Humpback could be derived from it. The fact that Humpbacks have the dorsal ridge of the peduncle distinctly crenulated from the flukes to the hump, in a way similar to that of the Gray Whales, is exceedingly interesting. There is a greater individual variation in the relative position of the dorsal fin in the *Megaptera* than in the *Balænoptera;* it is situated much further forward in the former genus than in the latter, and it has almost every possible shape between a prominent, falcate fin and a low rounded bunch.

Before the pectoral and caudal fins of the Humpback had reached their present high state of specialization it is very probable that the dorsal may have been much less prominent and that, as in the Gray Whales, it formed the terminal bunch at the anterior edge of the peduncle crenulations. As the specialization of the animal continued the dorsal hump increased in size, its shape became modified, and the crenulations in the remainder of the series grew less prominent.

It is possible, therefore, that we may see *Rhachianectes* developing a dorsal fin in a parallel way to the *Megaptera* and that, if specialization is continued, it may become as prominent as in the case of the Humpback and its relative position be more constant.

Hairs.— Both the fœtal and adult *Rhachianectes* possess longer hairs, and they are more widely and more uniformly spread over the entire head, than in any other baleen whale. The hairs were scattered in six irregular rows over the whole rostrum of fœtus No. 1*a*, and a line of 16 on the dorsal ridge extended from the blowholes to the snout. The most posterior hair was on the left side of the head opposite the posterior end of the blowholes.

On each rami of the mandible there were 21 hairs in three irregular rows, the most posterior being a little anterior to a point opposite the corner of the mouth. At the mandibular symphysis three irregular vertical rows, which closely approximated each other, contained 40 hairs. The areas most thickly covered with hirsute remains were the tips of the snout and mandible. Each hair was white, about 20 mm. long, and situated in a small pit surrounded by a dark ring.

On the head and lower jaw of the adult *Rhachianectes* the number and arrangement of the hairs is essentially the same as on the fœtus described above. The hairs are generally longer in the adult than in the fœtus, sometimes reaching a length of 40 mm.; on whale No. 18, male, in several places on the mandibular rami two hairs were found in a single follicle.

A careful examination was made of all parts of the body, both in the fœtus and adult, but in no place other than the head and jaws were there evidences of hair.

Blubber.— The blubber is very thick and fat, and varies in color from red to flesh-pink. Because of this, as noted by Dr. True, the Japanese recognize two kinds of Gray Whale, the "aosaki" (red blubber) and the "shirosaki" (white blubber). Although specimens with blubber strongly red, almost white, and of every intermediate shade, were taken during my stay at Ulsan, I could detect no differences, other than those purely individual, between them.

The blubber varies in thickness with individuals, and on different parts of the body, usually being from 20 cm. at the thinnest to 35 or 40 cm. at the thickest part.

The Japanese consider the meat and blubber to be of poorer quality for eating than those of any other baleen whale. In the winter, during the months of December and January when the price is at its highest, the blubber sells for about 4 sen (2 cents) per pound and the red meat 10 sen (5 cents).

In regard to the blubber Scammon says: "The coating of fat, or blubber, which possesses great solidity and is exceedingly sinewy and tough, varies from six to ten inches in thickness, and is of a reddish cast" (*l. c.*, p. 21).

Parasites.— The entire body of *Rhachianectes* is more or less thickly infested with the parasitic amphipod crustacean *Cyamus scammoni* Dall, and the hard barnacle *Cryptolepas rhachianecti* Dall. The barnacles embed themselves deeply on all parts of the body as well as on the flukes and pectoral fins.

The *Cyamus* are almost invariably to be found about the blowholes, the genital and anal openings, and on the tips and posterior edges of the flukes and flippers. Wherever a cluster of *Cryptolepas* have become embedded, *Cyamus scammoni* will also fasten and frequently cover a wide area having the barnacles as a nucleus; an injury or abrasion of the skin at once becomes the resting place of numbers of parasites. The snout of *Rhachianectes* for a distance of sixty or seventy cm. from the tip is usually cornified in a way similar to the "bonnet" of the Right Whale, and is produced, as in that species, by the action of the parasitic *Cyamus*. In some individuals the entire dorsal ridge of the rostrum from the snout nearly to the blowholes becomes cornified.

When a *Cryptolepas* detaches itself a circular grayish pit remains, which in time becomes white as the wound heals; these scars are exactly like those left by the barnacle *Coronula diadema* upon the *Megaptera*. No barnacles other than *Cryptolepas rhachianecti* were observed upon the Gray Whales, and it seems probable that none other infest this species.

A careful examination of the *Cyamus* taken from Korea specimens demonstrates that they are certainly identifiable with Dall's *Cyamus scammoni* described from the California examples of *Rhachianectes glaucus*. In any case it is doubtful if such highly specialized parasitic forms would show strong changes even if isolated for a long period and thus they furnish little information on the question as to whether or not the Gray Whales of the east and west sides of the Pacific actually mingle in the north.

Osteology.

The skeleton of *Rhachianectes*, other than the skull, has never been completely described, consequently a rather detailed account of its principal characters will be given in the following pages; also comparisons with other genera will be instituted whenever individual peculiarities can be emphasized thereby.

The length of the skeleton of the American Museum specimen, measured in a straight line, is 1107 cm. (36′ 4″). It was taken from a very old male (No. 20), 1250 cm. (41′ ½″) long, on January 19, 1912, at Ulsan, Korea.

The vertebral epiphyses are all firmly ankylosed, in most cases the lines of union being lost, and there are other evidences of extreme age.

SKULL.

Plates XXV–XXVII.

In general form the skull of *Rhachianectes* is directly intermediate between the skulls of *Eubalæna* and *Balænoptera,* and somewhat resembles *Neobalæna.* The dorsal outline is much curved and especially high from the nares posteriorly, thereby giving to the occipital plane a comparatively slight obliquity, scarcely greater than in *Eubalæna.* The skull, as seen in profile, is thus quite unlike that of a Fin Whale, not only the whole dorsal outline being more convex but the rostral portion more arched. The interorbital region is thus deep and quite constricted.

The rostrum is narrow and elongate and the lateral outline tapers regularly toward the tip. The premaxillæ in the distal portion are very deep and have almost vertical sides, as in *Eubalæna,* but become somewhat flattened where they spread apart for the narial opening. Proximally they end a considerable distance from the vertex of the skull *leaving a wide area of the frontals exposed,* a primitive condition. The proximal portions of the premaxillæ enclosing the nasals appear as broad strips, superiorly placed, and articulate with the frontals by a deep interdigitating suture.

The maxillæ instead of being almost horizontal as in the Balænopterinæ are sharply oblique. Their inner (superior) edges slope abruptly downward in the distal half of the rostrum but in the proximal half are almost parallel with the skull axis. Each maxilla sends a narrow projection backward toward the vertex of the cranium, ending beside the premaxillæ. The lateral extentions of the maxillæ are remarkable in the fact that each one *overlaps the anterior edge of the orbital process of the frontal,* and bears posteriorly a strong tubercle which, with the anterior end of the orbit, partially encloses a large oblique foramen.

The nasals are very broad and long, joining in the median line to form a prominent crest; they occupy half the space between the nares and the summit of the occipital bone.

Compared with *Balænoptera* and *Megaptera* the orbital processes of the frontals are narrower, shorter and consequently less massive, but are much wider and less elongate than in *Eubalæna.* Viewed from below they have the trumpet-shaped form so characteristic of the fossil genus *Plesiocetus.* The posterior edges of the orbital processes of the frontals from the skull-vertex to the orbits present irregular margins; a primitive character.

The squamosal is comparatively small and has a straight outer edge quite unlike the concave squamosals of either *Balænoptera, Megaptera* or *Eubalæna;* in this respect the squamosal of *Rhachianectes* resembles that of fossil genera. The "temporal ridge," formed by the anterior margins of the temporal fossa, is well marked, thus showing an interesting primitive condition.

The supraoccipital presents three deep concavities, and on the superior portion two prominent and peculiar rugosities. These are undoubtedly homologous with the similar processes just under the lambdoid crest on the supraoccipital of dogs and other mammals, where the *rectus capitis posterior major* and *minor* muscles, which assist in raising the snout, are attached.

Their development, and the presence of similar rugosities below upon the basi-sphenoid and basi-occipital bones, are probably correlated with the fact that the cervical vertebræ are all free, and the neck is somewhat less abbreviated than in other large cetaceans thus allowing greater movement of the head.

The most interesting characters of the inferior surface of the skull are the comparatively short posterior extension of the vomer and pterygoid bones, the heavy pterygoids and, as mentioned above, the strongly down-turned edges of the basioccipital and basi-sphenoid which are exceedingly thick and massive.

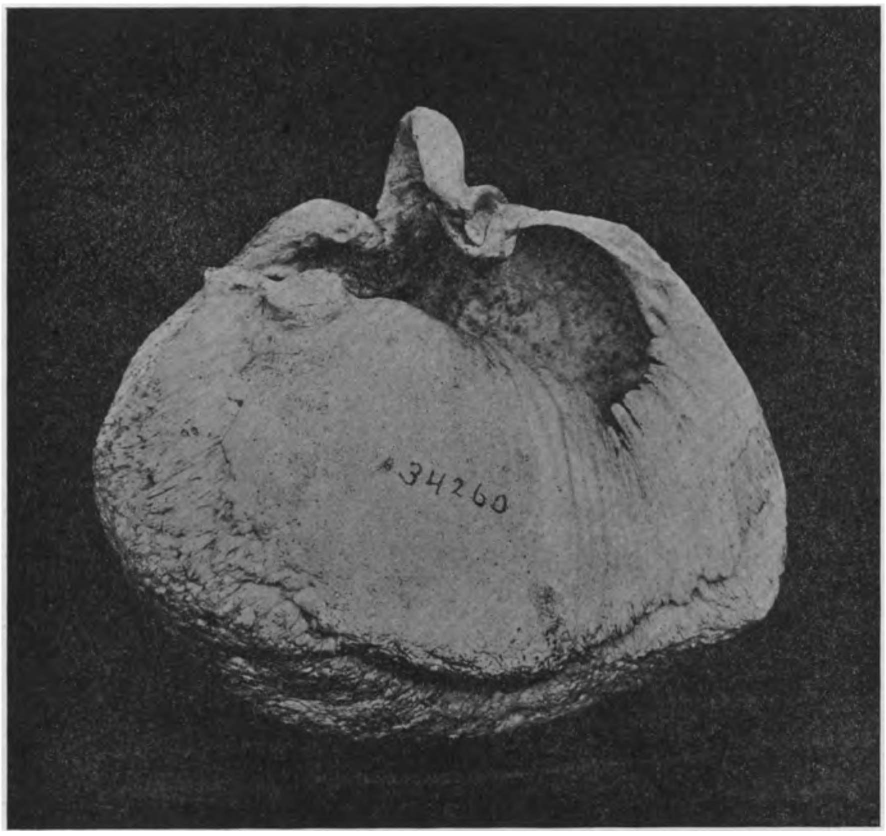

Fig. 1. Inner view of tympanic bulla of *Rhachianectes glaucus.*

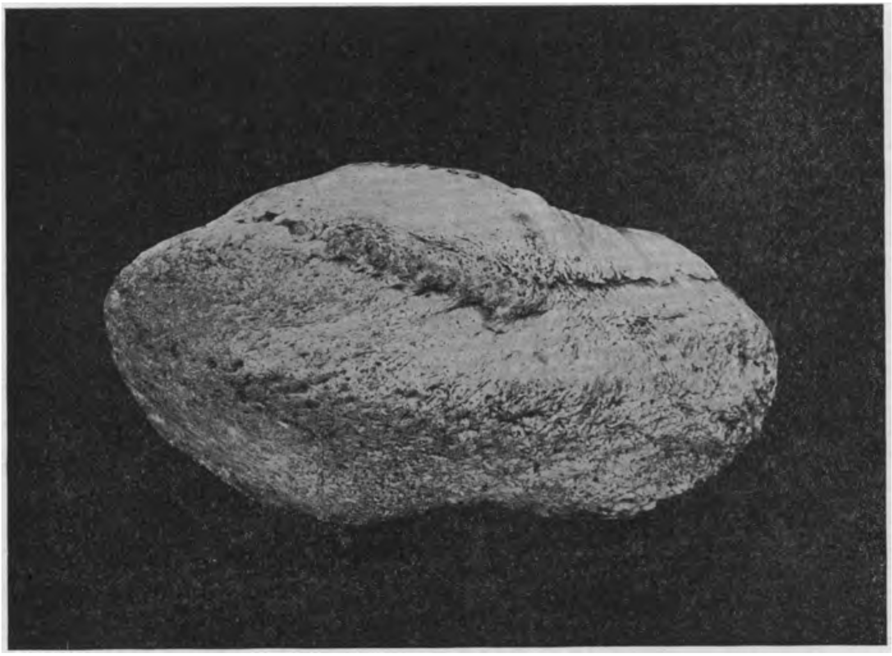

Fig. 2. Inferior view of tympanic bulla of *Rhachianectes glaucus.*

True remarks in regard to the peculiarities of the skull of *Rhachianectes:* "Most striking are the rugosities of the occipital, the large size of the nasals, the shortness of the nasal portion of the intermaxillæ, and their great depth anteriorly, the overlapping of the orbital processes of the frontal by the proximal portion of the maxilla, and the strong tubercle on the posterior margin of the former. All these characters are seen equally as well developed in the skulls figured by Malm as in the Monterey specimen.

"These and many other characters stamp it as a very distinct form, approaching closely neither *Balœna* nor *Balœnoptera*" (*l. c.*, p. 291). Dall, Van Beneden, Malm and Beddard have also more or less completely described the skull of *Rhachianectes.*

The mandibular rami are without coronoid processes these being represented only by flattened tubercles. Each

PLATE XXV.

PLATE XXV.

RHACHIANECTES GLAUCUS.

Fig. 1. Dorsal view of the skull from California in the U. S. National Museum.
Fig. 2. Dorsal view of the skull from Korea in the American Museum.

RHACHIANECTES GLAUCUS.

PLATE XXVI.

PLATE XXVI.

RHACHIANECTES GLAUCUS.

Fig. 1. Ventral view of the skull from California in the U. S. National Museum.
Fig. 2. Ventral view of the skull from Korea in the American Museum.

RHACHIANECTES GLAUCUS.

ramus is moderately bowed and the superior outline from the coronoid rudiment to the distal end is regularly convex; the inferior outline is a succession of slight convexities and concavities as shown by the figures. On the inner side of the superior edge for the distal three fourths of the ramus is a well-marked alveolar sinus which becomes very deep near the tip. Both rami show the effects of a former injury.

The mandible of *Rhachianectes* strongly resembles that of the Balæninæ, and shows little concavity on the inner side proximally; it is surprising to find a specialized mandible of this type when the many other primitive characters of the skull are considered.

The tympanic bullæ of *Rhachianectes* are small and remarkable because of their strong lateral compression and slightly grooved internal border (that is, the border nearest the median line of the skull). They are totally unlike those of *Eubalæna* in size and general shape and differ from *Balænoptera* in being much less elongate, wider, and more compressed as well as in other points. In size and general outline they somewhat resemble *Megaptera* but instead of being almost globular, as in the latter genus, are greatly flattened. By their compressed form and concave internal border they strongly suggest the tympanic bones of certain fossil genera.

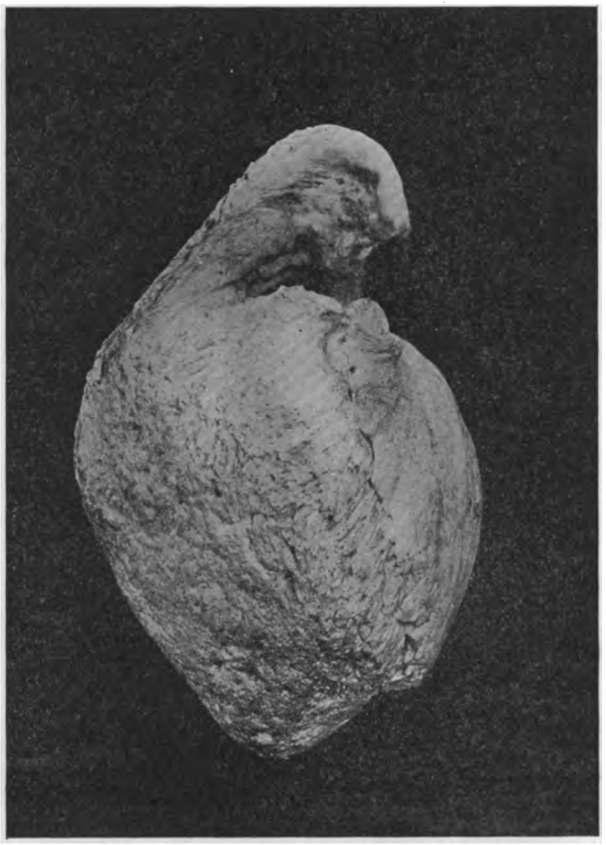

Fig. 3. Posterior view of tympanic bulla of *Rhachianectes glaucus.*

Table VI.—Measurements of skull of Rhachianectes glaucus.

	No. 34260 A. M. N. H. Andrews	No. 13803 U. S. N. M. Dall
	mm.	mm.
Total length from the tip of premx. to occipital condyle (straight)	2570	2464
Greatest breadth	1110	1041
Length of rostrum	2122	1740
Breadth “ “ at base	605	584
“ “ “ “ middle	429[1]	337[1]
“ across pmx. at same point	202	184
Length of mx. from frontal border	1761	1651
Greatest breadth across mx. proximally	908	851
Length of premx.	2115	2007
“ “ nasals in median line	320	305
Breadth “ “ at anterior end	196	171
Distance from anterior end of nasals to anterior end of supraoccipital	383	375
Length of orbit (least)	172	165
“ “ palatine bones	424[2]	394[2]
Breadth across anterior ends of zygomatic processes of squamosals	1130	940
Breadth across anterior angles of orbital processes of frontals	950	889
Breadth across posterior angles of orbital processes of frontals	1035	991
Depth of skull from crest of supraoccipital to lowest point of pterygoids	731	

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[1] Straight.

[2] The exposed position.

Table VI.— Continued.

	No. 34260 A. M. N. H. Andrews mm.
Length of mandible (straight)	2425
" " " (curved)	2500
Depth " " at middle	375
Greatest length tympanic bulla	102
" width " " posteriorly	79

Hyoid Bones.— The hyoid bones differ from those of all other baleen whales with which I am familiar.

The basihyal and two thyrohyals are ankylosed into a long, extremely massive and rugose bone. The central portion (basihyal) is dorso-ventrally compressed and has two short, anterior, conical projections (ceratohyals), but each thyrohyal rapidly thickens, becoming cylindrical in the distal two-thirds and curved slightly backward. The shape of this portion of the hyoidean apparatus is distinctly individual but resembles that of *Eubalæna* much more than any *Balænoptera.*

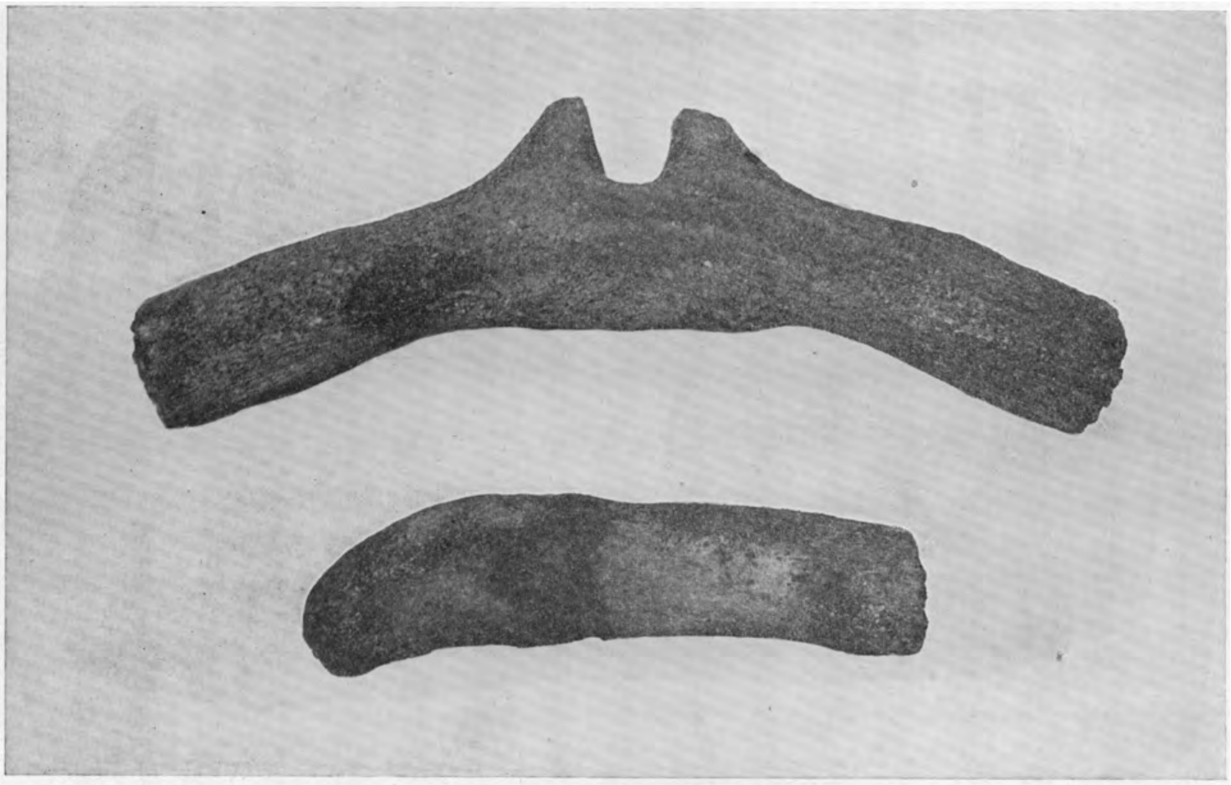

Fig. 4. Hyoid bones of *Rhachianectes glaucus.*

The stylohyals, on the other hand, are decidedly more like those of the latter genus than the former. Each is a massive, rugose bone, slightly curved upward and forward. The anterior edge for its greater part is sharp and the posterior margin rounded so that a cross section of the stylohyal would be an ovoid ellipse. These bones are nearly half again as long and twice wider than are the roughly cylindrical stylohyals of an adult 54 ft. female *Eubalæna glacialis* in this Museum.

PLATE XXVII.

PLATE XXVII.

RHACHIANECTES GLAUCUS.

Fig. 1. Lateral view of the skull from California in the U. S. National Museum.
Fig. 2. Lateral view of the skull from Korea in the American Museum.
Fig. 3. External side of the left ramus of the mandible; Korea specimen in the American Museum.
Fig. 4. Internal side of the left ramus of the mandible; Korea specimen in the American Museum.

Rhachianectes glaucus.

Measurements of the hyoid bones.

Extreme length of base (thyrohyals and basihyal)	631 cm.
Antero-posterior width across ceratohyal	149 "
Greatest thickness of thyrohyal distal end	105 "
" length of stylohyal	392 "
" width " "	106 "

VERTEBRÆ.

The vertebræ of *Rhachianectes*, through the combination of characters, differ widely from those of the other known genera of baleen whales, the general resemblance being rather more toward *Megaptera* than *Balænoptera* or *Eubalæna.*

The extremely rugose surfaces of practically all of the bones of the skeleton is interesting. I know of no other large Cetacean, except *Physeter macrocephalus,* in which this condition is so pronounced. Fifty-six vertebræ seems to be the normal number for *Rhachianectes glaucus,* the formulæ of three skeletons being as follows:

C	D	L	Ca.		Total		
7	14	12	23	=	56	Am. Mus. Nat. Hist.	(R. C. A.)
7	14[1]	12	23	=	56	U. S. Nat. Mus.	(R. C. A.)
7	14	14	21	=	56	British Mus.	(Beddard)

The differences in these formulæ will be discussed later.

Cervical vertebræ.— The cervical vertebræ are all free and show no tendency toward ankylosis.

The atlas differs strongly from that of both *Eubalæna* and *Balænoptera* but bears a considerable resemblance to *Megaptera.* Its most distinctive characters are the massive neural arch, the short transverse processes, and the small size of the condylar facets relative to the height of the vertebræ.

The neural arch is high and exceedingly thick and massive, having an irregular rugose superior surface and an indistinct spine; it is perforated by a transverse arterial foramen. The short bunch-like transverse processes are set obliquely to the vertical plane of the axis, have irregular rounded ends, and are directed slightly upward. They resemble the transverse processes of the *Megaptera* but are shorter and not so wide.

The centrum of the atlas at the bottom slopes strongly upward, and at the sides inward, so that the posterior face is considerably smaller than the anterior. The opening between the condylar facets in conjunction with the neural canal is much shallower than is usual with the atlas of other baleen whales; this character is not so pronounced in the National Museum specimen, the opening being roughly V-shaped, the point directed downward.

On the posterior surface, the internal-superior corners of the facets for articulation with the axis are produced inward appearing as two irregular tubercles when seen from the anterior face of the axis through the space between the condylar facets.

The axis resembles, in general, that of a *Balænoptera.* The neural arch is very thick and massive, has a rugose, truncated summit and an indistinct spine. Each of the posteriorly directed, wing-like transverse processes is perforated somewhat above the center by a rather small oval foramen; the processes are thick and have irregular, rugose surfaces. The articular facets for the atlas are small and between them is a rather prominent odontoid process.

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[1] Although but thirteen pairs of ribs are present in the U. S. National Museum specimen, the distal ends of the transverse processes of the twenty-first vertebra show distinct articular facets and indicate that the last pair of ribs has been lost.

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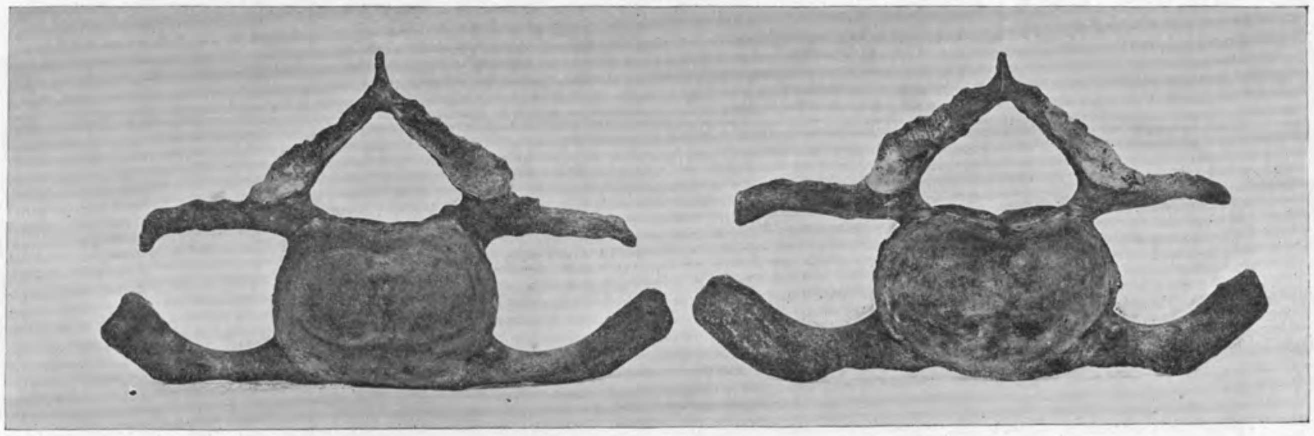

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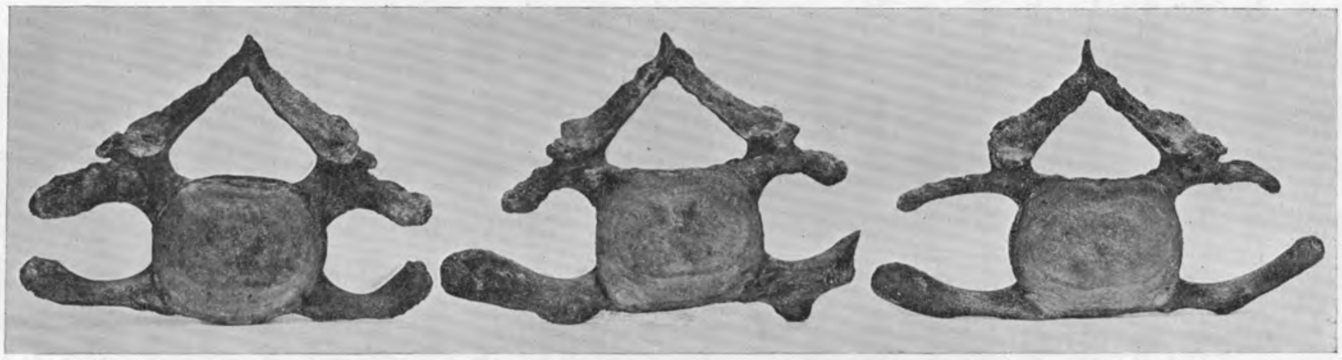

Fig. 5. Atlas and axis of *Rhachianectes glaucus.*
Fig. 6. Third and fourth cervical vertebræ of *Rhachianectes glaucus* (right to left).
Fig. 7. Fifth, sixth and seventh cervical vertebræ of *Rhachianectes glaucus* (right to left).

The third cervical vertebra has a circular body, somewhat compressed dorsally, and on either side two well developed transverse processes. The lower process is thick and roughly cylindrical for half its length, projecting somewhat downward but bends up and back in the distal half where it becomes compressed and blade-like. The upper process is straight, except at the distal end, and directed backward; the distal ends of the two processes stand widely apart (on the right side 50 mm.).

Both the upper and lower transverse processes of the fourth vertebra are similar to those of the third in length and direction, but the lower process is less massive and expanded distally.

On the fifth cervical the lower process is compressed throughout, especially so at the distal end where it is thin and expanded; instead of being directed slightly backward, as are those immediately preceding, it projects straight out and turns upward in the distal portion. The superior process is shorter than that of the fourth vertebra and curved slightly backward and downward.

The inferior transverse process of the sixth cervical is more massive than that of either the fifth or fourth, projects upward and forward and bears on the posterior side, proximally, a prominent flattened tubercle. The superior process of this vertebra is the shortest in the cervical series and projects strongly downward.

The seventh cervical has a lower transverse process which, although it is shorter than that of the sixth, is 135 mm. in length, roughly cylindrical and slightly expanded distally. The lower transverse processes of the seventh cervical of the U. S. Nat. Mus. specimen appear on the right side merely as a rounded tubercle and upon the left as a short process 64 mm. in length; neither seem to have been broken or otherwise injured.

The upper process is thick, compressed and considerably longer than that of the sixth vertebra; both are directed downward.

The anterior zygapophyses of the third vertebra are well developed, becoming larger on each succeeding cervical and appearing on the seventh as tubercles 43 mm. in length.

The spines of all the cervicals increase in height and thickness from the third to the seventh.

The laminæ of the neural arches of the third, fourth, and fifth vertebræ are wide at the bases, narrowing rapidly and uniting at the apices in erect and prominent spines. The arches of all the cervical vertebræ are high and triangular, considerably resembling those of *Megaptera.*

The cervical vertebræ of *Rhachianectes,* considered as a whole, are unique in the *combination* of the following characters:

1. An atlas of peculiar shape.
2. An axis having wing-like transverse processes.
3. Triangular neural arches and long inferior transverse processes in all cervical vertebræ posterior to the axis.[1]

Dorsal vertebræ.—The most distinctive character of the dorsal vertebræ is the zygapophyses, which are extraordinarily thick and massive with heavily rugose surfaces. They appear on the proximal ends of the transverse processes of the fifth dorsal as well developed tubercles rapidly enlarging on the succeeding vertebræ into prominent projections having massive globular ends.

The transverse processes are heavy throughout the series and have expanded, concave distal ends except in the case of the first and last dorsals; the ends of the transverse processes of the tenth thoracic vertebra are the widest of the series.

The neural spines of the first six dorsals are directed forward, those of the seventh, eighth, and ninth are vertical, and the remainder directed backward.[2] The spines increase steadily in antero-posterior width from the first to the twelfth dorsal, which bears the widest spine in the entire vertebral column.

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[1] As noted above, this was not entirely true of the U. S. Nat. Mus. specimen in which the lower transverse processes of the seventh cervical were small.

[2] The spines of the first four dorsal vertebræ of the U. S. Nat. Mus. specimen are directed backward, the fifth, sixth and seventh upward and the remainder backward.

The centrum of the first thoracic is circular except for a slight dorsal flattening; the dorsal compression of the centra becomes more pronounced in the posterior members of the series.

Lumbar vertebræ.— The lumbar vertebræ present certain individual peculiarities in the spines and zygapophyses, by means of which they may be distinguished from those of other whales. The spines of the entire lumbar series are directed strongly backward, that of the ninth being the most oblique of the vertebral column; the backward direction of the spines in the posterior vertebræ of the series is much greater than in *Megaptera* and somewhat more than in *Balænoptera*. All of the spines are regularly convex distally and that of the seventh lumbar is the longest.

The zygapophyses are prominent and show, in a modified form, the expanded distal ends so characteristic of the dorsal vertebræ. Those of the anterior half of the lumbar series are directed outward so that they overhang the anterior faces of the centra more strongly than is usual. The spines and zygapophyses differ in numerous minor ways from those of other genera.

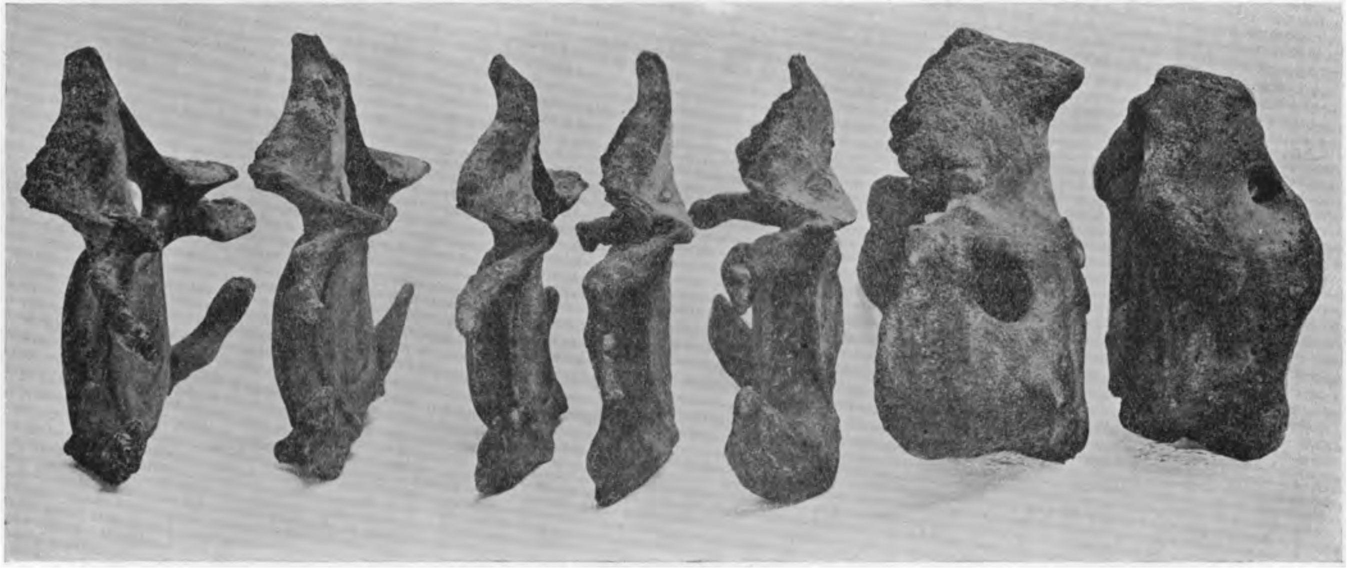

Fig. 8. Cervical vertebræ of *Rhachianectes glaucus*.

The transverse processes of the first four units of the lumbar series are curved somewhat upward, the fifth, sixth and seventh are horizontal, and those of the remaining vertebræ directed more or less downward. The transverse processes of the sixth lumbar are the longest.

Caudal vertebræ.— The caudal vertebræ do not agree closely with those of other baleen whales. In the size, shape, and direction of the transverse processes, spines and zygapophyses, and in the appearance and disappearance of the foramina and processes, many differences are apparent.

The spines decrease gradually in height from the first to the eleventh caudal where they become lost. The zygapophyses of the anterior caudal vertebræ in their expanded, globular distal ends resemble those of the dorsal series, and disappear with the neural spines upon the eleventh vertebra. The spines and zygapophyses show a decidedly greater resemblance to *Megaptera* than to *Balænoptera*.

The transverse process of the first caudal is the widest in the entire vertebral column and is directed strongly downward. The transverse process of the fourth, fifth and sixth caudals arise from the posterior part of the centra and project outward and forward, their inner edges almost meeting the expanded outer margins of the anterior faces of the centra; in this way a partially

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Fig. 9. Dorsal vertebræ of *Rhachianectes glaucus.*
Fig. 10. Lumbar " " "
Fig. 11. Caudal " " "

enclosed foramen is formed. On the right side of the sixth caudal this foramen is completely encircled [1] and the transverse process near the center is also perforated by a second vertical canal.

The antero-posterior diameter of the centrum of the first caudal is the greatest of the entire vertebral column and the anterior face is almost a perfect circle. Although the inferior median carina of the thirty-third vertebra is distinctly bifurcated posteriorly, the thirty-fourth is definitely indicated as the first caudal by the presence of the first pair of chevrons which have become firmly ankylosed to its centrum.

Beddard states that he counted in the British Museum specimen 14 lumbar vertebræ and 21 caudals, whereas both the American Museum and U. S. Nat. Mus. skeletons have 12 lumbars and 23 caudals. Since the total number of vertebræ, and also those of the dorsal series, are alike in the three specimens, I believe they will be found to possess a similar number of lumbar and caudal units. Unless the skeletons have been examined with the chevrons *in situ*, or there happens to be an ankylosis as in the case of our specimen, it is difficult to make an absolutely correct determination of the lumbar and caudal units. Although the inferior median carina is usually first distinctly bifurcated upon the first caudal, the division may sometimes occur upon the last lumbar and cannot, therefore, be taken as an infallible guide.

In the following table data as to the appearance and disappearance of the several processes and foramina in *Rhachianectes glaucus* is given. For convenience of reference similar data of other genera are placed in apposition.

	Rhachianectes glaucus		*Eubalæna glacialis*	*Megaptera nodosa*	*Balænoptera physalus*
	Am. Mus. Nat. Hist.	U. S. Nat. Mus.			
Last vertebra to bear a transverse process is No.	41	41	42	39	48
Last vertebra to bear a neural spine is No.	44	44	45	41	50
First vertebra with perforated transverse process is No.	39	38	39	—	43

Table VII.—Measurements of Vertebræ of Rhachianectes glaucus.

	mm.
Atlas, greatest breadth across transverse procesess	417
" " depth	312
" " breadth across condylar facets	317
" " depth of condylar facet	224
" breadth of condylar facet	124
" greatest depth of neural arch	69
" breadth of distal end of tr. proc.	109
Axis, greatest breadth across tr. proc.	662
" " depth	327
" " " of centrum	162
" " breadth " "	289
" " length of right tr. proc.	243
" length of foramen in tr. proc.	89

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[1] This foramen does not become enclosed in the U. S. Nat. Mus. specimen.

Table VII.—Continued.

	mm.
5th cervical, breadth across upper tr. proc.	446
“ “ “ “ lower “ “	528
“ “ greatest depth (vertical)	318
“ “ depth of centrum “	157
“ “ breadth of centrum	195
“ “ length of upper tr. proc.	130
“ “ “ “ lower “ “	176
7th cervical, breadth across upper tr. proc.	434
“ “ “ “ lower “ “	445
“ “ greatest depth (vertical)	329
“ “ “ “ of centrum	164
“ “ “ breadth “ “	189
“ “ “ length of upper tr. proc.	135
“ “ “ “ “ lower “ “	135
1st dorsal, breadth across tr. proc.	460
“ “ greatest depth (vertical)	371
“ “ “ “ of centrum	166
“ “ “ breadth of centrum	214
“ “ length of tr. proc.	155
“ “ “ “ spine	94
5th “ breadth across tr. proc.	—
“ “ greatest depth (vertical)	445
“ “ “ “ of centrum	175
“ “ “ breadth “ “	210
“ “ “ length of tr. proc.	173
“ “ “ height of spine	184
10th “ “ breadth across tr. proc.	636
“ “ “ depth (vertical)	496
“ “ “ “ of centrum	174
“ “ “ breadth “ “	227
“ “ “ length of tr. proc.	243
“ “ “ greatest height of spine	259
1st lumbar, breadth across tr. proc.	831
“ “ greatest depth (vertical)	542
“ “ “ “ of centrum	186
“ “ “ breadth “ “	229
“ “ “ length of tr. proc.	340
“ “ “ height of spine	323
5th “ breadth across tr. proc.	886
“ “ greatest depth (vertical)	600
“ “ “ “ of centrum	206
“ “ “ breadth “ “	240
“ “ “ length of tr. proc.	340
“ “ “ height of spine	363
10th “ “ breadth across tr. proc.	780
“ “ “ depth (vertical	580
“ “ “ “ of centrum	225
“ “ “ breadth “ “	265
“ “ “ length of tr. proc.	285
“ “ “ height of spine	363
1st caudal, “ breadth across tr. proc.	665
“ “ “ depth (vertical)	535
“ “ “ “ of centrum	243
“ “ “ breadth “ “	274
“ “ “ length tr. proc.	230
“ “ height of spine	265

Table VII.—Concluded.

		mm.
5th caudal,	breadth across tr. proc.	468
“ “	greatest depth (vertical)	465
“ “ “	“ of centrum	270
“ “ “	breadth “ “	281
“ “ “	length tr. proc.	115
“ “ “	height of spine	210
10th “ “	breadth across tr. proc.	275
“ “ “	depth (vertical)	330
“ “ “	“ of centrum	258
“ “ “	breadth “ “	275
“ “ “	length of tr. proc.	—
“ “ “	height of spine	83

CHEVRONS.

The American Museum skeleton has twelve chevrons and the National Museum ten; apparently two have been lost in the latter case and twelve would seem to be the normal number.

The first chevron in the American Museum series is firmly ankylosed to the centrum of the first caudal vertebra. It is 75 mm. in length, 118 mm. wide and free distally. The second chevron is 180 mm. long and 91 mm. wide, the laminæ uniting distally to form a long hæmal spine. The third chevron is the longest of the series, having a maximum length of 240 mm. and a width of 120 mm.

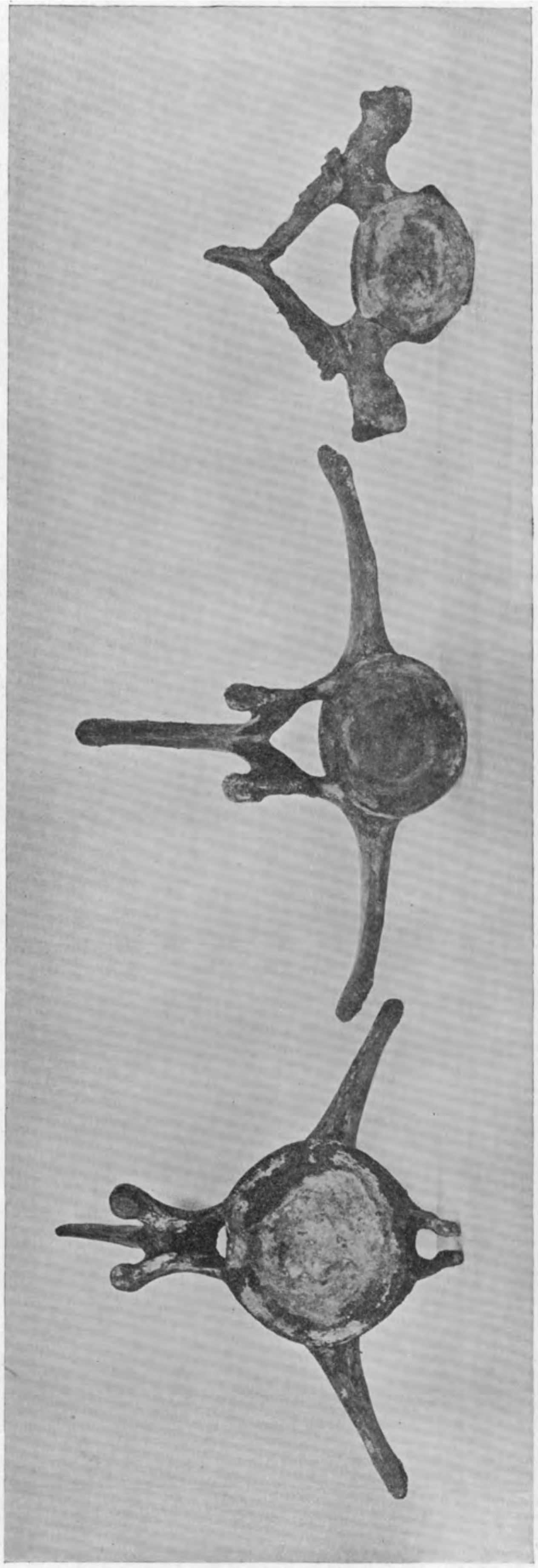
From the third backward, the chevrons increase rapidly in width and gradually decrease in length, the fifth being the widest of the series; its maximum width is 212 mm. The last two members of the series have their distal ends free.

RIBS.

The ribs of *Rhachianectes* are exceedingly interesting. The most important feature of their morphology is to be seen in the proximal ends of the third, fourth, fifth, sixth, and seventh, *on each of which a large tubercle, neck and head are developed.* The prominent tubercle, and the deep concavity between it and the head in all of these ribs gives them a shape very similar to those of the toothed whales and quite unlike any Mystacoceti.

In *Balænoptera* the second and third ribs usually have prominent tubercles and long necks while in the remainder of the series the necks and heads become atrophied, or lost. In *Rhachianectes* the necks and heads do not disappear until the *eighth rib* and up to this point are well developed and prominent. Thus the anterior half of the rib series is articulated to the vertebral column much more firmly than in other baleen whales, and presumably the thorax is capable of less lateral movement.

The proximal end of the first rib is thin and rounded but has a small, outwarding projecting tubercle (the head) near the lower edge. On the second rib this tubercle (the head) is more thoroughly developed, and on the third has become extended into a long neck and an expanded head which project outward at a right angle to the remainder of the rib. The tubercle is very prominent and has a large flattened articular fossa. On the fourth rib the neck is slightly shorter than that of the third and the angle it forms with the shaft is a little wider; its tubercle, however, is considerably larger than that of the third.



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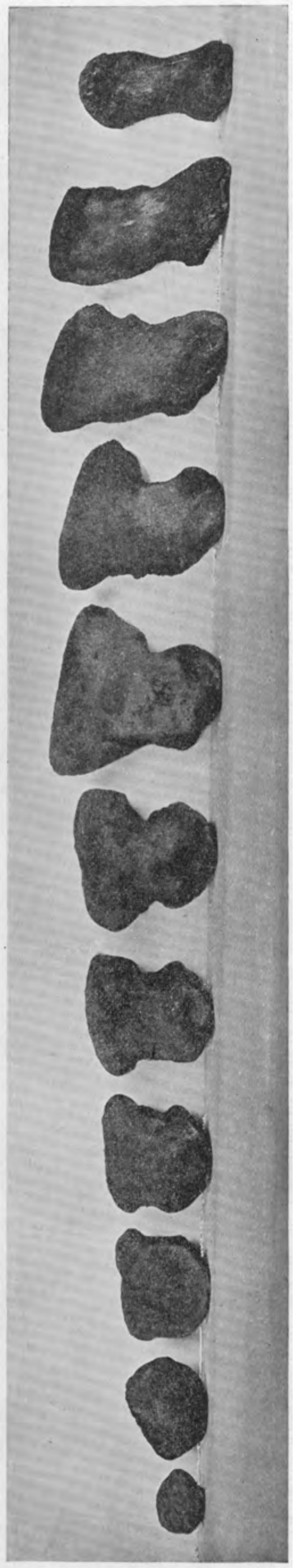

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Fig. 12. First dorsal, first lumbar and first caudal vertebræ of *Rhachianectes glaucus* (right to left).
Fig. 13. Chevrons of *Rhachianectes glaucus*.

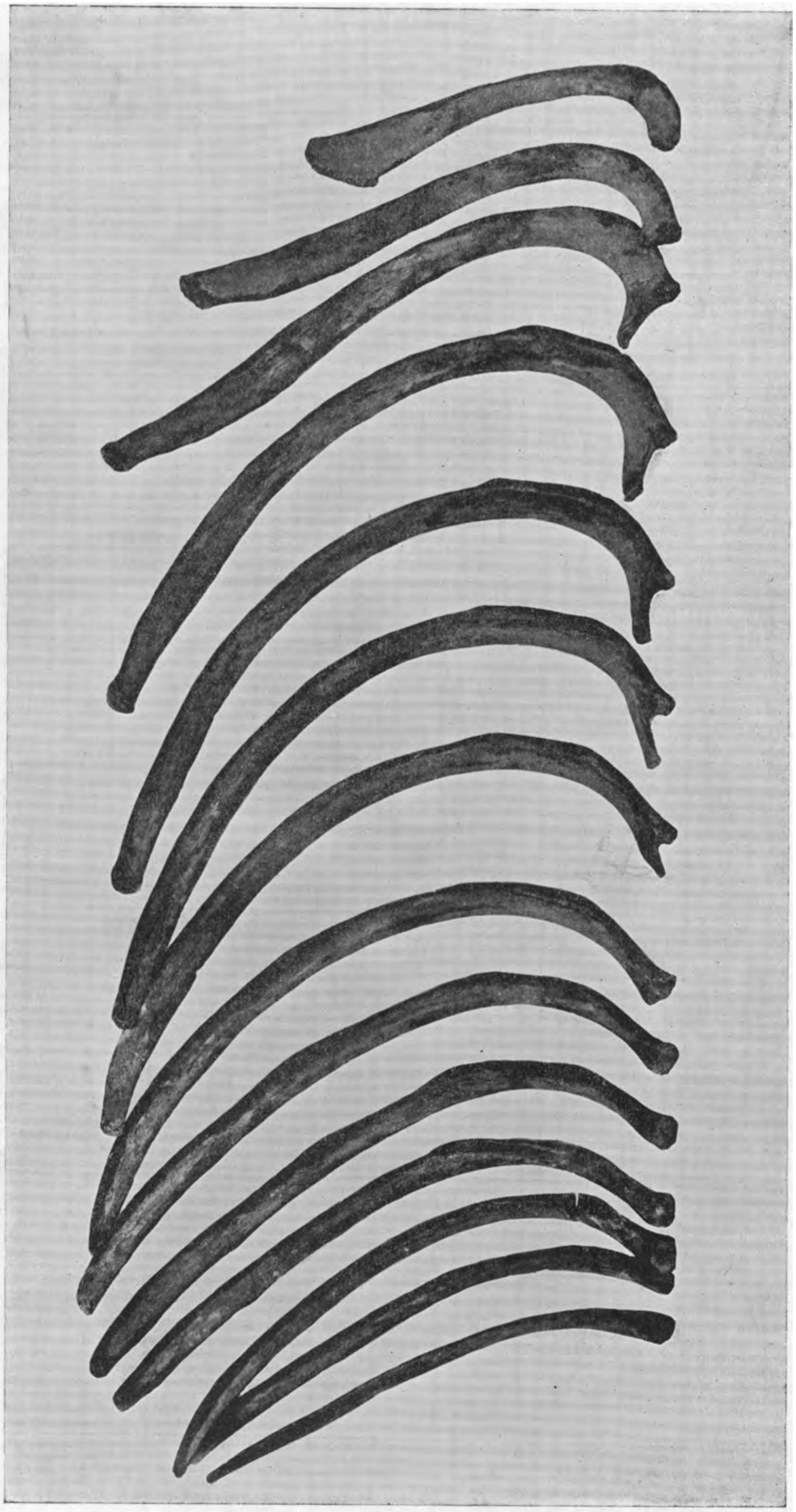

Fig. 14. Ribs of *Rhachianectes glaucus*.

The neck of the fifth rib is shorter and forms a wider angle with the shaft than does the fourth, but its tubercle is larger and more prominent and the concavity of the neck between it and the capitulum is deeper.

The neck of the sixth rib is similar to the fifth in length, size of tubercle and the angle with the shaft. That of the seventh is a little shorter than the sixth, the angle is somewhat wider and the tubercle a little larger.

Upon the eighth rib the neck and head disappear and are represented only by a small projection; the tubercle of the rib is greatly enlarged, however, and is separated from the process representing the neck by a well-marked concavity, which is present to a less extent upon all the succeeding ribs except the last two pairs.

The ribs are all long and massive, considerably exceeding in measurements those of the 40-foot *Megaptera* and the 50-foot *Balænoptera physalus* recorded by Struthers.[1]

The first is of uniform width in its proximal half but rapidly expands in the distal portion where it becomes the widest of the series; the fifth is the longest.

The ribs of the U. S. National Museum specimen differ in the important particulars that upon the first the portion representing the neck and head is considerably more produced than in the American Museum skeleton and that *the second rib bears a fully developed neck and head;* the distance from the tubercle to the end of the head of this rib is 225 mm.

Measurements of the ribs and of the capitular processes of the first eight pairs are given in the appended table:

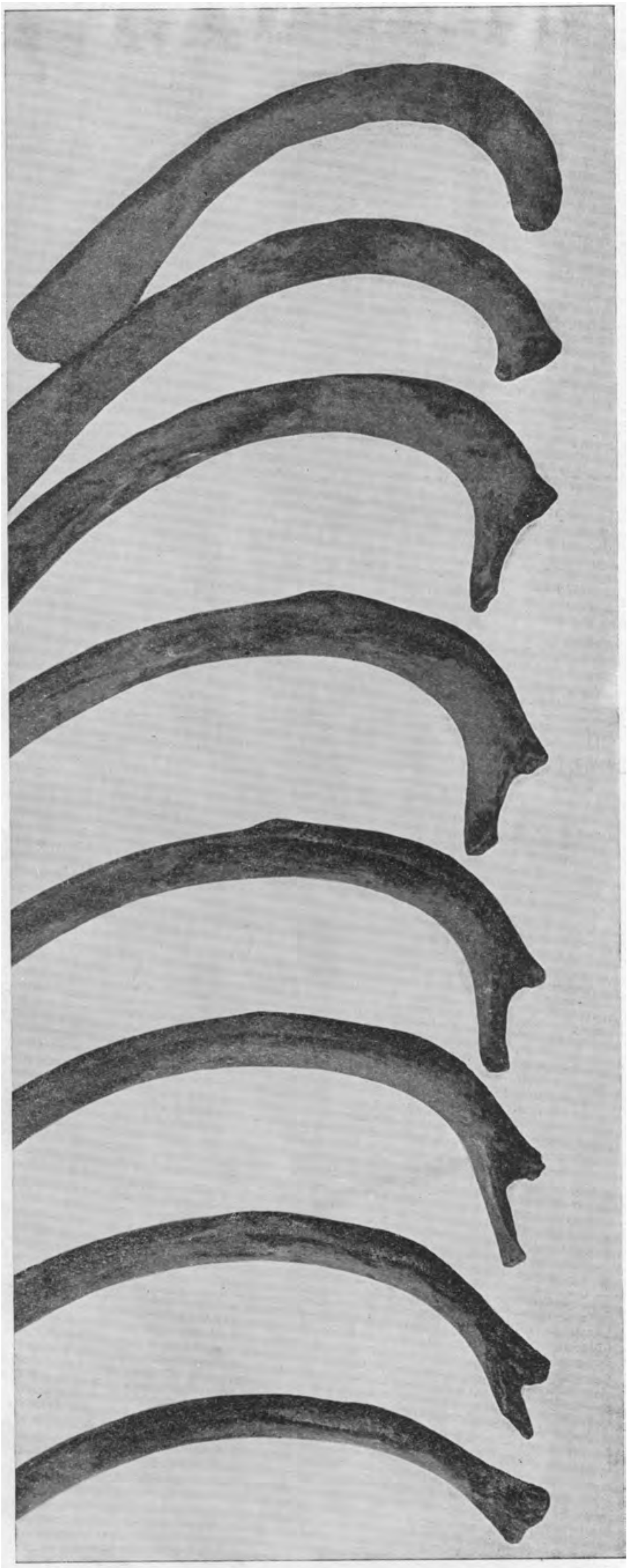

Fig. 15. Proximal portions of first eight ribs of *Rhachianectes glaucus.*

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[1] Journal of Anatomy and Physiology, Vol. XXIII (new ser. Vol. III), 1889, p. 143.

Table VIII.—Measurements of the ribs of Rhachianectes glaucus.

	1st	2nd	3rd	4th	5th	6th	7th	8th	14th
Length on outside curve from tip of head to distal end	mm. 1400	mm. 1855	mm. 2255	mm. 2455	mm. 2515	mm. 2490	mm. —[1]	mm. 2335	mm. 1430
Length, straight, from tubercle to distal end	1020	1335	1590	1700	1785	1750	1765	1725	1370
Distance from back of tubercle to end of head	—	125	251	233	213	213	—[1]	110	—

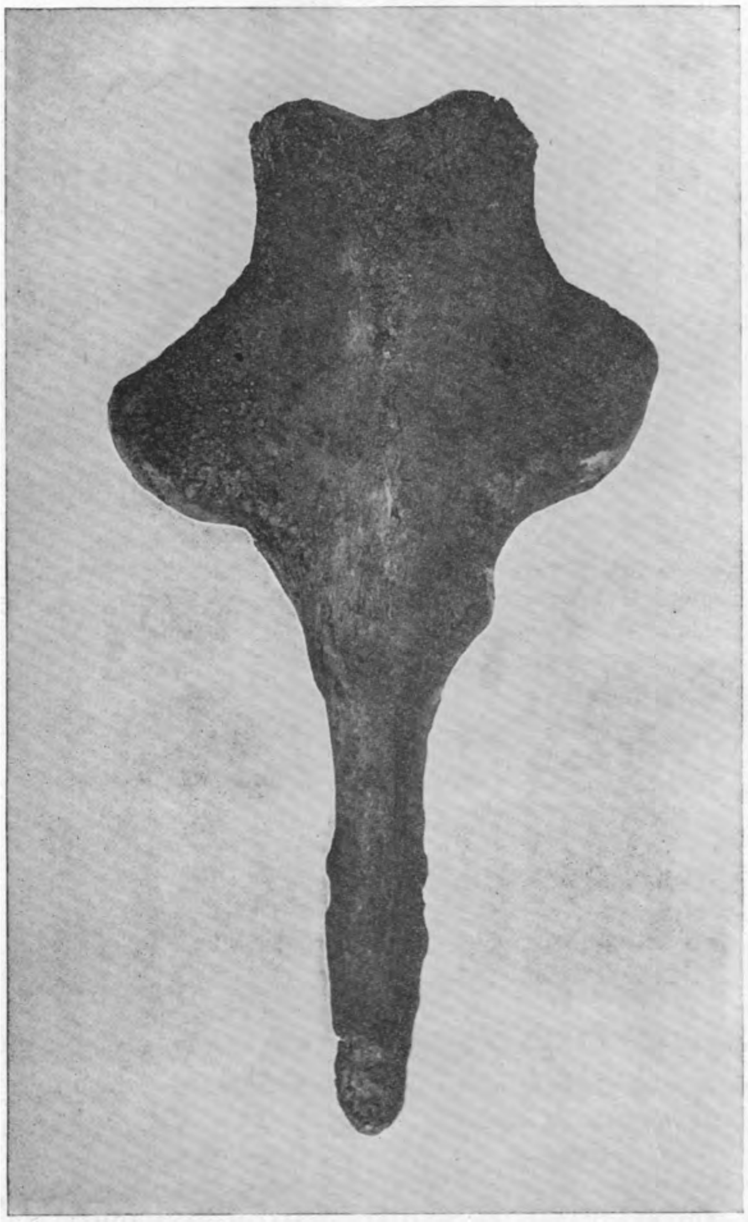

Fig. 16. Sternum of *Rhachianectes glaucus;* Am. Mus. skeleton.

Sternum.

The sternum belonging to the skeleton of *Rhachianectes* in the American Museum has the form of a Latin cross and closely resembles the corresponding bone of *Balænoptera acuto-rostrata.* The lateral arms of the cross are short and irregularly rounded and the summit of the superior portion is abruptly truncated and has a shallow concavity. The inferior prolongation of the sternum is irregularly cylindrical terminating in a blunt point, and is remarkable for its length. The entire sternum, but especially the anterior surface, is rugose and covered with small osseous tubercles which apparently are not due to exostosis but have been developed for tendon attachments.

The sternum of the United States National Museum specimen shows an extraordinary difference in shape from that described above and demonstrates the enormous individual variation to which such almost rudimentary bones are subject. The sternum is concave on the superior surface, has two rounded, wing-like lateral processes and terminates inferiorly in a short irregular spine.

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[1] End of neck injured.

Measurements of sternum.

	American Museum mm.	U. S. Nat. Museum mm.
Greatest height (vertical)	460	223
" breadth (across arms)	260	242
Length of lower process	276	165

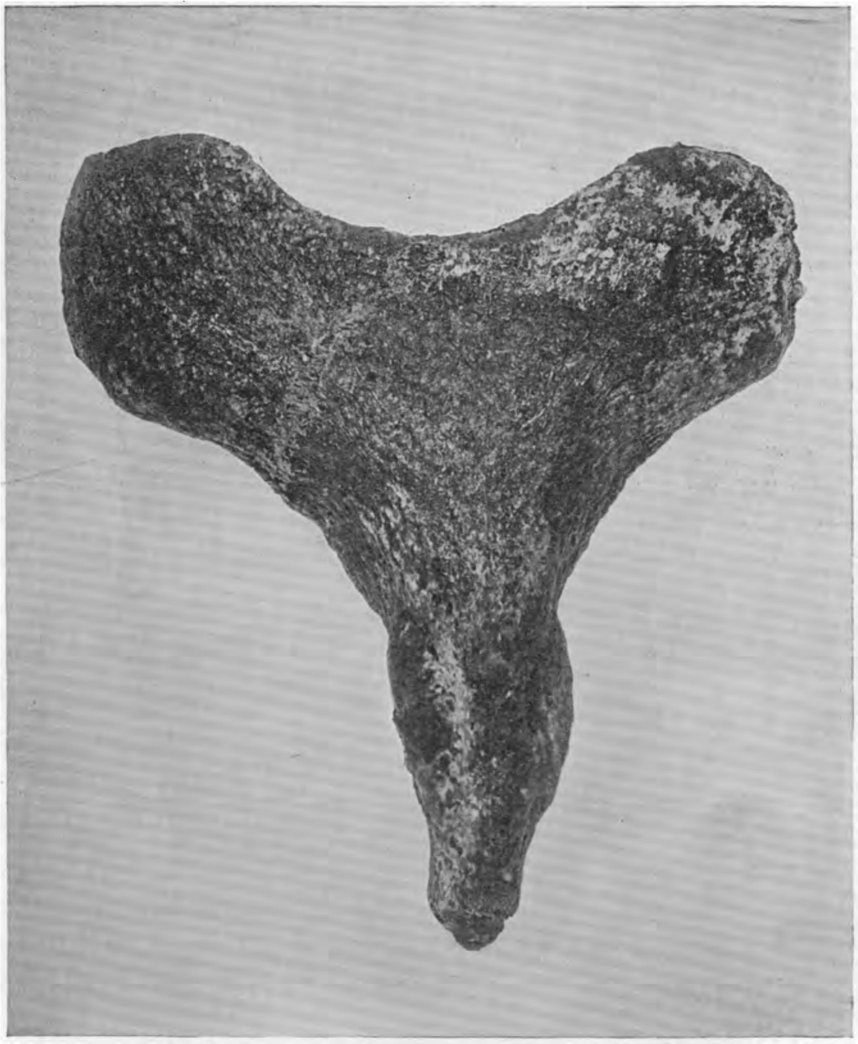

Fig. 17. Sternum of *Rhachianectes glaucus;* U. S. Nat. Mus. skeleton.

Pectoral Limb.

Scapula.— The scapula of *Rhachianectes* is distinctive being intermediate between the wide, low blade of *Balænoptera* and the high, narrower and more symmetrically fan-shaped scapula of *Eubalæna*. In the great height proportional to its width it approaches the latter genus while in the well developed coracoid and large acromion it resembles the former.

The superior margin is quite evenly convex, becoming slightly flattened posteriorly. The glenoid border is almost straight except for a short concavity where it rises from the glenoid fossa and neither it nor the coracoid border overhangs as strongly as in the scapulæ of *Balænoptera*.

The acromion is exceedingly wide throughout, expanded and irregularly rounded distally, and slightly curved.

The coracoid is thick and massive, turned sharply inward and directed somewhat upward from the margin of the glenoid fossa.

The external face of the scapula is quite strongly concave as in *Eubalæna*. It is much thicker and more massive than in *Balænoptera* but not as thick as that of a Right Whale.

Measurements of the scapula are given in Table IX.

Humerus. — The humerus is nearly straight, the superior edge is but slightly concave and the external tuberosity is prominent. In all of these characters the humerus differs from that of *Balæna, Eubalæna* and *Megaptera* and strongly resembles the fossil genus *Plesiocetus;* while in *Balænoptera* the head is almost directly upon the summit of the bone, the concavity of the sides gives the humerus quite a different appearance from that of *Rhachianectes.*

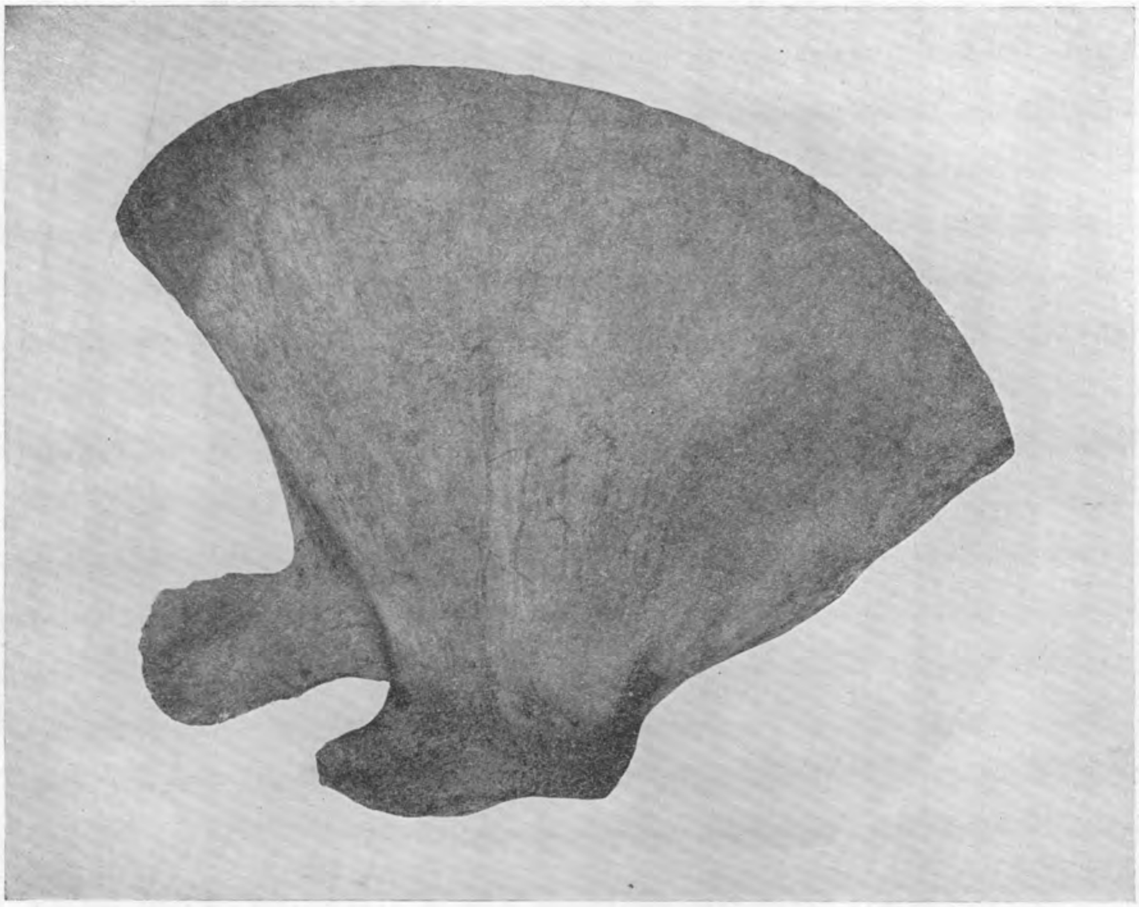

Fig. 18. Inner view of right scapula of *Rhachianectes glaucus;* Am. Mus. skeleton.

Radius.— The radius is remarkable for its width. The exterior edge for its proximal half is slightly convex and in the distal portion a little concave. The interior edge presents a shallow concavity due to the broadening of the bone at the carpal end. For the proximal half the radius is of almost uniform width but in the distal half rapidly expands.

Ulna.— The ulna has a nearly straight inner edge but a strongly concave outer margin due to the rapid broadening of the bone in the distal half. The olecranon process is prominent and projects upward.

The radius and ulna differ markedly from those of *Balæna*, *Eubalæna* and *Megaptera* but in general resemble *Balænoptera*. The broad radius is somewhat similar to that of *B. musculus* but the straight ulna is quite unlike the bone in that species. The radius and ulna of *B. physalus* and *B. borealis* are more slender, more curved and less expanded distally than in *Rhachianectes glaucus*.

Manus.— *Rhachianectes* has four digits in the manus. The phalangeal formulæ of the flippers of the U. S. National Museum specimen (which are more nearly perfect than are those of the American Museum skeleton) are as follows:

Fig. 19. Inner view of right scapula of *Rhachianectes glaucus,* photographed at Ulsan, Korea.

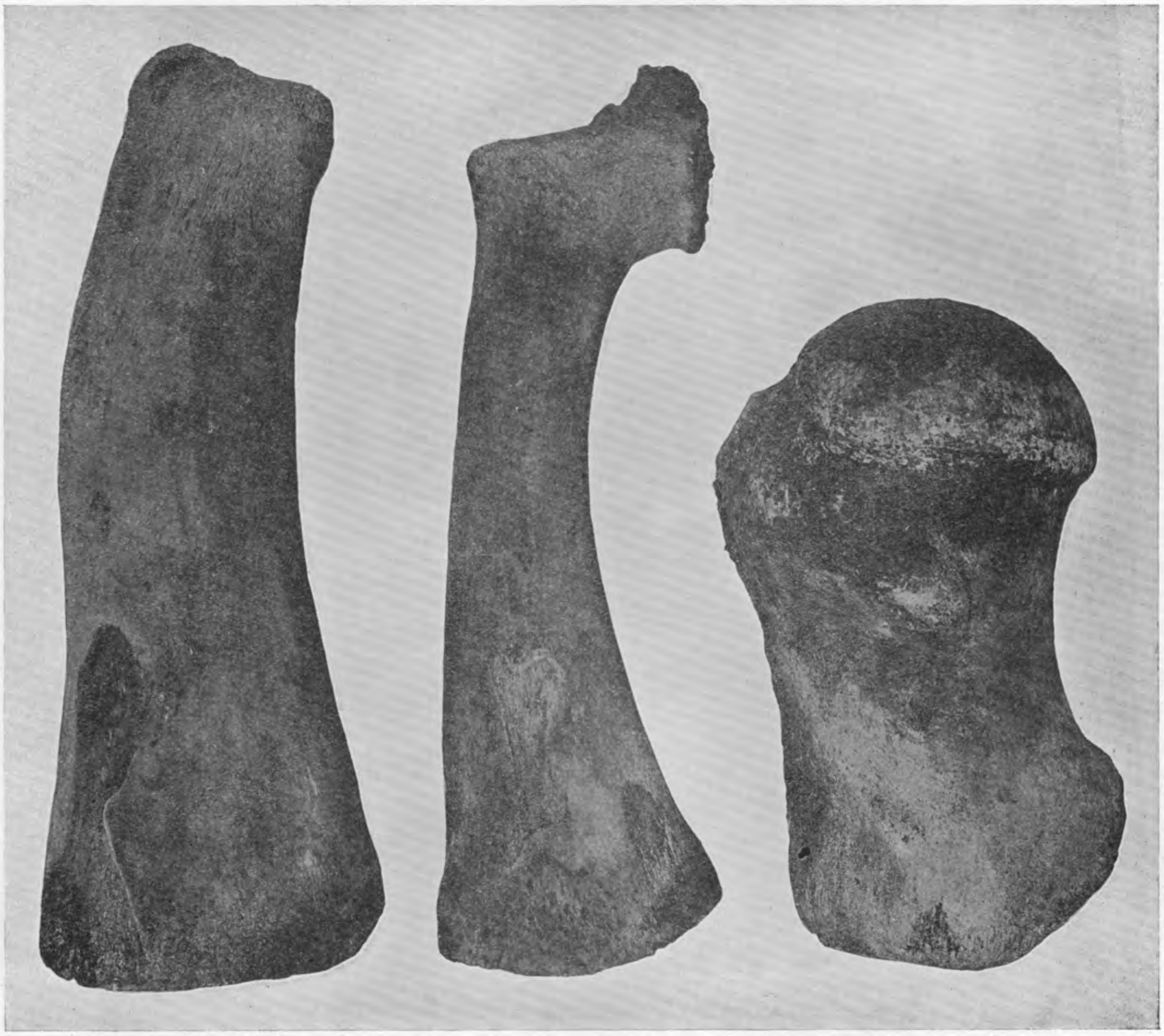

Fig. 20. Humerus, radius and ulna of *Rhachianectes glaucus;* Am. Mus. skeleton.

	II	III	IV	V
Right:	3	3	4	1
Left:	3	4	4	1

The terminal phalanx of the third digit of the left pectoral is a shell of bone and seems to be a normal phalanx which has been injured. This has all the appearance of bony tissue and not of hardened cartilage but it is not present in the right manus. Presumably the tips of both flippers were injured and the correct formulæ for the phalanges is that of the left. The terminal phalanx of the fourth digit of the right manus is also a bony shell but in the corresponding finger of the left hand it has a normal shape and size.

Table IX.—Measurements of Pectoral Limb of Rhachianectes glaucus.

	Am. Mus., No. 34260 mm.
Scapula, greatest height (vertical)	856
" " breadth	1125
" length acromion (inferior edge)	335
" breadth " distally	180
" length coracoid (inferior edge)	146
" breadth glenoid fossa	268
Radius, greatest length	750
" " breadth proximally	183
" " " distally	265
Ulna, greatest length	758
" " breadth proximally	222
" " " distally	226
Humerus, greatest length	520
" " breadth proximally	316
" " " distally	282

Pelvic Rudiments.

The pelvic elements of *Rhachianectes* are exceedingly interesting, the most remarkable features in comparison with other whales being their great size, the less reduction of the pubis and ischium, and the presence of a large foramen.

Those of the American Museum skeleton are two long, slightly curved bones of exactly the same length. The ilium is exceedingly massive, laterally compressed, and has a long dorsal and ventral ridge; a cross-section would be a wide ellipse. The ischium has the same length as the ilium but it is not as massive, is more compressed, and is deeply excavated at the distal end.

The pubis appears as a prominent, roughly cone-shaped tubercle, turned sharply downward and standing at right angles to the remainder of the bone instead of projecting directly outward as in other baleen whales.

Along the inner base of the pubis is a deep longitudinal concavity in the bottom of which, and slightly posterior to the pubis, is a large curved foramen which perforates the bone transversely, emerging on the dorsal surface almost opposite the point of entrance.

Although both the American and U. S. National Museum specimens from which the pelvic elements were secured were males, there is considerable variation in the size and shape of the bones in the two individuals. Those of the U. S. National Museum skeleton are shorter, due to a reduction of the iliac portion, wider through the pubis, slenderer throughout and more

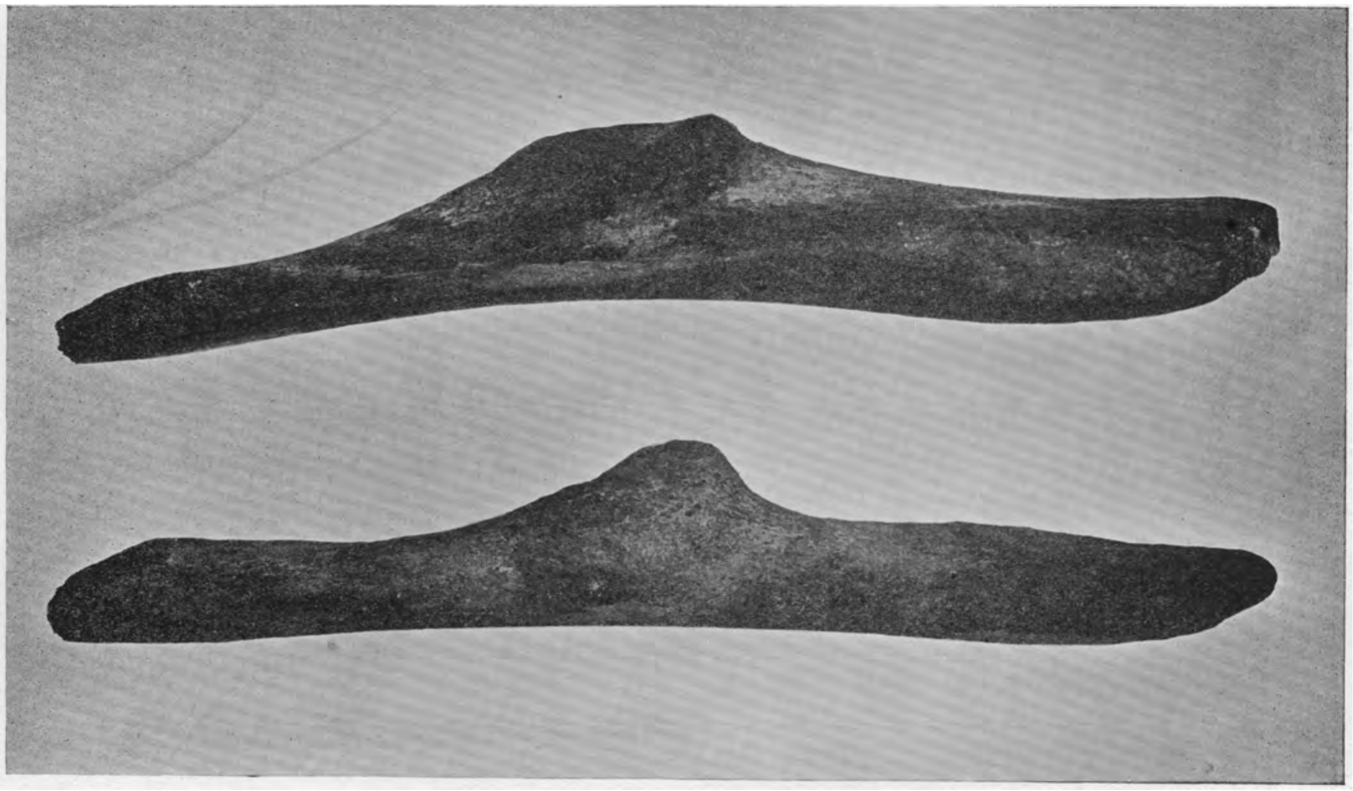

Fig. 21. Pelvic elements of *Rhachianectes glaucus;* Am. Mus. skeleton.

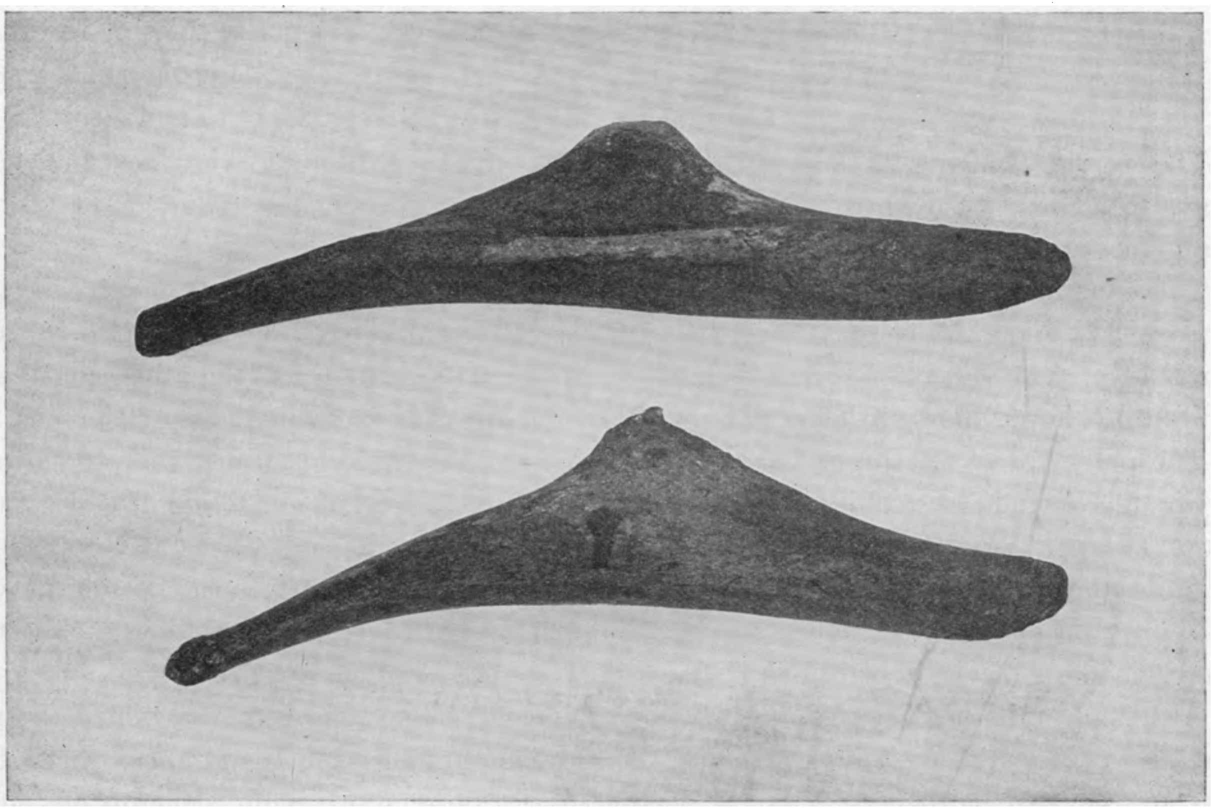

Fig. 22. Pelvic elements of *Rhachianectes glaucus;* U. S. Nat. Mus. skeleton.

curved. In both the ilium is considerably shorter than the ischium, the pubis is not turned as sharply downward as in the American Museum specimen, and the transverse foramen is larger; also there is no excavation of the distal end of the ischium.

The presence of a foramen perforating the pelvic rudiment has been recorded by Struthers in the case of *Balæna mysticetus* but it is rare in other Cetaceans.

It is to be regretted that it was not possible to make a careful examination of the flesh containing the pelvic elements to determine the condition of the femoral rudiments. I believe that *Rhachianectes* will be found to possess a femur larger than that of any other baleen whale when this subject has been more carefully investigated.

Measurements of the pelvic elements.

	American Museum mm.	U. S. Nat. Museum mm.
Length of entire pelvis	501	439
" " ilium	258	210
" " ischium	258	259
Breadth of ilium	74	62
" " ischium	53	49
" across pubis	75	100

CONCLUSIONS.

Specific relationship of California and Korea specimens of Rhachianectes.

Descriptions and measurements of the external anatomy and post-cranial skeleton of California examples of *Rhachianectes* are so general and inaccurate that they furnish few reliable data for use in deciding the specific relationship of the specimens from opposite sides of the Pacific. A discussion of this question, therefore, must rest almost entirely upon the basis of skull characters.

A careful comparison with our Korea specimen of the figures, descriptions and measurements of the American skulls presented by True and Malm shows a remarkably close agreement in all essential points. Examination of the table of measurements shows the only difference worthy of note to be in the proportionately shorter rostrum of the California skull and its less squamosal breadth. Judging from the figures the former difference seems to be due to the fact that the slender prolongations which the maxillæ send backward toward the vertex of the skull are somewhat broken, thus reducing the rostral length. The proportional squamosal breadth of the California skull is somewhat less than in the one from Korea, but since the orbital widths are almost exactly the same, this cannot be considered as of great importance.

There is, so far as I can discover, not the slightest ground for believing the Gray Whales of the east and west Pacific to represent other than a single species. Whether or not the animals mingle in the north during their summer migration has been discussed in the section of this paper relating to habits and need not be again taken up here.

Systematic Position.

Review of former classifications.

1871.— J. E. Gray places *Rhachianectes* in the family Agaphelidæ.

1874.— Gill makes Agaphelidæ of Gray a subfamily under Balænopteridæ and divides that family into the three subfamilies Agaphelinæ, Balænopterinæ and Megapterinæ.

1891.— Flower and Lydekker combine all genera under the family Balænidæ without subfamily divisions.

1897–1904.— Trouessart gives two subfamilies, Balænopterinæ and Balæninæ, under the family Balænidæ and includes *Rhachianectes* in the former.

1900–1902.— Beddard considers *Rhachianectes* as an aberrant genus of the family Balænopteridæ.

1901–04–05.— Elliot recognizes two subfamilies of the Balænidæ and in the Balæninæ includes *Balæna*, *Rhachianectes* and *Megaptera*.

1904.— Max Weber recognizes three families, Rhachianectidæ, Balænidæ and Balænopteridæ.

1910.— Osborn, under the family Balænidæ, recognizes the three subfamilies Rhachianectinæ, Balæninæ and Balænopterinæ.

It will be seen from this brief review of the various classifications of the genus *Rhachianectes* that there has been little agreement as to its systematic position. This is partly due to the fact that up to the present time only the skull has been studied, the post-cranial skeleton never having been described. The results of my work upon this remarkable animal, presented in the preceding pages, lead me to believe that it cannot be included in either of the subfamilies of the Balænidæ and must take rank as a separate family. For this designation Weber's Rhachianectidæ is available and a definition of the family and genus may be formulated as follows:

Family *Rhachianectidæ.*— Skull with a broad strip of the frontals exposed upon the vertex. Maxillæ overlapping the anterior edges of the orbital processes of the frontals. Nasals very long and broad. Mandible without a coronoid process. Cervical vertebræ free. Manus consisting of four digits. Ribs of the anterior half of the series provided with tubercles, necks and heads. Furrows few and short.

Genus *Rhachianectes.*— Head less than one-fourth the length of the body. Baleen laminæ few, short, and thick. No dorsal fin. Pectoral limbs of medium width. Furrows only upon the throat. Rostrum of skull narrow and moderately arched. Premaxillæ sending broad, overlapping projections toward vertex of skull. Prominent rugosities upon the supraoccipital and basioccipital bones of the skull. Tympanic bullæ compressed and somewhat concave on internal border. Scapula having both acromion and coracoid processes.

Primitive Characters of Rhachianectes.

The external and internal anatomy of *Rhachianectes glaucus* presents certain characters which seem to demonstrate that this animal is more primitive than any other existing baleen whale. These may be summarized as follows:

1. Long hairs scattered over the entire head and mandible and not confined to certain regions as in other whales.

2. Baleen plates very short, thick, fewer in number and more widely spaced than in other whales.

3. Skull:

a. Exposure of a wide strip of the frontals upon the vertex of the skull.

b. Long nasal bones.

c. Comparatively small squamosals having straight outer edges. This is noticeably different from the concave squamosals of existing baleen whales and is a character of fossil genera.

d. Proximal ends of the premaxillæ very broad, superiorly placed, and articulate with the frontals by a deep, interdigitating suture.

e. Orbital processes of the frontals anteriorly overlapped by the edges of the maxillæ, posteriorly with irregular margins, and trumpet-shaped; all well marked characters of certain fossil baleen whales.

f. A well emphasized temporal ridge.

g. Prominent rugosities upon the supraoccipital, pterygoids, and basioccipital bones of the skull.

h. Compressed tympanic bullæ having concave internal borders.

4. Cervical vertebræ entirely free and showing no evidences of ankylosis between any members of the series.

5. Atlas and axis possessing massive, rugose neural arches; axis with comparatively small foramina through the wing-like transverse processes.

6. Ribs possessing tubercles, necks and heads as far back as the eighth, and in these portions resembling an Odontocete.

7. A long and straight humerus of the *Plesiocetus* type.

8. Very large pelvic elements, the presence of a large foramen in them and the comparatively slight reduction of the pubis and ischium.

RELATIONSHIP OF RHACHIANECTES.

Rhachianectes glaucus is apparently not closely related to any of the existing baleen whales but in some respects it stands intermediate between the Balæninæ and Balænopterinæ being nearer the latter. In many skull characters it approaches closely the Pliocene whales of the genus *Plesiocetus* which is allied to the existing Balænopterinæ; in fact, were it not for its specialized mandible it must certainly be considered as nearly related to them. The fossil whales of the *Pleisiocetus* group possessed mandibles having the proximal portion of each ramus, internally, widely concave and leading into a large dental canal; in short, much as in the mandibles of the existing toothed whales. *Rhachianectes*, however, although resembling *Plesiocetus* in many important skull characters, possesses a specialized mandible similar to that of the Right Whales; that is the proximal portion, internally, is not concave and the dental canal is small. This type of mandible prevents the phylogenist from taking *Rhachianectes* off from the *Plesiocetus* group, unless he wishes to consider that while persisting until the present day with comparatively little modification of its primitive skull characters, it has undergone considerable specialization of the mandible alone. This is a perfectly possible supposition, which I am inclined to believe is true, since *Rhachianectes* shows such marked affinities to *Plesiocetus* and is so strongly separated from the other known genera of fossil and recent whales. It is, upon the whole, one of the most remarkable of existing Cetaceans and might be called a "living fossil."

ILLUSTRATIONS.

PLATES.

Plate XIX.

Fig. 1. Lateral view of peduncle showing white markings, mostly cirriped scars.
Fig. 2. Lateral view of peduncle showing normal gray and white markings and total absence of cirriped scars.
Fig. 3. Head, pectoral fin and section of back blubber.
Fig. 4. Direct lateral view of peduncle showing dorsal crenulations.
Fig. 5. Dorsal view of peduncle showing normal gray markings and flukes.
Fig. 6. Peduncle lying upon the wharf.
Fig. 7. Posterior portion of body showing inferior outline.

Plate XX.

Fig. 1. Direct lateral view of head showing few parasite scars.
Fig. 2. Three-quarters posterior view of head showing many parasite scars.
Fig. 3. Dorsal view of head and blowholes; note the barnacles *Cryptolepas rhachianecti* embedded in the skin, and the masses of *Cyamus scammoni*.
Fig. 4. Front view of head.
Fig. 5. Direct lateral view of head and mandible of fœtus No. 1*a*.
Fig. 6. Section of peduncle showing normal gray and white markings.

Plate XXI.

Fig. 1. Eye and ear.
Fig. 2. Inner view of baleen.
Fig. 3. Blowholes and *Cyamus scammoni*.
Fig. 4. Three-quarters view of tongue.
Fig. 5. Lateral view of anterior portion of snout showing cornified areas due to the action of parasites.
Fig. 6. Inferior view of anterior portion of snout.
Fig. 7. Fœtus No. 1*a*.

Plate XXII.

Fig. 1. Throat showing two grooves.
Fig. 2. " " " "
Fig. 3. " " three "
Fig. 4. " " " "
Fig. 5. " " " "
Fig. 6. Tongue in position.

Plate XXIII.

Fig. 1. Superior surface of uninjured pectoral fin.
Fig. 2. Pectoral fin injured and infested with parasitic *Cyamus scammoni*.
Fig. 3. Superior surface of slightly injured pectoral fin.
Fig. 4. Inferior surface of pectoral fin showing usual type of coloration (slightly injured).
Fig. 5. Inferior surface of pectoral fin.
Fig. 6. " " " " "
Fig. 7. " " " " " (injured).
Fig. 8. " " " " " "

Plate XXIV.

Fig. 1. Flukes showing barnacle scars; posterior edges slightly injured.
Fig. 2. Flukes; posterior edges very slightly injured.
Fig. 3. Posterior edge of flukes.
Fig. 4. Peduncle of fœtus No. 1*a*.
Fig. 5. Section of blubber at end of peduncle crenulations ("hump").
Fig. 6. Gray Whale spouting blood.
Fig. 7. Normal spout of a Gray Whale.

Plate XXV.

Fig. 1. Dorsal view of the skull from California in the U. S. National Museum.
Fig. 2. Dorsal view of the skull from Korea in the American Museum.

Plate XXVI.

Fig. 1. Ventral view of the skull from California in the U. S. National Museum.
Fig. 2. Ventral view of the skull from Korea in the American Museum.

Plate XXVII.

Fig. 1. Lateral view of the skull from California in the U. S. National Museum.
Fig. 2. Lateral view of the skull from Korea in the American Museum.
Fig. 3. External side of left ramus of mandible; Korea specimen in the American Museum.
Fig. 4. Internal side of left ramus of mandible; Korea specimen in the American Museum.

TEXT FIGURES.

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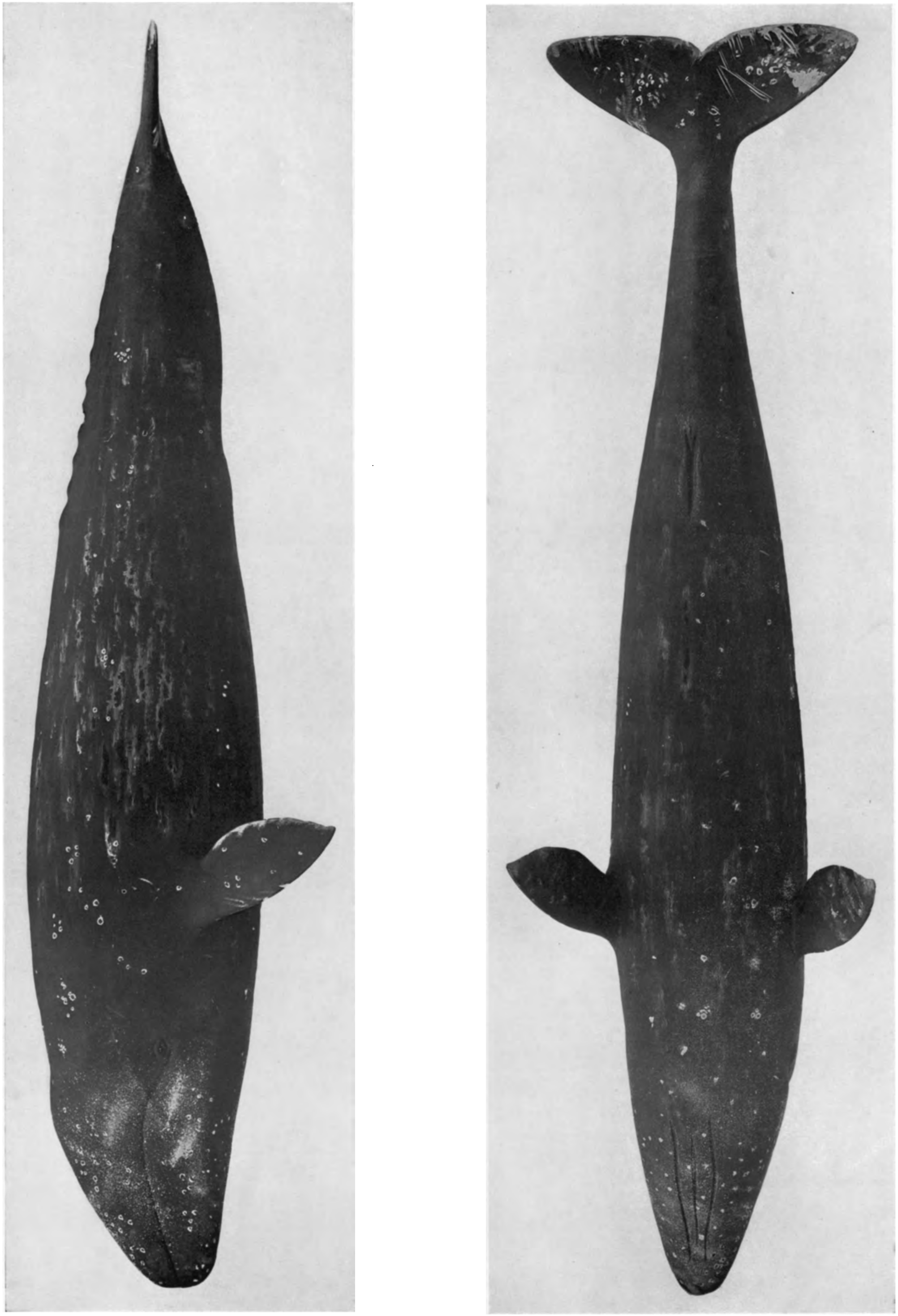
PLATE XXVIII.

PLATE XXVIII.

Rhachianectes glaucus.

Supplemental Plate for Part V.

Fig. 1. Lateral view.
Fig. 2. Ventral.
(From photographs of a model constructed under the direction of Roy C. Andrews.)



RHACHIANECTES GLAUCUS.

Grey Whales in the East Sea Area of Korea

BY

KAZUHIRO MIZUE

Introduction

Rhachianebtes goaucus is classified into a Suborder Mystacoceti but it is quite a different species from Balaenidae or Balaenopterynae. Apart from them, it forms a family Rhachianectes by itself. Due to its resemblance to the fossil whales of the Pleisiocetus group in the shape of the skull it is often called a "living fossil".

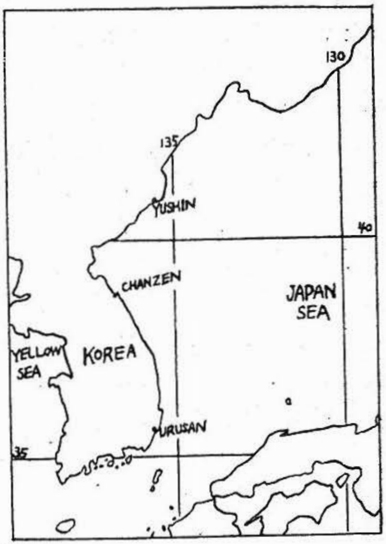


Fig. 1.

Whales of this species were captured so abundantly off the coast of California once that they are still called Californian grey whales. But the catch there began to decrease rapidly towards the middle of the 19th century. It is reported, however, they are on the increase in the recent years. Besides California, a considerable catch of grey whales was made in the East sea area of Korea, but their stock has completely been exhausted at present. Roy C. Andrews made a detailed study of grey whales at Urusan, the landstation in the East sea area of Korea during the season 1909-1910, which will be found in the Memoirs of the American Museum of Natural History-V. We shall here make some study of the same subject statistically based on the data after 1910.

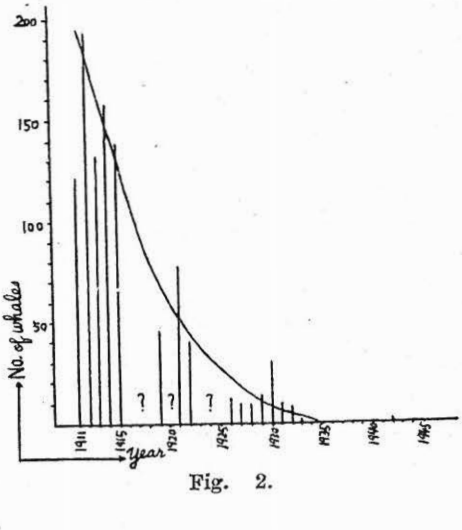


Fig. 2.

Number of the Catch

Fig. 2 shows a number curve of the catches of grey whales in our adjacent waters according to the years. It is based on the data from 1910 up to the present. In spite of the lack of the data of some years, the curve gives a clear idea of the rapid decrease of the catch. It is not before 1903 that Norwegian Whaling was adopted in the East sea area of Korea for the first time, and in thirty years, almost the last grey whale was hunted up there. The fact will indicate that the stock of grey whales in our adjacent waters was but a small one existing, as it were, independently, having no intercourse with the stocks of other waters.

At the middle of the 19th century when grey whales along the coast of California were feared to have gone to exhaustion, in the East sea area of Korea the stock was still kept intact, which began to decrease after 1903; during the fifteen years from 1934 up to the present not a single grey whale was captured there. Meanwhile, along the Californian coast, it is reported, grey whales are on the increase. It apparently proves the fact that there is no intercourse between the two stocks of grey whales on the east and the west sides of the Pacific.

No catch of Grey Whales has been made off the eastern coast of Korea since 1933. Of the thirty years' whaling history there, the records of the seven years, —1911, 1914, 1919, 1921, 1922, 1926, and 1932— are completely preserved in the monthly reports of the various whaling companies forwarded to the Japanese Whaling Society. Based on the data we shall here make some reports of the grey whales in this place.

Table 1.

Sea-area.	%	Whaling season
Kurile-Islands	0.2	August
Hokkaido-Okhotsk	0.2	May
Hokkaido-Pacific	0.2	July
Sanriku	0.7	October
Kinan	0.0	
Bonin-Islands	0.0	
Goto-Tsushima	4.2	December
West of Korea	0.4	May
East of Korea	94.2	November-May
Japan-Sea	0.0	
Formosa-Ryukyu	0.0	

Sea-Area is divided by location of the land-station

In Table 1 are shown percentages of the yearly catches in the seven years according to the sea areas; the division of the sea areas is based on the sites of the landstations. The whaling ground of gray whales in the Goto-Tsushima sea area actually belong to the east sea area of Korea. So 98% of the catch of grey whales are made off the eastern coast of Korea. Grey whales in our adjacent waters are different from other baleen whales in point of the distribution; they have seldom been captured in the ground belonging to the Pacific. Besiees the East sea area of Korea, three were caught at Ayukawa of the Sanriku sea area and one off Nemuro, Hokkaido in 1914, two in the northern part of the Yellow Sea in 1922, one off Sakhalin in 1826 and one off Otomae, the North Kurile Islands in 1942. The number is so small compared with that of the catch made in the East sea area of Korea that they may be regarded as exceptional. However, these eight grey whales were all caught in the waters north of 38°N.

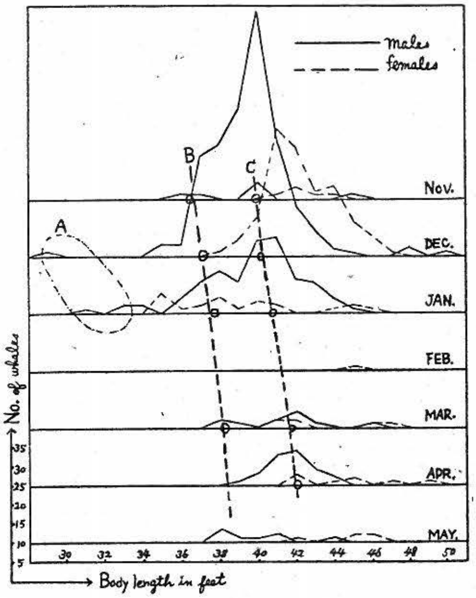


Fig. 3

In spite of the yearly decrease of the number, body-length frequency curves of the grey whales according to the years follow the same pattern every year rising into peaks in almost the similar months. Fig. 3 shows body-length frequency curves of the whale catch according to the months. Here monthly variations in number are noticable, and in the case of male grey whales, the peaks in the curves apparently move from the left to the right according to the months, showing the process of their growth. (As for the females, due to the scantiness of the number, the phenomenon is hardly discernible) A-group in Fig. 3 is composed of one-year-old male animals, B-and C-groups of two-years-old and three-years-old ones respectively. According to R. C. Andrews the period of delivery of grey whales lasts from the end of December to the beginning of January next year, and their body-length at birth is 14 feet, which gains no less than 18 feet during the first year after the birth. Seeing the growth speed of grey whales, like any other species, is extremely high in the first year, it is quite assumable that the young whale born during the previous winter, is some 30 feet long when it appears in the Korean waters the next season. The body-length of grey whales at birth, as it is calculated from my data is 15 to 16 feet.

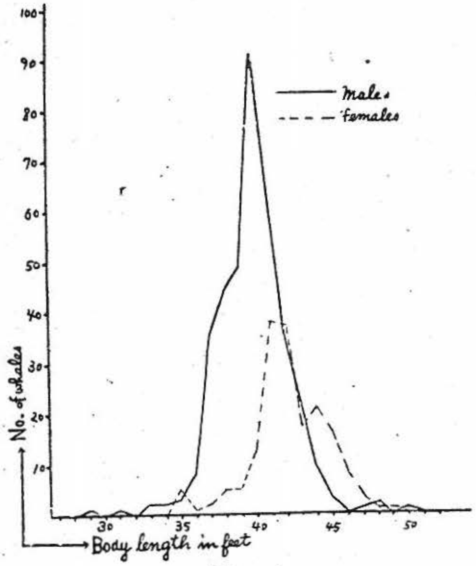


Fig. 4

Fig. 4 presents body length frequency curves of the whale catch according to the sexes. In the case of male grey whales the curve rises into a peak at 40 feet while in females a peak forms at 41 to 42 feet and again at 44 feet. According to Figs. 3 and 4 female grey whales, like any other species of baleen whales, are larger in size than males.

Table 2

	November			December			January			February			March			April			May			Total		
	♂	♀	to.	♂	♀	to.	♂	♀	to.	♂	♀	to.	♂	♀	to.	♂	♀	to.	♂	♀	to.	♂	♀	to.
Number of Whales	7	6	13	220	125	345	97	22	119		1	1	11	6	17	29	8	37	8	8	13	37.2	173	545
Average length in feet	39.7	42.3	40.9	39.6	42.3	40.5	39.8	39.0	39.6		45	45	41.4	43.5	42.1	41.8	44.8	42.6	39.8	44.8	41.7	39.9	42.1	40.6
Sex-ratio	53.8	46.2		63.8	36.2		81.5	18.5		0.0	100.0		64.7	35.3		78.4	21.6		61.5	38.5		68.3	31.7	

In Table 2 are shown average body lengths and sex ratios of the whole catch according to the months. There is two feet's variation between the body lengths of the two sexes, and the maximun body length of the males is 50 feet and that of the females 49 feet, while the minimum body length is 29 feet for the males and 35 feet for the females. In Table 3 you will find these particulars of the body length of grey whales compared with the measuring values calculated by other writers in the past.

Table 3

	Average for all Specimens of both sex		Average for all females		Average for all males		Max. of female	Max. of males	Min. of females	Min. of males
	No. of whale	length	No. of whale	length	No. of Whale	length	length	length	length	length
Korea, by Andrew	23	38′ 9½″	3	41′ 4″	20	38′ 6″	43′ 3″	41′ 1″	38′ 1″	32′ 2″
Korea, by Whalers	123	39′ 10″	50	41′ 2″	73	39′ 0″	45′ 0″	43′ 0″	32′ 0″	35′ 5″
California, by Scammon	4	40′ 8″			3	40′ 8″		48′ 0″		32′ 0″
Korea.	545	40′ 7″	174	42′ 1″	372	39′11″	49′ 0″	50′ 0″	35′ 0″	29′ 0″

Table 4

Month	%
November	2.4
December	63.1
January	21.8
February	0.8
March	3.1
April	6.8
May	2.4

Table 4 presents the percentages of the monthly catches shown in Table 2. According to it the catch of December forms the highest percentage of 63.1 and then comes the 21.8% of January. The catches of the other months cannot be compared with those of the above two months. When we divide the catches of both December and November into decades, it will be found that there is a small variation between the whaling seasons of the two sexes and that the best season for both males and females is from the middle of December towards the end, and the next best is either the beginning of January or that of December.

Table 5

Month	November		December			January			Feb.
	Middle	last	first	middle	last	first	middle	last	first
No. of male	0	6	28	81	111	74	23	1	0
No. of females	0	6	29	49	47	14	7	1	0
Total	0	12	57	130	158	88	30	2	0

Localities of the Catch

As has already been made clear by tables and figures, grey whales are quite regular in their appearance in the east sea area of Korea. According to Table 5, males begin to arrive there at the end of November, increase in number till they reach the greatest number at the end of December, which declines towards the middle of January. After that, male grey whales are no longer seen in this sea area. As for females, they begin to appear at the end of November, reach the greatest number at the middle of December towards the end and decrease in number till they leave the place for the north at the middle of January. Thus grey whales stay for only two months in this sea area; the place is also a good whaling ground for Fin Whales and many catcher-boats work during the season,—from September to March next year. They would have certainly caught grey whales if they had seen them in the months of October, November, February and March. The localities of the catch of grey whales, compared with those of fin whales, are quite near the coast. Their chief grounds are found within 10 sea-knots from the shore.

Grey whales come to the east sea area of Korea for the purpose of delivery as was already pointed out by R. C. Andrews. Female animals captured before the middle of December, are, with almost no exception, with big foetuses immediately before birth. It is quite assumable that delivery is made among the islands at the southern extremity of the Korean Peninsula. Pregnant whales hasten to the place of delivery by themselves, and a little later, herds of grey whales appear in this sea area. In the case of sperm ahales, many females led by one strong male, from so-called "Harem". The contrary is true of grey whales; in their case, the leader is a female and many males follow her. The fact will be made clear by a survey of the sex ratio of the catch. Mr. Andrews writes in his book, "One or two females lead ten to fifteen males." By this he must have meant the pairing migration, for the waters at the southern extremity of the Korean Peninsula present a place of pairing for grey whale as well.

After delivery, female animals accompanied by cubs and apart from the herd, go up north on their nursing migration.

According to Cap. H. G. Melson, the two female Grey Whales captured off Chanzen (39° N.) at the middle of March, 1912 are found with foetuses of seven and ten inches respectively,—both are two months and half after fecundation,

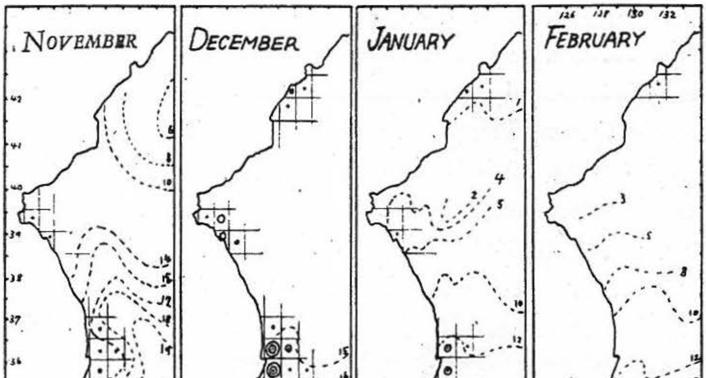


Fig. 5

From this and other data the pairing season of grey whales is assumed to be at the beginning of January. According to Mr. Scammon, the five female whales with small foetuses captured along the coast of California (31°-37° N) in up-season, had thick blubber contrary to the animals nursing cubs. It is not supposable that female grey whales copulate while nursing. So their delivery may happen, in the most favorable condition, every other year.

Grey whales in down-season do not seem to hunt for food, for the animals captured then have no food in their stomach but green colored gastic juice. In up-season, after delivery or pairing, they begin to search for food. Grey whales caught off Yushin, North Korea in up-season-from March to May, are sure to be found with Crustacea in their stomach. According to Mr. Tago, Nephrops thomsonii, small sized Crustacea, was found in the stomach contents of the two grey whales caught in the nothern waters of the Yellow-Sea in May, 1922.

Fig. 5 shows the localities of catch according to the months based on the data of the seven years. At the end of November a small number of grey whales appear both off Urusan and Chanzen. In December, catches are made in three places, the best ground being off Urusan. The animals start on their northwards migration in January and the catch off Urusan decreases. It is interesting to notice that no grey whale is caught in the month of February, except one at Yushin in the north. The fact may indicate that grey whales go up north through the distant offing during that month. In March catches begin to be made in the northern part of this sea area. Either in April or May the catch there forms a comparatively large percentage of the whole catch. These grey whales captured in the northern part, are assumably stray or belated animals from the main herd. Generally spreaking, grey whales on their southwards migration get up speed, but slacken it when they go up north.

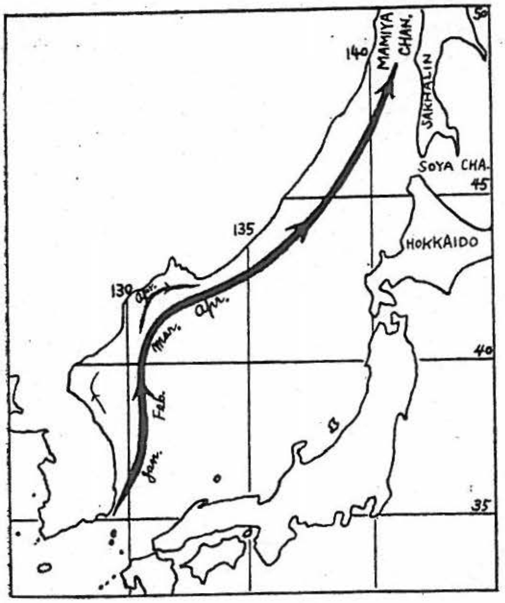


Fig. 6

The general routes of the migration of grey whales off the eastern coast of Korea, based on the various data at our disposal, is shown in Figs. 6 and 7.

From the above two figures, we

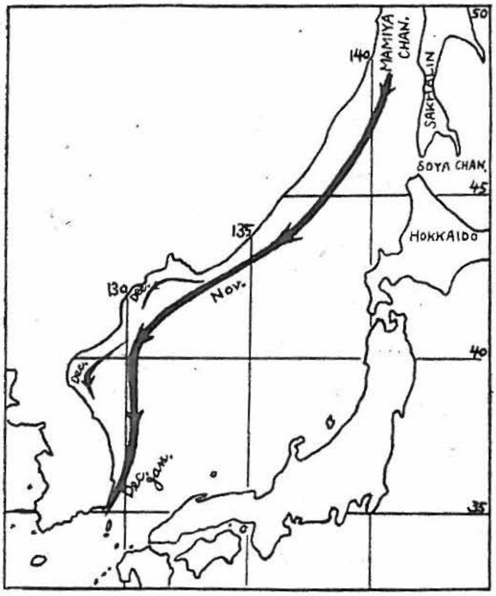


Fig. 7

can assume the movement of grey whales in the east sea area of Korea. As for there where about after then, it is reported by Mr. Tago that they reach Hokkaido or the western coast of Sakhalin in May or June and then through the Mamiya Channal go to the northern part of the sea of Okhotsk, where they seem to spend their summer. On their southwards migration they seem to take the same course as they come up north. It is not probable that grey whales pass through the Soya Channal to the farther north, for fin and hump-back whales are captured there from the landstation in Hokkaido but not grey whales. Nor is it assumable that they go between the Kurile Islands to the North Pacific and further to the Bering Sea, for the North Kurile Islands have many landstations from where both male sperm whales and fin whales were caught abundantly but no grey whale has ever been captured since 1919. (Though one was captured off Otomae, a landstation of the North Kurile Islands, in August, 1942, it ought to be regarded as exceptional.)

According to Mr. Scammon (1874), grey whales in the American side of the Pacific go down as far as 20° N. but in the Asian side they go no farther than 34° N. Nor will they go to the water whose temperature rises higher than 20°C. The right temperature of water for both delivery and pairing of grey whales is assumed to be 15°—20°C. In Fig. 5 the dotted lines show the distribution of the annual mean temperature of the surface water in the East sea area of Korea.

October 30, 1949

The Gray Whale

Eschrichtius robustus

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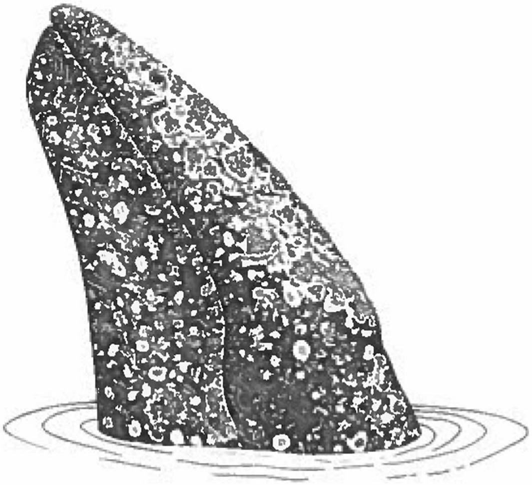

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3

History of Gray Whales in Japan

Hideo Omura

Introduction

The occurrence of gray whales in the coastal waters of Japan prior to the turn of the century was described by Omura (1974). He referred to a population occurring in the south of Wakayama and Kochi prefectures and very briefly to the presence of another population occurring off the north coast of Yamaguchi prefecture, in the Sea of Japan, and off the west coast of Kyushu, in the East China Sea. Catches were made from both populations in the days of net whaling (1675–1890).

The Wakayama/Kochi population is thought to have followed a migration route along the east coast of Japan (Nishiwaki and Kasuya, 1970; Omura, 1974). The Yamaguchi/Kyushu population is thought to have been a portion of the Korean stock. This stock migrated down the east coast of Korea in winter. The majority turned west along the south coast of Korea (Andrews, 1914) but a fraction is assumed to have continued southward until they reached the north coast of Yamaguchi prefecture (near Kayoi, a present Nagato city) and then to have turned along the west coast of Kyushu.

Subfossil mandibles excavated some years ago from the city of Ichikawa were recently identified as belonging to a gray whale. This further supports the contention that this species occurred in coastal waters of Japan.

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Brief History of Old Whaling in Japan

Whaling off Japan appears to have a very long history. A poem describing the catching of whales by a small boat is dated prior to the tenth century. Nothing is known, however, about the method and gear used or about the species of whales taken.

In the years of Genki (1570–1573), whaling in Mikawa and Qwari districts (now Aichi prefecture) facing Ise Bay was conducted by villagers who formed teams of 7–8 vessels and used hand harpoons (Otsuki, 1808; Fukumoto, 1960; Hashiura, 1969; Nagasaki, 1981). It can be assumed this whaling began as bay whaling and its center was Morosaki (see Fig. 7). Nothing is known about the species of whales taken, but there is a possibility that gray whales were the target. In the Edo era (1603–1867), gray whales en route to the Seto Inland Sea were thought to enter Ise Bay, passing sufficiently close to shore to become accessible to fishermen.

In years of the Bunroku (1592–1595), a skilled harpooner from Morosaki named Sukebei Mase came to Misaki (now in Kanagawa prefecture) and began whaling (Hashiura, 1969). The species of whales taken are not known, but a considerable number of whales was taken and local fishermen were stimulated to begin whaling with the same technique. It was reported this period did not last more than 20 years, because of a scarcity of whales.

There are grounds to believe that the harpoon method of whaling was transferred to Katsuyama, the village opposite Misaki across Tokyo Bay in Chiba prefecture. According to Yoshihara (1976a), new whaling started there in the years of the Keicho (1596–1603). This was the origin of the small cetacean whaling now in operation in Chiba prefecture, which takes mainly Baird's beaked whales (*Berardius bairdii*) and some other small toothed whales but no gray whales. Hand harpoons, and after 1907 small harpoon guns, were used for killing whales. Nets were not used at all in this fishery, contrary to the practice in other whaling sites in western Japan. The whaling grounds were later shifted to the east coast of Chiba prefecture.

Hand-harpoon whaling originated in Morosaki and spread to the south along the coast of Ise and Kumano districts (present Mie and Wakayama prefecture). In the eleventh year of Keicho (1606), Yorimoto, head of the then powerful Wada clan, established five whaling groups at Taiji, Kumano. He took command of the operation in the Taiji area, consulting with two fishermen, Denji from Morosaki and Jiemon from Sakai near Osaka (Hashiura, 1969). It is thought Denji, possibly a harpooner, assisted Yorimoto with the technical aspects and that Jiemon handled the commercial aspects of whaling. In 1618 a skillful harpooner named Yoheiji, from Onoura, near Morosaki, was employed at Taiji and given the name of Hazashi (chief harpooner), showing superior status to that of any other whaling crew.

In 1675, Yoriharu Wada, a grandson of Yorimoto later renamed Kakuemon Taiji, invented a new method of whaling using nets. Whales trapped and entangled by many folds of nets were easily harpooned. Straw nets were used at first, but they were too weak and were replaced in following years by hemp.

The use of nets was a revolutionary event in the history of whaling in Japan, allowing takes of humpback whales, other balaenopterid whales, and right whales, none of which could have been taken by hand harpoon previously. This method, however, required more fishing boats, more manpower, and a coordinated cooperative operation. At Taiji, five whaling groups were reorganized into one and Yoriharu Wada took the command.

The basic organization of the net-whaling fleet consisted of the following groups:

1. Seko-bune or beater boats (for driving and killing whales), one group of about 15–20 boats, 13 m long and 2.3 m wide, with eight oars. The crew of each boat consisted of 15 men, namely 1 captain, 13 sailors, and 1 apprentice.
2. Ami-bune or netting boats, one group of 6 boats, 13 m long and 3.5 m wide, with eight oars and a crew of 10 men.
3. Mosso-bune or tug boats, a group of 4 boats, nearly the same as beater boats but with a broader beam, and a crew of 1 captain and 12 sailors.

From a hillside hut commanding a wide view, watchmen scanned the sea surface for whale blows. When a whale was sighted within range, the watchmen sent signals with flags or rockets informing the boat crews of the species, position, and swimming direction of the whale. The boats described above waited in scattered positions and moved into action in an orderly fashion when the commander gave the order.

The beater boats surrounded the whale from a distance and drove it toward the netting boats which moved into proper position to set their nets. Nets were sometimes set two or three deep to prevent the whale's escape and to reduce its struggle. The netted whale was harpooned from the beater boats. When the whale was sufficiently weakened by a number of harpoons, a sailor jumped into the water and climbed onto the head of the whale with his knife to make a hole on the septum of the blowholes through which a rope was passed. Another hole was made in a similar way near the dorsal hump. In both cases the sailor stayed on the slippery surface of the whale body by grasping the handle of a struck harpoon. These harpoons also prevented the nets from slipping off.

The invention of net whaling was a major event in the economy of Japanese fishing villages. Whaling supported many hundreds of people, including workers processing the whale carcass, making nets, or engaged in other related activities, as well as sailors at sea.

Net whaling was soon introduced at Koza, a town close to Taiji, and at other places in Kumano district (part of the present Mie and Wakayama prefectures). In 1683 this method was transferred to Tosa (in the present Kochi prefecture), where the two whaling groups of Ukitsu and Tsuro were already in operation. In the following year a whaling boss named Gidayu Fukazawa from Omura, west Kyushu, came to Taiji and learned this method from Yoriharu (Hashiura, 1969). When Fukazawa returned to Kyushu, net whaling soon spread over the west coast of Kyushu and the north coast of Yamaguchi prefecture.

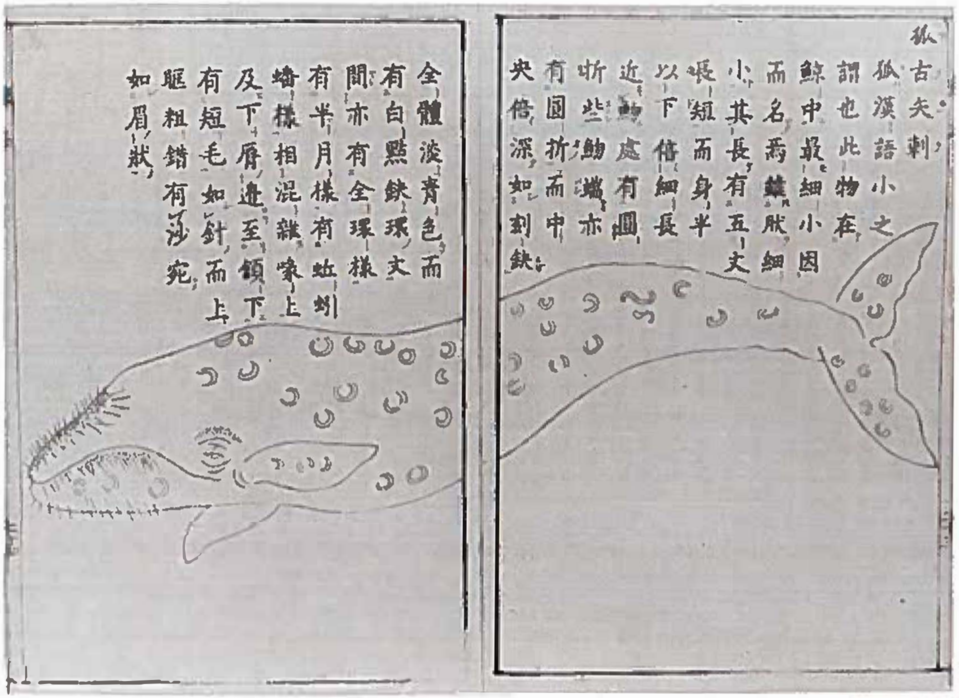
Descriptions of Gray Whales in Old Literature

Old Japanese whaling flourished in the Edo or Tokugawa era (1603–1867). Several books and picture scrolls of whales and whaling published during this period are useful because they contain such information on the whales migrating to Japanese waters as their species composition, migratory pattern, and catch statistics.

"Geishi" (the Treatise of the Whale), written in 1758 and printed in 1760 by Jiemon Kandoriya, the castellany of Wakayama, is the earliest printed monograph of the cetacea of Japan. It contains a drawing and brief description of the gray whale (Fig. 1), named Kokujira from *ko* meaning small and *kujira* meaning whale. The gray whale was so called because it was thought to be the smallest species among whales. There is evidence to suggest that at that time the minke whale was not identified as an independent species of baleen whale.

Kokujira had no dorsal fin but was illustrated as having several knobs in the posterior portion of the back. On both upper and lower jaws there were many hairs that spread over the entire head. This agrees with the description by Andrews (1914) who states "they (hairs) are more widely and more uniformly spread over the entire head, than in any other baleen whales."

The body color of Kokujira is described as pale blue, and there are many circular or



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古失刺孤漢語小之謂也此物在鯨中最細小因而名焉[illegible]狀細小其長有五丈喉短而身半以下倍細長近[illegible]處有圓[illegible]些[illegible]亦有圓折而中央倍深如刺鈌

全體淡青色而有白點鈌環文間亦有全環様有半月様有[illegible]蟠様相混雜象上及下脣邊至頷下有短毛如針而上軀粗錯有[illegible]宛如眉狀

Fig. 1. *Kokujira in Geishi, 1760 (from Hawley, 1958)*

various stages of semicircular markings on the body surface. These are thought to be scars left by detached barnacles (*Cryptolepas* sp.). These barnacles embed themselves deeply in all parts of the body as well as the flukes and pectoral fins. When a barnacle detaches, it creates a circular grayish wound which in time becomes white as it heals (Andrews, 1914).

Another drawing of Kokujira (Fig. 2) appears in a scroll appended to "A History of Whaling at Taijiura, Kumano," by the Committee for the Compilation of the History of Whaling at Taijiura (Hashiura, 1969). It is assumed this scroll was made during the early years of Kambun (1661–1673), 100 years before "Geishi" was printed. These two drawings are quite similar, except for the shape of markings on the surface which is shown as pale blue in color. In both there are needle-like white hairs approximately 6 cm long. In the second (Fig. 2), barnacles and lice are shown attached to the body. The positions of blowholes, eye, ear hole, mouth, flippers, navel, genital aperture, anus, and tail flukes are all correctly indicated by arrows.

Kiyonori Otsuki (1773–1850), a famous scholar in the Tokugawa era, left an undated manuscript on whales and whaling entitled "Geishiko (A Draft of a History of the Whale)." It was written perhaps in 1808, but remained unpublished until 1925 when it was printed in a series of various collections in Sendai. In March, 1951 this book was reprinted by the Japan Whaling Association. It is by far the most systematic survey of whales and whaling written in the Tokugawa period (Hawley, 1958).

The author of the "Geishiko" refers to various books on whales and whaling which

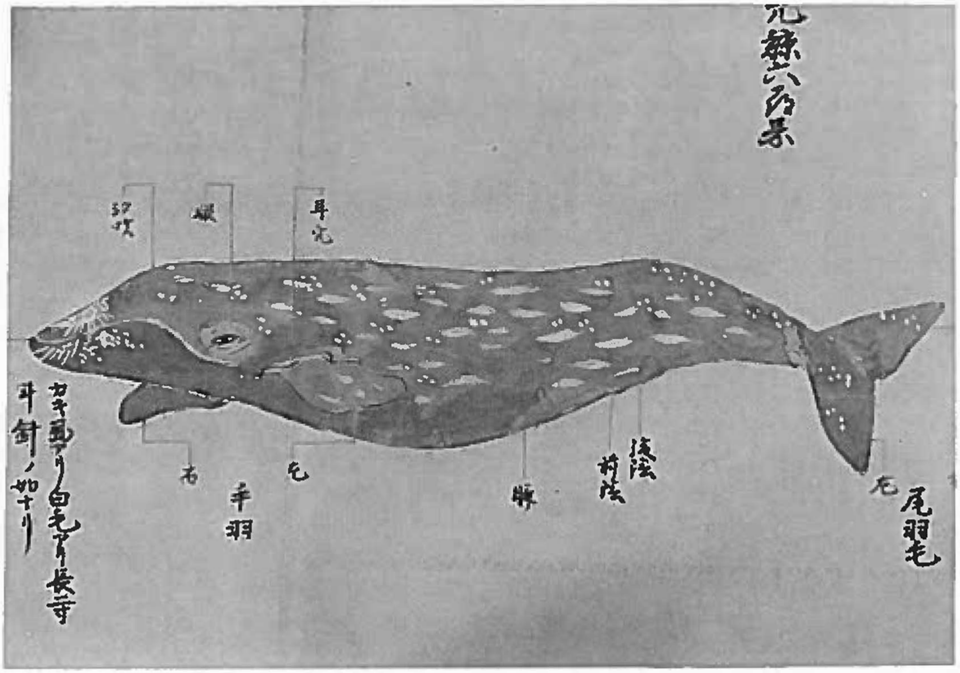

Fig. 2. *Kokujira drawn in 1661–73 (from Hashiura, 1969).*

were then available to him. Kokujira was also called Chikokujira, *chiko* also meaning small. The baleen plates of Chikokujira were described as being white. Two kinds of Kokujira were reported, one called *Aosagi* and the other *Share*. Aosagi was preferred to Share because its oil was white. However, interpretation of this old description became somewhat confused in later years. Andrews (1914) states

> The blubber is thick and fat, and varies in color from red to flesh pink. Because of this the Japanese recognized two kinds of gray whale, the 'Aosaki' (red blubber) and the 'Shirasaki' (white blubber). Although specimens with blubber strongly red, almost white, and of every intermediate shade, were taken during my stay at Ulsan, I could detect no difference, other than those purely individual, between them.

In Andrews' description, *Aosaki* is the same as Aosagi. There is only a slight difference in pronounciation of the two words, and Aosagi means blue heron.

I have been unable to find the names of *Shirasaki* or *Shirasagi* in any of the old books on whales and whaling. The only two kinds of Kokujira named are "Aosagi" and "Share." And, contrary to the above description, the color of blubber in Aosagi is said to be white. Hattori (1887–1888) thought that Share were young animals and Aosagi full-grown adults. This may be the correct interpretation. The individual differences in color of the blubber may be due to the different foods they took, as suggested by Andrews (1914). There is a description (Anonymous, 1890) in which the bigger whales which come from the west are called Aosagi (at Kawajiri). If this statement is correct, Aosagi referred to whales that were migrating from the calving ground to feeding grounds.

Biological Evidence of Occurrences

SUBFOSSIL EVIDENCE

In 1966, both mandibles, some vertebrae, and ribs of a whale were excavated from a depth of 4 m in a sand stratum in Ichikawa city, a neighboring city of Tokyo, during construction of the Ichikawa Telegram and Telephone Office. This stratum contained fossil shells, which were radiocarbon dated to 6000 years BP, or the time of the Jomon Sea Regression. The whale was erroneously identified as the sei whale, *Balaenoptera borealis*. The skeleton was then mounted with an artificial skull, vertebrae, and ribs, and exhibited in the main hall of the Ichikawa Municipal Museum.

In March, 1982 I visited the museum, with Dr. T. Kasuya of the Ocean Research Institute, University of Tokyo, and Mr. H. Kato of the Whales Research Institute and positively identified the specimen to be a gray whale. In gray whales the "lower jaws are massive, wide, and without coronoid processes: their inner surface somewhat concave at the proximal part" (Tomilin, 1967). There was no difficulty with the identification, because these features are very prominent even at a glance (Fig. 3).

Both mandibles of the Ichikawa whale have been broken anteriorly. The straight-line length of the right bone from broken tip to posterior end is 2.22 m. The height is 35

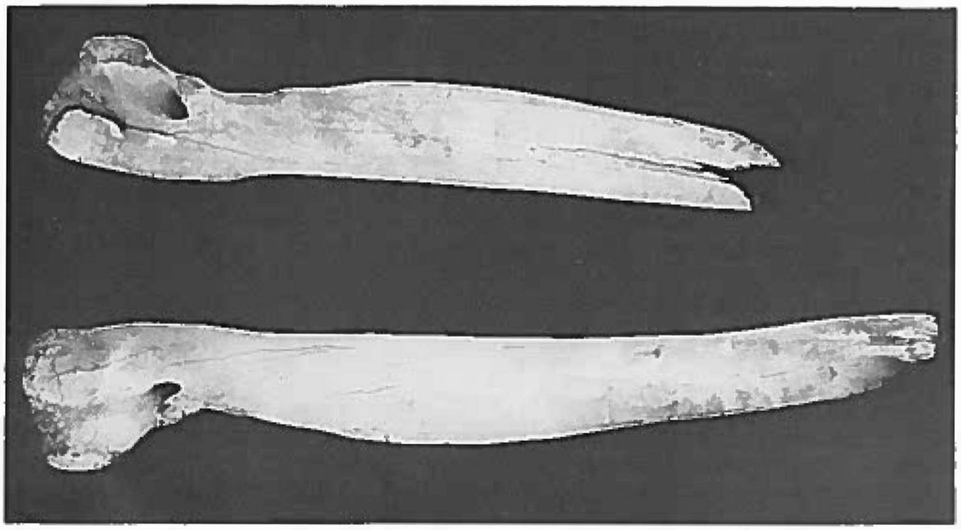

Fig. 3. *Mandibles of the Ichikawa whale (courtesy of the Ichikawa Municipal Museum).*

cm at the articulation, 21.5 cm at the lowest part just in front of articulation, and 29.7 cm at the top of the remaining part. Total length of this mandible is estimated to have been about 2.5 m and the body length of the whale approximately 12 m.

Ichikawa city is situated at the innermost part of the Tokyo Bay. The positive identification of this specimen is direct evidence that gray whales once occurred in the eastern coastal waters of Japan.

RECENT HISTORICAL EVIDENCE

In 1864 two gray whales were taken in the Seto Inland Sea, at Kawanoe, Ehime prefecture, the first on February 20 and the second on February 26. These whales were reported first by Shindo (1968) and then by Omura (1974). It is not necessary to describe them here in detail, but I wish to mention briefly their relationships to Aosagi and Share. Drawings of these whales are kept at the Kawanoe City Library (Figs. 4 and 5).

The first whale is smaller than the second and possibly would have been referred to as Share, although nothing was noted on the drawing (Fig. 4); the second whale (Fig. 5) was labeled as Aosagi. The body surface of the first whale was slightly infested with barnacles. The second whale bears heavy white markings of barnacle infestation, suggesting it was older than the first. A left scapula, possibly from the second whale, has been preserved at Hachiman shrine in the city, presented as Ema in memory of the whaling event (Fig. 6). The scapula of *Rhachianectes* (*Eschrichtius*) is distinctive in being intermediate between the wide, low scapula of *Balaenoptera* and the high, narrower, and more symmetrically fan-shaped scapula of *Eubalaena* (Andrews, 1914). Measurements of

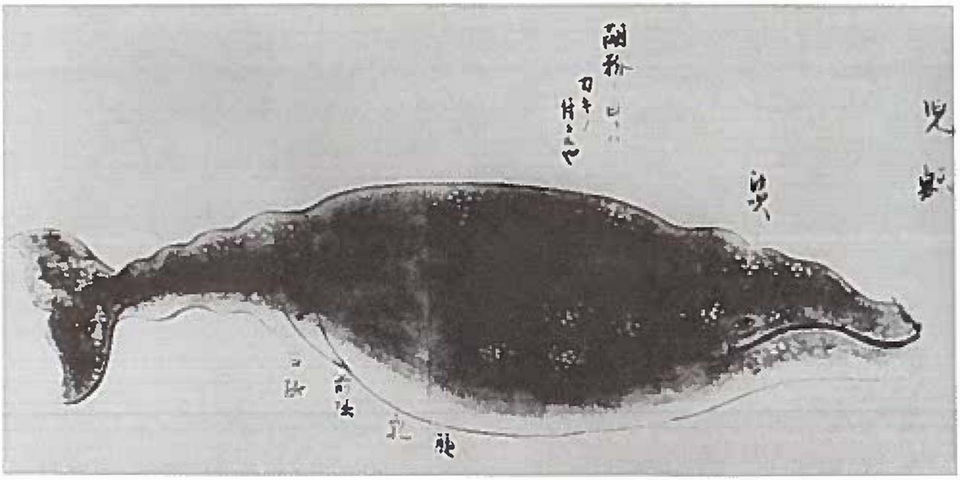

Fig. 4. *Kawanoe whale—first whale (from Omura, 1974).*

the at Hachiman shrine scapula were given by Omura (1974). Greatest breadth and greatest height are 99 and 74 cm, respectively, and the ratio of breadth to height is 1.34.

Omura (1974) thought the nearby waters of Iwaijima in the Seto Inland Sea was a calving ground of the gray whales, which occurred on the south coast of Japan. According to Saito (1977), Engelbert Kaempher, a German traveler and physician, sighted small whales in the waters near Mitajiri on April 30, 1691, while he was returning from a visit to the Shogun's capital of Edo (Tokyo). Mitajiri is close to Iwaijima and not far from Shimonoseki, the western entrance to the Inland Sea. Kaempher referred to these

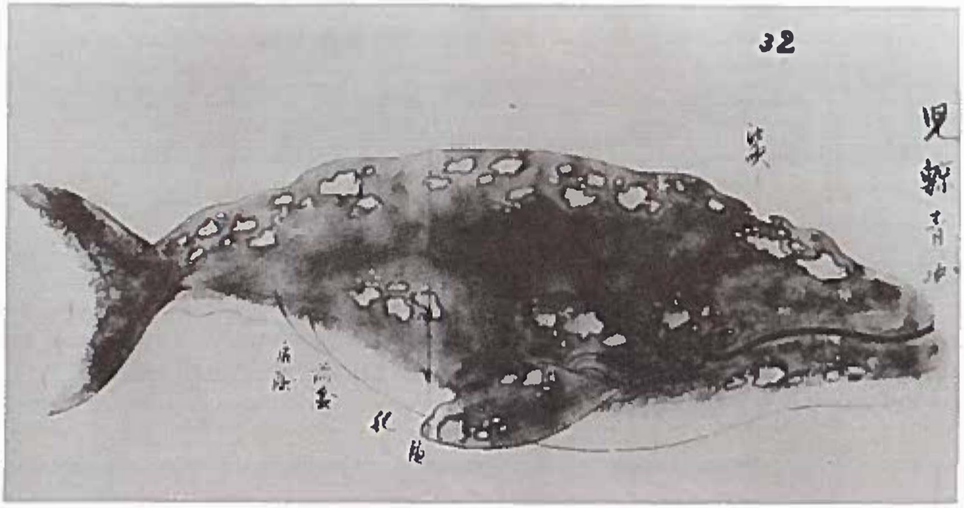

Fig. 5. *Kawanoe whale—second whale (from Omura, 1974).*

Fig. 6. *Left scapula of the Kawanoe whale (from Omura, 1974).*

whales as "Nordcaper," which means right whale, a species not reported from the Inland Sea; he further describes them as small whales. It is possible the whales he sighted were in fact gray whales. Gray whales and right whales have often been confused, even by gunners of modern whale catcher boats.

Nishiwaki and Kasuya (1970) report the accidental catch of a young female gray whale in 1968 at Shingu, Wakayama prefecture (the skeleton of this whale is maintained at Taiji Whale Museum). They also reported the sighting, by a skillful gunner of long experience, of a gray whale in nearby waters around 1959.

Catches of Gray Whales

Net whaling flourished nearly 200 years in the Edo era (1603–1867), during which time gray, right, humpback, and other species of whales were taken. The gray whales were usually taken without nets, because of their relatively smaller size (Taiji, 1937).

Practically no catch statistics exist for Wakayama and Mie prefectures. At Taiji, whaling continued after the Meiji Revolution (1868) until a tragedy occurred in 1878. In that year more than 100 people were killed by a heavy storm while they pursued a right whale accompanied by a calf. This incident was practically the end of old whaling at Taiji.

There remain at Taiji some fragmentary records of the catch. For example, from December 24, 1799 to January 15, 1800, a total of 9 whales was taken, including 1 right, 6 humpback, and 2 gray whales. However, because most of the records were lost by fire or during several floods, it is not clear whether this was an exceptionally good season. This seems to have been a good catch, but further comparison of catch records is not possible.

Whaling on the coast of the Sea of Japan, at Ine, Kyoto prefecture, had been conducted since very ancient times, probably as early as Tenmon (1532–1554). The methods were somewhat different from those used in other places. The village of Ine is located on a small inlet, called Inewan, into which whales occasionally swam. When this happened the fishermen of Ine blocked the entrance of the inlet with nets and then caught the whale using hand harpoons and nets. Catch records of the Ine whaling operation during a period from 1656 to 1913 are available by species (Yoshihara, 1976b). During this time a total of 357 whales, including 167 humpback, 149 "fin" (including minke), and 41 right whales, was taken. No gray whales were taken, evidence that gray whales did not occur on the east side of the Sea of Japan at that time.

Whaling was conducted, however, in several villages on the north coast of Yamaguchi prefecture, including Kayoi in the east and Kawajiri in the west (Tokumi, 1957; Tada, 1978). At Kayoi, at present Nagato city, there is a temple named Koganji where notes are preserved which contain the Buddhist names of each whale taken and from which catches of species have been summarized (Kimura, 1956). Japanese people were given special names from a Buddhist priest when they died, and in this respect the whales were treated somewhat like human beings. The first volume of the Koganji notes is missing, but from remaining volumes catch figures are available for about 50 years, from 1802 to 1850. During this period a total of 308 whales, including 116 fin, 105 humpback, 59 right, and 28 gray whales, was taken. The average catch per year was 6.3 animals; gray whales comprised 9% of the catch.

For Kawajiri, catch statistics arranged by species and by 10-year increments are available from 1699, when whaling was started, until 1888 (Anonymous, 1890). Yearly figures for the 8 years from 1894 to 1901 were given by Tada (1978) (Table I). For a period of 50 years, from 1769 to 1818, only the total number of catches was reported, but catches by species can be compared for the periods 1699 to 1768 and 1819 to 1888. Catches of gray whales increased from 12% in the former period to 16% in the latter. Both figures are greater than proportions of gray whales in catches at Kayoi. Catches of right and humpback whales decreased as those of "fin" whales (again possibly including minke whales) increased, possibly due to decrease of the former two species. Tada (1978) states that no right whales were taken after 1884. Catch statistics at Kawajiri in the later years are given by Tada (1978) for a period from 1894 to 1901. The decline of gray whale catches and the increase of "fin" whale catches during this period are remarkable. Whaling at Kawajiri was virtually terminated in 1902.

In addition to Kayoi and Kawajiri, whaling was conducted at several villages including Mishima (Tada, 1968), a small island about 45 km northwest of Hagi city. Whaling in these villages began around 1680 and lasted until near the end of the nineteenth century. Unfortunately, details of the catches are not available.

On the west coast of Kyushu, whaling was conducted at various places. Otsuki (1808), for example, listed 68 localities. This does not mean, however, that 68 whaling groups existed in Kyushu; rather, it represents the total number of places where whales,

Table IA
Catches of Whales at Kawajiri, Yamaguchi Prefecture: 1699–1888[a]

Years	Gray	Right	Humpback	Fin	Others[b]	Year total
1699–1708	11	29	94	2	7	143
1709–1718	17	17	103	14	9	160
1719–1728	21	29	103	3	9	165
1729–1738	12	31	92	3	2	140
1739–1748	21	26	93	—	—	140
1749–1758	13	20	48	—	—	81
1759–1768	15	14	58	—	1	88
Species totals	110	166	591	22	28	917
Average per year	1.6	2.4	8.4	0.3	0.4	13.1
Percentage	12.0	18.1	64.4	2.4	3.1	100
1769–1778						140
1779–1788						136
1789–1798						117
1799–1808						84
1809–1818						105
Species totals						582
Average per year						11.6
1819–1828	8	19	55	—	37	119
1829–1838	10	29	27	—	72	138
1839–1848	18	48	59	4	—	129
1849–1858	37	23	88	24	—	172
1859–1868	34	2	55	32	7	130
1869–1878	44	4	34	65	—	147
1879–1888	19	3	49	130	—	201
Species total	170	128	367	255	116	1036
Average per year	2.4	1.8	5.2	3.6	1.7	14.8
Percentage	16.4	12.4	35.4	24.6	11.2	100

[a] Anonymous (1890).

[b] Species were not noted.

Table IB
Catches of Whales at Kawajiri, Yamaguchi Prefecture: 1894–1901[a]

Year	Gray	Humpback	Fin	Others	Total
1894	0	3	10	1	14
1895	0	0	4	1	5
1896	4	1	7	1	13
1897	0	4	9	2	15
1898	1	4	10	1	16
1899	0	2	8	0	10
1900	2	1	4	1	8
1901	0	13	3	2	18
Species totals	7	28	55	9	99
Average per year	0.9	3.5	6.9	1.1	12.4
Percentage	7.0	28.3	55.6	9.1	100

[a] Tada (1978).

especially right whales, were taken. These numbers were reduced to only 3 a few years before the turn of the century, due to heavy reduction in numbers of right whales migrating there (Takahashi, 1899).

Whaling in Kyushu also started as a small enterprise using hand harpoons. After the invention of net whaling, this method spread over the west coast of Kyushu, and whaling flourished there more than in any other place (Anonymous, 1980). Whaling in Kyushu was operated by several groups, such as the Nakao group of Yobuko and Ogawajima (Saga prefecture), the Toi group of Iki Island (Nagasaki prefecture), and the Masutomi group of Hirado and Ikitsuki (Nagasaki prefecture). Among them the Masutomi group was the largest. From 1725, the year when the group was formed by Matazaemon Masutomi, to 1874, a total of 21,790 whales was taken (Yoshihara, 1977), a yearly average of 150 whales for all locations combined. The group operated at several locations in Kyushu, and sometimes at Mishima and Kayoi (both in Yamaguchi prefecture) as well. It was said this whaling group employed 3,000 people and about 200 fishing vessels when in operation.

Whaling at Ogawajima survived long after the introduction of modern whaling (Anonymous, 1980). A hut called Yamami, or lookout, was built on the top of a hill. When the watchmen sighted a whale he telephoned to a modern catcher waiting in the port of Yobuko. The catcher then pursued and killed the whale and returned it to the village, where it was processed by the villagers using traditional methods. This type of whaling lasted until 1948.

It is possible that gray whales were also taken in the waters west of Kyushu, but there are no catch statistics by species. Catch figures of whales at Iki Island in the 16 years from 1845 to 1860 are shown in Table II. Whaling from Iki Island was conducted by two whaling groups, Masutomi and Kuramitsu, operating at Katsumoto one season and

Table II
Catches of Whales at Iki, 1845–1860[a]

Year	Katsumoto	Maeme	Year totals
1845	60	78	138
1846	40	45	85
1847	42	32	74
1848	34	40	74
1849	14	11	25
1850	19	19	38
1851	22	19	41
1852	7	14	21
1853	12	4	16
1854	9	20	29
1855	10	14	24
1856	7	7	14
1857	19	Unknown	19
1858	Unknown	7	7
1859	Unknown	7	7
1860	4	7	11
Species totals	299+	324+	623+
Average per year	21.4	21.6	38.9+

[a] Anonymous (1890).

Maeme the next. The catches of whales at Iki decreased after 1849, probably because of the decrease of right whales.

In Tosa (present Kochi prefecture) whaling with hand harpoons dates from the years of Kanei (1624–1643) (Izukawa, 1943), and net whaling from 1683 when it was introduced from Taiji. Two groups of whalers, Ukitsu and Tsuro, operated on the coast of Tosa, splitting their activities between an east and a west whaling ground. There are two peninsulas in Kochi, the Muroto Peninsula in the east and the Ashizuri Peninsula in the west. The east whaling grounds were on the east side (in winter), and west side (in spring) of the Muroto Peninsula. The west ground was on the east side of the Ashizuri Peninsula in both winter and spring.

Each year the Ukitsu whaling group operated in one ground and the Tsuro whaling group on the other, and the two alternated grounds each year. Both groups left good catch records by year, from which general trends of the whaling in Kochi can be detected (Table III).

Table IIIA shows the total catches of whales by the Tsuro group in the years 1693–1712, inclusive. The average catch per year was 20.6 whales, but no species breakdown was available. For the 35 years from 1800 to 1835 (Table IIIB), the Ukitsu group took 959 whales, or 27.4 whales per year. Humpback whales comprise more than one-half of the total catch. In the years 1849 and thereafter (Tables IIIC, D, and E), right whales decreased considerably, while catches of Bryde's, blue, and fin or balaenopterid whales increased. Catches of gray whales appear to have been rather stable.

Table IIIA
Catches of Whales in Kochi Prefecture: Tsuro Group, 1693–1712[a]

Year	Catch	Year	Catch
1693	26	1704	11
1694	14	1705	32
1695	30	1706	16
1696	5	1707	26
1697	23	1708	26
1698	11	1709	26
1699	25	1710	21
1700	21	1711	22
1701	22	1712	22
1702	12		
1703	21		
		Total	412
		Average per year	20.6

[a] Anonymous (1931).

Table IIIB
Catches of Whales in Kochi Prefecture: Ukitsu Group, 1800–1835

Year	Gray	Right	Humpback	Bryde's	Others	Year total
1800	5	2	4	—	1	12
1801	0	1	5	—	2	8
1802	5	2	6	1	3	17
1803	1	4	17	—	—	22
1804	2	4	29	—	1	36
1805	0	11	17	—	—	28
1806	3	3	23	—	1	30
1807	2	5	15	—	—	22
1808	5	5	29	—	1	40
1809	4	11	11	—	—	26
1810	3	2	11	—	—	16
1811	1	7	20	—	—	28
1812	4	7	14	—	—	25
1813	6	5	10	—	—	21
1814	5	8	5	2	2	22
1815	6	3	41	—	—	50
1816	2	4	8	—	—	14
1817	4	5	13	—	—	22
1818	4	8	12	—	1	25
1819	4	3	10	—	6	23
1820	6	7	6	—	1	20
1821	4	5	9	—	5	23
1822	5	10	3	1	1	20

(continued)

Table IIIB (*Continued*)

Year	Gray	Right	Humpback	Bryde's	Others	Year total
1823	5	7	18	—	1	31
1824	3	8	20	—	—	31
1825	3	11	27	—	—	41
1826	1	16	8	—	—	25
1827	4	10	17	—	—	31
1828	2	5	12	—	—	19
1829	4	9	15	—	—	28
1830	7	9	25	—	2	43
1831	6	10	21	—	—	37
1832	7	12	16	1	—	36
1833	6	11	10	—	—	27
1834	7	15	4	—	2	28
1835	8	14	10	—	—	32
Species total	144	259	521	5	30	959
Average per year	4.0	7.2	14.5	0.1	0.8	26.6
Percentage	15.0	27.0	54.3	0.5	3.1	100

[b]Prepared from Yoshihara (1974).

Table IIIC

Catches of Whales in Kochi Prefecture: Tsuro Group, 1849–1865[c]

Year	Gray	Right	Humpback	Bryde's	Others	Year total
1849	4	—	10	3	—	17
1850	8	4	14	4	—	30
1851	6	1	25	—	—	32
1852	5	—	11	1	—	17
1853	5	1	22	—	—	28
1854	5	1	9	5	—	20
1855	8	2	10	2	—	22
1856	5	—	7	3	—	15
1857	2	—	14	1	—	17
1858	9	—	9	3	2	23
1859	6	1	8	1	1	17
1860	5	1	21	—	2	29
1861	9	1	3	1	1	15
1862	10	—	14	2	—	26
1863	6	3	7	5	—	21
1864	7	4	18	1	—	30
1865	1	—	7	3	—	11
Species total	101	19	209	35	6	370
Average per year	5.9	1.1	12.3	2.1	0.4	21.8
Percentage	27.3	5.1	56.5	9.5	1.6	100

[c]Prepared from Anonymous (1937).

Table IIID
Catches of Whales in Kochi Prefecture: Tsuro Group, 1874–1896[d]

Year	Gray	Right	Humpback	Bryde's	Others	Year total
1874	9	2	4	4	2	21
1875	5	—	5	2	—	12
1876	4	1	6	2	4	17
1877	5	3	6	—	2	16
1878	5	—	14	1	1	21
1879	7	—	5	2	—	14
1880	9	2	13	3	1	28
1881	4	2	—	1	3	10
1882	8	7	9	4	—	28
1883	3	—	1	3	3	10
1884	9	—	10	3	2	24
1885	2	1	2	1	1	7
1886	2	1	11	7	1	22
1887	3	1	5	2	5	16
1888	5	1	8	4	3	21
1889	1	—	2	—	3	6
1890	1	—	7	2	2	12
1891	2	2	3	4	3	14
1892	3	—	3	8	2	16
1893	2	—	—	1	4	7
1894	4	—	7	2	8	21
1895	4	—	4	3	4	15
1896	2	—	9	13	2	26
Species total	99	23	134	72	56	384
Average per year	4.3	1.0	5.8	3.1	2.4	16.7
Percentage	25.8	6.0	34.9	18.7	14.6	100

[d] Anonymous (1937).

Table IIIE
Catches of Whales in Kochi Prefecture: Ukitsu Group, 1875–1896[e]

Year	Gray	Right	Humpback	Bryde's	Others	Year total
1875	1	1	2	4	3	11
1876	2	—	6	5	4	17
1877	11	—	19	3	—	33
1878	1	6	4	4	3	18
1879	7	3	9	2	1	22
1880	6	1	2	8	6	23
1881	5	2	10	5	1	23
1882	3	—	4	2	3	12
1883	3	1	7	3	—	14
1884	1	2	1	2	6	12
1885	3	2	5	4	5	19

Table IIIE (*Continued*)

Year	Gray	Right	Humpback	Bryde's	Others	Year total
1886	1	—	6	3	10	20
1887	4	—	13	4	5	26
1888	1	—	6	4	4	15
1889	2	—	4	7	2	15
1890	1	—	—	4	3	8
1891	1	—	9	—	5	15
1892	1	1	1	3	2	8
1893	4	1	3	1	4	13
1894	1	1	3	4	1	10
1895	3	—	6	5	3	17
1896	2	—	6	4	7	19
Species total	64	21	126	81	78	370
Average per year	2.9	1.0	5.7	3.7	3.5	16.8
Percentage	17.3	5.7	34.0	21.9	21.1	100

[e]Shibusawa (1939).

Discussion and Conclusions

Except for a few stragglers, gray whales do not occur in the coastal waters of Japan at present. Prior to the turn of the century, however, they were found in two regions, one on the Pacific side of Japan, from Tokyo Bay to Kochi prefecture, and the other on the west side of Japan off Kyushu, including the north coast of Yamaguchi prefecture. This conclusion is supported by subfossil mandibles excavated from Ichikawa city, old books on whales and whaling, and catch statistics of old whaling operations in the Edo era (1603–1867). The whales in these two regions may represent different populations of gray whales. The latter (the Kyushu group) is clearly a portion of the Korean stock. Distribution of the two populations in the waters off Japan and Korea is shown in Fig. 7. The two populations may have intermingled in the Seto Inland Sea. If so, then both populations belong to the Korean stock.

In summer, the Korean stock of gray whales occupies, or at least formerly occupied, the northern Okhotsk Sea (Rice and Wolman, 1971). It is not clear whether or not the gray whale population occurring off the south coast of Japan also spends the summer in Okhotsk Sea mingling with the Korean stock. Bowen (1974) states that the young female gray whale accidentally taken in 1968 at Shingu (Nishiwaki and Kasuya, 1970) resembled members of the California stock in morphological features and should be regarded as a stray from the Bering Sea. There still exists the possibility, however, that the two populations occurring in the coastal waters of Japan intermingle with each other in the Seto Inland Sea.

The annual catch of gray whales in Kochi prefecture in the days of net whaling was rather small (Table III). The largest catch was 11 in 1877 by the Ukitsu group; the yearly

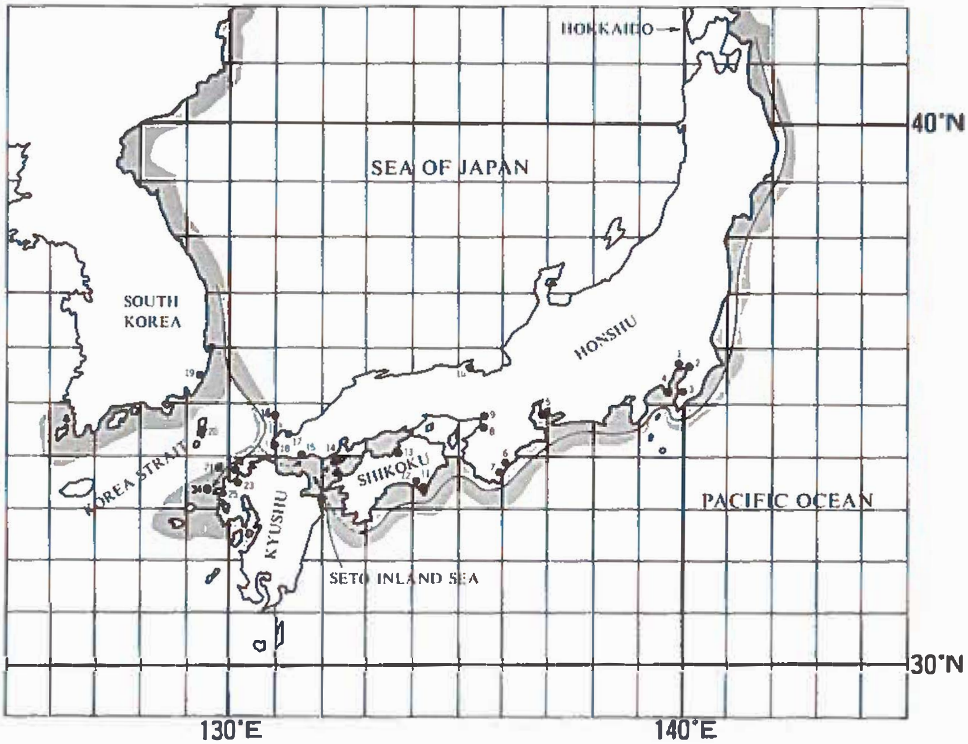

Fig. 7. *Map showing the distribution of gray whales in the coastal waters of Japan and Korea. Place names appearing in the text are indicated by numerals as follows: (1) Tokyo, (2) Ichikawa, (3) Katsuyama, (4) Misaki, (5) Morosaki, (6) Taiji, (7) Koza, (8) Sakai, (9) Osaka, (10) Ine, (11) Tsuro, (12) Ukitsu, (13) Kawanoe, (14) Iwaijima, (15) Mitajiri, (16) Mishima, (17) Kayoi, (18) Kawajiri, (19) Ulsan, (20) Tsushima, (21) Iki, (22) Ogawajima, (23) Yobuko, (24) Ikitsuki, (25) Hirado. Solid arrow, migration routes and area of distribution of Gray whales; broken arrow, movements uncertain.*

average was 2.9–5.9, and there were no remarkable differences between the two whaling groups or among different years. The total yearly catch of gray whales by the two groups in Kochi prefecture is estimated to have been around 10 whales. This suggests gray whales occupied a less important position than right and humpback whales.

Catch figures of gray whales in Wakayama and Mie prefectures are not known. Presumably gray whales were taken in numbers such as in the Kochi prefecture. If one assumes that equal numbers were taken in each of these prefectures, then the total catch of gray whales from the population would have been 30 per year. The catch of gray whales from this population appears to have been rather stable (Table III), suggesting that the catch rate from this population was not high.

The catch of gray whales at Kawajiri, Yamaguchi prefecture during the period of 1699–1768 totaled 110 whales, or an average of 1.6 whales per year (Table I). In the third period, 1819–1888, the corresponding figures are 170 total and 2.4 whales per year, indicating an average increase in take of 0.8 whales per year. These catches are very low compared with the corresponding figures in Kochi prefecture. For the period 1894–1901, the average catch per year was 0.9, less than in previous years. Kimura (1956) also shows a reduction in gray whale catch at Kayoi after 1831.

It is not known how many gray whales were caught on the west coast of Kyushu. It is assumed, however, these catches were far more dependent on availability of right, humpback, and fin whales, as in Kawajiri and Kayoi, and that gray whales were caught only secondarily to the whaling there. It is assumed as many as 20–30 gray whales were taken per year but the catch of gray whales decreased towards the end of net whaling around 1900 and these stocks were finally extirpated.

This reduction does not necessarily mean a reduction of the Korean stock. Mizue (1951) reports heavy catches of gray whales at Ulsan, Korea after 1910. Therefore, the decrease of gray whales migrating to the coast of Yamaguchi and to the west coast of Kyushu may have resulted in a change in migration route.

Modern-type whaling in Japan commenced in 1898, when the first catcher Hokamaru, built of wood, caught three whales (Akashi, 1910). After that year, whaling operated first on the east coast of Korea, the west coast of Kyushu, and the south coast of Japan, and then shifted to the northeast coasts of Japan and Hokkaido. As pointed out by Mizue (1951), only a few gray whales were taken during modern whaling, except in Korea and Tsushima. Omura (1974) speculated the gray whale population on the Pacific side of Japan was driven from its calving ground in the Seto Inland Sea sometime prior to this century by the increase in boat traffic and industrial development on the coast. It now appears this matter is more complicated and that additional material is needed to support firm conclusions.

Summary

Prior to the turn of the century, two populations of gray whales migrated to the coastal waters of Japan, one to the southern coast of Hokkaido and Honshu and the other to the west coast of Kyushu via the north coast of Yamaguchi prefecture. The former migrated along the east coast of Japan from the north and entered the Seto Inland Sea, the supposed calving ground for this population. The latter, considered to be a portion of the Korean stock, migrated along the east coast of Korea and then to southwest Honshu and northwest Kyushu. Intermingling of the two populations in the Seto Inland Sea cannot be denied.

The annual catch of gray whales in the days of net whaling (1675–1890) was approximately 30 whales from the former population and 20–30 from the latter. Virtually no gray whales, however, have been observed in the waters around Japan since about 1898 when modern-type whaling was introduced.

The southern coast population was probably driven from the Inland Sea sometime prior to this century due to increased industrial development and boat traffic on the coast. The matter is complicated, however, and additional material is needed before final conclusions can be drawn.

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灰鲸在中国近海的分布*

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灰鲸（*Eschrichtius gibbosus* Erxleben 1777）现仅存于北太平洋，曾因各捕鲸国滥捕而几近绝灭，是最早受到保护的鲸种之一。东太平洋群体，经数十年的保护，资源量已恢复到一万头左右。但沿亚洲侧洄游的西太平洋群体，资源仍未有恢复迹象，尚亟待保护。对中国近海的灰鲸只有过少量报道。本文根据作者在海上的实际观察和对南、北方重点渔区的数次调查，就灰鲸在中国近海的分布及洄游探讨如下。

一、骨　　骼

原大连展览馆曾收藏1具灰鲸骨骼（♂），系1949年在辽宁黄海岸的搁浅鲸，可惜骨骼已被丢失。浙江省博物馆的1具灰鲸骨骼（♀）系1933年收藏的，种名长期被误植，1977年经作者订正，并调查了当时运输和解剖鲸体的过程，推断该标本可能采自浙江近海。另1具骨骼保存在广东省广州市文化公园水产馆，1954年采自雷州半岛徐闻县的外罗港，经作者鉴定为灰鲸。这3具骨骼证明灰鲸在我国南、北方近海都有分布。3具标本的体长都在12米以上，均为成体。

从表1中看出，浙江省博物馆和广州的标本颅宽皆为颅长的42.3%；朝鲜东海岸所获标本体长12.50米，颅宽为颅长的43.2%（Andrews, 1914），相比差别不太大。从头骨照片看，Nishiwaki 和 kasuya 描述的日本标本的鼻骨前端边缘成凸形，浙江省博物馆标本的鼻骨（图1）同朝鲜标本近似，两块鼻骨的前缘均稍成凹形，广州标本的鼻骨损缺。从侧面看，朝鲜和日本标本的上枕骨向后的坡度都很大，同广州标本大体一样；但浙江省博物馆标本的上枕骨形态，由顶部开始向后微斜，继而骤然下垂，使头骨后部形成陡壁（图3），这些不同可能是属于个体上的差异。

浙江博物馆标本的椎式为$C_7+D_{13}+L_{13}+Ca_{23}=56$。大连1949年的标本和广州标本的胸椎数均为13。而大连1960年的标本的胸椎数为14（王丕烈，1978）。Andrews（1914）记述的朝鲜标本，Nishiwaki & Kasuya（1970）记述的日本标本的椎式皆为$C_7+D_{14}+L_{12}+Ca_{23}=56$。说明胸椎和腰椎数有个体差异。通常记述灰鲸的7块颈椎完全分离（西胁，1965，1970；Томилин 1957，1962），但作者检查浙江博物馆和广州标本的第2和第3颈椎的椎弓及较小的棘突愈合在一起，仅椎体分离（图1）。浙江博物

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* 承浙江省博物馆、广州市水产馆、广东省徐闻县水产局等单位大力支持，谨致谢意。

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表1　灰鲸头骨的测量

测量部位	浙江博物馆		广州水产馆		测量部位	浙江博物馆		广州水产馆	
	毫米	%	毫米	%		毫米	%	毫米	%
颅全长	2790	100	2970	100	枕髁宽　左	131	5.1		
颅宽	1180	42.3	1255	42.3	枕髁宽　右	124	4.4		
吻长	1945	69.7	1920	64.6	两枕髁外距	335	12.0	320	10.8
吻基部宽	645	23.1	670	22.6	枕骨大孔高	101	3.6		
吻中部宽	420	15.1	395	13.3	枕骨大孔宽	69	2.5		
眶间宽	930	33.3	960	32.3	翼骨长　左	420	15.1	410	13.8
眶前突间宽	900	32.3			翼骨长　右	430	15.4	470	15.8
上颌骨长　左	2232	80.0	2350	79.1	翼骨宽　左	155	5.6	175	5.9
上颌骨长　右	2158	77.3			翼骨长　右	144	5.2	185	6.2
前颌骨长　左	2390	85.7			两翼骨后端外距	380	13.6	400	13.5
前颌骨长　右	2425	86.9			下颌骨外曲线长　左	2540	91.0	2690	90.6
鼻骨长	425	15.2			下颌骨外曲线长　右	2495	89.4	2610	87.9
两鼻骨前端宽	207	7.4			下颌骨直线长　左	2470	88.5	2540	85.5
犁骨长	1765	63.3	1840	62.0	下颌骨直线长　右	2480	88.9	2570	86.5
犁骨后端宽	128	4.6	137	4.6	下颌骨中部高　左	313	11.2	315	10.6
额骨眶板宽	235	8.4			下颌骨中部高　右	325	11.6	325	10.9
枕髁高　左	199	7.1	140	4.7	下颌骨冠状突处高左	374	13.4	400	13.5
枕髁高　右	210	7.5	170	5.7	下颌骨冠状突处高右	382	13.7	430	14.5

图1　灰鲸的颈椎
A. 侧面　　B. 背面

馆标本骨骼全长11.48米，最后1个尾椎缺失。颈椎为脊柱全长5.5%，胸椎为21.3%，腰椎为32.4%，尾椎为40.8%。

二、分布、洄游

北太平洋的灰鲸分东、西2个群体。西太平洋群体，也称朝鲜群体。夏季在鄂霍次克海栖息索饵、冬季已知它们在朝鲜南部水域产仔。(Andrews, 1914; Mizue, 1951)。日本的濑户内海过去曾是灰鲸的一个生育场所。（Omura, 1914; Shindo, 1975）。东太平洋群体的个别灰鲸可能来到西太平洋群体的所在水域内（Nishiwaki and Kasuya, 1970)。

西太平洋灰鲸群体过去主要渔场在朝鲜东海岸，西海岸的猎捕量只占0.4%(Mizue, 1951）。说明游到中国海区的数量甚少。有的学者曾认为该群体可能灭绝（Mizue, 1951, Bowen, 1974)。但南朝鲜1967—1975年还继续捕获到（Brownell and Chun, 1977），证明该群体尚未灭绝。

在黄海由日本捕获的灰鲸，1917、1918和1922年各2头，1929年1头（笠原昊，1950），其中1922年的2头获自黄海北部。而后黄海北部曾多次发现，1949年9月中旬在辽宁省金县黄海岸的二道城子海边搁浅1头，1958年6月27日在山东烟台近海发现2头，1960年4月30日在辽宁省长海县的大长山岛后海发现1头，同年7月末在渤海海峡的隍城岛附近发现1头（王丕烈，1976，1978），此后十余年来未再发现。直至1977年6月长海县王家岛的渔民在该岛近海又发现1头；1979年1月长海县大长山岛的渔民在该岛后海再发现1头，该鲸在此处滞留10余天才离去。这些记录说明，经朝鲜东海岸洄游的灰鲸，有少量成年鲸沿朝鲜西海岸北上至黄海北部，尤以辽宁省的大长山岛后海发现次数较多。因此，灰鲸进入我国海洋岛渔场和烟威渔场并非偶然现象，为其向南洄游的延续。

浙江省博物馆的1具鲸骨，可为灰鲸游入我国东海近岸的凭证。

福建省及广东省在建国以前没有发现或捕获灰鲸的记载。台湾省缺少确切记录(杨鸿嘉，1964）。经作者数次深入重点渔区调查，确认广东省惠阳地区大亚湾内1954年春季搁浅1头；雷州半岛的徐闻县外罗港1949年曾搁浅1头，1953年春季发现4头，1954年春季发现1头，此后在该水域未再发现。另据徐闻县外罗港有经验的渔民介绍，1960年曾在海南岛东岸的铜鼓渔场（19°—20°N）发现过灰鲸。在五十年代初期广东沿海发现的记录远比北部黄海多，且又是在接近20°N线海域内发现的较多。 Fin whale

五十年代初期在我国近海发现较多的灰鲸，同当时东、黄海长须鲸资源得到恢复有类似原因，即由于长期停止捕鲸，各种鲸都得到生息的时机，而几将灭绝的灰鲸也有所增加。

浙江省博物馆1933年得的灰鲸标本，怀有将分娩的胎儿。广州市水产馆保存1灰鲸幼体的剥制标本，系1954年春季采自惠阳地区大亚湾。1953年春季在徐闻县外罗港发现的灰鲸，有2对母仔鲸伴游。据此分析，广东省海域也是灰鲸的生育区。

在《广东新语》（屈大钧，1680）中曾记述：“海䲡长者亘百里，背常负子，蛋人辄以长绳系铊飞刺之，候海䲡子斃，拽出沙潭，取其脂货，至万钱”。此处海䲡系指大型鲸类。在粤东地区的平海大嘴岛，渔民相传约百年前曾在近岸捕鲸。联系五十年代初

测广东近岸发现的灰鲸，根据其习性极近沿岸，并栖游于岩礁地带，原始方法即能捕获。因此估计过去在该地区发现的主要为灰鲸，在灰鲸种群的兴旺时期游来广东沿海的数量是较多的。

Scammon（1874）认为沿美洲侧洄游的灰鲸分布南限到达20°N。Mizue（1951）记载沿亚洲侧洄游的灰鲸，以往捕获水域南达34°N。但就 Shindo（1970，1975）对日本濑户内海灰鲸的研究，及Nishiwaki 和 Kasuya（1970）对日本太平洋岸获灰鲸的报道，西太平洋群体的分布水域向南达到了 32°N。根据作者的调查，过去在中国海区可能偶有个别灰鲸超越20°N线，向南达到海南岛的东部沿海（图２）。

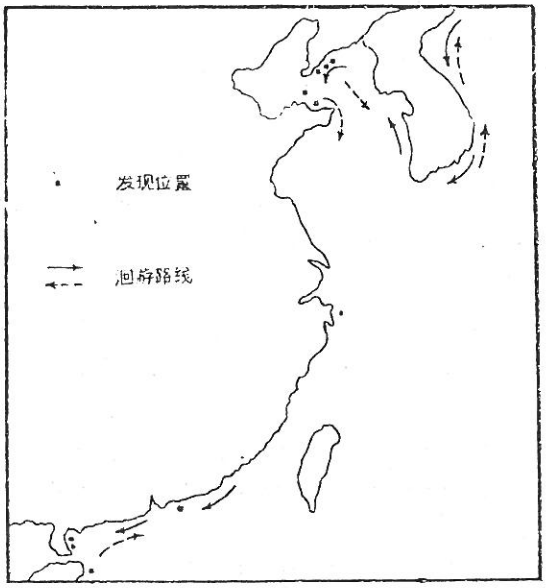

图２ 中国近海灰鲸洄游分布示意图

关于灰鲸在中国南部近海的洄游路线，尚缺乏完整资料。虽然由鄂霍次克海南下的灰鲸，以往有些沿日本太平洋侧沿岸洄游，且认为日本濑户内海曾是个生育场所，但进入二十世纪，濑户内海的灰鲸已绝迹，在太平洋侧的日本九洲南岸以及琉球群岛水域未见记录，我国台湾省也无确切记录。故我国广东沿岸所发现的灰鲸来自日本太平洋侧的可能性甚少。因此，广东沿岸的灰鲸同我国北方海区的有联系，即有少量的灰鲸沿东海中国海岸继续南下，到达广东省沿岸水域进行生育。

灰鲸的洄游规律性及其极近沿岸浅水域栖息的习性，使它易被捕杀。我国沿海在七十年代虽仍偶有发现，但西太平洋群体至今远未得到恢复，需要继续加强保护，为之创造生息的条件。我国颁布的《水产资源繁殖保护条例》，已将灰鲸列为保护对象。1980年我国已成为国际捕鲸公约签字国之一，今后我国也无意进行商业性捕鲸。因此呼吁西北太平洋沿岸国家为保护灰鲸继续做出贡献。

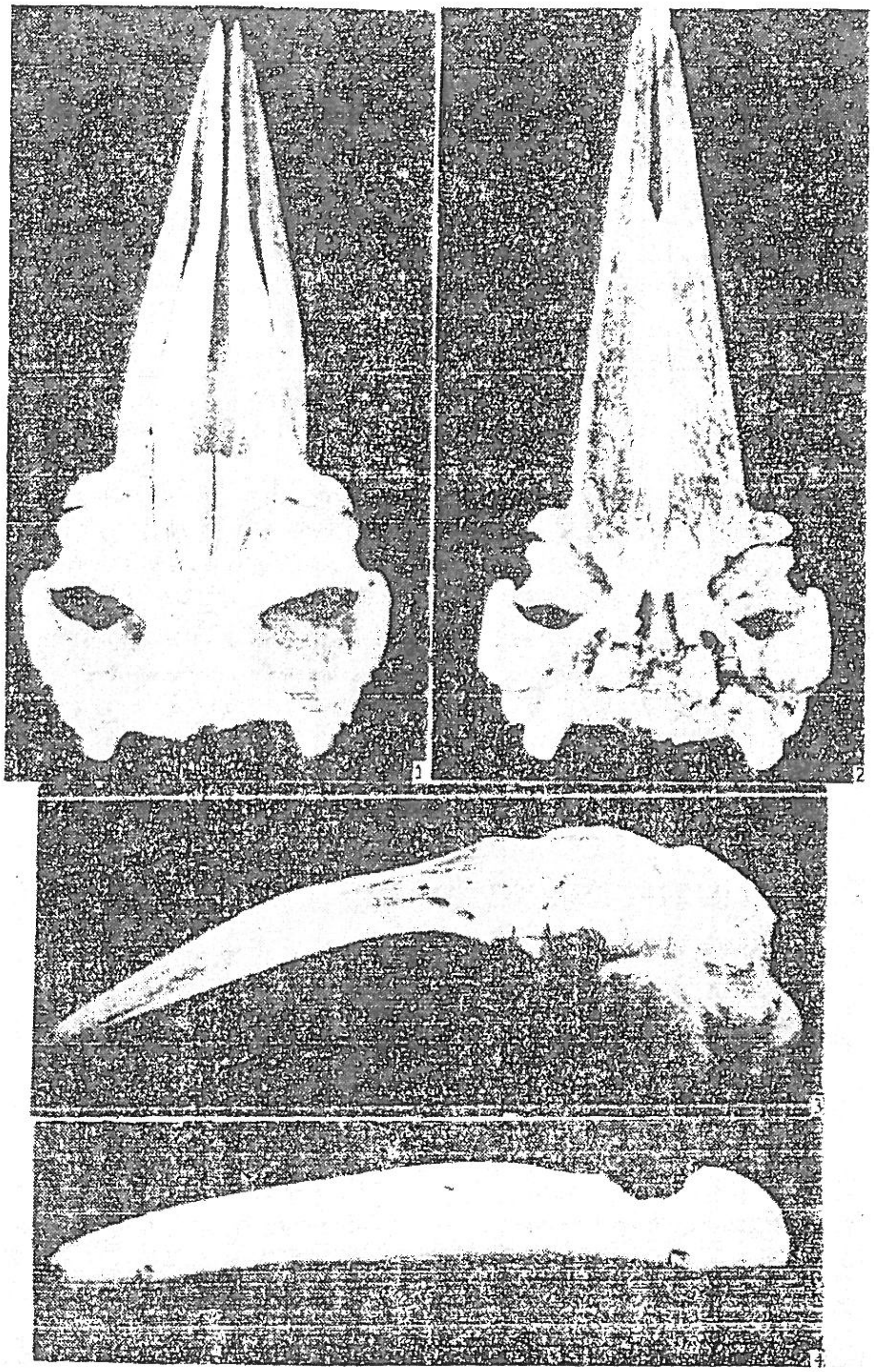

图3　灰鲸的头骨

1.背面　2.腹面　3.侧面　4.下颌骨

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外文摘要 (Abstract)

DISTRIBUTION OF THE GRAY WHALE(*ESCHRICHTIUS GIBBOSUS*) OFF THE COAST OF CHINA

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Three skeletons of the gray whales have been obtained off Liaoning, Zhejiang and Guangdong Province in the Yellow Sea, the East China Sea and the South China Sea respectively. It is believed that some individuals of the western Pacific stock migrated through the waters off the east coast of China, and entered the calving grounds in the coastal waters of Guangdong Province in former times, these calving grounds are possibly in the Daya Bay and Wailuo Harbour. Occasionally, a few individuals probably reached as far south as 20°N in the adjacent waters of the east coast of Hainan Island.

REPORT ON THE PHOTOGRAPHIC COMPARISON OF THE WESTERN AND MEXICAN GRAY WHALE CATALOGUES.

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ABSTRACT

Photographs of 217 identified gray whales obtained from the Sakhalin Island, Russia feeding grounds were compared with 6,546 photo-identified individuals from the Baja California Peninsula, Mexico breeding lagoons to identify matches between these two populations. A total of 13 matches of individuals were found, including six males, five females and two of unknown sex. Twelve whales had sightings prior to and after to their respective sighting in Mexico. Twelve whales were observed in Laguna San Ignacio and one in Laguna Ojo de Liebre. Ten of the 13 whales were photographed in Mexico only in one year and the other 3 in two years. Twelve whales were sighted in Sakhalin in the summer of 2011. Eleven whales were sighted in consecutive seasons, eight of them in three consecutive seasons (summer-winter-summer), three in two seasons (summer-winter), and four in two seasons (winter-summer). Three whales were sighted the same day in Laguna San Ignacio suggesting that these animals were traveling in association with each other. Four females with calves were sighted in the winter in Mexican waters and in the next summer off Sakhalin, three of them without calves suggesting that these females had either separated from their calves or that their calves did not survive. The time between the last sighting in one season and the first one in the next season was $\bar{x}=195.4$ days (n=11, 141-255) during the summer-winter migration, and $\bar{x}=150.9$ days (n=12, 131-213) during the winter-summer migration. The matches made between whales sighted off Sakhalin and the Mexican Pacific are the first results of the multinational collaboration "PACIFIC WIDE STUDY ON POPULATION STRUCTURE AND MOVEMENT PATTERNS OF NORTH PACIFIC GRAY WHALES" initiated under the coordination and support of the International Whaling Commission last year.

INTRODUCTION

Recent results of genetic and photographic identification comparisons between western and eastern North Pacific gray whales (see IWC, 2011) suggest a mixing of these populations during the winter reproductive season, and illustrate the great conservation and management importance of a more comprehensive examination of gray whale movement patterns and population structure in the North Pacific. The Scientific Committee recommended that a collaborative Pacific-wide study be developed under the auspices of the IWC, recognising that *inter alia* this will contribute to the Committee-endorsed Conservation Plan for western North Pacific gray whales and incorporate previous recommendations made by the Committee. Such a study will involve collaborative analysis and sharing of existing data as well as the collection of new data. This report summarizes the results of the "(Phase 1) photo-identification project". The purpose of this project was to undertake a comparison of two western gray whale catalogues from Sakhalin Island, Russia with the Mexican gray whale catalogue.

METHODS

The comparison was done based on two catalogues of photo-identified gray whales from Sakhalin Island and one catalogue of gray whales from Laguna San Ignacio and Laguna Ojo the Liebre on the west coast of the Baja California Peninsula, México.

The Sakhalin catalogues

The first step was to compare the two catalogues available at that moment:

1) The Russia-US catalogue (2012).

Burudin, A. M., Weller, D., Sychenko, O., and Bradford, A. 2012. *"WESTERN GRAY WHALES OFF SAKHALIN ISLAND, RUSSIA: A CATALOG OF PHOTO-IDENTIFIED INDIVIDUALS".*
205 individuals. Period 1994-2011

2) The IBM catalogue.

Tyurneva, Y. O. y Yakovlev, Y. M. 2010. "THE WESTERN PACIFIC GRAY WHALES OF SAKHALIN ISLAND 2002-2008, LEARING ABOUT A POPULATION OF WHALES THROUGH PHOTOGRAPHS".
165 individuals. Period: 2002-2008

As result of these comparisons 217 photo- identified gray whales from Sakhalin were used in the comparison with the Mexican catalogue. All are represented by the right-side dorsal flank and 215 are associated with the left-side dorsal flank

The Mexican catalogue

This catalogue includes 6,546 gray whales. 5366 photo-identified in Laguna San Ignacio between 1993 and 2011, and 1180 in Laguna Ojo de Liebre (Scammon´s Lagoon) between 2001 and 2003. Of the 6,546 whales in the catalogue 5,890 are represented by a right-side of the dorsal flank image and 1,837 were associated with a left-side dorsal flank image (Table 1).

Table 1. Number of photo-identified gray whales in the Mexican catalogue.
Laguna Ojo de Liebre = LOL, Laguna San Ignacio = LSI.

year	Total photo-id whales	Right and left sides	Only right side	Only left side	Lagoon
2001	398	0	398	0	LOL
2002	462	0	462	0	LOL
2003	320	0	320	0	LOL
1996	157	0	155	2	LSI
1997	310	0	310	0	LSI
1998	392	0	392	0	LSI
1999	253	0	253	0	LSI
2000	448	0	448	0	LSI
2003	247	0	247	0	LSI
2005	438	18	420	0	LSI
2006	249	22	226	1	LSI
2007	495	150	217	128	LSI
2008	358	114	137	107	LSI
2009	662	286	238	138	LSI
2010	750	250	319	181	LSI
2011	607	341	167	99	LSI
Total	**6546**	**1181**	**4709**	**656**	

RESULTS.

The Sakhalin to Mexico catalog comparison resulted in a total of 13 confirmed matches of individuals, including six males, five females and two of unknown sex. Twelve whales had sightings prior and after to their respective sighting in Mexico. Twelve whales were observed in Laguna San Ignacio and one (#3) in Laguna Ojo de Liebre. Ten of the 13 whales were photographed in Mexico only in one year and the other 3 in two years. Twelve whales were sighted in Sakhalin in the summer of 2011(Table 2).

Twelve whales were sighted in consecutive seasons, eight of them in three consecutive seasons (summer-winter-summer), three in two seasons (summer-winter), and four in two seasons (winter-summer). Whale #2, male, was sighted in summer-winter (2006-2007), and summer-winter-summer (2009-2010); similarly whale #9, female, was sighted in summer-winter-summer (2006-2007), and in the winter-summer (2011) (Table 3).

The whales #5, #6 and #12 were sighted the same day, February 24 2006, and whale # 20 was sighted two days later in Laguna San Ignacio. The whales #5 and #12 were in the same group and #6 in a different group, suggesting that these animals were traveling in association with each other (Table 3).

Four females with calves were sighted in the winter in Mexican waters and in the next summer off Sakhalin, three of them without calves (Table 3), suggesting that these females had either separated from their calves (e.g. weaned) or that their calves did not survive (e.g., due to predation).

The time between the last sighting in one season and the first one in the next season was $\bar{x}=195.4$ days (n=11, 141-255) during the summer-winter migration, and $\bar{x}=150.9$ days (n=12, 131-213) during the winter-summer migration. The shorter time was of the whale #13, of unknown sex, with 131 days followed by the whale #4, a male, with 139 days, and the whales #8 and #11, mothers with calves, with 144 and 143 days respectively (Table 3).

Table 2. Sighting summary information for 13 gray whales matched between Sakhalin and Mexico. * = With calf.

	Russia-US		**IBM**		**UABCS**		**Russia-US**
#	**No.**	**Years**	**No.**	**Year(s)**	**No.**	**year(s)**	**Sex**
1[1]	20	97,02-04,07,09,11	80	06,07	06-0209-D-LSI	06	M
2[1]	52	98,99,00,01,02, 03,05,06,08,09,10,11	26	02,05,08	07-0328-I-LSI, 10-0639-D-LSI	07,10	M
3	27	95,97,98,99,00,01,02, 04,05,06,07,09,10,11	2	02,05	02-0336-D-LOL	02	M
4	91	00,05,07,08,09,11	137	07	11-0273-D-LSI	11	M
5	28	97,98,99,00,01,03,04, 05,06,07,09,11	59	05,07	06-0131-D-LSI	06	M
6	69	98,00,01,02,03,04, 08,09,11	113	04,05,07	06-0176-D-LSI	06	M
7[1]	42	97,98,99,00,03, 04,05,11	90	03,05	09-0696-D-LSI-M	09*	F
8[1]	63	97,98*,00,01,02 05,07,08,10,11*	47	03,05,07	08-107-I-LSI-M	08*	F
9	103	01,02,04,05,11	119	05,06,07	07-0457-D-LSI, 11-0526-D-LSI-M	07,11*	F
10	29	97,98,00,01,02,03,04, 05,07,09,10,11	28	03,05	10-0739-D-LSI-M	10*	F
11	85	99,01,02,04,05,08*,09, 11	51	04,05,07	08-0051-D-LSI-M, 10-0396-D-LSI	08*,10	F
12	94	00,03,04,05,07,11	57	03,06,07,08	06-0132-D-LSI	06	U
13			166	09	09-0506-D-LSI	09	U

[1] Reported in Weller *et al.* 2011

Table 3. Gray whales sighted in consecutive seasons.

#	Sakhalin (Summer) RusUS	BMI	Mexico (Winter) UABCS	Sex	Summer	Days	Winter	Days	Summer
1	20	80	06-0209-D-LSI	M			26-Feb-2006	213	27-Sep-2006
2	52	26	07-0328-I-LSI, 10-0639-D-LSI	M	22-Aug-2006 07-Aug-2009	181 217	20-Feb-2007 13-Mar-2010	 177	 06-Sep-2010
3	27	2	02-0336-D-LOL	M	31-Jul-2001	217	06-Mar-2002	150	03-Aug-2002
4	91	137	11-0273-D-LSI	M			01-Mar-2011	139	18-Jul-2011
5	28	59	06-0131-D-LSI	M	07-Aug-2005	200	24-Feb-2006	179	22-Aug-2006
6	69	113	06-0176-D-LSI	M	23-Ags-2005	184	24-Feb-2006		
8	63	47	08-107-I-LSI-M	F	09-Sep-2007°	201	29-Mar-2008*	144	20-Aug-2008°
9	103	119	07-0457-D-LSI, 11-0526-D-LSI-M	F	17-Oct-2006”	141	08-Mar-2007° 08-Mar-2011*	189 170	13-Sep-2007” 25-Aug-2011°
10	29	28	10-0739-D-LSI-M	F	07-Aug-2009°	219	14-Mar-2010* 29-Mar-2010*	176	06-Sep-2010°
11	85	51	08-0051-D-LSI-M, 10-0396-D-LSI	F	16-Sep-2007” 24-Jul-2009	163 255	26-Feb-2008* 06-Mar-2010*	143	19-Jul-2008*
12	94	57	06-0132-D-LSI	U	06-Sep-2005	171	24-Feb2006	203	16-sep-2006
13		166	09-0506-D-LSI	U			04-Mar-2009	131	113-Jul-2009

*with calf
°without calf
“presence of calf unknown

DISCUSSION

The 13 individuals sighted in Mexican waters represent about 10% of the western gray whale population based on the population assessment of an estimate of 130 individuals (90% Bayesian CI = 120-142) (Cooke *et al.* 2008). If we combine these matches with the six matches found off the coast of Vancouver Island reported by Weller et al. (2011), presumably during their migration from the breeding lagoons along the Mexican coast, and the two genetic matches noted by Lang et al (2011) with whales sampled in southern California, a total of 21 whales identified as part of the western gray whale population have migrated, at least in some years, to the eastern North Pacific during the winter breeding season.

The presence of three of these whales the same day in Laguna San Ignacio, two in the same group, indicate that these whales may travel in association or in groups, as Weller *et al* (2011) observed based on six matches off Vancouver Island, British Columbia, Canada. This also suggests that these whales may stay together in groups while on the breeding grounds.

The sex of the whales (six males, five females and two of unknown sex) indicates that both sexes, in approximately equal numbers, migrate to Mexican waters during the winter breeding season.

The sighting of females without their calve on the Russian feeding grounds suggests a high mortality of the calves, based on the small sample of four mothers with calf sighted in Laguna San Ignacio and the next summer off Sakhalin (i.e., only a 25% survivorship). The long distance of their migratory destination compared to the Bering and Chukchi Seas could be an important factor in the survivorship of the calves. Alternatively, these females may have separated from their calves as the normal weaning process when the calves were of sufficient age to begin foraging for themselves.

The number of days between the last photograph of the season and the first one of the next season represents the maximum migration time and depends on the presence of the whale, the chance to find and photograph it, and the field work seasons of the different research teams. The shorter times observed 131-143 days could be close to the real migration times of these whales.

The matches made between whales sighted off Sakhalin and the Mexican Pacific are the first results of the multinational collaboration “PACIFIC WIDE STUDY ON POPULATION STRUCTURE AND MOVEMENT PATTERNS OF NORTH PACIFIC GRAY WHALES” initiated under the coordination and support of the International Whaling Commission last year. Additional comparisons and analyses of photographs from the Western and Eastern gray whales are ongoing and will include photographs from the IBM Kamchatka catalogue, and from Laguna San Ignacio and Bahia Magdalena winter aggregation and breeding areas, obtained during the winter 2012.

Acknowledgements

We wish to thank our field researchers and colleagues that assisted with the documentation of the gray whales in Laguna San Ignacio and Laguna Ojo de Liebre. We also thank The Ocean Foundation, and the World Wildlife Fund-Mexico for their support of the field work and analysis of our results. This research was conducted as part of the Laguna San Ignacio Ecosystem Science Program (LSIESP) under special scientific research permits No.SGPA/DGVS/11560/10 and SGPA/DGVS/00640/12from the Subsecretaría de Gestión Para La Protección Ambiental, Dirección General de Vida Silvestre, de Mexico.

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ENDANGERED SPECIES RESEARCH
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FEATURE ARTICLE

Movements of gray whales between the western and eastern North Pacific

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ABSTRACT: The western North Pacific (WNP) population of gray whales *Eschrichtius robustus* is redlisted by the IUCN as Critically Endangered. As part of a long-term study on whales off Sakhalin Island, Russia, photo-catalog comparisons of gray whales in the western and eastern North Pacific (ENP) were undertaken to assess population mixing. These comparisons involved 2 approaches: (1) a systematic comparison of the WNP 'Sakhalin Catalog' to an ENP 'Pacific Northwest Catalog' that consisted of images from the northwest coast of North America and (2) a non-systematic comparison of the WNP 'Sakhalin Catalog' to an ENP 'Laguna San Ignacio Catalog' that consisted of images from central Baja California, Mexico. The Sakhalin to Pacific Northwest comparison consisted of 181 and 1064 whales, respectively, and resulted in 6 matches (3 males, 2 females, and 1 whale of unknown sex). All sightings of 'Sakhalin whales' in the Pacific Northwest occurred off southern Vancouver Island, British Columbia, Canada. The Sakhalin to Laguna San Ignacio comparison consisted of 181 and 2514 whales, respectively, and resulted in 4 matches (2 males and 2 females). As the Pacific Northwest and Laguna San Ignacio catalogs represent only a small fraction of the total estimated number of individuals in the ENP population (~19 000), it is likely that more WNP/ENP exchange has occurred than was detected by these photo-catalog comparisons. Although these matches provide new records of movements between the WNP and ENP, recent observations of gray whales off Japan and China suggest that not all gray whales identified in the WNP share a common wintering ground.

Once thought to be extinct, an endangered western North Pacific gray whale breaches off Sakhalin Island, Russia.
Image: David W. Weller

KEY WORDS: Gray whale · Pacific Ocean · Movement patterns · Conservation

INTRODUCTION

Gray whales *Eschrichtius robustus* are presently recognized as 2 populations in the North Pacific Ocean. Recent genetic studies using both mitochondrial and nuclear markers have demonstrated significant differentiation between the western North

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Pacific (WNP) and eastern North Pacific (ENP) populations (LeDuc et al. 2002, Lang 2010, Lang et al. 2011). The ENP population ranges from calving areas off Baja California, Mexico, to feeding areas in the Bering, Beaufort, and Chukchi Seas. The WNP population feeds in the Okhotsk Sea off Sakhalin Island, Russia, and in nearshore waters of the southeastern Kamchatka Peninsula (southwestern Bering Sea). Little is known about the current migratory routes and wintering areas of the WNP population, but historic evidence indicates that the coastal waters of eastern Russia, the Korean Peninsula, and Japan were part of the migratory route and that areas in the South China Sea were used as wintering grounds (see review by Weller et al. 2002).

Both populations were dramatically reduced by commercial whaling during the 19th and 20th centuries (Henderson 1984, Weller et al. 2002, Reeves et al. 2010). The ENP population was removed from the U.S. List of Endangered and Threatened Wildlife in 1994 and is currently estimated to number approximately 19 000 individuals (Laake et al. 2009). At the single species-level unit, gray whales are redlisted by the International Union for Conservation of Nature (IUCN) as being of Least Concern (Reilly et al. 2008). The WNP subpopulation, however, is redlisted by the IUCN as Critically Endangered (Reilly et al. 2008). The most recent assessment of the Sakhalin population, using a Bayesian individual-based stage-structured model, resulted in a median 1+ (non-calf) estimate of 130 individuals (90% Bayesian CI = 120–142) in 2008 (Cooke et al. 2008).

Research on gray whales in the WNP has been ongoing since 1995, predominantly on the primary feeding ground off northeastern Sakhalin Island (Weller et al. 1999, Bradford et al. 2008, Lang et al. 2011), and more recently off southeastern Kamchatka (Vertyankin et al. 2004, Tyurneva et al. 2010, Burdin et al. 2011). These studies monitor gray whales using photo-identification methods, as gray whales are individually identifiable based on unique, permanent pigmentation features (Darling 1984). Such monitoring on the Sakhalin feeding ground has documented (1) pronounced seasonal site fidelity and inter-annual return of known individuals, (2) consistent use of the area by adult females when pregnant, resting (i.e. when not pregnant or lactating), and accompanied by calves, and (3) annual return by many individuals that were first identified there as young-of-the-year (Weller et al. 1999, 2002, Bradford et al. 2008, Bradford 2011).

Whales associated with the Sakhalin feeding area can be absent for all or part of a given feeding season (Bradford et al. 2008), indicating that they probably use other areas during the summer and fall feeding period. Some of the whales identified feeding in the coastal waters off Sakhalin, including reproductive females and calves, have also been documented off the southern and eastern coast of Kamchatka (Tyurneva et al. 2010, Burdin et al. 2011). Further, whales observed off Sakhalin have been sighted off the northern Kuril Islands in the eastern Okhotsk Sea and Bering Island in the western Bering Sea (Weller et al. 2003). Finally, Lang (2010) reported that 2 adult individuals from the WNP, sampled off Sakhalin in 1998 and 2004, matched the microsatellite genotypes, mtDNA haplotypes, and sexes (1 male, 1 female) of 2 whales sampled off Santa Barbara, California, USA (Area 3 in Fig. 1) on 20 and 23 March 1995. The study by Lang (2010) was the first to suggest that some level of interchange might be occurring between the WNP and ENP.

While information regarding the summer feeding areas of gray whales in the WNP has become increasingly available in the past decade, current data from the historic migratory corridor(s) are limited and data from the presumed wintering area(s) are essentially unavailable. There have been only 13 known sightings or strandings in Japanese waters since 1990 (Nambu et al. 2010). Between 2005 and 2007, 4 female gray whales were fatally entrapped in set nets along the Pacific coast of Honshu, Japan. One of these females, entrapped in January 2007, was matched to earlier photographs of it as a calf (with its mother) while on the Sakhalin feeding ground in July and August 2006 (Weller et al. 2008). This match provided the most contemporary link between the summer feeding ground off Sakhalin and a winter location along the coast of Asia.

In an effort to obtain more information about the southern migration route(s) and wintering area(s) of gray whales in the WNP, a satellite telemetry project was undertaken in 2010 by a team of Russian and American scientists (Mate et al. 2011). While the objective of that study was to document gray whale movements in the WNP, the only whale tagged was tracked from the WNP to the ENP. The result of this telemetry study, together with the genetic matches reported by Lang (2010), provided the impetus for WNP/ENP photo-identification catalog comparisons, which we conducted to further assess population mixing.

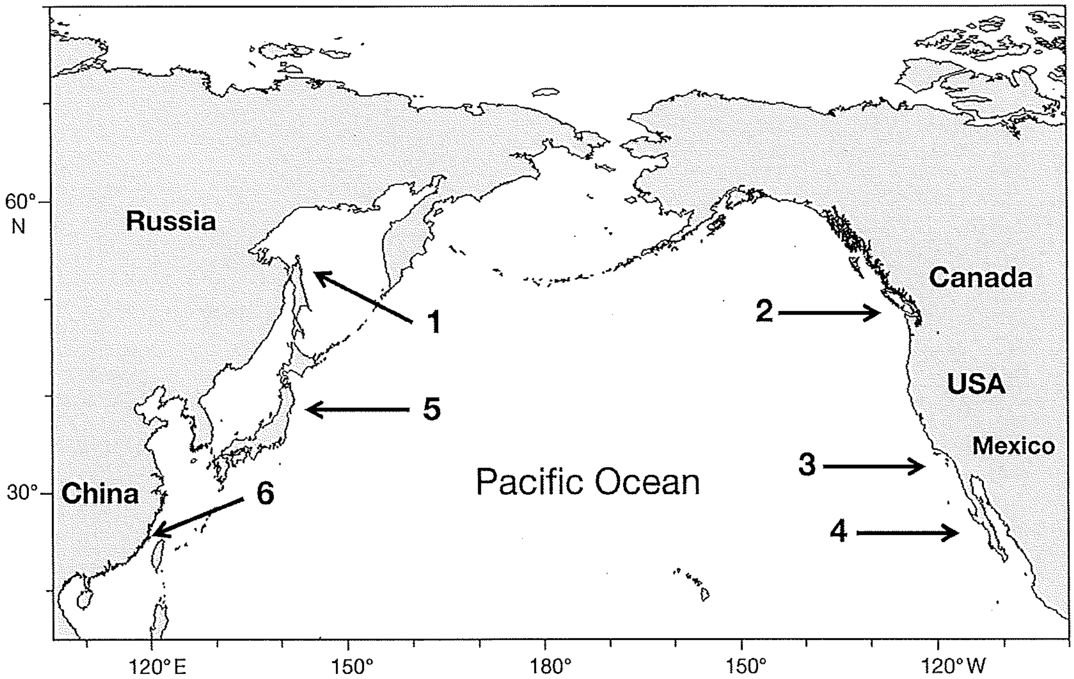

Fig. 1. *Eschrichtius robustus*. North Pacific Ocean, showing: (1) Western North Pacific (WNP) feeding ground off Sakhalin Island, (2) Eastern North Pacific (ENP) region off Vancouver Island where 6 photographic matches to Sakhalin individuals were found, (3) ENP region off California where 2 genetic matches were found (Lang 2010), (4) ENP region off Baja California where 4 photographic matches to Sakhalin individuals were found, (5) WNP region of Japan where a photographic match was found (Weller et al. 2008), and (6) WNP region of China where a gray whale stranded in November 2011 (Zhu 2012)

MATERIALS AND METHODS

Photo-identification images of 181 Sakhalin gray whales (the Sakhalin catalog, hereafter SAK catalog) collected off Sakhalin Island (Area 1 in Fig. 1) between 1994 and 2009 by a joint Russia-U.S. research program (Weller et al. 1999, 2002) were compared to a catalog of 1064 'Pacific Northwest gray whales' (hereafter, PNW catalog) identified by Cascadia Research Collective and collaborators working in U.S. and Canadian waters from California to Alaska (Area 2 in Fig. 1) primarily between 1998 and 2009 (Calambokidis et al. 2002, 2010). The PNW catalog focuses on gray whales that feed during summer and fall in coastal waters between northern California and the Gulf of Alaska, referred to as the Pacific Coast Feeding Group (PCFG), but also includes some migrating whales identified in the spring (March to May) during their northward passage to high-latitude feeding grounds.

Of the 181 whales in the SAK catalog, all were represented by a right-side dorsal flank image, and 179 were associated with a left-side dorsal flank image. Of the 1064 whales in the PNW catalog, 845 were represented by a right-side dorsal flank image, and 898 were associated with a left-side dorsal flank image. Each individual in the SAK catalog was compared in numerical order to all individuals in the PNW catalog as follows. First, the left-side dorsal flank of each individual in the SAK catalog was compared to the left-side dorsal flank of all individuals in the PNW catalog. This process was then repeated using the right-side dorsal flank and ventral aspect of the tail flukes. Comparisons were made by a single analyst (A.K.), but resulting matches were confirmed by 3 independent researchers skilled in gray whale photo-identification (including A.L.B. and J.C.).

Similarly, photo-identification images of 181 whales in the SAK catalog were compared to an online catalog of 2514 'Laguna San Ignacio gray whales' (hereafter, the LSI catalog) identified between 2006 and 2010 in Baja California, Mexico (Area 4 in Fig. 1). This assessment was not comprehensive or systematic, as was the case for the PNW catalog, because the LSI catalog represented a collection of 'annual working catalogs' rather than a single multi-year catalog of known individuals. Thus, the comparison to the SAK catalog reported herein was undertaken opportunistically. A single analyst (A.L.B.) conducted the appraisal, with identified matches confirmed by 2 additional observers (including D.W.W.).

RESULTS

The comparison of the SAK catalog to the PNW catalog resulted in a total of 6 confirmed matches of individuals, including 3 males, 2 females, and 1 whale of unknown sex (Table 1). None of these 6 whales is a known PCFG animal, and, to date, each one has only ever been photographed a single time during either April or May.

Remarkably, all 6 of the matches were from only 2 days of effort, with 3 whales identified on 2 May 2004 and 3 on 25 April 2008. The 3 whales identified on 2 May 2004 were together in a single group, while the 3 whales recorded on 25 April 2008 were in 2 separate groups but in close proximity. All of the sightings of Sakhalin whales in the Pacific Northwest occurred near Barkley Sound off the west coast of southern Vancouver Island, British Columbia, Canada.

Three of the 6 whales were first identified as calves (with their mothers) on the Sakhalin feeding ground during 1997 (no. RUS-U.S. 032/CRC 1045), 2003 (no. RUS-U.S. 119/CRC 1040), and 2004 (no. RUS-U.S. 135/CRC 1042; Table 1). Interestingly, a genetic analysis of paternity classified one of the matched males (no. RUS-U.S. 035/CRC 0809) as the putative father of 2, or possibly 4, calves identified off Sakhalin (Lang 2010). All 6 whales had sightings off Sakhalin prior to their respective sightings off Vancouver Island, and 5 (83%) had sightings off Sakhalin subsequent to their Vancouver sightings. Four whales were sighted off Vancouver Island and Sakhalin in the same year: 3 in 2004 and 1 in 2008. Of the 3 whales identified off Vancouver Island on 2 May 2004, 2 were resighted off Sakhalin on 31 July 2004, while the third was first resighted on 6 August 2004. Whale no. RUS-U.S. 032/CRC 1045 was sighted off Sakhalin in 2007 during July (29), August (4,18,25), and September (7,8,9), off southern Vancouver Island on 25 April 2008, and then back off Sakhalin on 19 July 2008. This whale is the same individual satellite-tracked from Sakhalin to the ENP in 2010/2011 (Mate et al. 2011).

The comparison of the SAK catalog to the LSI catalog resulted in a total of 4 confirmed matches of individuals, including 2 males and 2 females (Table 2). Three of these 4 whales were photographed in Laguna San Ignacio in only 1 year, while whale no. RUS-U.S. 052 was identified in both 2007 and 2010. All 4 whales had sightings off Sakhalin prior to their respective sightings in Laguna San Ignacio, and 3 (75%) had sightings off Sakhalin subsequent to their lagoon sightings. Two whales were sighted in Laguna San Ignacio and Sakhalin in the same year: one in 2008 (no. RUS-U.S. 063) and one in 2010 (no. RUS-U.S. 052).

One of the 4 whales (no. RUS-U.S. 020) was first identified as a calf on the Sakhalin feeding ground

Table 2. *Eschrichtius robustus.* Sighting summary information for 4 gray whales matched between Sakhalin Island, Russia (SAK), and Laguna San Ignacio (LSI), Baja California, Mexico. Years shown with a dash (–) are inclusive. RUS-U.S.: joint Russia-U.S. research program; M: male; F: female

Whale ID	Sex	Years sighted in SAK	Years sighted in LSI
RUS-U.S. 020[a]	M	97, 02–04, 07–09	2006
RUS-U.S. 042[b]	F	97–00, 03–05	2009
RUS-U.S. 052[c]	M	98–03, 05–06, 08–10	2007, 2010
RUS-U.S. 063[d]	F	97–98, 00–02, 05, 07, 08, 10	2008

[a] First identified off Sakhalin in 1997 as a calf. Photo-matched to Bering Island in June 2000 (Weller et al. 2003). [b] Identified as a mother with calf in LSI 2009. Never seen with calf off Sakhalin. [c] Putative father of a 1998 Sakhalin calf (Lang 2010). [d] Identified as a mother with calf in LSI 2008. Known mother from Sakhalin in 1998

Table 1. *Eschrichtius robustus.* Sighting summary information for 6 gray whales matched between Sakhalin Island, Russia (SAK), and the Pacific Northwest coast of North America (PNW). Years shown with a dash (–) are inclusive. RUS-U.S.: joint Russia-U.S. research programm; CRC: Cascadia Research Collective; M: male; U: unknown; F: female

Whale ID	Sex	Years sighted in SAK	PNW sighting	PNW sighting coordinates
RUS-U.S. 002 / CRC 0817	M	94–95, 97, 99–01, 04–09	02 May 2004	48° 41.41′ N, 124° 58.06′ W
RUS-U.S. 032 / CRC 1045[a]	M	97–98, 01–05, 07–10	25 April 2008	48° 53.81′ N, 125° 24.54′ W
RUS-U.S. 035 / CRC 0809[b]	M	95, 97, 98–07, 09–10	02 May 2004	48° 41.41′ N, 124° 58.06′ W
RUS-U.S. 078 / CRC 0825	U	97, 99, 02–04, 06–10	02 May 2004	48° 41.41′ N, 124° 58.06′ W
RUS-U.S. 119 / CRC 1040[c]	F	03, 10	25 April 2008	48° 44.01′ N, 125° 07.70′ W
RUS-U.S. 135 / CRC 1042[d]	F	04	25 April 2008	48° 44.01′ N, 125° 07.70′ W

[a] Same whale satellite-tagged in 2010 (Mate et al. 2011). First identified off Sakhalin as a calf in 1997. [b] Putative father of 2 (strict criterion) or 4 (relaxed criterion) Sakhalin calves (for definitions see Lang 2010). Years that these calves were first identified are: 1998, 2001, 2002, and 2003. [c] First identified off Sakhalin in 2003 as a calf. [d] First identified off Sakhalin in 2004 as a calf

during 1997 (Table 2) and photographically matched to the Commander Islands in June 2000 (Weller et al. 2003). A genetic analysis of paternity classified 1 of the matched males (no. RUS-U.S. 052) as the putative father of a calf identified in 1998 off Sakhalin (Lang 2010). Both of the matched females were identified as mothers with calves while in Laguna San Ignacio. Whale no. RUS-U.S. 042 was identified as a mother with a calf in 2009 but has never been seen with a calf off Sakhalin. Whale no. RUS-U.S. 063 was identified as a mother with a calf in 2008 and was also observed with a calf off Sakhalin (in 1998).

DISCUSSION

The photographic matches reported here provide new information that is of broad significance to understanding the migration patterns and mixing of gray whales in the North Pacific. The high number of matches made between the SAK and PNW catalogs is particularly intriguing given that the PNW catalog used for comparison focuses on PCFG whales and thus greatly underrepresents individuals that pass off the Pacific Northwest during the spring migration. Limited numbers of whales in the PNW catalog have been photographed during the spring off the coast of Vancouver Island where the 6 matched whales were observed (n = 26 for southern Vancouver Island; n = 48 for all of western Vancouver Island). Thus, 6 of the 74 (8.1%) whales identified off Vancouver Island in the PNW catalog were known Sakhalin individuals. Given that the PNW catalog contains only a small fraction (1064) of the estimated total number of individuals (~19 000) in the ENP population, it is likely that more WNP/ENP exchange has occurred than was detected during this comparison.

The high match rate observed between the SAK and PNW catalogs suggests a spatio-temporal behavioral factor that makes Sakhalin whales more likely to have been identified in the small PNW spring sample. The fact that all the matches came from sightings made on only 2 days, mostly in the same groups and in localized areas, indicates that whales from the Sakhalin feeding ground associate, at least to some degree, even when utilizing migratory routes in the ENP. These 6 whales were sighted in an area where some whales tend to linger and feed during the northbound migration (Darling et al. 1998). Feeding whales are often found in more nearshore waters and over extended periods of time, potentially making them more likely to be photographed than animals rapidly migrating past the area (Darling et al. 1998, Calambokidis et al. 2010). The long distance and potential open water crossing required for transit from the ENP to the WNP may make it advantageous for whales to spend time feeding in the Pacific Northwest (e.g. Vancouver Island) prior to undertaking a westerly passage to Sakhalin.

The preliminary comparison of the SAK and LSI catalogs revealed 4 additional matches. Since the SAK to LSI catalog comparison was conducted in a non-comprehensive manner, relying on long-term familiarity with whales in the WNP catalog, it is probable that additional matches exist. Given the importance of conducting further comparisons to the wintering lagoons of Baja California, Mexico, a systematic and comprehensive comparison of the SAK catalog to a recently compiled multi-year catalog from LSI and Laguna Ojo de Liebre (Scammon's Lagoon) is presently underway (see IWC 2011).

When the 10 WNP/ENP photo-identification matches reported here are combined with the 2 genetic matches noted by Lang (2010), a total of 12 gray whales (6 males, 5 females and 1 whale of unknown sex) identified in the WNP off Sakhalin Island have been matched to 3 locations in the ENP (Vancouver Island, Southern California, Laguna San Ignacio), providing evidence that both sexes, in approximately equal numbers, move between the WNP and the ENP. Despite this level of mixing, significant mtDNA and nuclear genetic differences between whales utilizing the Sakhalin feeding ground and those summering in the ENP support the continued recognition of Sakhalin animals as a distinct genetic unit (Lang et al. 2011).

Adding to the complexity of mixing between the WNP and ENP are contemporary records of gray whales off Japan and, to a lesser degree, China. As previously mentioned, there have been only 13 records of gray whales in Japanese waters since 1990 (Nambu et al. 2010). One of these reports includes a whale first identified as a calf accompanied by her mother on the Sakhalin Island feeding ground in July and August 2006 that was later fatally entrapped in a set net off the Pacific coast of Honshu (Area 5 in Fig. 1) in January 2007 (Weller et al. 2008). While observations of gray whales in Japan have been made between November and August, most of these records are concentrated between March and May. This March to May period coincides with the sightings in the ENP of the 10 matched whales described here. Observations of gray whales in China are exceptionally rare. Only 24 sightings and/or strandings have been recorded since 1933, including observations of 2 mother–calf pairs (Wang 1984, Zhu 2002). However, a 13 m female gray whale stranded in the Taiwan Strait near the town of Baiqingxiang (Pingtan County), China (Area 6 in Fig. 1), in November 2011 (Zhu 2012). These findings, in combination, suggest that not all gray whales identified in the WNP share a common wintering ground.

The use of photo-identification methods, together with genetic and telemetry techniques, is essential to furthering our understanding of gray whale population structure. We recommend that other existing photo collections and tissue samples of gray whales in the WNP and ENP (e.g. those from Sakhalin, Kamchatka, Chukotka, Mexico, and Japan) be used to further examine gray whale movement patterns and population mixing within the Pacific. Ideally, a collaborative Pacific-wide study should be undertaken, similar in scope to those conducted for humpback whales in the Atlantic and Pacific (Smith et al. 1999, Calambokidis et al. 2008).

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Genetic Differentiation Between Western and Eastern (*Eschrichtius robustus*) Gray Whale Populations Using Microsatellite Markers

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ABSTRACT

Within the North Pacific, gray whales (*Eschrichtius robustus*) are recognized as distinct eastern and western populations. Although both populations were severely reduced by whaling, the eastern population is generally considered to have recovered while the western population has remained highly depleted. Previous studies have documented genetic differentiation between the two populations on the basis of mtDNA haplotype frequencies. Since mtDNA represents only maternal inheritance patterns, the present study used bi-parentally inherited microsatellite markers (n=13) to measure differentiation between populations as well as to compare levels of nuclear genetic diversity retained in each. Mean levels of genetic diversity, as measured by the microsatellites, were similar between the eastern and western populations, indicating that the western population has retained relatively high levels of nuclear genetic diversity despite its small size. Comparison of microsatellite allele frequencies confirmed that eastern and western populations are genetically distinct. Although highly statistically significant, the level of differentiation between the two populations is relatively low, and sex-specific analyses suggest that some amount of male-biased dispersal may occur between populations. While these results suggest some movements between the eastern and western populations may take place, the maintenance of genetic differences between the two populations supports their recognition as separate eastern and western populations. Future efforts should focus on elucidating the nature and extent of any dispersal which is occurring in order to better understand factors potentially influencing the recovery of the small western population.

INTRODUCTION

Although gray whales (*Eschrichtius robustus*) once inhabited the North Atlantic Ocean (Mead and Mitchell 1984), the current distribution of the species is limited to the eastern and western margins of the North Pacific (Rice and Wolman 1971). Within this region, gray whales are recognized as having distinct eastern and western populations. Eastern gray whales winter in the lagoons and adjacent waters of Baja California, Mexico and then migrate north along the west coast of North America to feed in the Bering and Chukchi Seas during summer (Rice and Wolman 1971), with a small number of animals remaining in more southern waters between northern California and southeastern Alaska during summer months (Darling 1984, Calambokidis *et al.* 2002). For western gray whales, the primary feeding ground is in the coastal waters off northeastern Sakhalin Island, Russia (Weller *et al.* 1999, 2002). The location of the wintering ground(s) for this population remains unknown, but limited information from sightings, strandings, and catches shows that some animals winter in the coastal waters of southern China (Wang 1984, Henderson 1990, Zhu 1998).

Both gray whale populations were greatly reduced by intensive commercial whaling during parts of the 19th and 20th centuries, but the two populations have exhibited different trajectories in abundance following exploitation. Commercial whaling for eastern gray whales ceased in 1936 (Brownell and Swartz 2006), and the population's size has increased since that time (Rugh *et al.* 2005). Eastern gray whales were removed from the U.S. List of Endangered and Threatened Wildlife and Plants in 1994, and recent abundance estimates indicate that the population contains approximately 22,000 animals (Punt and Wade 2010). In the western population, however, hunting continued through at least 1966 (Brownell and Chun 1977). This population was reduced to a much smaller size than the eastern populations and was considered by some to be extinct as recently as the 1970s (Bowen 1974). Today western gray whales exist only as a small remnant population. Recent population assessment utilizing a Bayesian individually-based stage-structure model and photo-identification data collected between 1994 and 2007 projected a median non-calf population size of 130 individuals in 2008, assuming current demographic and population trends continue (Cooke *et al.* 2008). This population was listed as Critically Endangered by the IUCN in 2000 (Weller *et al.* 2002, Baillie *et al.* 2004), and its continued survival is jeopardized by problems associated with small population size (reviewed in Clapham *et al.* 1999), as well as by a wide range of potential anthropogenic threats, including the rapid expansion of oil and gas development on its summer feeding ground off Sakhalin Island, Russia (Weller *et al.* 2002, Reeves *et al.* 2005, IISG 2006) and mortality due to net entrapment while on the migratory route off Japan (Brownell *et al.* 2007, Weller *et al.* 2008b).

Concern for the conservation status of the western population led to the initiation of a joint Russia-U.S. research program in 1995. This program is based on the summer feeding ground off Sakhalin Island, Russia and has incorporated both photo-identification studies and biopsy sampling (Weller *et al.* 1999, 2002). Photo-identification research has shown that most whales demonstrate high rates of annual return and pronounced seasonal site fidelity to the Sakhalin feeding ground (Weller *et al.* 1999, 2002). The majority (83% of identified whales (n=169) have also been genetically sampled, allowing a male bias (58% males) to be documented among sampled individuals (Weller *et al.* 2002, 2008). This male bias is particularly pronounced in individuals first identified as calves, of which 66% are males (Weller *et al.* 2008).

Biopsy samples collected between 1995 and 1999 have been used to show that the eastern and western populations are genetically distinct based on mitochondrial DNA (mtDNA) haplotype frequencies (LeDuc *et al.* 2002). This study found that western gray whales have retained a relatively high number of mtDNA haplotypes for such a small population. Genetic differentiation between the eastern and western populations was based on differences in the frequency distributions of haplotypes within each population. While haplotypes were apportioned relatively evenly among the eastern gray whale samples, the haplotype distribution found within the western gray whale samples was highly skewed, with two haplotypes found in very high frequencies and the remaining haplotypes identified in only one or two individuals (LeDuc *et al.* 2002).

The work presented here used thirteen microsatellite markers to further examine population structure of gray whales. Unlike mtDNA, which is maternally inherited and provides information about historic gene flow of females only, microsatellites are nuclear bi-parentally inherited markers and reflect gene flow of both males and females. The primary goal of this study was to examine genetic differentiation between eastern and western populations using microsatellites, as well as to assess factors which might contribute to that differentiation. Secondarily, levels of nuclear genetic diversity were compared between the two populations to determine if substantial genetic variability has been lost in the much smaller western population and could thus be affecting its ability to recover. Finally, since additional western gray whale samples have been collected since the LeDuc *et al.* (2002) study, further analysis of population structure and genetic diversity using mtDNA was also conducted.

MATERIALS AND METHODS

Sample collection and DNA extraction

One hundred forty-two western gray whale samples were collected between 1995 and 2007 via biopsy darting of free-ranging whales on the population's feeding ground off Sakhalin Island, Russia. All except for one of the western gray whale samples are linked to a photographically identified animal, and this sample set represents 83.4% of all animals (n=169) identified on the western feeding ground through 2007. One hundred thirty-seven eastern gray whale samples obtained from the archive at the Southwest Fisheries Science Center were used for comparison to the western population. These samples were taken primarily from stranded animals (n=105), with some samples obtained from directed subsistence takes (n=12), fisheries bycatch (n=3), and biopsies (n=17) from free ranging whales. Collection locations ranged from southern California north to the Chukotka Peninsula in Russia.

DNA had been previously extracted for 120 of the eastern gray whale samples and 45 of the 142 western gray whale samples (those collected between 1995 and 1999) for use in an earlier study (LeDuc *et al.* 2002). For the remaining samples, whole genomic DNA was extracted using either the QIAGEN DNeasy™ tissue kit or the Corbett Robotics X-tractor Gene robot with the recommended protocols.

Molecular sexing and mtDNA control region sequencing

For those samples (n=114) not analyzed in the prior study by LeDuc *et al.* (2002), molecular sexing and mtDNA control region sequencing were conducted. For all of the eastern gray whale samples as well as the western gray whale samples which were collected prior to the 2006 season (n=94), a polymerase chain reaction (PCR) was used to determine sex utilizing primers described in Fain and Lemay (1995) and following the methods described in Gilson *et al.* (1998). For western gray whale samples collected in 2006 and 2007 (n=20), the protocol described in Morin *et al.* (2005) was used to determine the sex of individuals.

PCR was used to amplify a 523-base-pair fragment from the mtDNA control region using the primers 5'-TACCAAATGTATGAAACCTCAG-3' (H00034, Rosel *et al.* 1995) and 5'-CCTCCCTAAGACTCAAGGAAG-3' (L15812, Escorza-Trevino *et al.* 2005). Amplification products were cleaned through purification columns (QIAquick, Qiagen) and then sequenced using standard protocols with ABI-PRISM® Dye-DeoxyTerminator Big Dye™ v3.1 (Applied Biosystems) and the same primers. Following ethanol precipitation, sequenced products were run on an ABI 3100 or ABI3130 capillary sequencer. Consensus sequences for both strands were generated using ABI SEQSCAPE v2.5 software.

Microsatellite genotyping

Thirteen microsatellite loci isolated from other cetacean species were used to genotype the samples (*Table 1*). Reactions were performed in 25-uL volumes containing approximately 100 ng of genomic DNA and 2.5 uL of 2.0 mM $MgCl_2$ buffer, 1.5 uL of 10 mM dNTPs, 0.75 uL of each primer (at 10uM concentrations, with the forward primer of each pair fluorescently labeled), and 0.25 uL Taq. The thermal cycling profile included an initial hot start of 94°C for 2 min followed by 35 cycles of 94°C for 45 s, 1 min at the annealing temperature (see *Table 1*), and 1.5 min at 72°C, with a final 5-min extension at 72°C. Amplified products were mixed with a size standard and loaded onto an ABI 3100 or ABI 3130 sequencer. Sizing and binning of allele fragments using ABI GENESCAN and GENOTYPER analysis software were automated and relied on the use of internal lane standards, with subsequent manual evaluation of all labeled peaks.

Microsatellite scoring errors and identification of replicate samples

Prior to inclusion in this study, photo-identification data collected during biopsy sampling was used to identify and remove any duplicate samples (*i.e.,* samples taken from the same individual) from the western population sample set. Genotypic data were used to search for duplicates within the eastern gray whale sample set using MS Excel Toolkit v3.1 (Park 2001); one duplicate was identified and removed prior to analyses, leaving a total of 136 eastern gray whale samples. Microsatellite data were also examined for signs of large-allele dropout and null alleles using MICRO-CHECKER v2.2.1 (van Oosterhout *et al.* 2004).

Genetic variability within populations

ARLEQUIN v3.01 (Excoffier *et al.* 2005) was used with the mitochondrial control region data to calculate standard indices of genetic variation (nucleotide diversity, π, and haplotype diversity, *h*; Nei 1987) for each population. Genetic diversity at the nuclear level was characterized by generating the number of alleles, observed heterozygosity, and expected heterozygosity for each microsatellite locus in each population using ARLEQUIN. Within each sample set, a Markov-chain approximation of an exact test, as implemented in GENEPOP v3.4 (Raymond and Rousset 1995a), was used to test for departures from Hardy Weinberg expectations and for linkage disequilibrium between all pairs of loci.

Bottleneck analyses

Populations which have undergone recent bottlenecks are expected to exhibit genetic signatures characteristic of a reduction in effective population size (Cornuet and Luikart 1996, Luikart and Cornuet 1998, Luikart et al. 1998, Garza and Williamson 2001). One such signature is a transient excess of heterozygosity (H_e) relative to that expected in a population of constant size, which results from the rapid loss of rare alleles contributing little to overall heterozygosity (Cornuet and Luikart 1996). Here we utilized the program BOTTLENECK v1.2 (Piry *et al.* 1999) to determine if the gray whale microsatellite data demonstrated evidence of population bottlenecks. As recommended (Piry *et al.* 1999), a two-phase model assuming 95% single-step mutations and 5% multiple-step mutations was employed, with the variance among multiple steps set to 12. The distribution of gene diversity at equilibrium was estimated using a coalescent process with 10,000 simulations, and a one-tailed Wilcoxon test was used to determine if an excess of heterozygosity, relative to that expected in populations at equilibrium, was present (Cornuet and Luikart 1996).

The loss of rare alleles during a population bottleneck may also result in gaps in the size distribution of microsatellite alleles. This can be measured as the mean ratio (*M*) of the number of alleles to the allele size range across all loci (Garza and Williamson 2001); bottlenecked populations demonstrate reduced *M* values. Here we used ARLEQUIN to calculate *M* for both gray whale populations and then compared our values to those reported for reduced and stable populations by Garza and Williamson (2001).

Genetic differentiation among populations:

Two approaches were used to assess the degree of genetic differentiation between the two sampling regions. In the first approach, samples were divided *a priori* into populations based on the geographic location in which they were collected. The extent of genetic differentiation between populations was then examined using both mtDNA sequences and microsatellite data. For mtDNA data, an analysis of molecular variance (AMOVA, Weir and Cockerham 1984, Excoffier *et al.* 1992) was used to generate frequency-based (F_{ST}) estimates of differentiation using the program ARLEQUIN (20,000 permutations were used to test for significance). For microsatellite loci, genetic differentiation was examined using an AMOVA (ARLEQUIN) and allelic frequencies (with 20,000 permutations to test for significance) to generate F_{ST} values (Weir and Cockerham 1984). Modified exact tests based on genotype counts, as implemented in GENEPOP v3.4 (Raymond and Rousset 1995b), were also utilized to measure levels of differentiation. Significance was tested using 10,000 permutations. Since the western gray whale sample set included 57 mother-calf pairings, analyses of genetic differentiation were repeated after removal of the sample representing the calf in each pair, in order to avoid biasing the results by including known first-degree relatives.

As an alternative to *a priori* stratification of samples by geographic location, population structure was also explored using a Bayesian model-based clustering approach (STRUCTURE v2.2, Pritchard *et al.* 2000) with the microsatellite data. STRUCTURE assumes that within a set of samples there are K populations, each of which is characterized by allele frequencies at each locus. The program then divides all samples into K genetically distinct clusters by assigning individuals to putative populations such that Hardy-

Weinberg and linkage disequilibrium are minimized within each group. Five independent runs of K=1-5 were performed with a burn-in period of 50,000 iterations followed by 100,000 Markov-chain Monte Carlo repetitions, using a model based on admixture with correlated allele frequencies (Falush *et al.* 2003). After averaging across runs, the log probability of the data given K (Ln P(X|K) was used as the criterion to infer the number of clusters (K) most compatible with the our data.

Detection of sex-biased dispersal

The potential for sex-biased dispersal between populations was investigated using the microsatellite data with the methods described by Goudet *et al.* (2002) and implemented in FSTAT v2.9 (Goudet 2001). Since the signal of sex-biased dispersal disappears with mating (Goudet *et al.* 2002), animals first sampled as calves in the western population were omitted prior to analysis. This program generates a number of statistics aimed at identifying patterns of sex-biased dispersal. The statistics utilized here were 1) F_{st}, the proportion of genetic variation among populations; 2) the mean corrected assignment index (mAIc) and 3) the variance around the assignment index (vAIc) (Favre *et al.* 1997, Mossman and Waser 1999). The p values were estimated using 10,000 randomizations, and a one-tailed test was utilized based on the expectation that, as in most mammals, dispersal is biased toward males. F_{st} and mAIc are expected to be higher in the more philopatric sex, while vAIc should be lower (Goudet *et al.* 2002).

To further explore the potential for sex-biased dispersal between populations, sex-specific estimates of genetic differentiation were generated using the methods outlined above with both the mtDNA and microsatellite data. In addition, values of cluster membership (Q) produced by the STRUCTURE model assuming K=2 clusters were compared between males and females.

RESULTS

Genetic diversity

Forty haplotypes defined by 39 variable sites were identified from the 278 gray whale samples. Thirty-five haplotypes were found among the eastern gray whale samples, while 22 haplotypes were found in the western gray whale sample set. Seventeen haplotypes were shared between the two populations. The frequency of haplotypes in each population is shown in *Table 2*. When all samples were combined, nucleotide diversity (π) was 0.018 (SD=0.0092), while haplotypic diversity (*h*) was 0.89 (SD=0.012). When subdivided by population, nucleotide diversity was relatively similar in both populations (π=0.016 ±0.0081SD, eastern population; π=0.018 ±0.0093SD, western population), while measures of haplotype diversity were higher in the eastern (*h*=0.95 ±0.006SD) than the western (*h*=0.77±0.025SD) population (*Table 3*). Sex-specific diversity measures indicated that although haplotypic diversity was similar between the male (*h*=0.96) and female (*h*=0.95) subsets of the eastern population, lower levels of haplotype diversity were found among the western female subset (*h*=0.77) when compared to the western male subset (*h*=0.83).

No signal of large-allele dropout or null alleles was identified by MICROCHECKER for any locus in either of the two populations. No deviation from Hardy-Weinberg Equilibrium was detected in either population after controlling for the False Discovery Rate (FDR, Benjamini and Hochberg 1995). After correcting for the FDR, only one loci combination was found to be in significant linkage disequilibrium in the eastern population. However, significant linkage disequilibrium was detected for eight loci combinations in the western population. Given that the same loci pairs were not in disequilibrium in both populations, it is unlikely that this result was derived from physical linkage. Linkage disequilibrium can result from inclusion of related individuals within a sample set. Therefore, known relatives were removed and the tests were rerun on the remaining genotypes. Six loci combinations remained out of linkage disequilibrium after controlling for the FDR.

After averaging across loci, measures of microsatellite diversity were higher in the eastern population (H_o=0.74, H_e=0.74, K=9.8) than in the western population (H_o=0.71; H_e=0.70, A=8.8); however, these differences were relatively small (*Table 4*). A total of 18 private alleles were observed in the eastern population, while only 5 private alleles were found in the western population.

Statistical analysis of the microsatellite allele frequency data using the program BOTTLENECK did not detect evidence of a recent (2-4N_e generations) bottleneck in either population. Under the model utilized, heterozygosity excess was not observed in the eastern (Wilcoxon test, *P*=0.989) or the western population (Wilcoxon test, *P*=0.999). In addition, the calculated *M* values (0.823±0.15and 0.808±0.17) in the eastern and western populations, respectively) were more consistent with those described for stable populations and were considerably higher than the upper bound (0.70) that Garza and Williamson (2001) derived for reduced populations.

Genetic differentiation among populations

Significant genetic structuring between eastern and western populations on the basis of both mtDNA haplotypes and microsatellite allele frequencies was observed (*Table 5*). Similar results were also observed for the microsatellite data when genetic differentiation was assessed using the exact test; the overall results were significant ($p \leq 0.001$), with 11 of the 13 loci showing significant differences when analyzed independently (data not shown). These comparisons remained significant ($P \leq 0.001$) after known relatives (n = 57 calves which had sampled mothers) were removed from the analysis (*Table 5*); however, only three of the thirteen loci showed significant differences when analyzed independently.

STRUCTURE analyses (Pritchard *et al.* 2000, Falush *et al.* 2003) supported the presence of two populations (P ~1.0), with a clear increase in the log-likelihood of the data for K = 2 when compared to that for other numbers of clusters (*Table 6*). The probability that the data contained only one cluster was < 0.001, suggesting that eastern and western populations are not panmictic. When Q values, which represent the proportion of each individual's genotype that can be attributed to each of the clusters, were used to assign individuals into clusters, 80% (n = 109 of 136) of animals sampled in the east were grouped into the same cluster while 65% (n = 92 of 142) of animals sampled in the west were grouped into a cluster (*Figure 1*). However, average source population Q values were relatively low for both populations; they averaged 0.69 (± 0.209SD) for animals sampled in the east and 0.60 (± 0.296SD) for animals sampled in the west.

Sex-specific comparisons

Sex-specific estimates of differentiation were much more marked among females than among males. Using mtDNA haplotype frequencies (*Table 5*), both the male and female comparisons were highly significant, although the F_{st} value estimated for females ($F_{st} = 0.078$) was more than twice as high as that estimated for males ($F_{st} = 0.033$). Interestingly, while the male-specific comparisons remained significant (P = 0.029) in the microsatellite exact test, F_{st} estimates based on microsatellite allele frequencies suggested no significant differences between eastern and western males. The sex-biased dispersal tests in FSTAT also supported greater philopatry among females when compared to males. While difference in males and females were not significant for the mean assignment index (*P* = 0.365) or the variance in the mean assignment index (*P* = 0.9262), females demonstrated significantly higher F_{st} values (*P* = 0.0176).

Results of the STRUCTURE analysis provided further evidence that male-biased dispersal may be occurring. After removing animals first identified as calves, average Q values were similar between eastern males ($Q_{EM} = 0.70 \pm 0.211$SD) and females ($Q_{EF} = 0.67 \pm 0.208$SD, *P* = 0.26, t-test); 80% and 87% of males and females were assigned to their source population. In contrast, average Q values were lower for western males ($Q_{WM} = 0.47 \pm 0.339$SD) than for western females ($Q_{WF} = 0.63 \pm 0.250$; *P* = 0.010, t-test). Only 40% of western males had $Q \geq 0.50$ for the cluster representing the western population, in contrast to 75% of western females.

DISCUSSION

Genetic variability

Populations reduced to small sizes can suffer from a loss of genetic diversity, which in turn may compromise their ability to respond to changing environmental conditions (Willi *et al.* 2006) and negatively influence long-term viability (Spielman *et al.* 2004, Frankham 2005). Although little is known about the level of genetic diversity maintained in the western gray whale population prior to its depletion by commercial whaling, comparison of the levels of diversity found in this small population with those maintained in the much larger population in the eastern Pacific can provide some insight into whether reduced genetic diversity may influence its recovery. Previous studies utilizing mtDNA indicated that while the western gray whale population had retained a relatively high number of mtDNA haplotypes and levels of nucleotide diversity which were concordant with those found in the eastern population, the population had reduced haplotype diversity when compared to its eastern counterpart (LeDuc *et al.* 2002). Our results, using an extended sample set that included ~83% of photographically identified western gray whales, support these earlier findings. As previously noted, the reduced haplotype diversity found in the western population was not a reflection of the number of haplotypes present but rather of the skewed distribution of those haplotypes (LeDuc *et al.* 2002). This skew was even more marked with the added samples. While the frequencies of the two most common haplotypes changed little, new low frequency haplotypes were added, with 14 of the 22 western gray whale haplotypes being found in only one or two animals.

While approximately half (49%) of the mtDNA haplotypes identified in the eastern population were shared with animals sampled in the western North Pacific, a much larger proportion (77%) of the mtDNA haplotypes found in the western population were also identified in eastern animals. Given the relatively thorough sampling of animals on the western feeding ground, it is likely that most if not all haplotypes present in that area have been identified, indicating that the mtDNA haplotypes found only in the eastern Pacific are likely to be unique to that population. In contrast, the low proportion of animals sampled in the eastern population suggests that those haplotypes currently identified only among western animals (n=5) might also be discovered in the eastern population with additional sampling.

Although the relationship between population size and mtDNA diversity is not straightforward (Bazin *et al.* 2006; Nabholz *et al.* 2008), the number of haplotypes (n=22) found in the western gray whale population is surprising given its small size and history of exploitation. In a similar study of endangered North Atlantic right whales (*Eubalaena glacialis*), which are thought to number approximately 400 individuals, only five haplotypes have been documented (n = 180 samples, Malik *et al.* 2000). While sampling in other populations has been less comprehensive, similar patterns have been found in other small mysticete populations, including the Okhotsk Sea bowhead whale population (*Balaena mysticetus*), in which only four different haplotypes were found (n = 25 samples, LeDuc *et al.* 2005), as well as the Sea of Cortez fin whales (*Balaenoptera physalus*), in which three haplotypes have been identified (n = 56 samples, Berube *et al.* 2002). The number of haplotypes found in the western gray whale population is more consistent with numbers found in larger populations, such as the stock of right whales (*Eubalaena australis*) breeding off South Africa, which contains 21 haplotypes (n = 41 samples, Patenaude *et al.* 2007) and has an estimated abundance of 3400 animals (Best *et al.* 2005).

Although the number of haplotypes currently found in the western population is higher than might be expected, this pattern may not persist into the future. Eleven of the 14 haplotypes found in low frequencies have been identified only in a single male. Although little specific information is available on gray whale longevity, they are generally thought to live for approximately 40 to 60 years. It is possible that some of these “rare haplotype” males could be animals that escaped being killed by whalers which hunted gray whales until at least 1966. Given the maternal inheritance pattern of mtDNA, and assuming that these males are indeed the only animals in the population with these haplotypes, the eventual loss of these individuals has the potential to substantially decrease levels of mtDNA diversity in the future.

The level of nuclear genetic diversity found in the western population was slightly lower than, but very similar to, that found in the much larger eastern population. The number of microsatellite alleles found exclusively in the eastern population, however, was markedly higher than the number found in the western population. Given that the western population has been relatively thoroughly sampled, these results suggest that the western population’s depletion and continued small size may have resulted in the loss of rare alleles from the population. No genetic signature of a bottleneck was detected in the western population using the microsatellite data. However, simulations have shown that detection of bottlenecks using genetic methods is dependent on a wide range of conditions, including duration of the bottleneck, mutation rate, pre-bottleneck size, and post-bottleneck recovery (Williamson-Natesan 2005), and many studies have failed to detect the genetic signature of a bottleneck even when demographic data indicate population size collapse (*e.g.*, Queney *et al.* 2000, Spong and Hellborg 2002).

Overall, the western population appears to have retained relatively high genetic diversity despite its history of exploitation and continued small population size. In other populations, the maintenance of genetic diversity in the face of population decline has been attributed to long generation times (Dinerstein and McCracken 1990, Hailer *et al.* 2006, Lippe *et al.* 2006), which are characteristic of baleen whales and may have buffered the population against the rapid loss of variation. However, the relatively high level of genetic diversity that appears to have been maintained in the western population could also be the result of dispersal of eastern animals onto the western feeding ground. Even at low levels, dispersal has been shown to obscure bottleneck signatures (*e.g.,* Kellar *et al.* 2001, Busch *et al.* 2007) and genetically "rescue" populations from the loss of genetic diversity (Vila *et al.* 2003). Further exploration of this possibility is detailed below.

Population structure

The inclusion of additional samples to analyses employing mtDNA supported the previous conclusion that the two populations are genetically distinct (LeDuc *et al.* 2002). Nuclear differentiation estimates further confirm differences between the two populations and indicate that genetic separation between populations is not derived solely from female philopatry. These measures of differentiation remained significant after known first degree relatives (*i.e*., the calf from sampled mother-calf pairs) were removed from the dataset, suggesting that such differences are not solely an artifact of the inclusion of highly related individuals in the analysis.

Although highly significant, the degree of nuclear differentiation, as measured by F_{ST} values, between the two populations is relatively small. This pattern of differentiation is similar to that found in North Pacific bowhead whale populations, which also demonstrate a significant but small degree of differentiation between a smaller western population inhabiting the Okhotsk Sea and a much larger eastern population in the Bering-Chukchi-Beaufort Seas (LeDuc *et al.* 2005). The relatively small but highly significant genetic differences observed in gray whales, particularly when combined with the similar pattern observed in North Pacific bowhead populations, suggests that past Arctic environmental changes may have played a role in influencing patterns of historic mixing and separation of eastern and western animals. Both stranding records and radio-carbon dating of remains have indicated that changes in sea ice distribution may have mediated bowhead whale distribution in the Canadian Arctic (Dyke *et al.* 1996, SaVelle *et al.* 2000). Within the North Pacific, Arctic-wide cooling and glaciation brought on by the "Little Ice Age" (~400-750 years ago) may have resulted in a southern shift in sea ice distribution and reduced sea level (Overpeck *et al.* 1997), potentially facilitating mixing between eastern and western whales. Sea ice expansion during the Neoglacial (~4700 to 2500 years ago) may also have limited access to parts of the Bering Sea and has been hypothesized to have altered the distribution of North Pacific pinnipeds and cetaceans (Crockford and Frederick 2007).

A second explanation for the low level of differentiation is that some limited gene flow could be occurring between the two populations. Given the small size of the western population, it seems likely that even minimal gene flow from the eastern to the western population would quickly homogenize allele frequencies. However, genetic drift also acts more strongly on small populations, allowing differences between populations to develop more rapidly. As such, genetic drift could be acting to counterbalance some restricted degree of genetic interchange between populations.

A third scenario which might also explain our results involves dispersal of whales between feeding areas without genetic exchange. Since breeding in gray whales is thought to primarily occur along migratory corridors (Rice and Wolman 1971), movement between feeding regions does not necessarily imply gene flow between the populations. Given that all of the western gray whale samples were obtained on the feeding ground, low differentiation levels could potentially be generated by a small number of eastern gray whales traveling to the western gray whale feeding ground during summer months and consequently being sampled while mixed with members of the western population. If these eastern dispersers visit the western feeding ground but return to the eastern Pacific to breed, such extralimital movements would act to reduce measured levels of genetic differentiation between populations in the absence of significant gene flow.

Some support for a limited degree of dispersal and/or gene flow between populations can be derived from the results of the sex-specific comparisons. If the observed low level of differentiation were due to recent divergence, similar patterns of differences should be observed for males and females. Contrary to this expectation, all measures of differentiation were at least twice as high for female-only versus male-only comparisons. In addition, although comparisons between males remained significant for mtDNA, the F_{st}-based comparison of microsatellite allele frequencies did not identify significant differences among males, suggesting that some degree of male-biased dispersal may be occurring between populations. Such a pattern could also provide an explanation for the large proportion of mtDNA haplotypes (11 of 22) in the western population which are represented only by a single male. Given the higher diversity and number of mtDNA haplotypes found in the eastern population, any dispersers from the east would have a relatively high probability of carrying haplotypes considered "rare' in the west (LeDuc *et al.* 2002). Eight of the eleven haplotypes carried by only a single male in the west were also found in the east; given the low proportion of sampled animals in the east, it is plausible that the other three haplotypes would also be identified among eastern animals with additional sampling.

Although the analyses summarized here are not able to discriminate between gene flow and feeding ground dispersal, a combination of genetic assignment tests and parentage analysis in the future may be useful to distinguish between these two possibilities. In addition, simulation modeling could be utilized in the future to determine the degree of gene flow or feeding-ground dispersal which could occur while still allowing the two populations to maintain genetic distinctiveness.

Conclusions and conservation implications

The results presented here support past work indicating that eastern and western populations are genetically distinct, further highlighting the need for continued conservation and expanded protection of the critically endangered western gray whale population. Although highly statistically significant, the level of differentiation between the two populations is relatively low, which may reflect recent divergence of the two populations, perhaps mitigated by past environmental changes, but could also suggest that some limited degree of dispersal and/or gene flow may occur between the two populations. Discrimination between these proposed explanations is important, given that each scenario could have different effects on the recovery of the critically endangered western population. If a restricted amount of gene flow is taking place, that interchange could be important in providing "genetic rescue" for the western population, helping to maintain relatively high levels of genetic diversity in a small population which would otherwise likely suffer from inbreeding and a subsequent loss of fitness. However, if dispersal between feeding grounds without any gene flow is occurring, then any eastern dispersers are not contributing to the gene pool but could be artificially inflating our estimates of both genetic diversity and population size, which would suggest that the western population is even more vulnerable than currently thought. Given the wide range of threats, including entrapment in fishing nets as well as expanding oil and gas development, which challenge the recovery of the western gray whale population, further exploration of possible mechanisms of intermixing is needed to better understand the dynamics of this critically endangered population.

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Table 1. Microsatellite loci used in the study. Includes the species for which primers were initially designed, size of repeats, annealing temperature (T_a), size range, and reference listing primer sequences.

Locus	**Source Species**	**Repeat Size (bp)**	**T_a (°C)**	**Size Range (bp)**	**Reference**
DlrFCB17t*	*Delphinaptera leuca*	2	54	183-213	Buchanan *et al.* 1996
EV14t*	*Megaptera novaeangliae*	2	55	138-156	Valsecchi and Amos 1996
EV37	*Megaptera novaeangliae*	2	55	183-231	Valsecchi and Amos 1996
EV94t*	*Megaptera novaeangliae*	2	52	209-237	Valsecchi and Amos 1996
Gata028	*Megaptera novaeangliae*	4	54	159-187	Palsboll *et al.* 1997
Gata098	*Megaptera novaeangliae*	4	54	67-103	Palsboll *et al.* 1997
Gata417	*Megaptera novaeangliae*	4	54	198-222	Palsboll *et al.* 1997
Gt023	*Megaptera novaeangliae*	2	54	94-116	Palsboll *et al.* 1997
RW31	*Eubalaena glacialis*	2	54	114-136	Waldick *et al.* 1999
RW48	*Eubalaena glacialis*	2	55	112-124	Waldick *et al.* 1999
SW10t*	*Physeter macrocephalus*	2	55	119-151	Richard *et al.* 1996
SW13t*	*Physeter macrocephalus*	2	55	168-196	Richard *et al.* 1996
SW19t*	*Physeter macrocephalus*	2	55	122-142	Richard *et al.* 1996

* The sequence for the reverse primer has been modified from the original design by the addition of a tail (Brownstein *et al.* 1996)

Table 2. Frequency of mtDNA haplotypes in each population.

	# of Individuals	
Haplotype	**East**	**West**
A	15	51
B	10	44
C	13	9
D	7	5
E	4	3
F		1
G	9	2
H	1	2
I		1
J		1
K	5	
L	6	1
M	6	2
N	5	1
O	1	
P	2	
Q	1	1
R	7	
S	1	
T	7	1
U	3	
V	3	1
W	1	
X	6	
Y	3	1
Z	2	1
27	2	
28	2	3
29	2	
30	3	
31	1	
32	1	
33	1	1
34	1	
35		7
36	2	
37	1	
38		3
41	1	
42	1	
Total	136	142

Table 3. Genetic diversity estimates based on mtDNA control region sequences. Includes number of individuals (n), number of haplotypes (k), haplotype diversity (h) and percent nucleotide diversity (π). For haplotype diversity and nucleotide diversity, standard deviations are included in parentheses.

Population		**n**	**k**	**h**	**π (%)**
East	All	136	35	0.95 (±0.006)	1.57(±0.810)
	Females	49	23	0.95 (±0.014)	1.41 (±0.744)
	Males	87	30	0.96 (±0.008)	1.66 (±0.856)
West	All	142	22	0.77 (±0.025)	1.82 (±0.932)
	No known relatives	84	22	0.82 (±0.030)	1.83(±0.937)
	Females*	36	10	0.77 (±0.050)	1.89 (±0.984)
	Males*	42	15	0.83 (±0.041)	1.82 (±0.944)
Both		278	40	0.89 (±0.012)	1.81 (±0.922)

* Excludes animals first identified as calves

Table 4. Microsatellite data for gray whales. Includes number of alleles per loci (k), expected heterozygosities (H_e), observed heterozygosities (H_o), and number of private alleles (K_p). The overall results include averaged values over all loci for k, H_e, and H_o, and the sum of all private alleles for K_p.

	East				**West**			
Locus	**K**	**H_e**	**H_o**	**K_p**	**K**	**H_e**	**H_o**	**K_p**
D17t	15	0.89	0.90	1	15	0.88	0.85	1
EV14t	9	0.81	0.78	1	9	0.76	0.74	1
EV37	17	0.88	0.89	1	17	0.85	0.91	1
EV94t	11	0.79	0.74	2	9	0.75	0.75	0
Gata028	8	0.78	0.82	3	5	0.75	0.78	0
Gata098	10	0.65	0.65	3	7	0.63	0.61	0
Gata417	7	0.71	0.71	0	7	0.63	0.65	0
Gt023	9	0.72	0.76	1	8	0.68	0.68	0
RW31	10	0.82	0.83	1	9	0.82	0.85	0
RW48	5	0.40	0.42	0	5	0.36	0.34	0
SW10t	9	0.77	0.76	1	9	0.75	0.77	1
SW13t	8	0.63	0.67	1	8	0.67	0.68	1
SW19t	10	0.71	0.67	3	7	0.64	0.67	0
Overall	9.8	0.74	0.74	18†	8.8	0.70	0.71	5†

Table 5. Analysis of molecular variance (AMOVA) and pairwise comparisons among gray whale populations from microsatellites and mtDNA control region sequences. Significant P values (<0.05) are shown in bold. Comparisons using only females and only males did not include known relatives.

Comparison	**Microsatellites**			**mtDNA**	
	Genotype frequency			**Haplotype frequency**	
	F_{ST}	F_{ST} probability	Exact test probability	F_{ST}	F_{ST} probability
All individuals	0.009	**≤ 0.001**	**≤ 0.001**	0.068	**≤ 0.001**
No known relatives	0.005	**≤ 0.001**	**≤ 0.001**	0.045	**≤ 0.001**
Females	0.013	**≤ 0.001**	**≤ 0.001**	0.078	**≤ 0.001**
Males	0.002	0.117	**0.039**	0.033	**≤ 0.001**

Table 6. Results of STRUCTURE analyis using a model incorporating admixture with correlated allele frequencies. Includes the inferred number of genetic clusters (K), the estimated log likelihood value (after averaging across runs) for the data given K (Ln P(X|K)), and the posterior probability of K (Pr (K|X)). The value of K with the highest posterior probability is shown in bold. Details about the parameters incorporated in each model are described in the text.

K	**Ln P (X|K)**	**Pr (K|X)**
1	-11612.18	~0
2	**-11469.22**	**~1**
3	-11682.32	~0
4	-11808.74	~0
5	-12214.70	~0

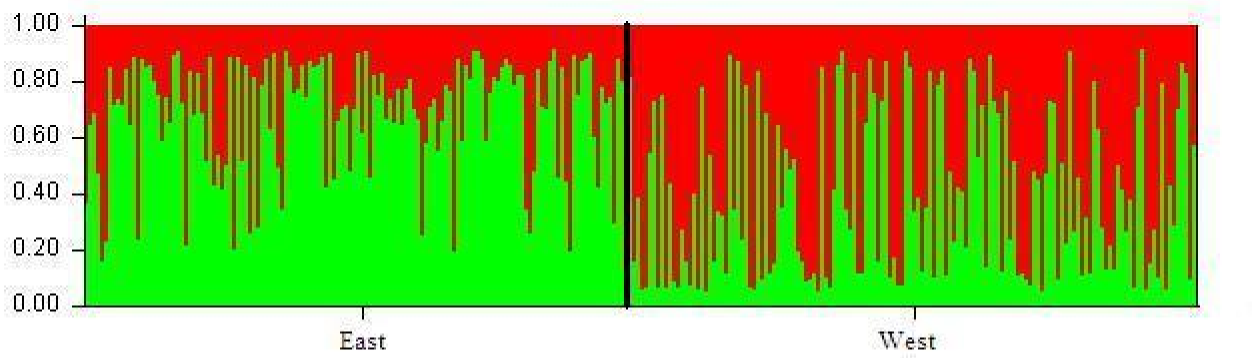

Figure 1. STRUCTURE barplot for K=2 using a model based on admixture with correlated allele frequencies. Individuals are represented by vertical bars, and the different colors of the bars represent the proportion of admixture (Q), or ancestry, from a each inferred genetic cluster. Individuals are grouped according to the population in which they were sampled, and the black line denotes the boundary between animals sampled in the eastern and western Pacific.

Assessment of stock structure among gray whales utilizing feeding grounds in the Eastern North Pacific

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ABSTRACT

Although the majority of Eastern North Pacific (ENP) gray whales spend their summers feeding in the Bering, Beaufort, and Chukchi Seas, a small number of individuals, referred to as the Pacific Coast Feeding Group (PCFG), feed in waters between northern California and southeastern Alaska during summer and fall. Many individuals identified within this southern feeding area demonstrate intra- and inter-seasonal fidelity to the region, suggesting that structure could be present among ENP gray whales utilizing different areas for feeding. Little is known, however, about patterns of site fidelity of individuals feeding in northern waters. We utilized samples collected from individual gray whales within both southern (n=100) and northern (n=106) feeding areas to assess possible stock structure using both mtDNA control region sequences and 8 microsatellite markers. Significant mtDNA differentiation was found when the subset of samples representing individuals (n=71) sighted over two or more years within the seasonal range of the PCFG were compared to the combined set of samples collected from the northern feeding area(s) (F_{ST}=0.01, p=0.005; Fisher's exact test, p=0.008) as well as when the PCFG samples were compared to only those samples which were collected off Chukotka, Russia (n=71, F_{ST}=0.01, p=0.012; Fisher's exact test, p=0.030). No significant differences were found for any of the comparisons utilizing microsatellites. These results indicate that structure is present among gray whales utilizing different feeding areas and suggest that matrilineal fidelity plays a role in creating such structure. The lack of differentiation detected using nuclear markers (χ^2 test, p=0.636, PCFG versus northern; p=0.753, PCFG versus Chukotka) suggests that individuals from different feeding areas may interbreed. These results are important in evaluating the management of the ENP gray whale population, especially in light of the Makah Tribe's proposal to resume whaling in an area of the Washington coast utilized by both feeding and migrating whales. Although the proposed hunt is designed to target whales migrating to/from the northern feeding grounds, the possibility of taking a PCFG whale cannot be eliminated. Increasing our understanding of recruitment into this group is needed to assess potential impacts of a hunt.

INTRODUCTION

The current distribution of gray whales is limited to the eastern and western margins of the North Pacific (Rice & Wolman, 1971), where a small western population (~130 individuals, Cooke *et al.,* 2008) and a much larger eastern population (~19,000 individuals based on surveys in 2006/2007, Laake *et al.,* 2009) are recognized. Much of what is known about the western population is derived from photo-identification and genetic studies of individuals on the population's primary feeding ground, which is located in the coastal waters of northeastern Sakhalin Island, Russia (Weller *et al.,* 1999; Weller *et al.,* 2008; LeDuc *et al.,* 2002; Lang *et al.,* 2010). Photo-identification studies have documented seasonal site fidelity and annual return of individuals to this feeding area (Weller *et al.,* 1999). Reproductive females are known to utilize the Sakhalin feeding ground in years when they are accompanied by calves as well as when they are pregnant or resting, and the return of many individuals first identified as calves accompanying their mothers has been documented (Weller *et al.,* 2009). Genetic comparisons of samples collected from gray whales feeding off Sakhalin with samples collected from whales in the eastern North Pacific (ENP) have supported recognition of the two populations as distinct, with differentiation in both mtDNA haplotype and microsatellite allele frequencies (LeDuc *et al.,* 2002; Lang *et al.,* 2010).

Gray whales in the ENP population feed in waters between California and the Bering, Beaufort, and Chukchi Seas during summer and fall. Most of the population then migrates south along the coast of North America to overwinter in the lagoons and coastal waters of Baja Mexico. Three primary calving lagoons are utilized, with some females known to make repeated returns to specific lagoons (Jones, 1990). Genetic studies have demonstrated small but significant mtDNA differentiation between females (mothers with calves) utilizing two of the primary calving lagoons and females sampled in other areas (Goerlitz *et al.,* 2003). An additional study, utilizing both mtDNA and microsatellites with samples collected from all three of the primary calving lagoons, also identified small but significant departure from panmixia between two of the lagoons using nuclear data, although no significant differences were identified using mtDNA (Alter *et al.,* 2009).

Sub-structuring within the feeding range of the eastern population could also be present. Although little is known about fidelity of gray whales feeding north of the Aleutians, a small number of individuals, referred to as the Pacific Coast Feeding Group (PCFG; IWC, 2010), are known to show fidelity to more southern feeding grounds located in the coastal waters between northern California and southeastern Alaska (Gilmore, 1960; Pike, 1962; Hatler & Darling 1974; Darling, 1984; Calambokidis *et al.,* 2002, 2010). Within these waters, photo-identification research, which commenced in the early 1970s, has identified some whales that demonstrate consistent return to specific areas within this larger region, although movements between areas within the region also occur regularly (Hatler & Darling, 1974; Darling, 1984; Calambokidis *et al.,* 2002, 2010). In addition, photographic evidence has shown that some whales considered part of the PCFG move at least as far north as Kodiak Island, Alaska (Calambokidis *et al.,* 2010, Gosho *et al*., 2011). Recent estimates of the annual abundance of the PCFG suggest that at most a few hundred individuals utilize this feeding area (Calambokidis *et al.,* 2010).

Satellite tagging studies of 18 whales off the coast of Oregon and California have provided additional information on the movements of individual whales considered part of the PCFG (Mate *et al.,* 2010). Although the duration of tag attachment differed between individuals, movement patterns of the tagged animals were variable, with some individuals remaining in a relatively small area within the larger PCFG seasonal range and others traveling more widely. Only two of the eighteen whales moved north of Washington while tagged; one of these animals traveled at least as far north as southeastern Alaska (Mate *et al.*, 2010). All six of the individuals whose tags continued to transmit through the southbound migration utilized the wintering area within and adjacent to Laguna Ojo de Liebre. Although this lagoon is by far the most heavily used of the three major wintering lagoons, these results raised the possibility that PCFG whales may demonstrate philopatry to this particular wintering area (Mate *et al.,* 2010).

Concern for the PCFG of gray whales has stemmed in part from recent interest in the resumption of whaling by the Makah Tribe in northwest Washington, an area used by migrating whales as well as by whales considered part of the PCFG. The current proposal by the Makah Tribe includes time/area restrictions which will limit the hunt to between 1 December and 31 May and will not allow hunting in the Strait of Juan de Fuca east of Cape Flattery. The Makah Tribe also proposes to compare photographs of any whales harvested in the hunt to a photo-identification catalogue of known PCFG whales and to suspend the hunt for the year if the number of known PCFG gray whales struck is equal to the annual allowable bycatch level calculated for the PCFG (Makah Tribal Council, 2011). These restrictions are designed to reduce the probability of killing a PCFG whale and to focus the hunt on whales migrating to/from feeding areas north of the PCFG. Nevertheless, it is impossible to ensure that no PCFG whales would be killed. Evaluating whether such kills would, over time, have the potential to deplete the PCFG requires an understanding of how individuals are recruited into the group. If recruitment into the area is exclusively driven by calves learning the location of feeding grounds from their mothers (i.e., internally), then a PCFG individual that is removed would not be replaced by immigration. However, if recruitment is largely external, such that some whales stop to feed during the migration and then return to the PCFG area as their primary feeding destination in subsequent years, then it is likely that any takes from the PCFG would be offset by immigration into the group by whales that in previous years fed in northern areas.

Understanding recruitment into the PCFG is relevant to management under the Marine Mammal Protection Act (MMPA). The goal of the MMPA is to maintain population stocks as functioning elements of their ecosystem. The National Marine Fisheries Service considers stocks to be demographically independent units, such that the population dynamics of the affected group is more a consequence of births and deaths within the group (internal dynamics) rather than of immigration or emigration (external dynamics). Thus, the exchange of individuals between population stocks is not great enough to prevent the depletion of one of the populations as a result of increased mortality or lower birth rates (NMFS, 2005).

Previous genetic studies of the PCFG whales have focused on evaluating patterns of recruitment. Initial work utilizing a simulation-based approach indicated that if the PCFG originated from a single recent colonization event in the past 40 to 100 years, with no subsequent external recruitment into the group, detectable mtDNA genetic differentiation would be generated (Ramakrishnan & Taylor, 2000). Subsequent empirical analysis, however, failed to detect such a signal when comparing 16 samples collected from known PCFG whales utilizing Clayoquot Sound, British Columbia, with samples (n=41) collected from individuals presumably feeding in more northern areas (Steeves *et al.,* 2001). Additional genetic analysis utilizing an extended set of samples (n=45) collected from whales within the range of the PCFG indicated that the level of genetic diversity and the number of mtDNA haplotypes identified were inconsistent with measures, based on simulations, which would be expected if recruitment into the group were exclusively internal (Ramakrishnan *et al.,* 2001). However, both simulation-based studies focused on evaluating only the hypothesis of founding by a single and recent colonization event and did not evaluate alternative scenarios, such as limited dispersal of whales from other areas into the PCFG, which could have implications for management (Ramakrishnan and Taylor 2000, Ramakrishnan *et al.,* 2001). More recently, Frasier *et al.* (In press) have shown significant levels of mtDNA differentiation when comparing samples collected from 40 individuals considered part of the PCFG with published data generated from 104 samples collected from ENP gray whales, most of which stranded along the migratory route (LeDuc *et al.,* 2002). These results suggest that matrilineally directed fidelity may play a role in use of this area and led the authors to support recognition of the PCFG as a distinct management unit.

The lack of available samples collected from gray whales feeding in northern areas has limited previous genetic studies from directly addressing the potential for demographic independence among whales utilizing different feeding regions within the ENP. Here we use samples collected from various locations north of the Aleutians as well as samples collected from within the seasonal range of the PCFG. A high proportion of the samples collected north of the Aleutians were collected from individuals harvested off Chukotka, Russia, where between 111 and 134 whales per year have been taken during aboriginal whaling over the last decade (IWC, 2010). We also increased the number of samples collected from whales within the seasonal PCFG range and, for those samples linked to photographed individuals, were able to further refine our representation of the PCFG by incorporating sighting histories of known individuals in some comparisons.

The primary goal of this study was to evaluate whether multiple demographically independent units of gray whales exist on feeding grounds, with a special focus on comparing PCFG whales with whales utilizing northern feeding areas. Although other scenarios are possible, here we test three hypotheses using data from both mitochondrial and nuclear markers (n=8 microsatellite loci):

1. No population structure (e.g., panmixia) is present among gray whales utilizing feeding areas in the ENP; individuals move between feeding areas and exhibit random mating. This hypothesis would be supported by a finding of no nuclear or mitochondrial differentiation between samples collected in northern versus southern feeding areas.
2. Utilization of feeding areas is influenced by internal recruitment, with calves following their mothers to feeding grounds and returning in subsequent years. Mating is random with respect to feeding ground affiliation. This hypothesis would be supported by a finding of significant differences in mtDNA haplotype frequencies when comparing samples collected on northern versus southern feeding grounds, but no significant differences are expected in microsatellite allele frequencies between groups of samples from specific geographic areas (i.e., "strata").
3. Utilization of feeding areas is influenced by matrilineal fidelity and mating is not random with respect to feeding ground affiliation. This hypothesis would be supported by a finding of significant differences in both mtDNA haplotype and microsatellite allele frequencies.

Support for the second hypothesis would indicate that groups of individuals feeding in northern and southern areas are demographically independent but not reproductively isolated, while support for the third hypothesis would provide support for both demographic independence and reproductive isolation.

METHODS

Sample Collection

A total of 277 samples were processed for this study. The majority of samples (n=185, including all samples collected between Northern California and British Columbia, Canada) were collected as biopsies from free-ranging individuals, with the remainder collected from individuals taken as part of the subsistence whaling (n= 75 samples from Chukotka) or from stranded individuals (n=17). Collection locations ranged from northern California to Barrow, Alaska and Chukotka, Russia (Figure 1).

For each of the biopsy samples collected, efforts were made to obtain a photograph of the biopsied whale. For whales biopsied between northern California and British Columbia, Canada, photographs were compared to photo-identification catalogues maintained by Cascadia Research Collective. This approach allowed sighting histories of individual individuals to be linked to samples and utilized (as described below) in the stratification of samples for comparisons.

Figure 1 shows that most of the PCFG samples utilized in this study came from the southern portion of the PCFG range. Although the original design of the study was to have both a Russian and a Barrow, Alaska strata, the sample size for the latter (n=14) was insufficient to characterize genetic frequencies from that area. We were therefore unable to directly address hypotheses about whether there are multiple demographically independent feeding units to the north of the Aleutian Islands.

Laboratory Processing

DNA extraction, PCR Amplification and Sequencing – DNA was extracted from samples using standard protocols. The 5' end of the hyper-variable mtDNA control region was amplified from extracted genomic DNA, using the polymerase chain reaction (PCR) and then sequenced using standard techniques (Saiki *et al.,* 1988; Palumbi *et al.,* 1991). DNA was amplified using a 25 ul reaction of 1ul DNA, 18.25 ul of water, 2.5 ul of buffer [10 mM Tris-HCl (pH 8.3), 50 mM KCl, 1.5 µl of 10 mM dNTP], 0.75 µl of each 10 µM primer, and 0.25 ul of Taq DNA polymerase. The PCR cycling profile consisted of 90°C for 2 min, followed by 35 cycles of 94°C for 50 sec, an annealing temperature of 60°C for 50 sec, and 72°C for 1 min, then a final extension of 72°C for 5 min. A 523 base pair region of the 5' end of the mtDNA control region was amplified using primers B (5'-TACCAAATGTATGAAACCTCAG - 3'; Rosel *et al.,* 1995) and TRO (5′- CCTCCCTAAGACTCAAGG-3′; developed at SWFSC). Both strands of the amplified DNA product were sequenced independently as mutual controls on the Applied Biosystems Inc. (ABI) model 3730 sequencer. All sequences were aligned using Sequencher v4.8

software (Gene Codes Corp., 2000). If discrepancies were found within the replication the sample was re-sequenced from extracted DNA. If the discrepancy was still not resolved, DNA was re-extracted from tissue and the sample was resequenced until the haplotype was confirmed. For a small number of samples (n=4), the mtDNA sequence contained an ambiguous base call which could not be resolved; these samples were excluded from the mtDNA analysis. In addition, if a sample was identified as having a mtDNA haplotype that was not found among any of the other samples, mtDNA amplification and sequencing was replicated to confirm the haplotype identity.

Nuclear DNA processing – Eight microsatellite loci isolated from other cetacean species were used to genotype the samples (Table 1). Extracted DNA was amplified using a 25 µl reaction of 1 µl of DNA, 18 µl of MilliQ water (Millipore, Bedford, MA), 2.5 µl of 10x PCR buffer (500 mM KCl, 100 mM Tris-HCl, pH 8.3, and 15 mM $MgCl_2$), 1.5 µl of 10 mM dNTP, 0.75 µl of each 10 µM primer, and 0.5 units of Taq DNA polymerase. The PCR cycling profile included 90 °C for 2.5 min, followed by 35 cycles of 94 °C for 45 sec, 1 min at the optimal annealing temperature (Table 1), and 72 °C for 1.5 min, then a final extension of 72 °C for 5 min. PCR products were assessed electrophoretically. Genotype data was generated on ABI's 3730 genetic analyzer and analyzed with ABI's Genemapper (version 4.0) software.

Sex determination - Samples were genetically sexed by amplification and Real-Time PCR (MX3000p, Stratagene Inc) of the zinc finger (ZFX and ZFY) genes. Sex was determined by the amplification pattern: males had two products and females had one (Morin *et al.,* 2005).

Quality Control – Quality control and sample tracking procedures, as detailed in Morin *et al.* 2010, were implemented for all laboratory processing by incorporating control samples (negative and positive) into all amplifications. In addition, a set of samples were randomly chosen to act as replicates for error tracking and error rate estimation. For these samples ("random replicates"), which represented ≥10% of all samples processed, the mtDNA sequence, sex, and microsatellite genotype were re-generated from DNA for each sample.

Analysis

Stratification of Samples – Two stratification hypotheses were tested in the analysis. The "Northern versus Southern" hypothesis assumed that individuals utilize each of these general regions in a relatively uniform manner such that sampling location within each stratum does not matter. The stratification used for the Northern-versus-Southern hypothesis included all samples described above (Figure 1). Those samples which were collected north of the Aleutian Island Chain were included in the "North" stratum, while all samples collected between northern California and southeastern Alaska (i.e. from within the described range of the PCFG) were included in the "South" stratum (Figure 1).

The second hypothesis is referred to as the "Fine-scale Feeding Aggregation" hypothesis. This hypothesis considers that there may be multiple feeding aggregations north of the Aleutians and hence sampling location within each stratum does matter. The only fine-scale area that was sampled adequately to capture genetic frequencies in the "North" stratum included the individuals hunted off Chukotka (Figure 2). The "Fine-scale Feeding Aggregation" hypothesis also used more stringent criteria than location and season to define individuals assigned to the PCFG stratum. The rationale for more stringent criteria is that photo-identification studies have indicated that whales utilizing the PCFG's seasonal range fall into two categories: 1) whales that return frequently and account for the majority of sightings, and 2) apparent stragglers from the migration that are sighted in only one year (Calambokidis *et al.,* 2010). The criteria for assigning samples to the PCFG stratum were intended to make this stratum representative of the first category of whales. Inclusion in the PCFG stratum for the "Fine-scale Feeding Aggregation" hypothesis relied on two criteria: 1) the sample was linked to a photographed animal with high or medium confidence, and 2) the photographed animal had been sighted two or more years within the season (June – November) and area representative of the PCFG.

Data Review – To avoid including duplicate samples, the Excel Microsatellite Toolkit (Park, 2001) was used to identify samples with identical genotypes, indicating that they may have been collected from the same animal. These sample pairs were then checked to see if they also shared the same mtDNA haplotype and sex, and, when possible, photo-identification records were used to confirm the genetic match. For all samples which shared identical mtDNA haplotypes, sexes, and genotypes, one sample from each pair was removed.

Genotyping Error Rate – For all plates of samples used to generate microsatellite genotypes, a random subset of samples, representing >10% of the samples on each plate, were assigned as replicates. Replicate and original genotypes were compared, and a per-allele error rate was calculated by determining the number of discrepant allele calls divided by the total number of allele calls compared across all loci.

Genetic Diversity – For the mtDNA, haplotypic diversity (h) and nucleotide diversity (π) were calculated using Arlequin 3.5.1.2 (Excoffier *et al.,* 2005). For the microsatellite data, the number of alleles per locus and observed and expected heterozygosities were calculated using custom R-code (eiaGenetics, available upon request[1]). Fstat (Goudet 1995) was used to calculate allelic richness for each stratum. Deviations from Hardy-Weinberg equilibrium (HWE) were assessed for each microsatellite locus using Genepop (version 4.0.11, Rousset 2008). Both the probability test (Guo & Thompson, 1992) and the test for heterozygote deficiency (Rousset and Raymond 1995) were conducted using the program defaults for the Markov chain parameters (10,000 dememorization steps, 20 batches, 5000 iterations/batch). Genepop was also used to test for linkage disequilibrium (LD) for each pair of loci. All tests were run for the combined dataset as well as for each stratum, and a sequential Bonferroni correction was applied across all tests for each stratum.

Genetic Structure – Pairwise estimates of genetic divergence were calculated using both F_{ST} and and Φ_{ST} (based on pairwise differences between sequences as the measure of genetic distance) for the mtDNA data as implemented in Arlequin 3.5.1.2 (Excoffier *et al.,* 2005). Statistical significance was assessed using 20,000 permutations. Fisher's exact test (Raymond & Rousset, 1995) was also used to test for mtDNA differentiation between strata using 100,000 replications to test for significance.

For the microsatellite data, F_{ST} (Weir &Cockerham, 1984), Jost's D (Jost, 2008), and a χ^2 test were used to assess genetic differentiation. These tests were implemented using custom code (eiaGenetics[1]) written in the statistical program language R (R Core Development Team, 2009). Statistical significance was determined from 10,000 permutations of each data set.

RESULTS

Data Review - Fifteen samples (including n = 11 samples collected from stranded whales) amplified at ≤5 microsatellite loci and were removed from the analysis. The remaining samples were genotyped for at least seven of the eight microsatellite loci. Fifty-six samples had microsatellite genotypes, mtDNA haplotypes, and sexes which matched at least one other sample in the dataset; these samples were removed from further analysis. No movements of animals between regions representing different strata were identified based on genetic matches (i.e., all samples sharing identical genetic profiles were part of the same stratum).

Genotyping Error Rate – Based on the samples randomly chosen for replication, a per-allele error rate of 0.16% was detected for the microsatellite data.

Genetic Diversity – Thirty-nine mtDNA haplotypes defined by 37 variable sites were identified from the 202 gray whale samples representing unique individuals (Table 2). Haplotype diversity (h) was high in all four strata ("Northern v. Southern" and "Fine-scale Feeding Aggregations") defined for the analysis (0.945 - 0.953). Nucleotide diversity (π) was also similar among the four defined strata (1.4 – 1.6%).

The frequency of each haplotype in the defined strata (including Barrow) is shown in Table 3. For the "Fine-scale Feeding Aggregations" strata, eighteen haplotypes were shared between Chukotka and the PCFG, with nine haplotypes found only in Chukotka and five haplotypes found only in the PCFG. For both Chukotka and the PCFG, many haplotypes were found in only one individual (n=12 haplotypes in Chukotka, n = 8 haplotypes in the PCFG).

The median-joining network shows the relationship among mtDNA haplotypes and their frequency in each stratum (Figure 4). MtDNA haplotypes from both Chukotka and the PCFG are dispersed throughout the network, and no phylogeographic pattern is apparent.

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A summary of microsatellite diversity for each locus is shown in Table 4. None of the tests for HWE were significant after the correction for multiple tests was applied. Significant linkage disequilibrium was found for only one pair of loci (EV14t and Gt023t) in the PCFG strata. No significant LD was found for these two loci in any of the other strata or for the combined dataset, so these loci were retained for the analysis.

Measures of genetic diversity for each stratum after averaging across loci are shown in Table 5. As in the comparisons of mtDNA diversity, nuclear diversity was similar across all strata.

Sex Ratio – A female bias was present among the samples, ranging from 1.3 – 1.5 females per male in each stratum (Table 6). This female bias is similar to that (1.47 females per male) described in Frasier *et al.* (In press) but contrasts with earlier studies (Steeves *et al.,* 2001; Ramakrishnan *et al.,* 2001). The male bias (1.7 males per female) described in Steeves *et al.* 2001 was based on a small sample size (n=16 samples). When the gender determination method utilized here was applied to the sample set used in the Ramakrishnan *et al.* 2001 study, only a slight male bias was identified (1.25 males/female). These results contrast with those presented in Ramakrishnan *et al.* (1.8 males/female) and indicates that an issue with the gender determination assay used at that time was responsible for falsely identifying some samples as males.

Genetic Structure – The results of the mtDNA comparisons are shown in Table 7. Low but statistically significant differences were detected when the PCFG stratum was compared with the North stratum (Φ_{ST} = 0.030, p= 0.0118; F_{ST}= 0.010, p=0.0052; Fisher's exact test p=0.0080) and with the Chukotka stratum (Φ_{ST} = 0.020, p=; F_{ST}= 0.012, p=0.0295; Fisher's exact test p = 0.0304). The F_{ST} comparisons for mtDNA were also significant when the North and South strata were compared (F_{ST}=0.007, p = 0.0272), although none of the other mtDNA comparisons involving the South stratum demonstrated significant differences. None of the comparisons across strata utilizing the microsatellite data were significant (Table 8), providing no evidence of nuclear structure among feeding areas.

DISCUSSION

The results presented here are consistent with the second hypothesis that was evaluated, indicating that utilization of at least some feeding areas is influenced by internal recruitment (e.g., matrilineal fidelity), but that individuals from different feeding grounds interbreed. The extent of differentiation, while significant, was low and was detected only in the mtDNA comparisons. Diversity within the PCFG strata was high and similar to that found among strata in the north.

The low level of mtDNA differentiation between strata, as well as the high diversity found in the PCFG, could be a reflection of relatively recent colonization (or re-colonization following depletion of the population by commercial whaling) of the PCFG area. If recruitment into the PCFG is driven exclusively by the return of individuals which followed their mothers to the area as calves, then over time those mtDNA haplotypes originally found only in males or non-reproducing females would be removed via genetic drift, while haplotypes found in females and their returning offspring would build to higher frequencies. By this process, genetic differences would develop between the PCFG and other feeding aggregations, and, given its small size, the PCFG would be expected to maintain low haplotypic diversity. However, if colonization of the PCFG area occurred relatively recently, strong mtDNA differences between the PCFG and individuals feeding further north may not have had time to develop, and the number and distribution of haplotypes in the PCFG may not yet have been affected by genetic drift.

The low level of mtDNA differentiation and high diversity is also consistent with a scenario in which the population structuring is largely driven by matrilineal fidelity (perhaps over longer time scales) but in which some low-level external recruitment also occurs. Some degree of external recruitment would slow the accumulation of genetic differences between the PCFG and northern individuals. As well, external recruits would likely carry haplotypes not previously found among PCFG individuals and would increase the number and diversity of haplotypes found.

These two explanations are not exclusive, and it is plausible that some combination of these scenarios (recent colonization and/or low-level external recruitment) may be occurring. The origin of the PCFG is unknown, and use of the area may date back to the "Little Ice Age" [ca. 1450-1850] when access to the Bering Sea feeding areas would have been limited by heavy ice and some whales may have started to use the PCFG range. Gray whales have been recorded feeding in the southern portion of the PCFG range as early as 1926, when a single gray whale, which was reported to have been feeding with four other whales, was taken by the Trinidad whaling station off the entrance to the Crescent City Harbor in July (Howell & Huey, 1930). The repeated return of individual whales to the area was first documented starting in the 1970s (Hatler & Darling, 1974; Darling, 1984). Photo-identification studies have identified some individuals that have consistently returned to the PCFG seasonal range over time, including some known reproductive females and their calves (Calambokidis *et al.,* 2010). However, "new" whales continue to appear annually and many are resighted in subsequent years (Calambokidis *et al.,* 2010). These new individuals may be internal recruits that were not sighted as calves, but could also be external recruits that return to the area following a successful feeding season. Even if some low-level external recruitment to the area is occurring, however, the differences in mtDNA haplotype frequencies observed in our comparisons indicate that matrilineal fidelity to the area does occur and is important in influencing population structure on the feeding grounds utilized by ENP gray whales.

Conception in gray whales is thought to primarily occur during a three week period between late November and early December (Nov 27 – Dec 13), although if no conception occurs during this first period, a second estrus may occur about 40 days later when whales are on or near their wintering grounds (Rice & Wolman, 1971). Rugh *et al.* (2001) estimate that the median (peak) sighting dates for the southbound migration are 12 December for Unimak Pass, Alaska, suggesting that many gray whales would be north of the PCFG seasonal range during the first mating period. In addition, of the eight individuals which had retained their satellite tags when they started the southbound migration, four (two males and two females) remained on the PCFG feeding ground after mid-December, with two staying until mid-January or later (Mate *et al.,* 2010). These findings raise the possibility that some segregation in breeding could occur based on feeding ground affiliation. However, while the results of the mtDNA comparisons indicate that matrilineal fidelity is generating structure among feeding areas utilized by ENP gray whales, the lack of differentiation found in the nuclear comparisons supports mixing of individuals from different feeding areas while breeding.

The genetic signal of matrilineal fidelity in the PCFG is less marked than that seen among gray whales feeding off Sakhalin Island in the western North Pacific (WNP). Although significant differences in F_{ST} and Φ_{ST} were observed in the mtDNA comparisons between the PCFG and the northern strata, the magnitude of differentiation is lower than that seen in the WNP versus ENP comparisons (F_{ST}=0.068, p≤0.001; Lang *et al.,* 2010). In addition, a pattern of matrilineal fidelity to the area is also reflected in the distribution of haplotypes among individuals in the western population, such that two haplotypes are found in very high frequencies (representing 36% and 31% of all sampled individuals, Lang *et al.,* 2010). This pattern would be expected if utilization of this area was driven in large part by the continued return over time of a small number of females and their offspring (and eventually their offspring's offspring), and examination of the haplotypes carried by individuals revealed that 16 of the 23 known reproductive females (between 1995 and 2007, Weller *et al.,* 2008) share one of these two common haplotypes (Lang, 2010). In the PCFG stratum, however, the three highest frequency haplotypes are found in only 10 to 13% of sampled individuals, which is consistent with more recent colonization of the PCFG area by a relatively large number of founders. In addition, genetic differentiation based on microsatellite allele frequencies was observed between the Sakhalin and ENP strata (F_{ST} = 0.009, p≤0.001; Exact test, p≤0.001), indicating that, unlike what has been suggested in the PCFG, some degree of reproductive isolation also occurs between these groups.

The results presented here are consistent with those presented in Frasier *et al*. (In press), which also found evidence of maternally driven structure when comparing samples collected from PCFG whales with samples from LeDuc *et al*. 2002, which were collected primarily from animals which stranded along the migratory route. The samples utilized in the Frasier *et al*. (In press) study were all collected from Clayoquot Sound, British Columbia. In contrast, the majority of samples representing the PCFG in this study were collected from animals in the waters off northern California, Oregon, and Washington, with only 11 samples collected from waters off British Columbia. Although some whales are known to move throughout the range of the PCFG, sightings of most whales are concentrated within subareas of the range (Calambokidis *et al*. 2010). This pattern is illustrated in Figure 7 of Calambokidis *et al.* (2010), which shows the distribution of latitudes of sightings for whales with 6 or more sightings after 1 June from 1998-2008. The patterns evident in this figure reveal that individual gray whales do not utilize the range of the PCFG randomly and indicate that, while there is likely overlap among the individuals sampled in Frasier *et al*. (In press) and the current study, neither represents random sampling across the range of the PCFG. To date, the photographs and/or genetic identities of sampled whales in the Frasier *et al*. (In press) study have not been compared with those used in the current study. In the future, such comparisons, along with the collection of additional samples from whales in the northern portion of the PCFG range, would be valuable in allowing sampling effort to be more evenly distributed throughout the range of the PCFG.

As aforementioned, the results presented here are consistent with the hypothesis that utilization of at least some feeding areas by ENP gray whales is influenced by internal recruitment. Within the PCFG, these findings are concordant with photo-identification records demonstrating site fidelity of individuals, including some known reproductive females and their calves, to the seasonal range (Calambokidis *et al.,* 2010). However, interpretation of the results is complicated by our lack of understanding of the potential for structuring within the northern feeding ground(s). If there is no structure on the feeding grounds north of the Aleutians, then the northern strata (both "north" and "Chukotka") can be considered representative of the genetic diversity of whales feeding throughout the northern feeding area. As such, the mtDNA differences observed here would be driven by fidelity of individuals to the PCFG seasonal range. However, if structuring is present among northern feeding areas, then the differences demonstrated here may be influenced by fidelity of individuals in either or both areas (Chukotka and PCFG). The collection of additional samples from northern feeding areas would be valuable in further elucidating the mechanisms creating the observed differences and in evaluating whether structuring is present among whales utilizing the northern feeding grounds.

Although the lack of nuclear differentiation found in our study indicates that gray whales from different feeding regions may be interbreeding, the significant differences in mtDNA haplotype frequencies that were identified in the study suggest that groups of gray whales utilizing different (northern versus southern) feeding regions are demographically independent. A similar pattern has been observed among humpback whales in the North Atlantic, where four feeding regions are present (Katona & Beard, 1990; Stevick *et al*., 2006). Within feeding regions, individuals demonstrate intra- and inter-seasonal site fidelity, with only low levels of interchange between regions (Stevick *et al*., 2006). Although most of the whales from these four feeding regions share a common mating ground in the West Indies (Katona & Beard, 1990; Clapham *et al.,* 1993; Palsbøll *et al.,* 1997; Stevick *et al.,* 1998), individuals utilizing the Gulf of Maine have been classified as a separate feeding stock, based on matrilineally-derived fidelity of individuals to this area and the assumption that, should this subpopulation be extirpated, repopulation by whales using adjacent areas would not occur on a management timescale (Waring *et al.,* 2000). It has been suggested that the timeframe for management should be, at most, decadal in scope (i.e., <100 years; Clapham *et al*., 2008).

Future Work - The low level of differentiation identified, as well as the high diversity found in the PCFG strata, may indicate relatively recent colonization of the PCFG but is also consistent with a scenario in which some low-level external recruitment into the PCFG may occur. Relatedness analysis, in which microsatellite genotypes are used to identify putative parent-offspring pairs, would provide insight into the proportion of internal versus external recruitment that is occurring. Such analysis would require genotyping additional microsatellite loci for sampled individuals and would benefit from the collection of additional samples from individuals within the PCFG.

As part of previous work exploring genetic differentiation between gray whales in the eastern and western North Pacific (Lang *et al.,* 2010), the genetic profiles of samples collected from individuals on the Sakhalin feeding ground (n=142) were compared to those generated from samples collected in the eastern North Pacific (n=136). Two individuals that were sampled off Sakhalin had matching genders, genotypes (n=13 loci), and mtDNA haplotypes to two individuals sampled off central California in 1995 (Lang, 2010). Although subject to caveats, these genetic matches may have represented movements of gray whales between the eastern and western North Pacific. Given that additional gray whale samples from feeding grounds in the ENP have been processed as part of this study, an expanded genetic comparison of all processed samples is currently underway to look for additional matches between the eastern and western populations.

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Figure 1. Map of sample collection locations showing the "Northern versus Southern" stratification

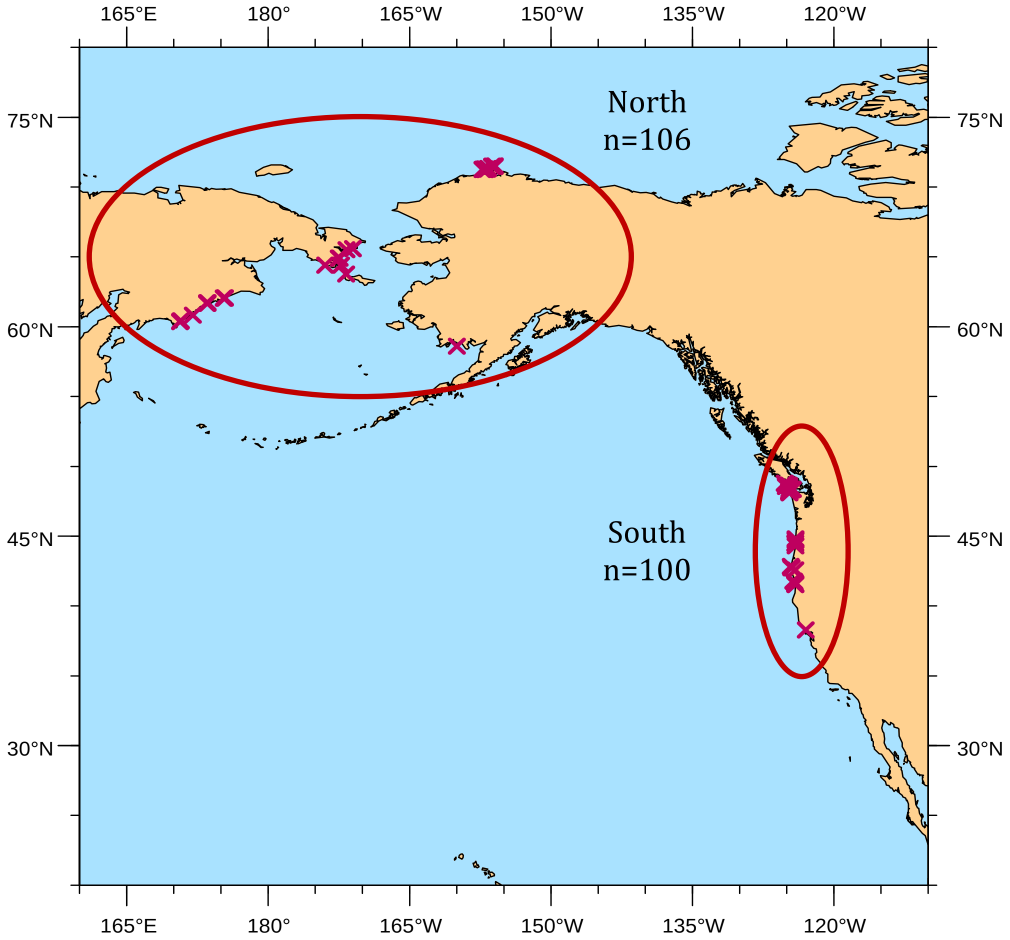

Figure 2. Map of sample collection locations showing the “Fine-scale Feeding Aggregations” stratification

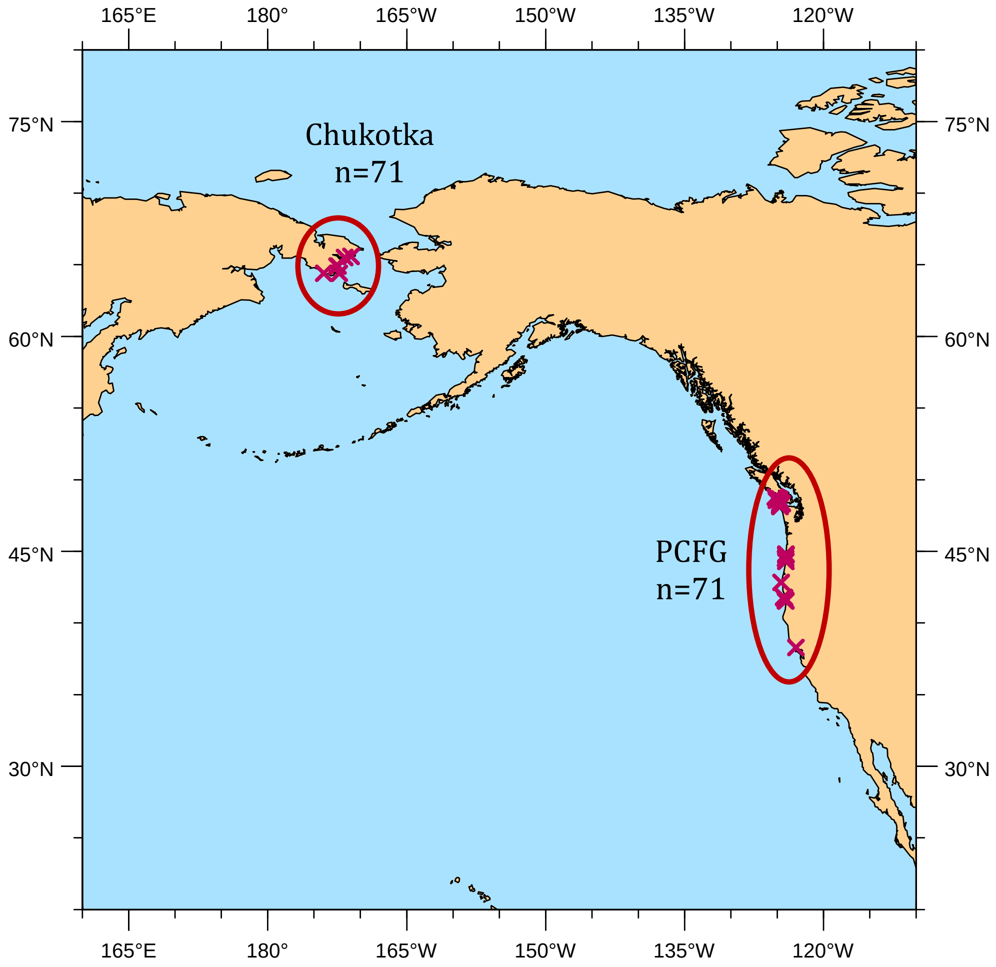

Table 1. Microsatellite loci used in the study. Includes the species for which primers were initially designed, size of repeats, annealing temperature (T_a), and reference listing primer sequences.[2]

Locus	Source Species	Repeat Size (bp)	T_a (°C)	Reference
EV14t	*Megaptera novaeangliae*	2	55	Valsecchi and Amos 1996
EV94t	*Megaptera novaeangliae*	2	52	Valsecchi and Amos 1996
Gata028t	*Megaptera novaeangliae*	4	54	Palsboll *et al.,* 1997
Gata417t	*Megaptera novaeangliae*	4	54	Palsboll *et al.,* 1997
Gt023t	*Megaptera novaeangliae*	2	54	Palsboll *et al.,* 1997
RW31t	*Eubalaena glacialis*	2	54	Waldick *et al.,* 1999
SW13t	*Physeter macrocephalus*	2	55	Richard *et al.,* 1996
SW19t	*Physeter macrocephalus*	2	55	Richard *et al.,* 1996

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[2] For all primers, the sequence has been modified from the original design by placing the sequence GTTTCTT on the 5' end of the reverse primer (Brownstein *et al.,* 1996)

Table 2. Sequence statistics for gray whale mitochondrial DNA control region sequences for the strata used in the population structure analysis

Strata		No. of Samples	No. of Haplotypes	Gene Diversity (h)	Nucleotide Diversity (π)
All		202	39	0.955 (±0.004)	0.0151 (± 0.008)
"Northern v. Southern"	North	103	32	0.952 (± 0.008)	0.0141 (± 0.007)
	South	99	29	0.953 (± 0.007)	0.0160 (± 0.008)
"Fine-scale Feeding Aggregations"	PCFG	71	23	0.945 (± 0.010)	0.0148 (± 0.008)
	Chukotka	69	27	0.953 (± 0.011)	0.0142 (± 0.007)

Table 3. The number of samples with each mtDNA haplotype for each stratum.

	"Northern v. Southern"		"Fine-scale Feeding Aggregations"		
MtDNA Haplotype ID	North (n=103)	South (n=99)	Chukotka (n=69)	PCFG 2 (n=71)	Barrow (n=14)
1	10	7	8	7	2
2	3	7	2	4	0
3	14	4	9	1	1
4	5	9	4	6	0
5	1	2	1	1	0
7	7	8	4	6	0
8	1	3	1	2	0
9	1	0	1	0	0
11	3	3	2	3	1
12	5	4	4	3	1
13	5	10	3	9	0
14	1	9	1	7	0
15	3	0	0	0	2
16	1	0	0	0	1
17	1	0	0	0	0
18	3	2	3	2	0
20	6	4	1	2	2
21	2	3	1	3	1
22	1	0	1	0	0
23	5	1	4	0	0
24	2	3	2	3	0
25	6	2	4	1	0
26	2	1	1	0	1
27	0	4	0	4	0
28	2	2	2	2	0
29	2	1	2	0	0
30	0	1	0	1	0
31	1	0	1	0	0
33	5	3	4	1	0
35	1	0	0	0	1
36	1	1	0	1	1
38	1	0	1	0	0
39	0	1	0	0	0
42	1	0	1	0	0
43	1	0	1	0	0
44	0	1	0	0	0
45	0	1	0	0	0
46	0	1	0	1	0
47	0	1	0	1	0

Figure 4. Median joining network

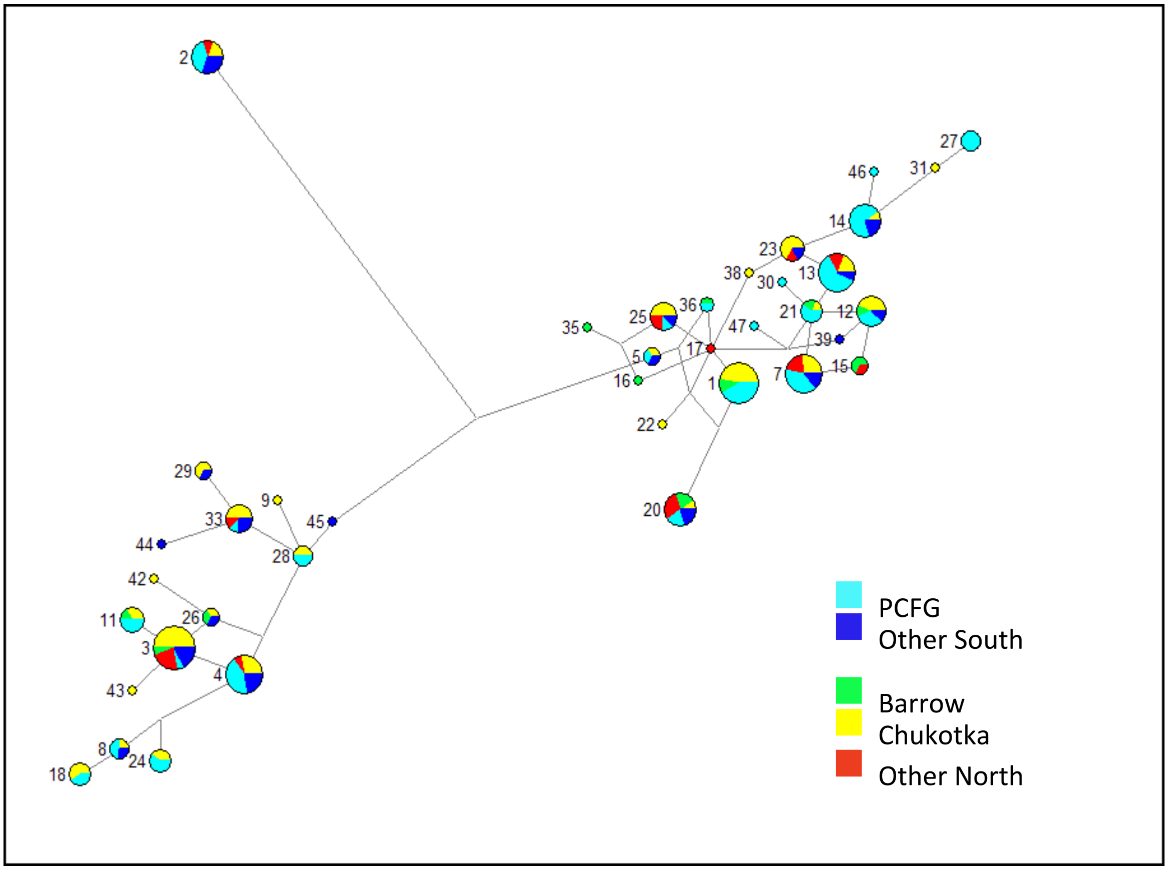

Table 4. Characteristics of the microsatellite loci utilized in the study.

Locus	**Number of alleles**	**Number of missing genotypes**	**He**	**Ho**	**HWE (prob)**
EV14t	10	0	0.829	0.850	0.533
EV94t	11	1	0.790	0.766	0.065
Gata028t	7	0	0.766	0.777	0.656
GATA417t	6	1	0.715	0.737	0.690
Gt023t	8	0	0.730	0.714	0.220
RW31t	10	0	0.830	0.782	0.017
SW13t	7	0	0.603	0.612	0.775
SW19t	10	1	0.709	0.707	0.213

Table 5. Gene diversity for the nuclear DNA data set, including the mean number of alleles, mean observed heterozygosity, and mean allelic richness.

Strata		No. of Samples	Mean number of alleles	Mean Ho	Mean allelic richness
"Northern v. Southern"	North	106	8.25	0.728 (±0.068)	8.18
	South	100	8.38	0.758 (±0.088)	8.36
"Fine-scale Feeding Aggregations"	PCFG	71	7.38	0.752 (±0.085)	7.37
	Chukotka	71	7.88	0.737 (±0.095)	7.86

Table 6. The sex ratio for each strata.

Strata		No. of Females	No. of Males	Ratio
Overall		117	85	1.4
"Northern v. Southern"	North	61	42	1.5
	South	56	43	1.3
"Fine-scale Feeding Aggregation"	PCFG	42	29	1.5
	Chukotka	41	28	1.5

Table 7. Results of MtDNA comparisons across strata. Significant p-values are shown in bold.

Pairwise Comparison	φst	p-value	F_{st}	p-value	Fisher exact test p-value
North (103) v. South (99)	0.006	0.1295	0.007	**0.0272**	0.0693
North (103) v. PCFG (71)	0.020	**0.0232**	0.012	**0.0052**	**0.0080**
Chukotka (69) v. South (99)	0.011	0.0872	0.005	0.0932	0.2234
Chukotka (69) v. PCFG (71)	0.030	**0.0118**	0.010	**0.0295**	**0.0304**

Table 8. Results of nuclear comparisons across strata

Pairwise Comparison	F_{st}	p-value	Jost's D	p-value	X^2 p-value
North (106) v. South (100)	-0.002	0.9740	-0.003	0.9491	0.9331
North (106) v. PCFG (71)	-0.002	0.8362	-0.001	0.8032	0.7532
Chukotka (71) v. South (100)	-0.002	0.9520	-0.003	0.9021	0.9021
Chukotka (71) v. PCFG (71)	-0.001	0.7303	0.000	0.6813	0.6364

Late-Feeding Season Movements of a Western North Pacific Gray Whale off Sakhalin Island, Russia and Subsequent Migration into the Eastern North Pacific

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ABSTRACT

The western population of North Pacific gray whales (WGW), once thought extinct, is now estimated at 130 individuals and feeds primarily off northeastern Sakhalin Island, Russia, during summer. The population is critically endangered, facing anthropogenic threats throughout its range from nets, ships, and oil development, but present migration routes and wintering areas remain unknown. On 4 October 2010, a subcutaneous Argos tag was applied following protocols established by the International Whaling Commission to a 13-year-old male (named “Flex”) in good body condition off Piltun Lagoon, northeastern Sakhalin Island. Flex was first seen as a calf off Sakhalin in 1997. State-space modeling of fall near-shore movements for 68 days post-tagging identified a small home range foraging area within 45km of the tagging site. These data are unique as local weather conditions during this time generally prevent other forms of whale observation. On 11 December, Flex departed Sakhalin and began migrating across the Okhotsk Sea, Bering Sea, and Gulf of Alaska. By 5 February, Flex was within 20 km of the central Oregon coast, overlapping spatially and temporally with the last few weeks of the usual eastern gray whale southbound migration. Flex’s migration segments were linear, high speed (averaging 6.5 km/h), and included deep water far offshore, suggesting open-water navigation skills not previously attributed to gray whales, who are considered coastal and shallow-water oriented. State-space modeling (considering directionality and speed) identified the basin-wide movements as “migration” rather than “wanderings" associated with foraging behavior. Flex’s movements do not preclude other migration routes or winter destinations for WGWs. Additional WGW tagging is needed to identify other areas of use. The resulting data will have high conservation value and be useful in potential mitigation of anthropogenic activities.

BACKGROUND

The western population of North Pacific gray whales (Eschrichtius robustus, WGW) once thought to be extinct was re-discovery off northeastern Sakhalin Island, Russia and is critically endangered (IUCN, 2008). The population is estimated to contain about 130 individuals age one or older, of which only about 25 are reproductive females (Cooke et al., 2008), and it faces a number of anthropogenic threats throughout its range, including fatal interactions with coastal net fisheries off Japan (Weller et al., 2008; Bradford et al., 2009) along its presumed migration route(s) and oil development in and near its principal summer feeding area (IUCN, 2009). The wintering area of the present population is unknown but, based on the limited available information, has been suggested as south of Honshu, Japan, off the coast of southern China in the South China Sea and the Gulf of Tonkin (Weller et al., 2002), or possibly off North America (Ilyashenko, 2009).

Satellite telemetry has been proposed repeatedly as an efficient way to investigate the migratory routes and wintering grounds of western gray whales and scientists have been cautious about tagging because of the population's very low numbers. After considerable discussion by the IWC Scientific Committee from 2006-10 and various panels convened under the auspices of IUCN from 2006-8 (summarized for the U.S. Marine Mammal Commission and IUCN by Weller, 2008), the research tagging effort reported here was undertaken to tag and track up to 12 of whales during the late summer of 2010 to ascertain winter migration route(s) and reproductive area(s).

METHODS

We used Wildlife Computers Spot-5 Argos transmitters epoxy-cast in Stainless steel cylinders for nearly complete implantation. Insertion blades and attachments for WGWs were similar to those used on 18 eastern NP gray whales (EGW) in 2009/10 (Mate, 2010). The latter field study was an efficacy test prior to using the tags on WGWs. The tags were applied by using a modified air-powered ARTS applicator and specialty pushrods (Mate et al. 2007).

The research was based from the 50 m M/V Igor Maximov, which was at sea from 3 September to 7 October 2010. Although we encountered technical difficulties with the supplied small tagging vessel and significant weather problems (including remnants of two typhoons and two gales), we tagged a whale on the last field-operational day of the extended cruise.

We followed the protocols established by the IWC special steering committee on western North Pacific Gray whale telemetry, which required tagging only known adult males in good body condition. On 4 October 2011, we tagged a13 year old male known as Flex off the northeast coast of Sakhalin Island, Russia (Figure 1 inset), where the whale had first been seen as a calf in 1997. Although the tag was not completely deployed, it provided location data for 124 days.

RESULTS

Flex stayed along the Sakhalin Island coast within 45 km of the tagging site and within 5 km of shore for 68 days (Figure 1). These near shore movements suggest foraging behavior. In mid-December Flex crossed the Sea of Okhotsk to the west side of the Kamchatka Peninsula, went around the southern end of the peninsula and departed the east coast in early January. The tagged whale crossed the western and central Bering Sea in one week to arrive at the shallow shelf break near a major canyon and then proceeded south passed the Pribilof Islands and through the eastern Aleutian Islands before crossing the Gulf of Alaska and heading south 20-25 Km off the Washington and Oregon Coasts (Figure 2). He was last located by satellite 20 Km off Siletz Bay, Oregon (~45*N) on 5 February, which over-lapped with the last few weeks of the usual ENP gray whale southbound migration through this same area.

Despite ambiguities in the accuracy of many Argos location classes, the course heading across the western Bering Sea varied within just a few degrees for a week. Such linearity in the Argos track makes significant errors in the actual distance traveled unlikely compared to the Argos-derived path. The Argos track length may actually be a conservative estimate, but still resulted in sustained swimming speed estimates for various segments of travel (Table1) substantially higher than those normally observed for EGWs during their southbound migration (Herzing and Mate, 1989; Granite Canyon ref).

CONCLUSIONS AND DISCUSSIONS

The very liner movement of Flex so far from shore suggests good open water navigation skills not previously attributed to gray whales. ENP gray whales have been considered more coastal or shallow-water oriented. State-space modeling suggests the long-range movements of Flex across the Sea of Okhotsk, Bering Sea, and Gulf of Alaska are directed migration movements rather than “wanderings", usually indicative of foraging behavior. During the Bering Sea and North Pacific travel segments, the whale's average speeds were >6.5 km/h, 50% higher than average speeds observed for six 2009-tagged EGWs migrating south in 2010 (Mate, 2010).

Flex has previously visited the eastern North Pacific, confirmed by photo matching (Weller et al., IWC/SC63/BRG6) and two other WGWs have been genetically matched to southern California (Lang et al., IWC/S63/BRG10). The results demonstrated by this whale do not preclude other migratory destinations for other WGWs or even this whale during other winters. The possibilities identified from the tagging, genetics, and the photo-ID papers suggest additional WGW taggings would be useful to identify other possible winter migratory routes and/or destinations. We took 13 tags to Russia in anticipation of tagging 12 whales in 2010. The remaining 12 tags are still in Russia. We suggest tagging 12 more WG whales to increase the total sample size to 10% of the estimated population. The use of a mother ship would help assure our ability to move more widely if necessary to find adequate candidate whales for tagging. An improved tagging boat would increase the probability of success. An earlier tagging season would avoid seasonally predictable bad weather. Being able to tag both males and females would dramatically improve the probability of successfully deploying additional tags and develop information about possible sexual differences in: winter migratory routes; foraging area departure timings; reproductive destinations; wintering area arrival timings; the amount of time spent in wintering areas; turnover rates in wintering areas, and spring migration re-entry routes and timing back into the summer feeding areas. All of these issues might identify areas or specific anthropogenic activities that could be risks to WGWs, as well as mitigation possibilities.

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Table 1. The durations, estimated distances, and speeds of Flex, a western gray whale, during the late summer and early fall feeding season near Sakhalin Island, Russia and subsequent migratory movements to the eastern North Pacific.

Waypoint	Date	Distance-km	Days	Avg. Speed
Deploy	10/4/2010 0:22:00			
Depart Sakhalin	12/11/2010 21:44:00	1018	68.9	0.6
Arrival W Kamchatka	12/16/2010 23:59:00	899	6.0	6.2
Depart E Kamchatka	1/2/2011 6:04:00	1185	16.4	3.0
Arrival Bering Shelf	1/9/2011 21:28:00	1324	7.7	7.1
Arrival Shumagin Islands	1/18/2011 21:44:00	1540	10.0	6.4
Arrival west coast U.S.	2/2/2011 23:33:23	2520	14.9	7.1

Cumulative		
Distance-km	Days	Avg. Speed
899	6.0	6.2
2084	22.4	3.9
3408	30.1	4.7
4948	40.1	5.1
7468	55.0	5.7

Figure 1. The study area at the northeast end of Sakhalin Island in the southern Sea of Okhotsk (inset), showing the near shore movements of “Flex” for 69 days within the traditional summer feeding area (4 October to 11 December 2010) just east of Piltun Lagoon.

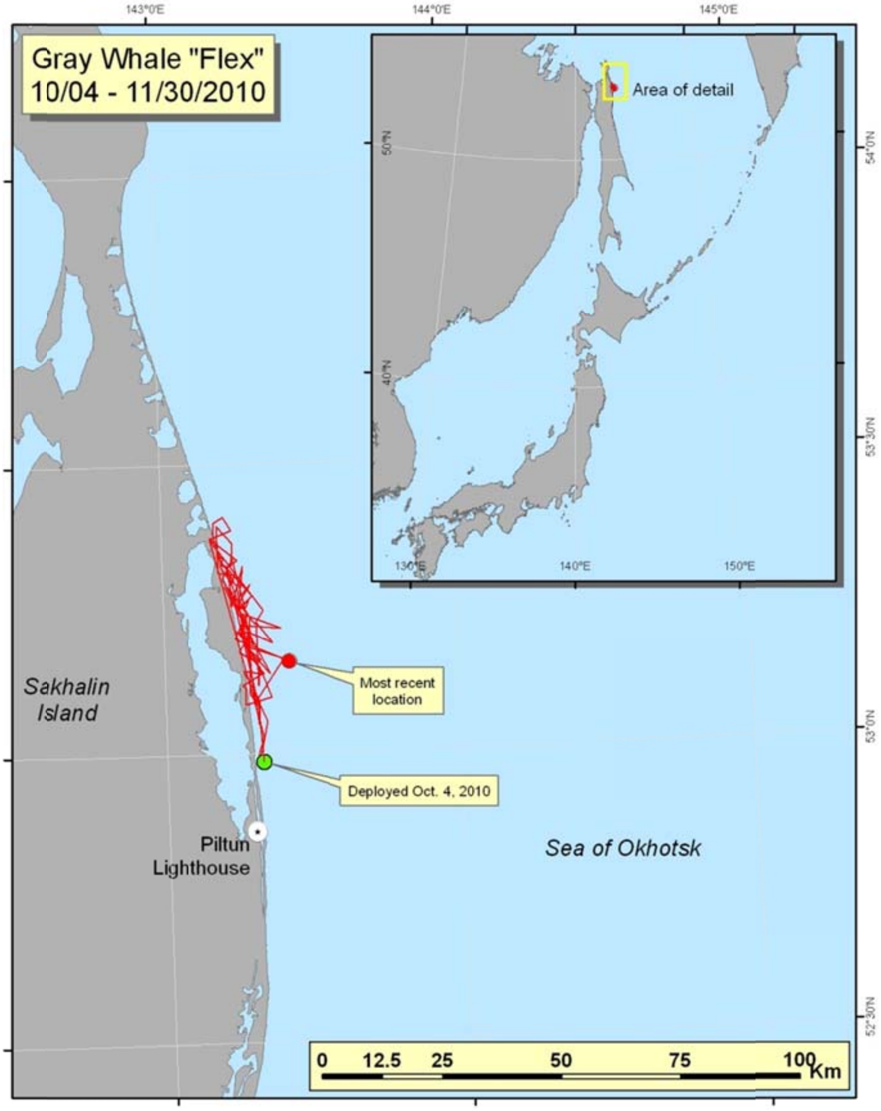

Figure 2. The 124 day movements of a 14 year old male western North Pacific gray whale “Flex” from 4 October 2010 to 5 February 2011.

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Marine biology

Critically endangered western gray whales migrate to the eastern North Pacific

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Western North Pacific gray whales (WGWs), once considered extinct, are critically endangered with unknown migratory routes and reproductive areas. We attached satellite-monitored tags to seven WGWs on their primary feeding ground off Sakhalin Island, Russia, three of which subsequently migrated to regions occupied by non-endangered eastern gray whales (EGWs). A female with the longest-lasting tag visited all three major EGW reproductive areas off Baja California, Mexico, before returning to Sakhalin Island the following spring. Her 22 511 km round-trip is the longest documented mammal migration and strongly suggests that some presumed WGWs are actually EGWs foraging in areas historically attributed to WGWs. The observed migration routes provide evidence of navigational skills across open water that break the near-shore north–south migratory paradigm of EGWs. Despite evidence of genetic differentiation, these tagging data indicate that the population identity of whales off Sakhalin Island needs further evaluation.

1. Introduction

Gray whales (*Eschrichtius robustus*) occur in both the eastern and western North Pacific Ocean [1]. Considered separate populations, both were severely depleted by commercial whaling. Eastern gray whales (EGWs) have recovered and are now thought to be near carrying capacity [2]. Western gray whales (WGWs), once thought to be extinct, currently number approximately 130 individuals and are listed as critically endangered by the International Union for Conservation of Nature [3]. Historically, widely ranging along the Asian coast, contemporary WGW aggregations are known primarily from summer feeding grounds off Sakhalin Island (SI), Russia [4]. WGWs were thought to winter off southern China [4], but current winter reproductive areas and migratory corridors are unknown. Here, we use satellite-monitored tracking data to conduct the first investigation of WGW migratory corridors and breeding areas to better evaluate threats to the population. The tag data reveal extensive migrations to traditional EGW breeding habitats, calling into question the identity of the WGW stock.

2. Material and methods

The International Whaling Commission's WGW Satellite Tagging Steering Committee established tagging protocols followed throughout two expeditions [5,6]: from 1 September to 7 October 2010 and 21 August to 22 September 2011. Only adult males in good body condition [7] were considered 2010 tagging candidates. Prior to a tagging approach, we visually identified whales from unique pigmentation patterns,

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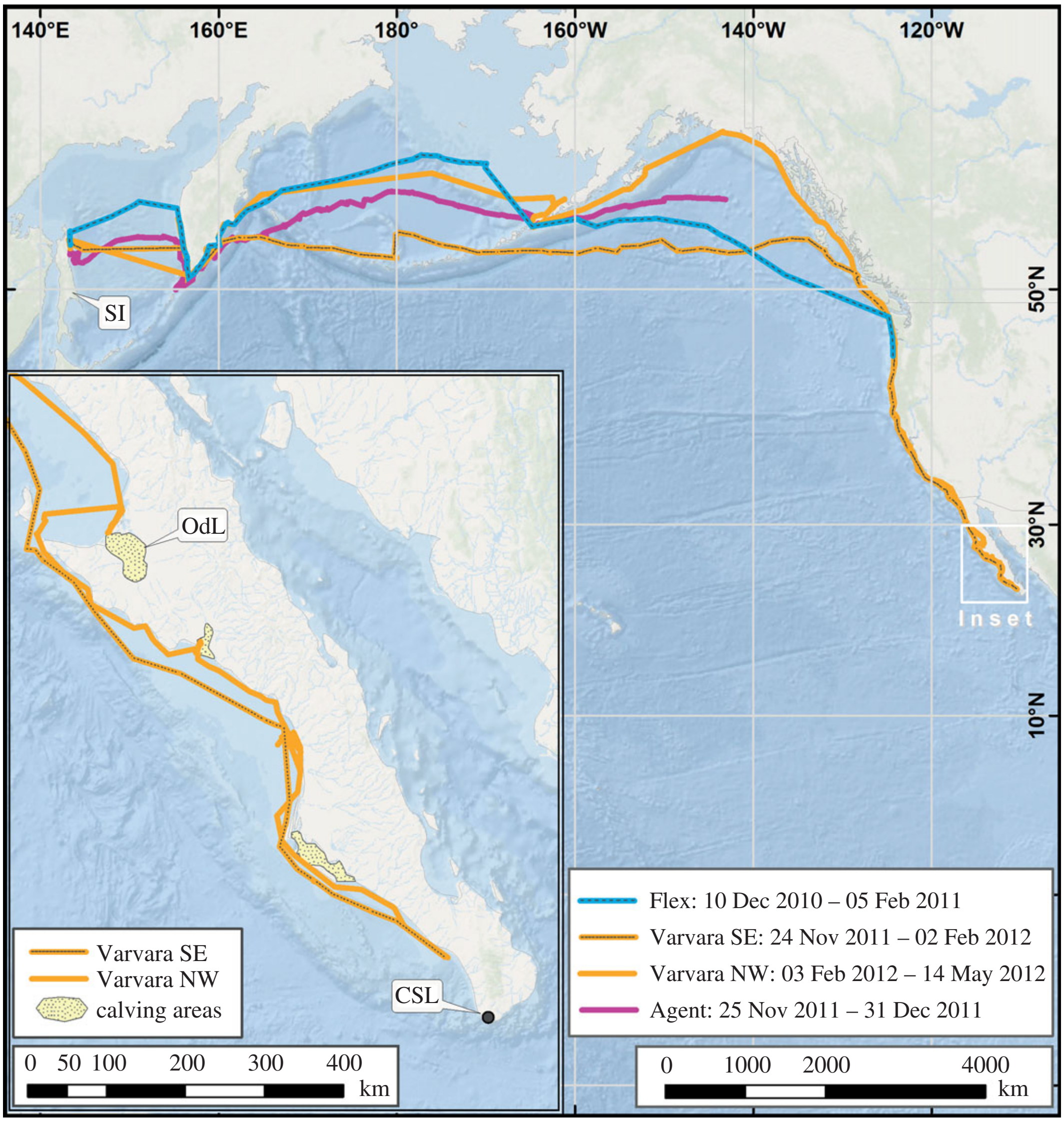

Figure 1. Routes of three western gray whales migrating from Sakhalin Island, Russia, to the eastern North Pacific. The legend depicts departure and arrival/end dates. Varvara visited all three major eastern gray whale reproductive areas off Baja California, Mexico (inset). (Online version in colour.)

using a WGW photo-identification catalogue. Sex is known for almost 80% of catalogued individuals from previous biopsy sampling, and many individuals were photographed as calves allowing age determination. Initially in 2011, only juveniles less than 6 years and females that had calves that year were not candidates. The latter criterion was later amended to allow tagging of females in good body condition that had weaned a calf.

We conducted tagging from a variety of small (less than or equal to 7 m) vessels powered by inboard diesel or four-stroke gas outboard engines, which were launched from the 50 m *Igor Maximov* support ship. We deployed tags from a distance of less than 4 m using a modified air-powered line-thrower [8]. Photos and videos were taken of tag deployments to document whale identity, tag penetration and location.

Tags consisted of a Wildlife Computers Spot-5 Argos transmitter and three Saft A-cell lithium batteries cast in an epoxy-filled stainless steel cylinder. The implantable tags were 28.2 cm long and 2.0 cm in diameter with attachments similar to those used for tagging other large whales [8]. To reduce the likelihood of infections, we partially coated tags with 2.5 g of Gentamycin sulfate, a broad-spectrum antibiotic, in a bio-soluble methacrylate for long-term release of the antibiotic into the tag site. Tags were sealed in gas-permeable bags for 12 h of ethylene-oxide sterilization.

Tags were programmed to transmit during four 1 h periods daily, coinciding with good satellite coverage over a broad range of possible North Pacific migration paths and destinations. Service Argos calculated locations with estimated accuracy based on the timing and number of transmissions received during individual satellite passes [9]. Three of seven location classifications have specific accuracies from less than 150 m (LC 3) to approximately 1 km (LC 1) [10]. We filtered unreasonable data by removing poor quality locations and limiting swim speeds to less than 10 km h^{-1} [8]. Distances travelled and swim speeds were calculated using ArcGIS 10.1 and are minimum estimates calculated from straight lines between consecutive locations.

3. Results

Three of seven tagged adult WGWs off SI during the two expeditions transmitted long enough to document migration away from SI after 68–89 days of near-shore movements: a male (13 year old 'Flex') in 2010 and two females (6 year old 'Agent' and 9 year old 'Varvara') in 2011. Each whale took different outbound routes across the Bering Sea, through the Aleutian Island chain, and across the Gulf of Alaska (figure 1), travelling an average of 6.2 km h^{-1} (table 1).

Tags attached to Flex and Varvara functioned long enough to document the whales entering the EGW southbound migration corridor. The last received location from Flex was 5 February 2011 off Lincoln City, OR, USA, after

Table 1. Tracking summary information of three western gray whales instrumented with satellite-monitored radio tags off Sakhalin Island, Russia.

whale	tracking segment	start date	end date	distance km (nmi)	days	speed km h^{-1} (nmi h^{-1})
Flex	feeding	4 Oct 2010	10 Dec 2010	938 (506)	68.0	0.6 (0.31)
Agent		28 Aug 2011	24 Nov 2011	2600 (1403)	88.7	1.2 (0.66)
Varvara		31 Aug 2011	24 Nov 2011	1280 (691)	84.2	0.6 (0.34)
Flex	southeast migration	10 Dec 2010	5 Feb 2011	7661 (4137)	56.1	5.7 (3.1)
Agent		24 Nov 2011	31 Dec 2011	5464 (2950)	36.3	6.3 (3.4)
Varvara		24 Nov 2011	2 Feb 2012	10 880 (5875)	69.5	6.5 (3.5)
Varvara	reproductive areas (end of migration—Ojo de Liebre)	2 Feb 2012	26 Feb 2012	1147 (619)	24.0	2.0 (1.1)
Varvara	northwest migration	26 Feb 2012	14 May 2012	10 484 (5661)	78.8	5.5 (3.0)

travelling at least 7661 km. Flex was re-sighted in good body condition during the 2011 SI tagging expedition. Varvara departed SI on 24 November 2011, 17 days earlier than Flex, and passed Lincoln City on 8 January 2012, during the peak of the EGW southern migration. She travelled 10 880 km south to within 103 km of Cabo San Lucas, Baja California Sur, Mexico (CSL), on 2 February 2012, 69.5 days after departing SI (figure 1). Varvara spent 42 days off Baja California, Mexico including 32 days of generally northward movement, passing all three major EGW reproductive areas [11]. From CSL to the northernmost breeding area at Laguna Ojo de Liebre (OdL), Varvara travelled 1147 km, averaging 2.0 km h^{-1} (figure 1, inset). Her 10 484 km migration from OdL back to SI followed a different route from her eastward trip, crossing the eastern Bering Sea near the southerly face of the retreating ice edge and took 79 days, ending on 14 May 2012. Some slower movement segments were recorded along the north side of the Alaska Peninsula and while crossing the Bering Sea. The overall average speed for her spring migration was 5.5 km h^{-1}. The entire 22 511 km round-trip migration lasted 172 days.

4. Discussion

Varvara's 10 880 km autumn migration constitutes the longest recorded distance travelled during a mammal migration [12]. The linear travel segments over deep water made by tagged whales in this study indicate excellent navigation abilities [13] in sharp contrast with the slower-paced, near-shore and shallow-water migration of EGWs along North America [11]. Varvara's near-shore spring migration route until reaching the Bering Sea was typical of EGWs. However, her more northerly westward route across the Bering Sea indicates she was not obliged to return by the same specific route of her eastward migration, further reinforcing a strong ability to navigate. The occasional slow movement segments observed along the Alaska Peninsula and during the western crossing of the Bering Sea may indicate opportunistic feeding.

New-born gray whale calves follow their mothers during the spring migration to the mother's foraging area, where weaning occurs in late summer [11]. Juvenile and adult WGWs first identified as calves off SI have returned there to feed [4], indicating a very strong allegiance to their mother's migratory destination. Similar natal philopatry has been observed in humpback whale calves, in the North Pacific and elsewhere, returning to their mothers' migratory destinations [14]. Thus, the three migratory tracks documented by this study strongly suggest the tagged whales were born in EGW reproductive areas.

The utilization of feeding areas in the western North Pacific by whales that winter in the eastern North Pacific raises questions about the present status of WGWs. Since these tracking data became available, a preliminary comparison between WGW and EGW photo-ID catalogues discovered 10 WGWs have been photographed near British Columbia and in San Ignacio Lagoon, Baja California, Mexico [15]. Those sightings, combined with two genetic matches, further strengthen the linkage between these two presumed stocks and question whether the present WGWs came from the population previously thought to be extinct or from recovered EGWs with an expanded range [16].

Recent evidence that 'true' WGWs (i.e. whales breeding in Asian waters) are extant includes: four fishing net deaths off the Pacific coast of Japan between 2005 and 2007, including a yearling first observed as a calf off SI [17]; a gray whale stranded in November 2011 off the Fujian Province in southern China [15], adjacent to the region speculated to serve as a reproductive area for WGWs [17]; and a March 2012 live sighting in Mikawa Bay, Japan [15]. EGWs have been sighted well outside their established ranges [18], so it is possible that WGWs are extinct and these western North Pacific sightings represent a wider EGW foraging range, and more variable migratory timing than is presently thought. It is also possible that the SI region is a foraging area where EGWs and a smaller-than-estimated 'true' WGW population co-mingle, with the latter group making a southerly migration along the Asian coast to an as yet undiscovered breeding area or that spatial and temporal concentrations of whales from SI, during their occupancy in the regular winter range of EGWs, allow them to maintain genetic separation from other EGWs. Overall, the tagging and photo-ID data indicate that the population identity of whales off SI needs further evaluation.

Ethics statement. The procedures used in this study were reviewed and approved by the International Whaling Commission's Western Gray Whale Satellite Tagging Steering Committee and the Oregon State University Institutional Animal Care and Use Committee.

Data accessibility. Data for this study are archived at the International Whaling Commission (http://iwc.int/data-availability) and at the Oregon State University Marine Mammal Institute.

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Author contributions. B.M. participated in the conception, design and coordination of the study, participated in field work and drafted the manuscript. V.I. participated in the conception, design and coordination of the study and reviewed the manuscript. A.B. participated in the design of the study, participated in field work and reviewed the manuscript. V.V. led the field work. G.T. participated in the design of the study and participated in the field work. V.R. participated in the conception, design and coordination of the study and reviewed the manuscript. L.I. participated in the field work and reviewed the manuscript. All authors gave final approval of the version to be published.

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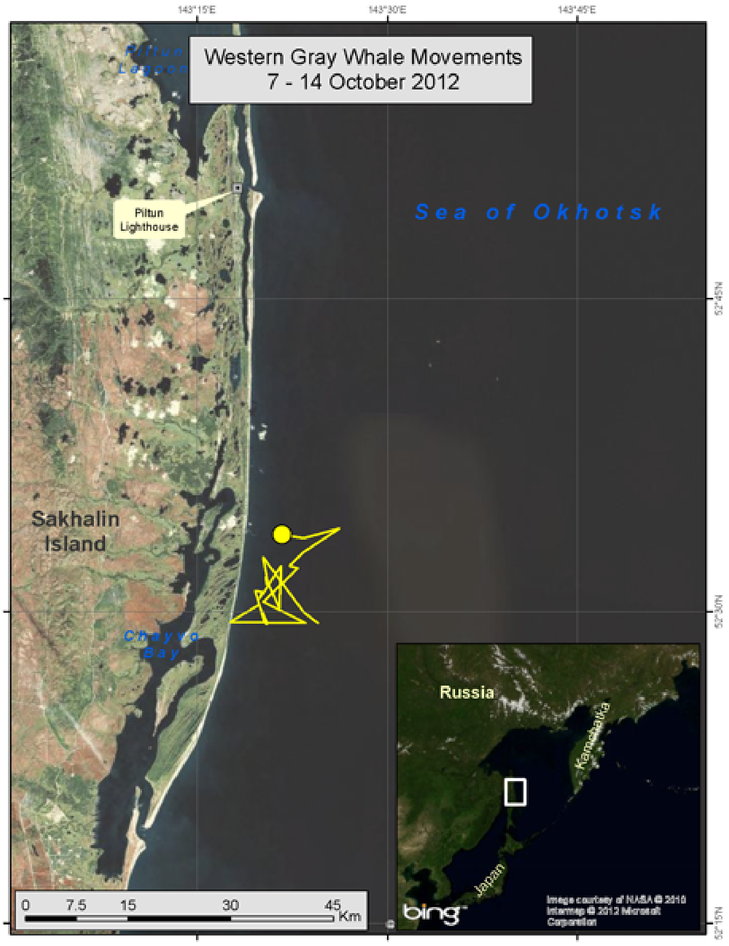

The last map on the website was in fact the last one for Varvara's tag, which ended operations on 12 October, 408 days after tagging, which is consistent with the original tag-life estimate. Varvara provided us some truly amazing data and insights that will be written up for peer-reviewed publications. Thanks for your enthusiastic interest and support of this project.

To learn more about the life history of the tagged whales, we asked our colleagues at the Kamchatka Branch of the Pacific Institute of Geography (KBPIG) and at the National Marine Fisheries Service (NMFS), who have been studying gray whales off Sakhalin Island since 1995. Kol, a male, was first sighted off Sakhalin as a calf in 2004, meaning that he is approximately seven and a half years of age. He has been observed off Sakhalin almost every summer since he was a calf. Agent is a six and a half year old female who has been seen frequently off Sakhalin since she was first sighted as a calf in 2005

Varvara, an eight and a half year old female, has been seen intermittently off Sakhalin since she was first sighted as a calf in 2003. Varvara has a reputation for being particularly curious and playful during small boat encounters! Blaze was accompanied by a calf when first identified off Sakhalin in 1995, making her at least 26 years of age. She has been sighted in almost all subsequent years and has been observed with five calves during this period. We are no longer hearing from the tag on Blaze, but it was not well attached and has probably fallen off.

Svetlana leaves an impression on all who encounter her because of her calm demeanor, her enormous size (potentially the biggest of the Sakhalin whales), and a large scar on her back (most likely the result of a previous vessel collision). Svetlana was an adult when first identified in 1997 and has been sighted off Sakhalin in virtually every year since. Svetlana has been observed with four calves over the years, and we know that she is at least 23 years of age, although we suspect she is quite a few years older. Bud, so-called because she is also especially tolerant of the research vessel, has other characteristics in common with Svetlana. Bud is also a reproductive female, was first identified off Sakhalin as an adult in 1997, and has been sighted there in most of the following years. Based on when she was first observed with a calf, we know that Bud is at least 19 years of age, but she may indeed be older. Bud has had at least four calves, including one that she weaned earlier in the 2011 tagging season. Bud’s calf from 2006 was unfortunately fatally entrapped in a set net off Japan in early 2007. To date, Bud represents the only known connection between Sakhalin and the historical western gray whale migratory corridor.

During our tagging efforts this summer, we saw Flex (the whale tagged in 2010) on several occasions. He appeared to be in good body condition and, while scarred, the tag area has healed.

Anyone making reference to these data needs to acknowledge the source of the data by using the following text: "This research was conducted by A.N. Severtsov Institute of Ecology and Evolution of the Russian Academy of Sciences (IEE RAS) and Oregon State University Marine Mammal Institute in collaboration with the U.S. National Marine Fisheries Service, Kronotsky State Nature Biosphere Reserve and the Kamchatka Branch of the Pacific Institute of Geography. The research was contracted through the International Whaling Commission (IWC) and International Union for Conservation of Nature (IUCN) with funding from Exxon Neftegas Ltd. and Sakhalin Energy Investment Company Ltd.

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Western Gray Whales 2010

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Status Review of the Eastern North Pacific Stock of Gray Whales

by
D. J. Rugh, M. M. Muto, S. E. Moore, and D. P. DeMaster

U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
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Abstract

The National Marine Fisheries Service (NMFS) conducted a review of the status of the Eastern North Pacific stock of gray whales (*Eschrichtius robustus*). This review culminated in a workshop held by the National Marine Mammal Laboratory (NMML) in Seattle, Washington, on 16-17 March 1999. Based on the continued growth of this population (rising at 2.5% annually; currently at an estimated 26,600 individuals) and the lack of evidence of any imminent threats to the stock, workshop participants recommended the continuation of this stock's classification as non-threatened. They also concluded that abundance monitoring should continue at some level, especially as this stock approaches its carrying capacity, and that, ideally, research should continue on human impacts to critical habitats. This stock's annual migrations along the highly populated coastline of the western United States and their concentration in limited winter and summer areas may make them particularly vulnerable to impacts from commercial or industrial development or local catastrophic events. The Western North Pacific gray whale stock has not recovered and should continue to be listed as endangered.

The workshop and status review conclude the 5-year assessment of the Eastern North Pacific gray whale stock following its removal from the List of Endangered and Threatened Wildlife and Plants on 16 June 1994.

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Appendices

Background

Under the Marine Mammal Protection Act (16 U.S.C. 1361 *et seq.*; the MMPA), the National Marine Fisheries Service (NMFS) has jurisdiction over most marine mammal species[1], including whales. Under section 4(a) of the Endangered Species Act (16 U.S.C. 1531 *et seq.*; the ESA) and 50 CFR part 424 of NMFS' listing regulations, NMFS makes determinations as to whether a marine mammal species should be listed as endangered or threatened, or whether it should be reclassified or removed from the List of Endangered and Threatened Wildlife and Plants (the List). Accordingly, NMFS conducted comprehensive evaluations of the status of the Eastern North Pacific gray whale stock, *Eschrichtius robustus,* (sometimes referred to as the "California stock") in 1984 (Breiwick and Braham 1984). Based upon their review, NMFS concluded that this stock should be listed as threatened instead of endangered (49 FR 44774, 9 November 1984); however, no further action was taken at that time. Another review was completed and made available to the general public on 27 June 1991 (56 FR 29471). The 1991 review showed the best available abundance estimate, in 1987/88, was 21,296 (CV = 6.05%; 95% CI = 18,900 to 24,000) whales and the average annual rate of increase was 3.29% (SE = 0.44%) (Buckland et al. 1993). Back-calculations, dynamic response, and Bayesian estimations indicated that this stock was probably approaching current carrying capacity (Reilly 1992). Therefore, NMFS determined that the Eastern North Pacific stock no longer met the standards for classification as an endangered "species." Although individual and cumulative impacts might have the potential to adversely affect these whales, it was determined that this stock was neither in danger of extinction throughout all or a significant portion of its range (i.e., not endangered), nor was it likely to again become endangered within the foreseeable future (i.e., not threatened). Therefore, on 22 November 1991 (56 FR 58869), NMFS proposed that this stock be removed from the List. Of note, changes to the listing of this stock had no bearing on the status of the Western North Pacific gray whale stock (sometimes referred to as the "Korean stock"), which has not recovered and is still considered endangered throughout its range (USFWS 1997). After an extensive public comment period (22 November 1991 to 6 March 1992), NMFS published a final notice of determination that the Eastern North Pacific stock should be removed from the List (58 FR 3121, 7 January 1993). The population abundance and trends in the population's growth rate were deemed sufficient to allow this stock to be removed from the List without first being down-listed to threatened status.

As a result of NMFS' determination, the U.S. Fish and Wildlife Service (USFWS) removed the Eastern North Pacific stock of gray whales from the List under the ESA on 16 June 1994 (59 FR 31094) with the amendment of 50 CFR 17.11(h). To correspond with that ruling, NMFS also removed this stock from the List under its jurisdiction (50 CFR part 222) through an amendment of 50 CFR 222.23(a).

As required under section 4(g) of the ESA, NMFS drafted the "5-year Plan for Research and Monitoring of the Eastern North Pacific Population of Gray Whales"

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[1] The U.S. Fish and Wildlife Service (USFWS) has jurisdiction over polar bears, sea otters, manatees, dugongs, and walrus.

(NMFS 1993) to monitor the status of the stock for a period of at least 5 years following the delisting. This plan (NMFS 1993:25) states that a "Task Group will conduct a comprehensive 'status review' of the gray whale . . . Included in that report will be a recommendation on whether to 1) continue the monitoring program for an additional 5-year period; 2) terminate the monitoring program; or 3) consider changing the status of the gray whale under the ESA." The draft plan, dated October 1993, was not finalized by the NMFS Office of Protected Resources; however, it has provided the framework and guidelines for research, monitoring, and management over the past 5 years. The plan was prepared by 11 NMFS scientists (the Gray Whale Monitoring Task Group), including Howard Braham (Chair), Jeffrey Breiwick, Robert Brownell, Jr., Marilyn Dahlheim, Douglas DeMaster (Vice-Chair), Kenneth Hollingshead, Jeffrey Laake, Stephen Reilly, John Stein, Steven Swartz, and Grant Thompson.

On 16-17 March 1999, 3 months prior to the conclusion of the 5-year period following the delisting of the Eastern North Pacific gray whale stock, a workshop was convened by NMFS at the Alaska Fisheries Science Center's National Marine Mammal Laboratory (NMML) in Seattle. Most of the original Task Group participated in this workshop, and other participants were invited as well, depending on their expertise and contributions that could help in the review process (see the participant list, Appendix A). The workshop provided an opportunity for interactions among researchers conducting studies pertinent to the evaluation of the status of gray whales. Agenda and abstract materials were circulated prior to and following the workshop to provide additional time for detailed reviews. An expanded agenda, with summaries of critical information, is included in the following report under "Outline of Available Information." Most of this material is explained further in the attached abstracts (Appendix B). Research documents from the past 5 years that pertain to this subject are in the literature section, including the literature cited in the Status Review.

Information included in the Outline of Available Information is inclusive of all pertinent studies and available data collected up to and including 16 June 1999, the 5-year anniversary of the removal of the Eastern North Pacific stock of gray whales from the List.

This Status Review document will be forwarded to the NMFS Assistant Administrator for Fisheries for approval and release to the public. The NMFS Office of Protected Resources will publish a Federal Register notice to announce the availability of this document and invite public comment.

Workshop objectives

The central objective of the status review and workshop held 16-17 March 1999 was to evaluate available information pertinent to the health of the Eastern North Pacific stock of gray whales. Questions to be answered through this process were:

1. Was it appropriate to delist this stock 5 years ago?
2. Should this stock continue to be considered non-endangered and non-threatened?
3. Should the monitoring process continue for another 5-year period?

Factors to be considered in determining the status of gray whales

The ESA specifies regulatory elements that were used to determine the status of the Eastern North Pacific stock of gray whales both in the delisting process in 1993-94 (see above) and in the review of scientific materials available during the 5 years that followed delisting (i.e., this report). Listing, reclassifying, or removing a species from the List is based on review of five factors, of which only one need apply for a "species" to be listed as either endangered or threatened (ESA: 16 U.S.C. 1533(a)(1); NMFS: 50 CFR 424):

1. Present or threatened destruction, modification, or curtailment of its habitat or range.
2. Overutilization for commercial, recreational, scientific, or educational purposes.
3. Disease or predation.
4. Inadequacy of existing regulatory mechanisms.
5. Other natural or manmade factors affecting its continued existence.

The workshop participants used these five factors as a guide to determine whether or not the current status of the Eastern North Pacific gray whale stock should be changed from non-threatened. The following information is a collection of research pertinent to this decision. The outline was adapted from the list of research needs in the 5-year monitoring plan (NMFS 1993:52).

Outline of Available Information

1) Abundance, distribution, population trend, and status

1.1) Abundance

1.11) **1993/94 abundance:** Systematic counts of southbound migrating gray whales were conducted 10 December 1993 to 18 February 1994 at Granite Canyon, California (Laake et al. 1994), the census site used most years since 1975 by NMML. In total, 1,864 pods (3,411 whales) were recorded during 447 hours of good or better watch conditions at the primary observation site. The abundance estimate was 23,109 (CV = 5.42%; 95% CI = 20,800 to 25,700).

1.12) **1995/96 abundance:** Systematic counts of gray whales were conducted from 13 December 1995 to 23 February 1996 at Granite Canyon (Hobbs et al. in press). As during previous surveys, census methods included double-counting to assess observer performance as well as aerial surveys and high-powered binoculars to document that a negligible fraction of migrating whales passed beyond the sighting range of the observers. There were 2,151 pods (3,928 whales) counted during 472.7 hours of standard watch effort. Data analysis procedures were modified to account for differential sightability by pod size. Population size was estimated to be 22,263 whales (CV = 9.25%; 95% log-normal CI = 18,700 to 26,500).

1.13) **1997/98 abundance:** Systematic counts of gray whales were conducted from 13 December 1997 to 24 February 1998 at Granite Canyon and Point Lobos, California (Hobbs and Rugh 1999). Counting methods, similar to previous surveys, included double-counting to assess observer performance and high-powered binoculars to document that a negligible fraction of migrating whales passed beyond the sighting range of the observers. In total, 2,318 pods (3,643 whales) were counted during 435.3 hours of standard watch effort. Data analysis procedures were identical to those used for the 1995/96 census. The population was estimated to be 26,635 whales (CV = 10.06%; 95% log-normal CI = 21,878 to 32,427).

1.14) **Counting methodology:** Systematic counts of gray whales have been conducted by NMML during 3 of the past 5 seasons (1993/94, 1995/96, 1997/98) (Hobbs and Rugh 1999). These surveys covered the duration of the southbound migration past the Granite Canyon research station. In addition to the standard primary watch, a second, independent watch was conducted once or twice daily. Offshore distribution of sightings was documented by comparing the paired counts on the standard watch; by searches through paired, fix-mounted 25 X binoculars; and by aerial surveys. In January 1993 and January 1994, pod-size estimation experiments involved an airplane circling pods of whales as several observers independently estimated pod sizes (Withrow in press). Tests of the counting system, but not full-season counts, were conducted in January 1995 and January 1997 (Rugh[2]). Analytical methods are described in Breiwick and Hobbs (1996).

1.15) **Night travel rates:** In studies conducted by Perryman et al. (1999a) in January 1994, 1995, and 1996, there was no significant diel variation in gray whale swimming speed. Prior to 15 January each year (the median migration date), diurnal and nocturnal rates (average number of whales/hour) were not significantly different; after 15 January, the nocturnal rate was significantly higher (28%, SE = 11.6%) than the diurnal rate.

1.16) **Database management:** Census data have been collected on gray whales during their southbound migration since 1952 (Shelden[3]). Currently the "raw" count data are not readily available to the scientific community or the general public. Therefore, researchers at NMML are in the process of creating a single, uniform, and easily accessible database. Before this can occur, the following tasks must be completed: 1) convert all computerized databases (Yankee Point/Granite Canyon/Point Lobos study sites used from 1967/68 to1997/98) into a common format, and place all data into one master database; 2) find and incorporate data from Point Loma (1952-78) into the master database; and 3) store the master database on CD-ROM for distribution to the public. It is anticipated that this product will be available by September 2000, pending support from the NMFS Office of Protected Species.

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[2] Pers. comm. Dave Rugh, National Marine Mammal Lab, AFSC, NMFS, 7600 Sand Point Way NE, Seattle, WA 98115-0070.

[3] Pers. comm. Kim Shelden, National Marine Mammal Lab, AFSC, NMFS,7600 Sand Point Way NE, Seattle, WA 98115-0070.

1.2) **Distribution**

1.21) **Migration**

1.211) **Relative to the census station**

1.2111) **Shore-based observations:** In January 1995 and 1996, using fixed-mounted 25X binoculars, paired independent searches for gray whales resulted in detection probabilities of 0.97 for pod sizes greater than 1 and 0.87 for single whales (5% of sampled population) within the critical sighting range of 1-3 nautical miles (nmi) (1.8-5.6 km) of shore (Rugh et al. in press).

1.2112) **Aerial observations:** Shelden and Laake (in press) compared the distribution of whales within 3 nmi (5.6 km) north and south of Granite Canyon during six aerial surveys (conducted concurrently with shore-based surveys in 1979, 1980, 1988, 1993, 1994, and 1996). They found that whale distributions within the typical viewing range of shore-based observers (3 nmi from shore) differed by year, but the shifts in the distribution were minor (< 0.3 nmi; < 0.5 km). Inshore (< 2.25 nmi; < 4.17 km) and offshore (> 2.25 nmi) distribution of gray whale pods did not differ significantly between survey years. A mean of 4.76% (SE = 0.85%) of the whale pods were observed beyond 2.25 nmi, and only 1.28% (SE = 0.07%) were observed beyond 3 nmi.

1.212) **Timing in 1998/99**

1.2121) **Oregon:** Alternate half-hour counts were made during the morning hours from 5 December 1998 through mid-February 1999 from the Yaquina Head Lighthouse (49 m above sea level) near Newport, Oregon (Mate and Poff 1999). The first whale was sighted on 23 December, and the peak passage occurred on 7 January. By comparison with previous data from the same site (1978-81), the migration started 3 weeks later than normal, and the migration peaked 6 days later than the latest date reported previously. Whales did not tend to come nearshore to the degree experienced in previous years. In this study, 60% of the sightings were greater than 5 nmi (> 9 km) offshore and 20% were less than 3 nmi (< 5.6 km).

1.2122) **Washington - aerial:** Shelden et al. (1999a, 1999b) conducted six (4 complete and 2 partial) surveys in November and December 1998 and January 1999. Four pods (6 whales) were observed on offshore transect lines from 5.5 to 47 km offshore, and two pods (2 whales) were observed on coastal tracklines from Cape Flattery to Carroll Island, Washington. The authors compared their results to surveys conducted off Granite Canyon, California, and suggested several factors that may have influenced the likelihood of detecting gray whales off the northern Washington coast: timing of the peak of the migration, lulls in the migration, width of the migration corridor, and limitations in the field of view from the aircraft. Of these four factors, corridor width appeared to be the most likely contributor to reduced observer detection rates.

1.2123) **Washington - shore-based:** Gray whales were seen on three occasions (2, 4, and 13 December) during a survey conducted from the tower of the Tatoosh Island lighthouse, on the northwesternmost tip of Washington State, between 30 November and 16 December 1998 (Jones 1999). The maximum possible sighting distance was estimated at 25 km, but gray whales were only seen at a range of 0.6-5.9 km from shore. It is possible that whales passed offshore, out of the observer's sighting range, or that this time period represented the very early stages of the southbound gray whale migration past Washington.

1.2124) **California to Alaska:** According to Rugh et al. (1999a, 1999b), the median sighting date of southbound gray whales prior to 1980 was 8 January (ranging from 5 to14 January) at the Granite Canyon research station. However, since 1980 there has been a 1-week delay in the peak of the migration such that the median date is now closer to 15 January (ranging from 12 to 19 January). Using a travel rate of 144 km/day (Swartz et al. 1987) between shore stations, the expected peak dates in 1998/99 should have been 5 January for Tatoosh Island; 8 January for Yaquina Head; 15 January for Granite Canyon; and 18 January at Point Vicente, near Los Angeles, California. Although no observations were made at Granite Canyon in 1998/99, sightings collected at Yaquina Head (Mate and Poff 1999) and Point Vicente (Schulman-Janiger 1999a) indicate that the southbound migration was within 1 or 2 days of the expected date.

1.213) **Travel rates:** Gray whales migrate at a rate of approximately 144 km/day (SD = 31 km/day), based on radio tags placed on whales near the Granite Canyon research station (Swartz et al. 1987). This travel speed was similar to rates calculated from a comparison of timings of peaks in sightings as whales migrated south past several shore stations ($\bar{x}$ = 139 km/day; SD = 18 km/day) (Rugh et al. 1999a, 1999b).

1.214) **Relative to Arctic and subarctic conditions:** Rugh et al. (1999a, 1999b) determined that gray whale migratory timing is remarkably regular: the 20 peaks observed at Granite Canyon during the southbound migration from 1967/68 to 1997/98 varied less than 4 days from the overall median dates. Regularity of this sort is likely driven by photoperiod (that is, shortening day lengths), not by weather. Arctic and subarctic temperatures and ice conditions are far from being so regular. Inter-year variations of a few days in migratory dates may be explained in part by variations in the median location of whales in the Bering or Chukchi Seas just prior to the onset of the migration. The farther north the whales are in autumn, the shorter the photoperiod will be, which might accelerate the onset of their southbound migration.

1.22) **Summering areas**

1.221) **Arctic and subarctic:** During aerial surveys in the Alaskan Chukchi and Beaufort Seas in 1982-91 (Moore and DeMaster 1997), gray whales were associated with virtually the same habitat throughout the summer (40 m depth and ≤ 1% ice cover) and the autumn (38 m depth and ≤ 7% ice cover), unlike bowhead and beluga whales. Moore and DeMaster (1997) believe that shallow coastal and offshore-shoal areas provide habitat rich in gray whale prey, and there is little reason for whales to abandon this habitat prior to winter onset. The association of gray whales with discrete offshore shoals in the northern Chukchi Sea may indicate that these are important feeding areas for the expanding population.

1.222) **Washington:** From 1984 to 1997, 168 individual gray whales were photo-identified (as seasonal resident whales from spring through fall) in coastal areas of Washington State (Calambokidis and Quan 1999, Gosho et al. 1999a, 1999b). Gray whales showed some localized site fidelity but also moved widely within and between years. Expanded research in 1998 (Calambokidis and Quan 1999) revealed that seasonal resident gray whales in Washington also used coastal areas from northern California to southeast Alaska from spring to fall. This large feeding range may account for inconsistent year-to-year resightings. Whales in northern Puget Sound showed strong site fidelity for part of the season and then moved to unknown areas. Use of southern Puget Sound was variable, mortality was high, and whales were rarely seen more than once.

1.23) **Wintering areas:** According to Urbán et al. (1997, 1998a, 1998b), the annual maximum count of all whales in San Ignacio Lagoon during the winters of 1978-85 averaged 348.7 (SE = 35.2) adults, of which 238.2 (SE = 36.7) were single whales and 110.5 (SE = 27.6) were cow-calf pairs. From 1996 to 1998, there was an average of 230 (SE = 18.4) adults in the lagoon, of which 140 (SE = 33.5) were single whales and 90 (SE = 37) were cow-calf pairs. During photo-identification studies in the lagoon in 1996-98, 752 whales were identified, including 411 single whales, 332 cow-calf pairs, and 9 whales which could not be classified. Of these, 120 whales were resighted: 14 single whales and 106 cow-calf pairs. Cow-calf pairs stayed in the lagoon an average of 19.1 days (± 4.8 95% CI) in 1996, 19.6 days (± 3.5 95% CI) in 1997, and 20.6 days (± 4.1 95% CI) in 1998, while single whales used the lagoons an average of 2.6 days (± 0.9 95% CI) in 1996, 6.2 days (± 3.2 95% CI) in 1997, and 5.6 days (± 2 95% CI) in 1998. During surveys in 1996 and 1998 (Urbán et al. 1998b), most whales were observed heading west off the coast of Bahía Ballenas, Baja California Sur, Mexico. Single whales were observed farther offshore than the cow-calf pairs. The number of single whales recorded in 1996 and 1998 was higher than the recorded number of cow-calf pairs. Similar traveling patterns and group composition were reported by Sánchez Pacheco and Valdés Aragón (1997) in 1997.

1.3) **Population trend:** Between 1967/68 and 1995/96, the Eastern North Pacific gray whale population increased 2.5% per annum (SE = 0.3%), and the estimated asymptote from a logistic model was 26,046 (SE = 6,281) with the inflection point in 1971 (SE = 6.5) (Buckland and Breiwick in press). Using a generalized linear model to fit abundance estimates from 1967/68 to 1997/98, the *ROI* (rate of increase) was 2.52% per annum (SE = 0.27%); using a logistic model, *K* (carrying capacity) was estimated to equal 37,364 (SE = 24,854), which is larger by 11,000 than a similar estimate based on the 1967/68 to1995/96 data; and *RY* (replacement yield) equaled 612 (Breiwick 1999). Density-dependent slowing of the population growth rate was supported by use of a Bayesian statistical method to compare the fit of the data to density-dependent versus density-independent models. Point estimates of the equilibrium population size ranged from 24,000 to 32,000, depending on the model (Wade and DeMaster 1996). Using a Bayesian statistical method to assess the stock with 1966/67 to1995/96 data, point estimates of carrying capacity ranged from 24,640 to 31,840; the median depletion (population size as a fraction of carrying capacity) was 0.75, with a lower 2.5th percentile of 0.36; the probability that the population is still below one-half of the carrying capacity was 0.21, and the probability that it is still below its maximum sustainable yield level was 0.28 (Wade in press).

1.4) **Population status**

1.41) **Criteria for ESA listing status:** Using 19 years of abundance estimates for the Eastern North Pacific gray whale, Gerber et al. (in press) sampled subsets of the original survey data to identify the minimum number of years of data required to consistently recommend removing the population from the ESA List of Endangered and Threatened Wildlife. These subsets of data were then analyzed using their proposed classification criteria. It was found that a quantitative decision to delist was unambiguously supported by 11 or more years of data, but precariously uncertain with fewer than 10 years of data.

2) **Calf production and pregnancy rate**

2.1) **Southbound migration at Granite Canyon/Yankee Point and Point Loma:** Calf sightings (number of calves/total whales) recorded by NMFS observers during the gray whale southbound migrations were summarized by Shelden et al. (in press) for 1952-95 and by Shelden and Rugh (1999) for 1995-98. Percentages of calves ranged from 0.0 to 0.2% from 1952-74, 0.1-0.9% from 1984-95, and 0.3-1.5% from 1995-98. The apparent increase in the percentage of calf sightings may be related to a trend towards successively later migrations over the 43-year observation period, or it may be due to an increase in spatial and temporal distribution of calving as the population has increased. The distribution of cows with calves relative to shore was similar to earlier years where the majority of sightings occurred inshore of the main migration corridor (1.4-2.8 km) during both shore-based and aerial surveys. Aerial surveys (between 1979 and 1994) indicated that shore-based observers missed 62% of the calves within their viewing area

(0-2.6 km from shore), suggesting that calves are under-represented in the data (Shelden et al. in press).

2.2) **Southbound migration at Point Vicente:** Schulman-Janiger (1999b), of the American Cetacean Society, Los Angeles Chapter (ACS/LA), reported that percentages of calves in the southbound migrations from 1983/84 to 1989/90 ranged from 0.5% to 2.5%, averaging 1.7%. From 1990/91 to 1992/93, these percentages increased to 3.0-3.9%, averaging 3.5%. The calf percentages from 1993/94 to 1998/99 ranged from 2.0% to 8.6%, averaging 4.6%. However, the calf count in the 1998/99 migration (n = 15; 2.2%) was one of the lowest in the past nine seasons. The highest calf count (n = 106; 8.6%) was in the 1997/98 season.

2.3) **Northbound migration at Point Vicente:** Schulman-Janiger (1999b) reported that percentages of newborn calves sighted in the ACS/LA surveys of the northbound migrations from 1983/84 to 1991/92 ranged from 0.9% to 8.3%, averaging 3.4%. From 1992/93 to 1997/98, these percentages generally increased, ranging from 4.3% to 13.8% and averaging 9.6%. Some of the highest percentages, ranging from 9.4% to 13.8% (averaging 11.2%), occurred in recent years (1995/96 to1997/98). These were substantially higher than previously published figures for California waters. The highest calf count (n = 222, 13.8%) occurred in the 1996/97 season and was more than double the count of any of the preceding nine seasons. However, the percentage of calves in the 1998/99 northbound migration was only 2.5% (n = 34), well below percentages seen in recent years.

2.4) **Northbound migration at Piedras Blancas:** Perryman et al. (1999b) conducted shore-based surveys at Piedras Blancas in central California to estimate the number of calves in the northbound migration. There were 1,000 calves (SE = 88.85) in 1994; 601 calves (SE = 69.56) in 1995; 1,141 calves (SE = 72.23) in 1996; 1,439 calves (SE = 78.62) in 1997; a preliminary estimate of 1,316 calves (SE = 77.56) in 1998; and a preliminary estimate (Perryman[4]) of 471 calves (SE = 77) in 1999. Calf production indices (calf estimate/total population estimate) were 4.5%, 2.6%, 5.1%, 6.5%, 5.9%, and 1.8% for the years 1994-99, respectively .

2.5) **Photogrammetric studies:** According to Perryman and Lynn (1999), the southbound migration is led by large whales, many of them pregnant females; juvenile whales usually arrive late in the migration. Based on the proportion of pregnant and recent postpartum females, 15 January was estimated to be the median birth date for the Eastern North Pacific stock of gray whales. The estimated length at 1 year was 8.6 m. Results indicated that relatively small changes in condition or fatness of gray whales are detectable in measurements from photographs.

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[4] Pers. comm. Wayne Perryman, Southwest Fisheries Science Center, NMFS, P.O. Box 271, La Jolla, CA 92038-0271.

3) **Habitat use**

3.1) **Climate trends:** Changes in the extent and concentration of sea ice in the Arctic Ocean over the past 20-30 years, coincident with warming trends, may alter the seasonal distributions, geographic ranges, patterns of migration, nutritional status, reproductive success, and ultimately the abundance and stock structure of some species (Tynan and DeMaster 1997a). Effects of climate warming on Eastern North Pacific gray whales are unknown, but studies of benthic-pelagic coupling in the Arctic and subarctic (e.g., Grebmeier and Barry 1991) suggest depression of production in surface waters that may lead to reduced availability of gray whale prey in primary feeding areas offshore of Alaska.

3.2) **Food resources:** According to Highsmith and Coyle (1992), gray whales rely on rich benthic amphipod populations in the Bering and Chukchi Seas to renew fat resources needed to sustain them during their winter migration to and from Baja California Sur. Gray whale feeding areas offshore of northern Alaska are characterized by low species diversity, high biomass, and the highest secondary production rates reported for any extensive benthic community. Stoker (in press) studied one of the high-use areas, the central Chirikov Basin between St. Lawrence Island and the Bering Strait, and found that gray whales disturb at least 6% of the benthos each summer and consume more than 10% of the yearly amphipod production. There are indications that this resource is being stressed and that the gray whale population may be expanding its summer range in search of alternative feeding grounds. Specifically, Highsmith and Coyle (1992) showed that the abundance and biomass of the amphipod community decreased during the 3-year period from 1986 to 1988, resulting in a 30% decline in production. They noted that high-latitude amphipod populations are characterized by low fecundity and long generation times, and that large, long-lived individuals are responsible for the majority of amphipod secondary production. Therefore, a substantial reduction in the density of large individuals in the population will result in a significant, long-term decrease in production.

4) **Potential anthropogenic concerns**

4.1) **Contaminants:** Tilbury et al. (1999) studied contaminants in gray whales. During migrations, prolonged fasting may alter the disposition of toxic chemicals within the whales' bodies. Gray whales feeding in coastal waters may be at risk from exposure to toxic chemicals in some regions. The higher concentrations of polychlorinated biphenyls (PCBs) found in stranded animals compared to harvested animals may be due to the retention of organochlorines in blubber during fasting rather than to increased exposure to these contaminants. The elevated concentrations of certain trace elements (e.g., cadmium) found in some tissues, such as kidneys, of stranded animals and the high levels of aluminum found in the stomach contents and tissues of harvested whales, compared to other marine mammal species, is consistent with the ingestion of sediment by gray whales.

4.2) **Oil spills:** Moore and Clarke (in press) reported that gray whales were seen swimming through surface oil from the *Exxon Valdez* oil spill along the Alaskan coast. Also, gray whales showed only partial avoidance to natural oil seeps off the California coast. Laboratory tests suggest that gray whale baleen, and possibly skin, may be resistant to damage by oil, but spilled oil or oil dispersant in a primary feeding area could negatively affect gray whales by contaminating benthic prey.

4.3) **Noise:** Moore and Clarke (in press) summarized studies of short-term behavioral responses to underwater noise associated with aircraft, ships, and seismic explorations. These studies indicate a 0.5 probability that whales will respond to continuous broadband noise when sound levels exceed *ca.* 120dB, and to intermittent noise when levels exceed *ca.* 170dB, usually by changing their swimming course to avoid the source. They also reported that preliminary results from studies to determine gray whale responses to a low-frequency active (LFA) anthropogenic source indicate that whales avoided exposure to transmissions in the 100-500 Hz frequency band at levels of 170-178 dB by deviating from their swimming path. Moore and Clarke (in press) noted that gray whales 'startled' at the sudden onset of noise during playback studies but demonstrated a flexibility in swimming and calling behavior that may allow them to circumvent increased noise levels. Conversely, some whales swim toward small skiffs deployed from whale watching boats in breeding lagoons, seemingly attracted by the noise of idling outboard engines. Gray whales sometimes change course and alter their swimming speed and respiratory patterns when followed by whale watching boats. Dahlheim (1984, 1988) found that gray whales respond to variation in underwater noise by changing the structure and timing of their calls. Ambient noise (both natural and man-made) has a profound affect on the behavior of this coastal species, causing them to modify their calls to optimize signal transmission and reception. Jones et al. (in press) described the significant decline in the number of whales using San Ignacio Lagoon during acoustic playback research conducted in the winter of 1984, and the re-occupation of this lagoon the following winter, although the numbers seen in 1985 were lower than observed during the 1978-82 period. The noise playback experiments documented alterations in vocal behavior and a significant decline in the number of whales occupying the lagoon during continuous playback (24-hour periods) of industrial noise (Dahlheim 1988). This experiment demonstrated the sensitivity of gray whales to noise disturbance within the lagoon.

4.4) **Entanglement in fishing gear:** From 1990 through 1998, 47 gray whales were reported entangled in fishing gear off the coasts of Alaska, Washington, Oregon, and California. Of these animals, 13 appeared to have survived; the remaining 34 were either mortalities or their status was unknown (Hill 1999a). A whale mortality, due to entanglement in a net pen, was reported in British Columbia in 1999 (Lochbaum[5]).

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[5] Pers. comm. Ed Lochbaum, Marine Mammal Coordinator, Department of Fisheries and Oceans, 3225 Stephenson Point Road, Nanaimo, B.C., V9T 1K3 Canada.

4.5) **Salt extraction in Mexico's lagoons:** Exportadora de Sal, sometimes referred to as ESSA, has operated a salt extraction facility at the town of Guerrero Negro, midway along the Pacific Coast of Baja California Sur, since 1954, and it is planning to expand its operation to San Ignacio Lagoon (Mate 1995). In 1994, ESSA entered into negotiations with the Mexican environmental authorities to expand its salt extraction and marketing activities within the buffer zone of the El Vizcaíno Biosphere Reserve. Specifically, they propose development of a 52,150 ha salt production facility on the shore of San Ignacio Lagoon (Dedina and Young 1995a). In 1995, due to insufficiencies in the Statement of Environmental Impact (MIA, acronym in Spanish), the Mexican authorities denied the permit for the San Ignacio Lagoon expansion and established a Scientific Committee, made up of seven specialists of different nationalities, to specify the terms of reference necessary for a new MIA. This task was completed in July 1996; however, to date, no proposal based on the new terms of reference has been received (SEMARNAP 1997).

4.6) **Commercial developments in Bahía Magdalena:** The growth of gray whale tourism in the North Zone of Bahía Magdalena has led to a proposed Japanese owned and financed tourist resort development at Bahía Magdalena (Dedina and Young 1995a). Although this represents a potential threat to the whales and their habitat, at this time, there are no plans to proceed with this development (Rojas Bracho[6]).

4.7) **Whale watching**

4.71) **Regulations in Baja California Sur, Mexico:** Urbán Ramírez[7] reported that whale watching is allowed in every lagoon in Baja California Sur except in the southern part of Bahía Magdalena (also see Sánchez Pacheco 1997a). Since 1997, government whale watching regulations (modified annually) have existed for commercial operators. There are currently four specific whale watching areas in the lagoons where the numbers of boats and methods of approach are regulated. There are no minimum approach distances, but whales cannot be chased.

4.72) **Whale disturbance in Ojo de Liebre and San Ignacio Lagoons:** A change in a whale's direction of movement is considered an indicator of disturbance. Sánchez Pacheco (1997b) defined a procedure to estimate the Maximum Simultaneous Number (NMS, acronym in Spanish) of vessels that can watch whales in an area without disturbing more than 50% of them. The procedure was applied in Ojo de Liebre Lagoon and San Ignacio Lagoon during 1995. Vessels followed selected whales, while observers recorded whale reactions and the distance between the vessel and disturbed whales.

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[6] Pers. comm. Lorenzo Rojas Bracho, Bahía Vizcaíno 476, Col. Moderna, Ensenada, B.C., 22860 México.

[7] Pers. comm. Jorge Urbán Ramírez, Programa de Investigacion de Mamiferos Marinos, Dept. de Biologia Marina, Universidad Autonoma de Baja California Sur, Ap. Post. 12-B, La Paz, B.C.S., 23081 México.

The NMS was 6 vessels in each of two areas in Ojo de Liebre Lagoon and 13 vessels in San Ignacio Lagoon.

4.73) **Whale disturbance and regulations in Bahía Magdalena:** A shore-based study was conducted in the northern part of Bahía Magdalena, Estero A. Lopez Mateo, to observe the effect of whale watching boats on whale behavior (Pérez-Cortés Moreno[8]). In this narrow and shallow area of the lagoon, single-day visits predominate and enforcement is difficult. Regulations permit a maximum of 22 boats in the area at one time; boats must have a permit and fly a flag when whale watching; and only two boats can be close to a whale at one time. Preliminary results indicated that whales did not interact with the boats in 65.3% of the sightings; no impacts were recorded in 28.4% of the sightings; and behavior changes were recorded in only 6.3% of the sightings. Not all of these changes were negative as there were some "friendly" whales that approached boats. Although there did not appear to be any negative impacts on the whales, increased enforcement was recommended since there was an "observer effect" on the boat operators (i.e., they were more likely to obey regulations if under observation).

4.74) **Whale watching off California:** Schulman-Janiger[9] described whale watching guidelines and activities off the coast of California. The guidelines specify a minimum approach of 100 yards (100 m) and recommend that vessels approach whales from the rear and avoid separating cow-calf pairs. However, there is very little enforcement, and it is hard to prove harassment. Whale watching is a major seasonal industry off California. For example, a total of 44,125 people in 1996 and 41,879 people in 1997 participated in the Cabrillo Whalewatch Program trip cruises alone (on 6 vessels) off Los Angeles, California . During the mid-1980s, abundant nearshore gray whale sightings prompted many operators to start to guarantee whale sightings, which led to increased pressure to locate whales. During 1989-91, the number of nearshore gray whale sightings decreased, and commercial vessels began to cooperate to locate whales. Several vessel operators combined assets to charter a spotting plane, and another vessel hired staff to spot whales from the ACS/LA survey site. A significant problem is the number of private boats that follow commercial boats. Off Los Angeles, there can be 8-12 boats following one whale. Jet-skis are also a significant problem; they harass whales and can separate cows from calves close to shore.

4.75) **Regulation suggestions in California:** Recommendations for improved regulations (Schulman-Janiger[9]) include: 1) issue permit numbers to whale watching vessels and require them to fly flags while following a whale; 2) make ship traffic aware of whales in the area; 3) set speed limits for vessels moving in and out of harbors; 4) do not extend the current whale-watching season

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[8] Héctor Pérez-Cortés Moreno, Instituto Nacional de la Pesca, CRIP, Km 1, Carretera a Pichilingue, La Paz, B.C.S., 23020 México.

[9] Alisa Schulman-Janiger, American Cetacean Society, 2716 S. Denison, San Pedro, CA 90731

(26 December-31 March) to target cow-calf pairs; 5) do not guarantee sightings; and 6) schedule boat races to avoid concentrations of whales, especially cow-calf pairs, in the area.

4.8) **Strandings:** From 1990 to 1998, there were 250 gray whale strandings (excluding the stranded whales in which the cause of death was due to entanglement) reported along the coasts of Alaska, Washington, Oregon, and California (Hill 1999b). In 1999 (as of 16 June), there were 24 gray whale strandings reported in Alaska (Sternfeld[10]); 6 in British Columbia--not including one death due to entanglement (Lochbaum[5]); 21 in Washington (11 on the coast; 10 within inland waters) (Norberg[11]); 1 in Oregon (Norberg[11]); and 32 on the California coast (Cordaro[12]). Pérez-Cortés Moreno (1999) reported that from 1975 to 16 June 1999, there were 518 strandings in Mexico (also see Sánchez Pacheco 1998). Thorough surveys were conducted in Mexico in the early 1980s and in 1998 and 1999, while relatively high numbers of strandings were recorded only in 1980 (53 whales), 1982 (46), 1991 (45), and 1999 (114). Although the number recorded in 1999 was high relative to other years, this was in part due to increased survey effort. These strandings occurred in many locations between December 1998 and June 1999 and were not related to a single stranding event. Of 89 stranded whales examined, 72% were adults, and of these, 78% were females.

4.9) **Ship strikes:** From 1990 to 1998, seven vessel strikes of gray whales were reported off the coasts of Alaska, Washington, Oregon, and California (Hill 1999c). Three of these animals appeared to have survived, while the other four were either mortalities or their status was unknown. Additional mortalities probably go unreported if the whales do not strand or are not thoroughly necropsied.

5) **Aboriginal harvest**: The current International Whaling Commission (IWC) quota (for 1998-2002) allows for a harvest of 140 gray whales per year for local consumption by aborigines (IWC 1998a).

5.1) **Russian:** From 1970 to 1998, an average of 139 gray whales were taken annually along the coasts of the Chukotka Peninsula (Quan 1999, Brownell[13]). The Russian Federation has agreed to take no more than 135 whales annually from 1998 to 2002 (IWC 1998a).

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[10] Pers. comm. Mary Sternfeld, NMFS, AK Region, Protected Resources, P.O. Box 21668, Juneau, AK 99802.

[11] Pers. comm. Brent Norberg, NMFS, WASC, 7600 Sand Point Way NE, Seattle, WA 98115-0070.

[12] Pers. comm. Joe Cordaro, NMFS, WASC, 501 West Ocean Blvd, 4200 Long Beach, CA 90802-4213.

[13] Pers. comm., Robert Brownell, Jr., Southwest Fisheries Science Center, NMFS, P.O. Box 271, La Jolla, CA 92038-0271.

5.2) **Alaskan:** No gray whales have been allocated by the IWC to Alaskan Native subsistence hunters since 1991 (Quan 1999). Two incidental takes of gray whales by an Alaskan Native occurred in 1995 (Brownell[13], Quan 1999).

5.3) **Makah:** The Makah Indian Tribe received a 5-year quota from the IWC in 1997 to harvest 20 gray whales for ceremonial and subsistence purposes. The Tribe may harvest up to five gray whales per year from 1998 through 2002 (IWC 1998a, Gearin 1999). Makah whalers struck and killed one gray whale on 17 May 1999 (Gosho[14]).

6) **Review of potential research projects:** As a part of the conclusions of the workshop, it was recommended that the Eastern North Pacific stock of gray whales be monitored for another 5-year period. This would occur between June 1999 and June 2004. Monitoring could provide information relevant to the regular reviews conducted by NMFS (e.g., Hill and DeMaster 1998) and the IWC (e.g., IWC 1998b). The high visibility of this stock along the west coast of North America has made it very popular, so there is considerable public awareness and concern for the gray whales' status. This stock's annual migrations along highly populated coastlines and their concentration in limited winter and summer areas may make them particularly vulnerable to impacts from commercial or industrial development or local catastrophic events. Also, the ease and efficiency of monitoring this stock during its migration past shore stations has provided scientists a rare opportunity to document a large whale species recovering from near extinction. Never before has there been as good an opportunity to study life history parameters of a cetacean population approaching its carrying capacity–a study which will be very beneficial to research on other, less accessible whale stocks. The following list includes potential projects that will help in this monitoring and further improve our understanding of the status of this whale stock. Inherent in this research is the encouragement to keep open lines of communication among scientists studying gray whales, which includes researchers in Mexico, the United States, Canada, and Russia.

6.1) **Abundance and trends in abundance**

6.11) **Granite Canyon, California:** NMML frequently conducts full-season counts of gray whales during the southbound migration past this shore station in central California (Shelden et al. in press). This has proven to be an optimal site both logistically (easy access in an area with a relatively mild climate) and biologically (where most of the gray whale population passes close to shore each year). The census conducted at Granite Canyon has provided a long-term, consistent monitoring of stock abundance and trends (since 1968). Although this stock is not considered to be at risk, the continuation of the seasonal counts will provide an ideal opportunity to study a large cetacean population as it approaches carrying capacity. The Granite Canyon census is considered to be a low risk investment as it is a system that has been well tested. Further testing is needed to improve corrections for pod-size estimates,

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[14] Pers. comm. Merrill Gosho, National Marine Mammal Lab, AFSC, NMFS, 7600 Sand Point Way NE, Seattle, WA 98115-0070.

continue studies of observer performance, and increase the accuracy of statistical variances within the observation data.

6.12) **Point Vicente, California:** Every year, ACS/LA volunteers conduct full-season counts of both the southbound and northbound migrations past Point Vicente, near Los Angeles (Schulman-Janiger 1999a) . These counts have been collected consistently since 1984 and are beneficial to time-series analyses; however, only a portion of the population passes this site during the southbound and northbound migrations.

6.13) **Yaquina Head, Oregon:** A volunteer from Oregon State University conducted counts of gray whales at Yaquina Head, near Newport, Oregon, in the 1998/99 season (Mate and Poff 1999). This site was also used for counts of the southbound and northbound migrations in 1978-81 (Herzing and Mate 1984).

6.14) **Other sites:** NMFS has no plans for systematic counts at locations other than Granite Canyon since this has proven to be the best site for shore-based counts.

6.141) **Cape Sarichef, Alaska:** Cape Sarichef, on the west edge of Unimak Island, is an ideal location for studying the gray whale migration in and out of the Bering Sea. This site was used for gray whale counts during several southbound and northbound migrations in the 1970s (e.g., Rugh 1984). However, the U.S. Coast Guard no longer maintains a facility there, making it logistically impractical to conduct research.

6.142) **Narrow Cape, Kodiak Island, Alaska:** Narrow Cape, on the south side of Kodiak Island, is an accessible site with a good view of the migratory corridor in the area, but gray whales also migrate on the north side of Kodiak Island, so the portion of the population passing Narrow Cape each year is unknown. No full-season counts have been conducted from this site.

6.15) **Stock assessment:** NMFS conducts an assessment of the Eastern North Pacific stock of gray whales at least every 3 years (Hill and DeMaster 1998); the stock assessment is currently being updated. The IWC conducts comprehensive assessments of stocks before harvest quotas are set (IWC 1998b); the next gray whale assessment will be in 2003.

6.16) **Stock identification and discreteness:** Genetic analysis may provide information on the degree of genetic variety within the Eastern North Pacific gray whale stock as well as determine differences between this stock and the Western North Pacific (Korean) stock (e.g., Rosel and Kocher 1997). Genetic discreteness of summering populations may be a factor in management decisions (Darling et al. 1998), specifically with regard to the whales in northwestern Washington where Makah Indians are whaling.

6.2) **Population health and viability**

6.21) **Calf counts**

6.211) **Granite Canyon, California:** The whale counts conducted by NMML at Granite Canyon during the southbound migration include counts of calves (Shelden et al. in press).

6.212) **Piedras Blancas, California:** During the past several years, the NMFS Southwest Fisheries Science Center (SWFSC) has conducted shore-based counts of gray whale calves during the northbound migration (Perryman et al. 1999b). Sighting rates at Piedras Blancas are compared to abundance estimates made by NMML during the southbound migration.

6.213) **Point Vicente, California:** The ACS/LA chapter includes calf counts in their ongoing effort at Point Vicente. The results show the percentage of calves seen during both the southbound and northbound migrations (Schulman-Janiger 1999b).

6.214) **Baja California Sur:** Counts of calves will continue to be a part of the studies of gray whales in Baja California Sur (e.g., Urbán et al. 1997).

6.22) **Condition index:** Photogrammetric studies conducted by the SWFSC help provide data on number of pregnant whales, proportion of sightings with calves, and lengths and other dimensions of whales. Dimension data can indicate animal health as a function of fat reserves (Perryman and Lynn 1999).

6.23) **Biological sampling**

6.231) **Harvest:** Data from harvested whales can help establish pregnancy rates and indicate health of individuals (e.g., Reilly 1992, Blokhin in press c).

6.232) **Natural mortality:** Samples from stranded whales may provide information on biological parameters, including reproductive condition, age, length, contaminant loads, stock discreteness, types of parasites or diseases, and cause of death (e.g., Heyning and Dahlheim in press).

6.3) **Distribution and habitat use**

6.31) **Baja California Sur:** Proposed studies include photo-identification of individual whales, radio-telemetry, and satellite-tagging. Results will provide information on persistence and consistency of use of certain lagoons. There was an intense study in 1980-85 that involved several of the lagoons (e.g., Jones and Swartz 1984). A multi-dimensional study over another 5-year period would provide a valuable comparison to the previous research.

6.32) **Washington State:** Photo-identification studies conducted by Cascadia Research Collective and the NMML (e.g., Calambokidis and Quan 1999, Gosho et al. 1999a, 1999b) provide information on how often individual whales are found in areas around northwestern Washington. This research will help answer questions about the "resident" vs. "transient" whales in the area where Makah Indians hunt whales.

6.33) **Migration and foraging**

6.331) **Satellite tagging:** Satellite tagging of gray whales would provide information on the timing and location of whales during their northbound migration and where they spend time feeding.

6.332) **Distribution information:** Distribution data may be collected from a variety of marine mammal surveys, such as the NMML cetacean surveys across southern Alaska, observations on fisheries research cruises, records collected in the Platforms of Opportunity Program, etc.

6.333) **Migratory timing:** Migratory timing can be documented through shore-based observations at sites used in the past, such as Point Vicente, Granite Canyon, and Yaquina Head (Rugh et al. 1999a, 1999b).

6.34) **Summer distribution:** Aerial and/or vessel surveys may provide information on current gray whale use of historic feeding grounds in the Bering and Chukchi Seas. Oceanographic sampling could document potential changes in prey production and availability (e.g., Grebmeier and Barry 1991).

6.4) **Anthropogenic concerns**

6.41) **Contaminant loads:** Contaminant loads are documented by the NMFS Northwest Fisheries Science Center (NWFSC) from samples collected from strandings and biopsies (Tilbury et al. 1999).

6.42) **Oil spills and post-spill monitoring:** There is a need for an oil-spill response protocol to minimize the effects of oil spills on gray whales. To develop this protocol, experimental designs are needed to minimize impacts of oil spills and better understand the risks to gray whales relative to different locations and intensities of oil spills.

6.43) **Noise:** Peter Tyack (Woods Hole Oceanographic Institute) and Chris Clark (Cornell University) have recently conducted and will probably continue to conduct acoustic studies relative to the response of large cetaceans, including gray whales, to Low Frequency Active (LFA) underwater transmissions (Tyack and Clark 1998).

6.44) **Fishery interactions:** The degree of impact of commercial and recreational fisheries on gray whales may be assessed through examinations of stranded whales, permit reports, and ships' log books. In particular, more information is needed from Mexico and Canada.

6.45) **Commercial development in critical habitats**

6.451) **Salt extraction in Baja California Sur:** A large salt evaporation facility is proposed for San Ignacio Lagoon (SEMARNAP 1997). If this facility is developed, the impact on whales using this lagoon should be studied. A comparison could be made between potential impacts of proposed salt work developments in Baja California Sur and the observed impacts of northwestern Australian salt works on humpback whales.

6.452) **Oil and gas exploration and extraction:** Oil and gas exploration and extraction have the potential of impacting whales along much of the migratory route, including feeding areas in the Bering and Chukchi Seas.

6.453) **Coastal development:** Coastal development, and the concomitant increase in human activities offshore, along much of the western shores of Mexico, the United States, and Canada has the potential of adversely impacting gray whales along their migration route (Moore and Clarke in press).

6.46) **Whale watching**

6.461) **Regulations:** A monitoring system should be established for operators of whale watching vessels; for example, through permit reports and/or log books. The IWC has established a subcommittee to provide guidelines for whale watching (IWC 1997d).

6.462) **Studies:** Studies should be conducted to evaluate the impact of whale watching operations. Whales and boats could be tracked using theodolites based on strategic shore-based sites. In Bahía Magdalena and San Ignacio Lagoon there are ongoing studies of whale watching operations (Pérez-Cortés Moreno[8], Sánchez Pacheco 1997b)

6.463) **Photographs:** Whale watching operations can be a source of photographs that may be used to identify individual whales. This could be beneficial in determining the amount of time individual whales stay in an area relative to the number of boats.

6.47) **Strandings:** Currently there are stranding networks in the United States and Mexico. On the U.S. West Coast, stranding information is collected by the NMFS Alaska Regional Office in Alaska, Northwest Regional Office in Washington and Oregon, and Southwest Regional Office in California. Besides aerial and vessel surveys of the lagoons in Mexico (Pérez-Cortés Moreno 1999), there is an ongoing research project in Scammon's Lagoon (Pérez-Cortés Moreno[8]).

6.48) **Ship strikes:** The number of strikes can be partially recorded through adequate documentation of marks on stranded whales and through ship logs (e.g., Hill 1999c, Heyning and Dahlheim in press).

6.5) **Research priorities:** Workshop participants were asked to select the five research projects that they would consider to be of the highest priority in evaluating the status of the Eastern North Pacific stock of gray whales. Preference was given to (in order of priority):

1) survey of the southbound migration at Granite Canyon (Section 6.11);
2) studies in the lagoons (Section 6.214, 6.31, 6.451, 6.453, 6.462, and 6.47);
3) photogrammetry/condition index (Section 6.22, 6.31, and 6.32);
4) calf counts (Section 6.21); and
5) Bering and Chukchi Sea surveys of foraging habitat/regime shifts (Section 6.34).

Summary

The workshop convened by NMFS at NMML in Seattle, Washington, on 16-17 March 1999, culminated the review of the status of the Eastern North Pacific stock of gray whales. This review was based on research conducted during the 5-year period following the delisting of this stock and includes information collected through 16 June 1999. The workshop followed guidelines outlined in the NMFS 5-year Plan to conduct the status review and recommend whether to: 1) continue the monitoring program for an additional 5-year period; 2) terminate the monitoring program; or 3) consider changing the status of the gray whale under the ESA. The 28 invited participants determined that this stock was neither in danger of extinction, nor was it likely to become endangered within the foreseeable future, according to the determining factors listed in section 4(a)(1) of the ESA. Therefore, there was no apparent reason to reverse the previous decision to remove this stock from the List.

Canada's Committee on the Status of Endangered Wildlife in Canada lists the "Northeast Pacific population" of gray whale as "not at risk." This is the lowest category for animals in their classification system, which also includes vulnerable, threatened, endangered, extirpated, or extinct.

The status of the Eastern North Pacific stock does not in any way alter the status of the still-endangered Western North Pacific ("Korean") stock of gray whales.

There was a consensus among the workshop participants that the Eastern North Pacific stock of gray whales should be monitored for an additional 5-year period (1999-2004), especially as this stock may be approaching its carrying capacity. Monitoring should include a continuation of surveys at Granite Canyon during the southbound migration; collaborative research with Mexican scientists on phenology of gray whales and the use of the lagoons in Baja California Sur; photogrammetry as a study of whale condition; calf counts; and an examination of the affect of environmental parameters, especially climate warming, on the whales' use of foraging areas.

Although the Eastern North Pacific stock of gray whales no longer receives protection under the ESA, it continues to be protected under the MMPA. As required by the MMPA, NMFS conducts an assessment of this stock every 3 years, or when new information becomes available. The last assessment occurred in 1997 (Hill and DeMaster 1998); it is currently being updated. Subsistence take is managed under quotas set by the IWC. Comprehensive assessments of gray whales are conducted by the IWC before quotas are set; the last assessment occurred in 1997 (IWC 1998b); the next will be in 2003 (IWC 1999a). There is no allowable commercial take of any gray whales, and the Convention on the International Trade in Endangered Species (CITES) regulates the transportation of animal parts. Furthermore, if there is evidence of a significant negative decline and research indicates that such a change would be warranted, this stock can be proposed to be listed again as threatened or endangered under the ESA.

This status review concludes the 5-year assessment of the Eastern North Pacific stock of gray whales (required by section 4(g)(1) of the ESA) that commenced on 16 June 1994 (59 FR 31094) when this stock was removed from the List.

Acknowledgments

Funding for travel to the workshop was provided by the NMFS Office of Protected Resources. Doug DeMaster was the chair for the workshop. Scientists making presentations at the workshop included: Héctor Pérez-Cortés Moreno, Lorenzo Rojas Bracho, and Jorge Urbán Ramírez from Mexico; Alisa Schulman-Janiger, from the American Cetacean Society/LA Chapter; John Calambokidis from Cascadia Research Collective; Jen Quan from the University of Washington; Bruce Mate from Oregon State University; Bob Brownell, Meghan Donahue, and Wayne Perryman from the NMFS Southwest Fisheries Science Center; John Stein and Gina Ylitalo from the NMFS Northwest Fisheries Science Center; and Jeff Breiwick, Marilyn Dahlheim, Doug DeMaster, Pat Gearin, Merrill Gosho, Scott Hill, Rod Hobbs, Sue Moore, Dave Rugh, and Kim Shelden from the NMFS Alaska Fisheries Science Center (National Marine Mammal Laboratory). Rod Hobbs provided the initial outline for the potential research projects. Helpful guidance at the workshop was provided by Greg Silber from the NMFS Office of Protected Resources, Steve Swartz from the NMFS Southeast Fisheries Science

Center, and Judy Zeh from the University of Washington. Greg Donovan, Helen Sharp, and staff of the International Whaling Commission provided abstracts of manuscripts from the IWC Journal of Cetacean Research and Management Special Issue 2 (in press) on gray whales. We are grateful to Ken Hollingshead and Greg Silber for their careful review of the Background section. Gary Duker and James Lee, of the AFSC Publications Unit, provided formatting edits. This document was improved by review comments from Héctor Pérez-Cortés Moreno, Lorenzo Rojas Bracho, Jorge Urbán Ramírez, José Sánchez Pacheco, Alisa Schulman-Janiger, Kim Shelden, Rod Hobbs, Tom Loughlin, and Steve Swartz.

Literature

The following list includes publications and unpublished documents dealing with gray whale research that has been conducted since 1993, following the circulation of the NMFS 5-year Plan for Research and Monitoring of the Eastern North Pacific Population of Gray Whales. Also included is any literature cited in the current status review and attached abstracts (indicated with an asterisk).

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APPENDIX A

PARTICIPANTS AT THE WORKSHOP TO REVIEW THE STATUS OF THE EASTERN NORTH PACIFIC STOCK OF GRAY WHALES

16-17 March 1999
At the National Marine Mammal Laboratory, Seattle, Washington

Participants	Affiliation and address	Attended
Will Anderson	PAWS 2122 8th Ave N, 201, Seattle, WA 98109	Yes
Mike Barber	Seattle Post-Intelligencer 101 Elliott Ave. W, Seattle, WA 98119	Yes
Howard Braham**	NMML, AFSC, NMFS (retired) 800 Acorn Circle, P.O. Box 1064, Ashland, OR 97520	No
Jeff Breiwick**	NMML, AFSC, NMFS 7600 Sand Pt Way NE, Seattle, WA 98115-0070	Yes
Robert Brownell, Jr.**	SWFSC, NMFS P.O. Box 271, La Jolla, CA 92038	Yes
Steve Buckland*	School of Mathematical and Computational Sciences University of St. Andrews, North Haugh, St. Andrews Fife, KY18 9SS, Scotland, UK	No
John Calambokidis*	Cascadia Research Collective 218 ½ W 4th Ave, Olympia, WA 98502	Yes
Leigh Calvez	naturalist	Yes
Marilyn Dahlheim**	NMML, AFSC, NMFS 7600 Sand Pt Way NE, Seattle, WA 98115-0070	Yes
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Meghan Donahue*	SWFSC, NMFS P.O. Box 271, La Jolla, CA 92038	Yes
Toni Frohoff	Humane Society of the US 321 Highschool Rd, 374 Bainbridge Island, WA 98110	Yes
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Rod Hobbs*	NMML, AFSC, NMFS 7600 Sand Pt Way NE, Seattle, WA 98115-0070	Yes
Robert Hofman*	Marine Mammal Commission 4340 East-West Hwy, Room 905, Bethesda, MD 20814	No
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Marcia Muto*	NMML, AFSC, NMFS 7600 Sand Pt Way NE, Seattle, WA 98115-0070	Yes
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Alisa Schulman-Janiger*	American Cetacean Society, Los Angeles Chapter 2716 S. Denison, San Pedro, CA 90731	Yes
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Kim Shelden*	NMML, AFSC, NMFS 7600 Sand Pt Way NE, Seattle, WA 98115-0070	Yes
Greg Silber*	Office of Protected Resources, NMFS 1315 East-West Hwy, Silver Spring, MD 20910-3282	Yes
John Stein**	NWFSC, NMFS 2725 Montlake Blvd. E., Seattle, WA 98112-2097	Yes
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Paul Wade*	NMML, AFSC, NMFS 7600 Sand Pt Way NE, Seattle, WA 98115-0070	No
Janice Waite*	NMML, AFSC, NMFS 7600 Sand Pt Way NE, Seattle, WA 98115-0070	Yes
Gina Ylitalo*	NWFSC, NMFS 2725 Montlake Blvd. E., Seattle, WA 98112-2097	Yes
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*Invited or asked to review workshop material.
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APPENDIX B

ABSTRACTS

Agenda Section 1.11

PRELIMINARY ESTIMATES OF POPULATION SIZE OF GRAY WHALES FROM THE 1992/93 AND 1993/94 SHORE-BASED SURVEYS

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Laake, J.L., D.J. Rugh, J.A. Lerczak, and S.T. Buckland. 1994. Preliminary estimates of population size of gray whales from the 1992/93 and 1993/94 shore-based surveys. Unpubl doc. SC/46/AS7 submitted to Sci. Comm. of Int. Whal. Commn. 13 p.

The California stock of gray whales (*Eschrichtius robustus*) has been recently proposed for removal from the U.S. list of endangered and threatened species. As part of the delisting regulation under the U.S. Endangered Species Act, the National Marine Fisheries Service has begun a monitoring effort that has included shore-based surveys conducted 10 December 1992 to 7 February 1993 and 10 December 1993 to 18 February 1994, during the whales' southbound migration past Carmel, California. Survey methods were the same as those used in previous seasons. Paired, independent counts were made whenever possible but not during every watch as occurred in 1987/88. In total, 1,180 pods (2,112 whales) were recorded during 343 hours of watch from the main (south) observation site when visibility was classified as excellent to good in 1992/93, and 1,864 pods (3,411 whales) were recorded during 447 hours in 1993/94. The survey data were analyzed using methods consistent with those used in the 1987/88 data analysis. The population estimate from the 1992/93 survey is 17,674 (CV = 5.87%, 95% confidence interval, 15,800 - 19,800), which is significantly lower than the 1993/94 estimate of 23,109 (CV = 5.42%, 95% confidence interval, 20,800 - 25,700) (z = -3.36, P = 0.0004). Possible reasons for the difference are: 1) changes in the number of whales migrating as far south as Carmel; 2) poor sighting conditions in 1992/93, particularly during the peak of the migration; 3) missing sources of variation. The 1993/94 estimate is not significantly different than the 1987/88 estimate of 20,869 (CV = 4.37%) (z = 1.46, P = 0.072).

Agenda Section 1.12

ABUNDANCE OF GRAY WHALES IN THE 1995/96 SOUTHBOUND MIGRATION IN THE EASTERN NORTH PACIFIC

R.C. Hobbs, D.J. Rugh, J.M.Waite, J.M. Breiwick and D.P. DeMaster

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Hobbs, R.C., D.J. Rugh, J.M. Waite, J.M. Breiwick, and D.P. DeMaster. In press. Abundance of gray whales in the 1996/96 southbound migration in the eastern North Pacific. J. Cetacean Res. Manage. Special Issue 2.

Systematic counts of gray whales (*Eschrichtius robustus*) were conducted from 13 December 1995 to 23 February 1996 at Granite Canyon, California. This study is the second of three during the 5-year period following the removal of gray whales from the U.S. government list of endangered and threatened wildlife. The counts were made at the same research station used most years since 1975 by the National Marine Mammal Laboratory to observe the southbound migration of the eastern North Pacific stock. Counting methods were kept similar to those used in previous surveys and included double counting to assess observer performance. In addition, aerial surveys and high-powered binoculars provided documentation that a negligible fraction of migrating whales passed beyond the sighting range of the counting observers. A total of 2,151 pods (3,928 whales) was counted during 472.7 hours of standard watch effort with a visibility recorded as fair to excellent. Data analysis procedures were substantially the same as in previous years with a modification to account for differential sightability by pod size. Population size is estimated to be 22,263 whales (CV = 9.25%; 95% log-normal CI = 18,700 to 26,500). This estimate is similar to the previous estimate of 23,109 (CV = 5.42%; 95% CI = 20,800 to 25,700) from the 1993/94 survey.

Agenda Section 1.13
1.14

THE ABUNDANCE OF GRAY WHALES IN THE 1997/98 SOUTHBOUND MIGRATION IN THE EASTERN NORTH PACIFIC

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Hobbs, R.C., and D.J. Rugh. 1999. The abundance of gray whales in the 1997/98 southbound migration in the eastern North Pacific. Unpubl. doc. SC/51/AS10 submitted to Sci. Comm. of Int. Whal. Commn. 18 p.

Systematic counts of gray whales (*Eschrichtius robustus*) were conducted from 13 December 1997 to 24 February 1998 at Granite Canyon and Point Lobos, California. This study is the third of three during the 5-year period following the removal of gray whales from the U.S. government list of endangered and threatened wildlife. The counts were made at the same research station used most years since 1975 by the National Marine Mammal Laboratory to observe the southbound migration of the eastern North Pacific stock of gray whales. Counting methods were kept similar to those used in previous surveys and included double counting to assess the performance of observers. In addition, high-powered binoculars provided documentation that a negligible fraction of migrating whales passed beyond the sighting range of the counting observers. In total, 2,318 pods (3,643 whales) were counted during 435.3 hours of standard watch effort when visibility was recorded as fair to excellent. Data analysis procedures were substantially the same as those used in previous years and identical to those used for the 1995/96 census. The population is estimated to be 26,635 whales (CV = 10.06%; 95% log-normal confidence interval = 21,878 to 32,427). This estimate is similar to the previous estimates of 23,109 (CV = 5.42%; 95% confidence interval = 20,800 to 25,700) from the 1993/94 survey and 22,263 whales (CV = 9.25%; 95% log-normal confidence interval = 18,700 to 26,500) from the 1995/96 survey.

Agenda Section 1.14

PRELIMINARY DOCUMENTATION OF GRAY WHALE ABUNDANCE ESTIMATION PROCEDURES

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Breiwick, J.M., and R.C. Hobbs. 1996. Preliminary documentation of gray whale abundance estimation procedures. Unpubl. doc. SC/48/AS2 submitted to Sci. Comm. of Int. Whal. Commn. 5 p.

The National Marine Mammal Laboratory (NMML) produces abundance estimates of the Eastern North Pacific stock of gray whales based on counts made from Granite Canyon, near Carmel, California. These abundance estimates are based on the number of pods observed and the average recorded pod size obtained directly from the field data. These numbers are corrected for 1) number of pods passing outside of count periods; 2) rate of night travel; 3) pods missed within the viewing range of observers while on watch; and 4) mean pod size. In conjunction with recent counts, aerial surveys have been flown to compare the offshore distribution of gray whale sightings with the distribution based on shore counts. Results since 1988 have indicated, however, that a correction factor for whales passing beyond the viewing range of shore-based observers is not necessary. Aerial observations of pod size have been used in comparison with shore-based pod size estimates to compute a correction factor for pod size bias. This document summarizes the analytical procedures used during the past decade.

Agenda Section 1.15

DIEL VARIATION IN MIGRATION RATES OF EASTERN PACIFIC GRAY WHALES MEASURED WITH THERMAL IMAGING SENSORS

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Perryman, W.L., M.A. Donahue, J.L. Laake, and T.E. Martin. 1999a. Diel variation in migration rates of eastern Pacific gray whales measured with thermal imaging sensors. Mar. Mammal Sci. 15(2):426-45.

We recorded the blows of southbound gray whales from central California in January 1994, 1995, and 1996 using thermal imaging sensors. For our sampling purposes, we defined day (0730-1630) and night (1630-0730) to coincide with the on/off effort periods of the visual surveys being conducted concurrently. We pooled data across the three years of sampling and tested for diel variation in respiration interval, pod size, offshore distance, migration rate, and swimming speed by comparing paired day/night means for samples collected within the same 24-hour period. We performed these tests using data from the entire migration period and then repeated the tests for samples collected prior to and after the approximate median migration date (January 15th). Over the entire migration period we observed significantly larger daytime pod sizes ($\bar{x}_{day} = 1.75 \pm 0.280$ km, noted here and throughout with one standard deviation, $\bar{x}_{night} = 1.63 \pm 0.232$km) and offshore distances ($\bar{x}_{day} = 2.30 \pm 0.328$ km, $\bar{x}_{night} = 2.03 \pm 0.356$ km), but found no significant diel variation in respiration interval. For the entire migration period, the nocturnal migration rate (average number of whales passing per hour) was significantly higher ($t = -2.65$, $\bar{x} = 20$, $p = 0.02$). During the early migration period, we detected no significant diel variation in pod size or respiration interval, but daytime offshore distances were significantly larger ($\bar{x}_{day} = 2.28 \pm 0.273$ km, $\bar{x}_{night} = 1.96 \pm 0.318$ km). Diurnal and nocturnal migration rates prior to January 15th were not significantly different. During the late migration period, there was no significant diel variation in respiration interval, pod size, or distance offshore, but the nocturnal migration rate was significantly higher (28%, SE = 11.6%) than the diurnal rate. We found no significant diel variation in swimming speed in any comparison. We propose later migrants socialize more during the day, which effectively slows their diurnal rate of migration even though they maintain equal speeds day and night when swimming.

Agenda Section 1.2111

EVALUATION OF HIGH-POWERED BINOCULARS TO DETECT INTER-YEAR CHANGES IN THE OFFSHORE DISTRIBUTION OF GRAY WHALES

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Rugh, D.J., J.A. Lerczak, R.C. Hobbs, J.M. Waite, and J.L. Laake. In press. Evaluation of high-powered binoculars to detect inter-year changes in the offshore distribution of gray whales. J. Cetacean Res. Manage. Special Issue 2.

Paired, independent searches for gray whales (*Eschrichtius robustus*) were conducted through fix-mounted, 25-power binoculars during January 1995 and 1996 at Granite Canyon, California. This study was a test of an efficient method for documenting inter-year changes in the offshore component of the gray whale migration. The research site has been used most years since 1975 by the National Marine Mammal Laboratory to make gray whale counts for abundance estimates. Matching sightings between these paired observation efforts showed a very high agreement between observers (detection probability 0.97) for whale groups consisting of more than one animal within 1 to 3 nmi of shore, and a fairly high agreement (0.87) for animals that appeared to be traveling alone (5% of the sampled population) within 1 to 3 nmi of shore. Therefore, sighting probability remained high out to 3 nmi, a distance which includes most (98.7%) of the whale migration. For the critical sighting range of 1 to 3 nmi, the method we applied here, using paired, fix-mounted binoculars, is considered a feasible, cost-effective technique for detecting inter-year differences in the offshore tail of the distribution of gray whales.

Agenda Section 1.2112

COMPARISON OF THE OFFSHORE DISTRIBUTION OF SOUTHBOUND MIGRATING GRAY WHALES FROM AERIAL SURVEY DATA COLLECTED OFF GRANITE CANYON, CALIFORNIA, 1979-96

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Shelden, K.E.W., and J.L. Laake. In press. Comparison of the offshore distribution of southbound migrating gray whales from aerial survey data collected off Granite Canyon, California, 1979-96. J. Cetacean Res. Manage. Special Issue 2.

Aerial surveys provide an assessment of the offshore distribution of gray whales and an estimate of the proportion of whales that migrate beyond the visual range of shore-based observers. Six surveys were conducted concurrent with shore-based surveys during 1979, 1980, 1988, 1993, 1994 and 1996. Annual differences were tested for in the distribution of whales within an area 3 nmi north and south of Granite Canyon, and it was found that the distributions within 3 nmi of the shore differed by year but the shifts in the distribution were minor (<0.3 nmi). The inshore (<2.25 nmi) and offshore (>2.25 nmi) distribution of gray whale pods did not differ significantly between survey years. An average of 4.76% (SE = 0.85%) of the whale pods were observed beyond 2.25 nmi and only 1.28% (SE = 0.07%) were observed beyond 3 nmi.

Agenda Section 1.2121
1.2124

THE SOUTHBOUND MIGRATION OF GRAY WHALES
WINTER 1998/99

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Mate, B.R., and A. Poff. 1999. The southbound migration of gray whales, winter 1998/99. Unpubl. doc. submitted to the Workshop to Review the Status of the Eastern North Pacific Stock of Gray Whales, 16-17 March 1999, Seattle, WA.

Alternate half-hour counts were made during the morning hours from 5 December through mid-February from the Yaquina Head Lighthouse (162 feet above sea level). Observations were made on all fair-weather days (< Beaufort 4).

The first whale was sighted on 23 December and the peak passage of whales per hour occurred 7 January. By comparison with previous data from the same site (1978/81: Herzing and Mate 1984), the migration started 3 weeks later than normal and the migratory population peaked 6 days later than the latest date.

Aerial surveys in early December showed a number of animals along the coast but not moving consistently in southerly directions. Surveys closer to Christmas about 10 miles offshore showed more animals beyond 5 miles than inside 5 miles. This was an unusual distribution from efforts in previous years when most of the population was within 3 miles of the coast. Despite periods of good weather, whales did not tend to come nearshore to the degree experienced in previous years. In this study, 60% of the animals were 5 miles or farther offshore and 20% of the animals were within 3 miles of shore judging from lighthouse observations.

Agenda Section 1.2122

FIELD REPORT ON THE WINTER DISTRIBUTION OF GRAY WHALES IN WASHINGTON WATERS, 1998/99

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Shelden, K.E.W., J.L. Laake, P.J. Gearin, D.J. Rugh, and J.M. Waite. 1999a. Field report on the winter distribution of gray whales in Washington waters, 1998/99. Unpubl. doc. submitted to the Workshop to Review the Status of the Eastern North Pacific Stock of Gray Whales, 16-17 March 1999, Seattle, WA.

The winter distribution of gray whales along the Washington coast has been difficult to characterize primarily because of low survey effort (due to poor surveying conditions). Aerial surveys were conducted during the months of November and December 1998 and January 1999 between Cape Flattery and Carroll Island, Washington. Flights included a coastal trackline extending from Cape Flattery (48°23' N, 124°44' W) to Carroll Island (48°00' N, 124°43' W) and 8 east-west oriented transect lines spaced at 7.4 km intervals, extending 55.6 km offshore. Survey flights were scheduled at 10-day intervals with modifications to the schedule occurring when weather conditions were not optimal. Four complete surveys and two partial surveys were flown between November 1998 and January 1999 for a total of 19.5 on-effort hours and 40 transect lines. Four gray whale pods (6 individuals) and two gray whale pods (2 individuals) were observed on offshore transect lines and coastal tracklines, respectively. Distances off the Washington coast for pods observed on transect ranged from 5.5 km to 47 km. One sighting of an extremely rotund whale on 22 December suggests that pregnant animals continued to pass the Washington coast late in December. No calves were seen. Other marine mammal sightings included aggregations of humpback whales and Pacific white-sided dolphins feeding in the survey area in November and early December. Based on this study and other reports, it appears that gray whales are widely dispersed across the outer continental shelf of Washington State during both migratory and non-migratory periods. Sightings indicate that some may migrate close to shore while others may be nearly 50 km offshore. Gray whales were also observed within Washington State's inside waters during the southbound migration period. Because gray whales utilize the inside waters and outer coast throughout the year, determining when a "resident" becomes a "migrant" has been based on migratory timing. Although migratory timing cannot be confirmed by the aerial survey results reported here because too few whales were seen during the flights, it does appear that the peak of the southbound migration passes through the area in early to mid-January.

Agenda Section 1.2123

GRAY WHALE OBSERVATIONS FROM TATOOSH ISLAND, WASHINGTON, DECEMBER 1998

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Jones, B. 1999. Unpubl. doc. submitted to the Workshop to Review the Status of the Eastern North Pacific Stock of Gray Whales, 16-17 March 1999, Seattle, WA.

Gray whales (*Eschrichtius robustus*) were surveyed from the tower of the Tatoosh Island lighthouse from 30 November - 16 December 1998. The purpose of the study was to determine the onset of the southbound migration of gray whales past Cape Flattery, the most northwestern point of Washington State. Observations were conducted primarily without the use of optical aids. 7 X 50 Fujinon binoculars, equipped with reticles and a magnetic compass, were used to document sighting location. Gray whales were seen on three occasions (2, 4, and 13 December) during 49.3 hours of observation effort over a total of 12 days. The average daily observation effort for this time was 4.1 hours. The maximum possible sighting distance was estimated at 25 km. Gray whales were seen at a range of 0.6 - 5.9 km from shore. Although few migrating gray whales were observed during this period, it is possible that whales passed offshore, out of the observer's sighting range. It is also possible that this time period (30 November - 16 December) represented the very early stages of the southbound gray whale migration past Washington, thus few whales were in the vicinity. Aerial and vessel surveys conducted by the National Marine Mammal Laboratory in November and December 1998, and January 1999 support the latter hypothesis.

Agenda Section 1.2124

SOUTHBOUND GRAY WHALE MIGRATION TIMING OFF LOS ANGELES, 1985-99

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Schulman-Janiger, A. 1999a. Southbound gray whale migration timing off Los Angeles, 1985-99. Unpubl. doc. submitted to the Workshop to Review the Status of the Eastern North Pacific Stock of Gray Whales, 16-17 March 1999, Seattle, WA.

TENTH PERCENTILE, MEDIAN DATES, AND NINETIETH PERCENTILE FOR THE SOUTHBOUND GRAY WHALE MIGRATION OFF PT. VICENTE/LONG POINT, CALIFORNIA, 1985-99

Season number	Census dates	10th percentile Sightings (whales)	Median (50th percentile) Sightings (whales)	90th percentile Sightings (whales)
3	1 Dec 85 - 17 May 86	7 Jan (5 Jan)	30 Jan (29Jan)	20 Feb (18 Feb)
4	1 Dec 86 - 3 May 87	2 Jan (4 Jan)	28 Jan (28 Jan)	12 Feb (12 Feb)
5	1 Dec 87 - 14 May 88	5 Jan (5 Jan)	18 Jan (18 Jan)	5 Feb (5 Feb)
6	1 Dec 88 - 30 Jun 89	2 Jan (4 Jan)	15 Jan (17 Jan)	31 Jan (31 Jan)
7	1 Dec 89 - 6 Jun 90	1 Jan (1 Jan)	24 Jan (24 Jan)	11 Feb (11 Feb)
8	1 Dec 90 - 12 May 91	25 Dec (30 Dec)	19 Jan (19 Jan)	16 Feb (16 Feb)
9	1 Dec 91 - 3 May 92	2 Jan (3 Jan)	21 Jan (23 Jan)	14 Feb (14 Feb)
10	1 Dec 92 - 8 May 93	30 Dec (30 Dec)	18 Jan (16 Jan)	15 Feb (11 Feb)
11	1 Dec 93 - 7 May 94	3 Jan (5 Jan)	28 Jan (27 Jan)	15 Feb (14 Feb)
12	1 Dec 94 - 5 May 95	22 Dec (24 Dec)	17 Jan (18 Jan)	11 Feb (11 Feb)
13	1 Dec 95 - 10 May 96	30 Dec (31 Dec)	24 Jan (26 Jan)	17 Feb (16 Feb)
14	1 Dec 96 - 16 May 97	30 Dec (30 Dec)	18 Jan (18 Jan)	12 Feb (9 Feb)
15	1 Dec 97 - 15 May 98	1 Jan (2 Jan)	17 Jan (17 Jan)	9 Feb (5 Feb)
16	1 Dec 98 - 15 May 99	28 Dec (31 Dec)	21 Jan (22 Jan)	8 Feb (8 Feb)

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1.213
1.214

TIMING OF THE SOUTHBOUND MIGRATION OF GRAY WHALES IN 1998/99

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Rugh, D.J., K.E.W. Shelden, and A. Schulman-Janiger. 1999a. Timing of the southbound migration of gray whales in 1998/99. Unpubl. doc. submitted to the Workshop to Review the Status of the Eastern North Pacific Stock of Gray Whales, 16-17 March 1999, Seattle, WA.

The southbound migration of gray whales has been documented most seasons since 1967 from Granite Canyon, a shore-based observation station in central California. Prior to 1980, median dates of sightings ranged from 5-14 January, with an overall median date of 8 January. Since 1980, there has been a 1-week delay in the peak, such that the median date is now closer to 15 January (ranging 12-19 January). Allowing for this delay, and using a travel rate of 144 km/day between shore stations, expected peak dates in 1998/99 should have been 11 December for Cape Sarichef, at the tip of the Alaska Peninsula/Unimak Island; 18 December for Narrow Cape near Kodiak, Alaska; 5 January for Tatoosh Island, the northwesternmost tip of Washington State; 8 January for Yaquina Head, near Newport, Oregon; 15 January for Granite Canyon, central California; and 18 January at Point Vicente, near Los Angeles, California. Although no observations were made at Granite Canyon in 1998/99, sightings collected at Yaquina Head and Point Vicente indicate that the southbound migration was within 3 days of the expected date. Inter-year variations of a few days in migratory dates may be explained in part by variations in the median location of whales in the Bering or Chukchi Seas just prior to the onset of the migration. The further north the whales are in late October, the shorter the days will be (i.e., a perceived reduction in photoperiod), which seems to be the primary cue to initiating the southbound migration.

Agenda Section 1.221

CETACEAN HABITATS IN THE ALASKAN ARCTIC

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Moore, S.E., and D.P. DeMaster. 1997. Cetacean habitats in the Alaskan arctic. J. Northwest Atl. Fish. Sci. 22:55-69.

Marine mammals can be used as indicators of environmental productivity because they must feed efficiently and therefore aggregate where prey is plentiful. Three species of cetaceans, bowhead whales (*Balaena mysticetus*), gray whales (*Eschrichtius robustus*), and white whales (*Delphinapterus leucas*) migrate to the Alaskan arctic each year to feed. These species have distinctly different feeding modes and forage at dissimilar trophic levels. Bowhead whales filter zooplankton from the water column, gray whales siphon infaunal crustaceans from the benthos and white whales catch a variety of nekton including crustaceans, cephalopods and fishes.

Line transect aerial surveys were conducted over the Alaskan Chukchi and Beaufort Seas each late summer and autumn 1982-91. The resulting database, consisting of 634 flights, was post-stratified by survey type and sea state (Beaufort $\leq$ 04) to provide a database of cetacean sightings made along random transects during good survey conditions. Sightings made during connect and search legs of the survey, and in rough seas were excluded. Post-stratification resulted in a cumulative (1982-91) database of 276,754 transect-km of survey effort during which there were 554 bowhead, 608 gray and 831 white whale sightings.

Habitat partitioning and variability in habitat use among cetaceans in offshore areas of northern Alaska is poorly defined. Available data suggest that cetacean distribution and abundance patterns can be quantified on the basis of water depth and surface ice cover, and that these indices can be linked to large-scale oceanographic processes. In summer, mean depth and percent surface ice cover were significantly different ($p < 0.001$) among bowhead (900 m, 52%; $n = 79$), gray (40 m, 1%; $n = 497$) and white whales (1,314 m, 60%; $n = 146$). All pairs were significantly different ($p < 0.003$), except for bowhead-white whale ice cover ($p < 0.13$). Similarly in autumn, mean depth and percent ice cover were significantly different ($p < 0.001$) among bowhead (109 m, 22%; $n = 475$), gray

(38 m, 7%; $n = 111$) and white whales (652 m, 52%; $n = 685$); all pairs were significantly different ($p < 0.001$). In addition, mean depth and percent ice cover were significantly different ($p < 0.001$) between summer and autumn for bowhead and white whale sightings. Currents are bathymetrically driven, and ice cover influenced by currents and wind, in the Chukchi and Beaufort Seas. The association of cetaceans with specific bathymetric and ice cover regimes provides a foundation for further investigation of inter-specific habitat selection, zones of productivity and insight to the role of cetaceans in Alaskan arctic ecology.

Agenda Section 1.222

PHOTOGRAPHIC IDENTIFICATION RESEARCH ON SEASONAL RESIDENT WHALES IN WASHINGTON STATE

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Calambokidis, J., and J. Quan. 1999. Photographic identification research on seasonal resident whales in Washington State. Unpubl. doc. submitted to the Workshop to Review the Status of the Eastern North Pacific Stock of Gray Whales, 16-17 March 1999, Seattle, WA.

Photographic identification of gray whales in Washington State has been conducted by Cascadia Research since 1984. This has been part of an ongoing research effort to study the abundance, movements, residence times, and return rate of seasonal resident gray whales that spend the spring, summer, and fall feeding in these areas. Starting in 1992, surveys were more frequent and encompassed a broader region. Since 1996, this effort has also included identifications from the National Marine Mammal Laboratory from systematic surveys along the northern Washington Coast and western Strait of Juan de Fuca.

Through 1997, more than 600 identifications of whales have been made, representing 168 unique individuals. In 1996 and 1997, 47 and 37 different gray whales were identified primarily on the northern coast of Washington State and near the western entrance to the Strait of Juan de Fuca (both the Washington and Vancouver Island sides). Movements among these three regions were very common and most animals were seen multiple times (up to 11) over periods of up to 163 days. Of whales identified in northwest Washington in 1996 and 1997, 64%-83% had been identified in a previous year. Gray whales identified near Grays Harbor in the spring were less likely to have been seen multiple times (52%) or a previous year (26%). Comparison of photographic catalogs with researchers working in British Columbia revealed that many of the whales that feed along the Washington coast through the summer range along the British Columbia coast to areas north of Vancouver Island. Gray whale occurrence in Puget Sound has been more variable from year to year.

Analysis is currently underway of the 1998 sample which is the largest and most comprehensive to date. Effort by Cascadia Research included surveys and identifications off California, Oregon, several regions of Washington State (including Puget Sound), southern British Columbia, and southeast Alaska. Photographs of animals in specific regions within this range were also obtained by collaborating researchers with NMML, West Coast Whale Research Foundation, Humboldt State University, University of Victoria, University of British Columbia, Department of Fisheries and Oceans, Vancouver Aquarium, Juan de Fuca Express, and Coastal Ecosystems Research Foundation. These represent close to 500 records of over 150 different individuals. Preliminary results of this analysis has provided new information on the status and movements of these seasonal resident whales.

Overall conclusions include:

1. Seasonal resident gray whales utilize coastal areas from northern California to southeast Alaska from spring to fall with some interchange of animals among most of these areas.
2. Gray whales show some localized site fidelity to certain areas but also move widely within and between years. Gray whales seen in northern Puget Sound show a strong site fidelity to this area but only for part of the season and then move to other unknown areas (not currently sampled).
3. Utilization of some areas, such as southern Puget Sound, are highly variable year to year and whales seen in this area have a high mortality rate and are rarely seen in more than one year.
4. The total number of seasonal resident animals is not known (in the hundreds), nor is how they are recruited to this group, or the degree to which they need to be managed as a separate unit.

Agenda Section 1.222

THE SUMMER AND FALL DISTRIBUTION OF GRAY WHALES IN WASHINGTON WATERS

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The National Marine Mammal Laboratory has been studying gray whale distribution and identification since 1996 in the Strait of Juan de Fuca, off the northern Washington coast, and off the southwest coast of Vancouver Island. Each year the animals were concentrated in different locations. In 1996, the largest concentration of gray whales occurred off Portage Head and Makah Bay on the northern Washington coast. In 1997, the majority occurred in the westernmost Strait of Juan de Fuca from Bullman Beach to Mushroom Rock. In 1998, most of the gray whales were sighted off the southwest coast of Vancouver Island. Photographs of gray whales allowed the identification of 18 individual animals in 1996 and 28 animals in 1997. Photo-identification and co-operation with other researchers showed that gray whales moved freely between areas in the Strait of Juan de Fuca, off the Washington coast, and off the southwest coast of Vancouver Island.

Agenda Section 1.23

GRAY WHALE STUDIES AT LAGUNA SAN IGNACIO, B.C.S., MÉXICO, WINTER 1996

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Urbán R., J., A. Gómez-Gallardo U., V. Flores de Sahagún, J. Cifuentes L., S. Ludwig, and M. Palmeros R. 1997. Gray whale studies at Laguna San Ignacio, B.C.S., México, winter 1996. Rep. Int. Whal. Commn. 47:625-633.

Laguna San Ignacio, located on the west coast of the Baja California Peninsula, is one of the four main calving-breeding lagoons of the eastern Pacific gray whale (*Eschrichtius robustus*). Uncertainty exists concerning the potential effects of both whale watching and the development of a proposed salt project on gray whales and the lagoon ecosystem. This note documents the current use of Laguna San Ignacio by gray whales for comparison with previous studies and, as far as possible, to provide a baseline to detect and analyse changes in the whales' use of this lagoon. Twenty boat censuses were carried out from 17 January to 27 March 1996. The maximum combined count was 207 (115 single whales and 92 cow-calf pairs). The peak numbers of both single whales and cow-calf pairs were at the same time in early March when almost 40% fewer whales were observed in 1996 than the 1978-82 average. Density estimates at the maximum combined count were: 8.6 whales/km^2 in the lower zone, 3.8 whales/km^2 in the middle zone and 1.3 whales/km^2 in the upper zone. Of the 329 identified whales, 164 were singles, 141 cow-calf pairs and 24 undetermined; 51 whales were seen more than once (43 cow-calf pairs and 8 singles). Different residency intervals were documented: cow-calf pairs stayed in the lagoon 18.3 ± 4.8 (95% C.I.) days and single whales 2.6 ± 1 (95% C.I.) days. Four systematic aerial surveys were carried out at Bahía Ballenas between 1 February and 4 March. The maximum count in this bay was on 28 February with 127 adult whales (119 single whales and 8 cow-calf pairs). These observations must be continued for a period of years to establish a new basis for comparison with previous research results. Further photographic and tagging studies may help in developing turnover rates, which will allow the number of whales using the lagoon to be calculated, based on visual surveys.

Agenda Section 1.23

A NOTE ON THE 1997 GRAY WHALE STUDIES AT LAGUNA SAN IGNACIO, B.C.S., MÉXICO

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Urbán R., J., A. Gómez-Gallardo U., and M. Palmeros R. 1998a. A note on the 1997 gray whale studies at Laguna San Ignacio, B.C.S., México. Rep. Int. Whal. Commn. 48:513-516.

This note includes the results of our second year of gray whale studies at Laguna San Ignacio, B.C.S., México. Uncertainty exists concerning the potential effects of both whalewatching and the development of the proposed salt project on gray whales and the lagoon ecosystem. The purpose of this report is to document the current use of Laguna San Ignacio by the gray whales for comparison with previous studies. Eleven complete censuses of the lagoon were done by boat to determine whale abundance and distribution from 11 February to 29 March 1997. The maximum combined count was 253 (127 single whales and 126 cow-calf pairs) during the last week of February. Six dead calves (four males and two females) were found inside the lagoon. The upper zone of the lagoon was the most important for cow-calf pairs and the lower zone for single whales. There were 22% more whales than in the 1996 winter season, but this is still 36% lower than the highest count in 1985. Different residency intervals were documented: cow-calf pairs stayed in the lagoon 19.6 ± 3.5 days (95% C.I.), and the single whales 6.2 ± 3.2 days (95% C.I.). Nine whales photo-identified in 1996 were also photographed during the 1997 winter season.

Agenda Section 1.23

TRANSITO DE BALLENA GRIS (*ESCHRICHTIUS ROBUSTUS*) EN BAHÍA BALLENAS, BAJA CALIFORNIA SUR, MÉXICO

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Sánchez Pacheco, J.A., and J.L. Valdés Aragón. 1997. Transito de ballena gris (*Eschrichtius robustus*) en Bahía Ballenas, Baja California Sur, México. [The transit of the gray whale (*Eschrichtius robustus*) in Bahía Ballenas, Baja California Sur, Mexico.] Boletín Pesquero CRIP-La Paz 7:26-33.

Results are presented on observations of the transit of gray whales at different distances from the coast in Bahía Ballenas, Baja California Sur, during the 1996 and 1997 seasons. Whales that moved northwards prevailed (96%). There were fewer single whales in 1997 than in 1996; the reverse situation occurred in whales with calves. Single whales transited further from the coast (75.4% ≥2 km) than whales with calves (82.32% within 3 km). The number of single whales estimated to migrate north from the observation point was 2,888 and 2,195 for 1996 and 1997, respectively. There were 418 cow/calf pairs seen in 1996 and 621 in 1997.

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ESTIMATED TRENDS IN ABUNDANCE OF EASTERN PACIFIC GRAY WHALES FROM SHORE COUNTS, 1967/68 TO 1995/96

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Buckland, S.T., and J.M. Breiwick. In press. Estimated trends in abundance of eastern Pacific gray whales from shore counts, 1967/68 to 1995/96. J. Cetacean Res. Manage. Special Issue 2.

Estimates of abundance of eastern Pacific gray whales are obtained from counts made during their southbound migration past a shore-based station near Monterey, California. Assuming an exponential rate of increase, the population is estimated to have increased at 2.5% per annum (SE = 0.3%) between 1967/68 and 1995/96. However, there is some indication that the population growth is slowing, so that an asymptotic growth curve may be more appropriate. The estimated asymptote from a logistic model is 26,046 (SE = 6,281) and the inflection point is approximately in 1971 (SE = 6.5). The onset of the migration, when 10% of the whales have passed the station, has occurred increasingly later through this sample period, by approximately one day every 2 years. Median dates show a similar trend of roughly one day every 3 years. However, there is no significant change in the date at which 90% of whales have passed the station.

Agenda Section 1.3

GRAY WHALE ABUNDANCE ESTIMATES, 1967/68 - 1997/98: *ROI*, *RY*, AND *K*

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Breiwick, J.M. 1999. Gray whale abundance estimates, 1967/68 - 1997/98: *ROI*, *RY* and *K*. Unpubl. doc. submitted to the Workshop to Review the Status of the Eastern North Pacific Stock of Gray Whales, 16-17 March 1999, Seattle, WA.

Gray whale abundance estimates for the period 1967/68 to 1997/98 were fit using a generalized linear model (Poisson error, logarithmic link), giving a rate of increase of 2.52% per annum (SE = 0.27%). In addition, a (continuous) logistic model fit to the data gave a *K* (carrying capacity) of 37,364 (SE = 24,854), larger by 11,000 than a similar estimate based on the 1967/68 - 1995/96 data. Both estimates have very large CVs associated with them. A discrete logistic model was also used to estimate R_{max} and *K*. A replacement yield (*RY*) of 612 was calculated based on the rate of increase estimate, average catches and the abundance estimates. A Monte Carlo procedure was used to calculate a 95% confidence interval for *RY*.

Agenda Section 1.3

A BAYESIAN ANALYSIS OF EASTERN PACIFIC GRAY WHALE POPULATION DYNAMICS

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Wade. P.R., and D.P. DeMaster. 1996. A Bayesian analysis of eastern Pacific gray whale population dynamics. Unpubl. doc. SC/48/AS3 submitted to Sci. Comm. of Int. Whal. Commn. 21 p.

A Bayesian statistical method was used to investigate the population dynamics of eastern Pacific gray whales. Apparent stability in the three most recent abundance estimates may be due to a density-dependent slowing of the population growth rate. This hypothesis was tested by comparing how well density-dependent population models fit the data relative to density-independent population models. Additionally, a second hypothesis was tested, which was whether using a parameter representing additional variance in the abundance estimates provided a better fit to the data than not including it. In total, the fit of eight different models were compared through the use of the Bayes factor. Density-dependent models were decisively supported by the data over density-independent models when the additional variance term was not used. However, the use of the additional variance term was also decisively supported by the comparisons. When the additional variance term was included, the data still favored the density-dependent models, but only marginally. Point estimates of the equilibrium population size ranged from 24,000 to 32,000 depending upon which model was used, but values as high as 70,000 still had some probability.

Agenda Section 1.3

A BAYESIAN STOCK ASSESSMENT OF THE EASTERN PACIFIC GRAY WHALE USING ABUNDANCE AND HARVEST DATA FROM 1967 TO 1996

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Wade. P.R. In press. A Bayesian stock assessment of the eastern Pacific gray whale using abundance and harvest data from 1967 to 1996. J. Cetacean Res. Manage. Special Issue 2.

Abundance and harvest data since 1966/67 were used to assess the eastern Pacific stock of gray whales. A Bayesian statistical method was used to estimate probability distributions for the parameters of both a simple and an age and sex structured population dynamics model, as well as output quantities of interest. Model comparisons using the Bayes Factor provided conclusive evidence that an additional parameter should be used to account for unexplained variation in the abundance time series. Incorporating the additional variance parameter decreased the precision of the estimates of the other parameters. Point estimates of carrying capacity ranged from 24,640 to 31,840 for the different models, but the posterior distributions from the selected models were very broad and excluded few values. The current depletion level (population size as a fraction of carrying capacity) was estimated to be about 0.75, with a lower 2.5th percentile of 0.36. The probability that the population was still below one-half of its carrying capacity was estimated to be 0.21, with a corresponding probability of 0.28 that the population was still below its maximum sustainable yield level. Quantities from which catch limits could potentially be calculated were estimated, including current replacement yield, maximum sustainable yield and the quantity Q_1 (described in Wade and Givens 1997).

Agenda Section 1.41

GRAY WHALES ILLUSTRATE THE VALUE OF MONITORING DATA IN IMPLEMENTING THE ENDANGERED SPECIES ACT

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Gerber, L.R., D.P. DeMaster, and P.M. Kareiva. In press. Gray whales illustrate the value of monitoring data in implementing the Endangered Species Act. Conserv. Biol.

Many scientists lament the absence of data for endangered species and argue that more funds should be spent acquiring basic information regarding population trends. Using nineteen years of abundance estimates for the eastern North Pacific gray whale *(Eschrichtius robustus)*, we sampled subsets of the original survey data to identify the number of years of data required to remove the population from the Endangered Species Act's (ESA) List of Endangered and Threatened Wildlife. For any given duration of monitoring, we selected all possible combinations of consecutive counts. To incorporate variability in growth rates we extracted a maximum likelihood estimator of growth rate and confidence interval about that growth rate on the assumption that the population changes can be approximated by a simple diffusion process with drift. We then applied a new approach to determine ESA status for each subset of survey data and found that a quantitative decision to delist is unambiguously supported by eleven years of data, but precariously uncertain with fewer than ten years of data. The data needed to produce an unequivocal decision to delist gray whales cost the National Marine Fisheries Service an estimated $660,000, a surprisingly modest expense given the fact that delisting can greatly simplify regulatory constraints. This example highlights the value of population monitoring in administering the ESA, and provides a compelling example of the utility of such information in identifying both imperiled species and recovered species. The economic value of such data should be clear: they provide the foundation for delisting, which could ultimately save much more money than the collection of the data would ever cost.

Agenda Section 2.1

GRAY WHALE CALF SIGHTINGS COLLECTED DURING SOUTHBOUND MIGRATIONS, 1952-95

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Shelden, K.E.W., D.J. Rugh, and S.A. Boeve. In press. Gray whale calf sightings collected during southbound migrations, 1952-95. J. Cetacean Res. Manage. Special Issue 2.

For the past 43 years, scientists at the National Marine Mammal Laboratory and preceding organizations, have collected information on sightings of gray whale calves during the whales' annual migration between Alaska and Mexico. The data document the timing and location of calving during the southbound migration along the California coast. Calf-sighting data were collected by observers conducting abundance surveys of gray whales from shore-based sites at Point Loma, near San Diego, in 1952-69 and 1975-78; Yankee Point, Carmel, in 1967-74; and Granite Canyon, Carmel, during most years between 1974 and 1995. Although some reporting methods have changed over the years, all records indicate that observers searched for and recorded calves. In addition to shore-based surveys, aerial surveys were conducted in five seasons between 1979 and 1994. Results indicate that shore-based observers missed 62% of the calves within their viewing area (0-2.6 km from shore), suggesting that calves are significantly under-represented in the shore-based data record. For many of the early census years (1952-74), the percentage of calves sighted (number of calves/total whales) was within the range 0.0-0.2%. In 1975 the percentage of calves sighted at Point Loma increased substantially (to 0.7%) but it did not show up at the Carmel shore stations, 570 km north of Point Loma, until 1984. The highest calf count (n = 36; 0.8%) occurred during 1993/94 at Granite Canyon, when migration dates were later than for any other year. The apparent increase in calf sightings may be related to a trend towards successively later migrations over the 43 year observation period, or to an increase in spatial and temporal distribution of calving as the population has increased. As the population reaches carrying capacity, food resources may be more limited, resulting in pregnant females departing from the feeding grounds later and with reduced fat reserves. As a result, parturition may be occurring prior to reaching the preferred calving grounds at Baja California, Mexico.

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Agenda Section 2.1

GRAY WHALE CALF SIGHTINGS DURING SOUTHBOUND MIGRATIONS, 1995-98

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Shelden, K.E.W., and D.J. Rugh. 1999. Gray whale calf sightings during southbound migrations, 1995-98. Unpubl. doc. submitted to the Workshop to Review the Status of the Eastern North Pacific Stock of Gray Whales, 16-17 March 1999, Seattle, WA.

As an addendum to Shelden et al. (in press), this report provides data on sightings of gray whale calves that were collected during aerial surveys conducted in January 1996 and shore-based surveys conducted during the winters of 1995/96, January 1997, and 1997/98 near the shore station at Granite Canyon, California. The proportions of calves to adults observed from 1995 to 1998 (0.003 - 0.015) were similar to those recorded from 1984 to 1995 (0.001 - 0.009). The highest number of sightings occurred during the 1997/98 season with 61 calves reported. The proportion of calves visible from the air in 1996 (0.0308) was much higher than the proportion observed in 1988 (0.0024) but fell between the proportions observed in 1993 and 1994 (0.0238 and 0.0440). The distribution of cows with calves relative to shore was similar to earlier years where the majority of sightings occurred inshore of the main migration corridor (1.4 - 2.8 km) during both shore-based and aerial surveys. The median distance for shore-based sightings was 0.79 km compared to 1.34 km from the air during the 1995/96 season. Although calves appeared to be closer to shore in 1995/96 when comparing shore-based observations from earlier years (1.1 km from pooled data 1987-95); median distances during aerial surveys were not different (1.3 km from pooled data 1988, 1993 and 1994). Shelden et al. (in press) noted that it was rare that more than one independent observer at a time recognized the presence of a calf. During the 1995/96 season, 12 calves were identified during paired-independent observations of which only 3 were also seen by the second observer. In January 1997, only 1 of 7 sightings were matched between observers, and during the 1997/98 season only 5 matches occurred among 40 sightings.

Agenda Section 2.2
2.3

SOUTHBOUND AND NORTHBOUND GRAY WHALE CALF SIGHTINGS OFF LOS ANGELES, 1984-99

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Schulman-Janiger, A. 1999b. Southbound and northbound gray whale calf sightings off Los Angeles, 1984-99. Unpubl. doc. submitted to the Workshop to Review the Status of the Eastern North Pacific Stock of Gray Whales, 16-17 March 1999, Seattle, WA.

For the past 16 seasons, trained volunteers have conducted the shore-based full-season Gray Whale Census and Behavior Project, sponsored by the Los Angeles Chapter of the American Cetacean Society (ACS/LA), at or near Point Vicente (near Los Angeles, California). Gray whales and other cetaceans are counted from shore, 10-12 hours per day, 7 days a week, for 5 to 6 months. Southbound counts have ranged from 301 to 1,301 per year, including 3 to 106 newborn calves. The percentage of southbound calves sighted (number of calves/total southbound whales) during the first 7 years of our study (1983/84 to 1989/90) ranged from 0.5% to 2.5%, averaging 1.7%. During the next three seasons (1990/91 to 1992/93) these percentages increased to 3.0-3.9%, averaging 3.5%. The calf percentages from 1993/94 to 1998/99 ranged from 2.0% to 8.6%, averaging 4.6%. However, the calf count in the 1998/99 migration (n = 15; 2.2%) was one of the lowest in the past nine seasons. The highest calf count (n = 106; 8.6%) was in the 1997/98 season. These calf percentages are considerably higher than those published for other censuses. As their numbers increase, more gray whales may delay departures from northern feeding grounds (especially in seasons that include warmer arctic waters and late ice formation); more females may give birth off southern California rather than in Mexican calving lagoons, possibly subjecting calves to higher mortality rates. Gray whales with newborns appear to favor a more protected coastal (rather than offshore) migratory corridor, thus raising nearshore percentages of southbound calves. The relatively high (and apparently increasing) percentage of southbound gray whale calves documented here indicate that births off southern California are more common than previously thought.

The northbound migration of cow/calf pairs peaks between 6 April and 27 April, generally during the last half of April; this peak occurs 4-8 (averaging 6) weeks after the earlier migration peak that primarily consists of whales with no calves. Northbound counts have ranged from 793 to 3,412 per year, including 11 to 222 newborn calves. The percentage of newborn calves sighted (number of calves/total number of northbound whales) during the first nine seasons of our study (1983/84 to1991/92) ranged from 0.9% to 8.3%, averaging 3.4%. During three seasons (1987/88, 1989/90, and 1990/91) the percentage of northbound calves observed was actually lower than the percentage of southbound calves observed earlier in those migrations; this occurred during a period of generally lower whale counts. During the next six seasons (1992/93 to 1997/98) this percentage generally increased: it ranged from 4.3% to13.8%, averaging 9.6%. Some of the highest percentages, ranging from 9.4% to 13.8% (averaging 11.2%), have occurred in recent years (1995/96 to1997/98). These were substantially higher than previously published figures for California waters. The highest calf count (n = 222, 13.8%) occurred in the 1996/97 season and was more than double the count of any of the preceding nine seasons. However, the percentage of calves in the 1998/99 northbound migration was only 2.5% (n = 34), well below percentages seen in recent years. Factors that may be contributing to this increase in northbound calf percentages include: shore-based observers are detecting a higher percentage of calves; there may be some shortening of gray whale calving intervals; and, more calves may be surviving the first few months of life. These annual counts, complementing those conducted from other areas, could help indicate whether gray whale calf production is decreasing, stabilizing, or increasing.

Agenda Section 2.4

ANNUAL CALF PRODUCTION FOR THE CALIFORNIA STOCK OF GRAY WHALES 1994-98
[Preliminary Analysis]

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Perryman, W.L., M.A. Donahue, S.B. Reilly, and P.C. Perkins. 1999b. Annual calf production for the California stock of gray whales 1994-98 [Preliminary analysis]. Unpubl. doc. submitted to the Workshop to Review the Status of the Eastern North Pacific Stock of Gray Whales, 16-17 March 1999, Seattle, WA.

We conducted shore-based sighting surveys to estimate the number of northbound migrating gray whale calves passing Piedras Blancas, California, for four consecutive years (1994-98). In addition, we conducted aerial surveys to determine offshore distribution of the migration in 1994 and 1995, measured day/night migration rates with thermal sensors in 1994-96, and maintained concurrent replicate watches near the peak of each migration to estimate the proportion of the northbound cow-calf pairs missed by the census team. During good weather conditions, we counted 325, 194, 408, 501, and 440 calves during 1994-98 respectively. Correcting these counts for periods not on watch, calves passing far offshore (1994 only), and for calves missed by the census team produced final estimates of 1,000 calves (SE = 88.85) for 1994; 601 calves (SE = 69.56) for 1995; 1,141 calves (SE = 72.23) for 1996; 1,439 calves (SE = 78.62) for 1997; and a preliminary estimate of 1,316 calves (SE = 77.56) for 1998. Calf production indices (calf estimate/total population estimate) are 4.5%, 2.6%, 5.1%, 6.5%, and 5.9% for the years 1994-98, respectively.

Agenda Section 2.5

RESULTS OF PHOTOGRAMMETRIC WHALING FOR GRAY WHALES ALONG THE CENTRAL AND SOUTHERN CALIFORNIA COAST BETWEEN 1994 AND 1998

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Perryman, W.L., and M.S. Lynn. 1999. Results of photogrammetric whaling for gray whales along the central and southern California coast between 1994 and 1998. Unpubl. doc. submitted to the Workshop to Review the Status of the Eastern North Pacific Stock of Gray Whales, 16-17 March 1999, Seattle, WA.

More than 25 years after the last gray whale was taken along the California coast under a special permit issued by the IWC to study the biology and ecology of this population, we began an aerial photogrammetric sampling effort with the goal of revisiting some of the results derived from the examination of specimens. Analysis of length, maximum width, and fluke width data for southbound gray whales indicate that the migration is led by large whales, many of them ?pregnant females," and that juvenile whales are most common late in the migration. Calves photographed around the California Channel Islands averaged 4.60 m in length. Based on the proportion of ?pregnant" and recent postpartum females, we estimate 15 January to be the median birth date for eastern Pacific gray whales. Northbound calves photographed in late May averaged 7.10 m in length which is inconsistent with the accepted growth curve for young gray whales. We estimate length at 1 year to be 8.6 m and propose a new growth curve. There was a significant positive linear relationship between the length of a cow and her associated northbound calf. Lengths of cows with calves were shorter on average than adult females examined by Rice and Wolman (1971: 12.3 m versus 12.7 m), which may reflect gunner selection for large whales, stretching of specimens during processing, or bias in the photographic sample. Based on the relationship between log length and log width, northbound whales were significantly thinner than those photographed southbound. This difference was most pronounced between ?pregnant females" and northbound cows with calves. Our results indicate that relatively small changes in condition or fatness of gray whales are detectable in measurements from photographs.

Agenda Section 3.1

OBSERVATIONS AND PREDICTIONS OF ARCTIC CLIMATIC CHANGE: POTENTIAL EFFECTS ON MARINE MAMMALS

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Tynan, C.T., and D.P. DeMaster. 1997a. Observations and predictions of arctic climatic change: potential effects on marine mammals. Arctic 50(4):308-322.

Recent analyses have revealed trends over the past 20-30 years of decreasing sea ice extent in the Arctic Ocean coincident with warming trends. Such trends may be indicative of the polar amplification of warming predicted for the next several decades in response to increasing atmospheric CO_2. We have summarized these predictions and nonuniform patterns of arctic climate change in order to address their potential effects on marine mammals. Since recent trends in sea ice extent are nonuniform, the direct and indirect effects on marine mammals are expected to vary geographically. Changes in the extent and concentration of sea ice may alter the seasonal distributions, geographic ranges, patterns of migration, nutritional status, reproductive success, and ultimately the abundance and stock structure of some species. Ice-associated seals, which rely on suitable ice substrate for resting, pupping, and molting, may be especially vulnerable to such changes. As recent decreases in ice coverage have been more extensive in the Siberian Arctic (60°E-180°E) than in the Beaufort Sea and western sectors, we speculate that marine mammal populations in the Siberian Arctic may be among the first to experience climate-induced geographic shifts or altered reproductive capacity due to persistent changes in ice extent. Alteration in the extent and productivity of ice-edge systems may affect the density and distribution of important ice-associated prey of marine mammals, such as arctic cod *Boreogadus saida* and sympagic ("with ice") amphipods. Present climate models, however, are insufficient to predict regional ice dynamics, winds, mesoscale features, and mechanisms of nutrient resupply, which must be known to predict productivity and trophic response. Therefore, it is critical that mesoscale process-oriented studies identify the biophysical coupling required to maintain suitable prey availability and ice-associated habitat for marine mammals on regional arctic scales. Only

an integrated ecosystems approach can address the complexity of factors determining productivity and cascading trophic dynamics in a warmer Arctic. This approach, integrated with monitoring of key indicator species (e.g., bowhead whale, ringed seal, and beluga), should be a high priority.

Agenda Section 3.1

THE INFLUENCE OF OCEANOGRAPHIC PROCESSES ON PELAGIC-BENTHIC COUPLING IN POLAR REGIONS: A BENTHIC PERSPECTIVE

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Grebmeier, J.M., and J.P. Barry. 1991. The influence of oceanographic processes on pelagic-benthic coupling in polar regions: a benthic perspective. J. Mar. Syst. 2:495-518.

Benthic community abundance and biomass in polar marine systems is directly influenced by food supply from the overlying water column. Variability in hydrographic regimes, ice coverage, light, water column temperature and pelagic food web structure limit the amount of organic carbon reaching the benthos. Data from the high Arctic and Antarctic indicate that a large percentage of surface-produced organic matter is consumed by both macro- and micro-zooplankton as well as recycled in the water column via the microbial loop. This results in food-limited regimes for the underlying benthos. The few exceptions are nearshore continental shelf systems, such as in the Bering and Chukchi Seas in the western Arctic and portions of the Canadian Archipelago and Barents Sea in the eastern Arctic, where high benthic abundance and biomass occurs due to a tight coupling between water column primary production and benthic secondary production. A major difference between the Antarctic and Arctic is that the nearshore deep Antarctic is characterized by relatively high benthic abundance and biomass despite low water column production, suggesting that stability, low disturbance levels and cold temperatures enable benthic organisms to grow larger than in the Arctic. Both physical and biological disturbance levels are high in the marginal seas of the Arctic and may directly influence benthic productivity. The relationship between primary production and sedimentation of organic material to the benthos is nonlinear due to its dependence on the role of the pelagic food web. Therefore, in this review we will only discuss the pelagic system with respect to how it impacts the net food supply reaching the benthos. A major objective of this review paper is to demonstrate the influence of oceanographic processes on pelagic-benthic coupling in polar regions from a "bottom-up" perspective, using benthic studies from various regions in both the Arctic and Antarctic. Similarities and differences in oceanographic processes, benthic abundance and biomass, and benthic carbon cycling within these polar marine systems are discussed and areas for further research identified.

Agenda Section 3.2

PRODUCTIVITY OF ARCTIC AMPHIPODS RELATIVE TO GRAY WHALE ENERGY REQUIREMENTS

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Amphipod crustaceans dominate the benthic community in vast areas of the northern Bering Sea; they are the major prey of the California gray whale *Eschrichtius robustus*. The protected whale population is growing steadily and may be approaching the carrying capacity of the amphipod community, one of the most productive benthic communities in the world. The abundance and biomass of the amphipod community decreased during the 3-year period 1986 to 1988, resulting in a 30% decline in production. High-latitude amphipod populations are characterized by low fecundity and long generation times. Large, long-lived individuals are responsible for the majority of amphipod secondary production. A substantial reduction in the density of large individuals in the population will result in a significant, long-term decrease in production.

Agenda Section 3.2

DISTRIBUTION AND CARRYING CAPACITY OF GRAY WHALE FOOD RESOURCES IN THE NORTHERN BERING AND CHUKCHI SEAS

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Stoker, S.W. In press. Distribution and carrying capacity of gray whale food resources in the northern Bering and Chukchi seas. J. Cetacean Res. Manage. Special Issue 2.

During their summer residency in the Bering and Chukchi Seas, gray whales rely on the rich benthic amphipod populations of the region to renew fat resources needed to sustain them during their winter migration to and from the breeding lagoons of Mexico. Surveys of gray whale population distribution on these northern grounds indicate that concentrations of feeding whales return annually to certain locations, and that these locations coincide, in most cases, with high density and high productivity amphipod communities.

The annual impact of gray whales feeding within these preferred areas is probably considerable. Studies of one of the high-use areas, the central Chirikov Basin between St. Lawrence Island and the Bering Strait, indicate that gray whales disturb at least 6% of the benthos each summer and consume more than 10% of the yearly amphipod production. Whether or not this rate of consumption is within sustainable bounds is unclear since it is impossible, at this time, to assess additional demands imposed upon amphipod populations by other predators such as epibenthic invertebrates and demersal fishes. There are indications, however, that this resource is being stressed and that the gray whale population is expanding its summer range in search of alternative feeding grounds.

Agenda Section 4.1

CHEMICAL CONTAMINANTS IN GRAY WHALES (*ESCHRICHTIUS ROBUSTUS*) FROM THEIR WESTERN BERING SEA ARCTIC FEEDING GROUNDS AND THE CALIFORNIA AND WASHINGTON COASTS

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The gray whale (*Eschrichtius robustus*) is a coastal migratory baleen whale (Mysticete) with a benthic feeding strategy and a long period of fasting during its southbound migration and residence in the breeding grounds. The prolonged fasting may alter the disposition of toxic chemicals within the animal. Additionally, gray whales have been observed feeding in coastal waters, which may present a risk of exposure to toxic chemicals in some regions. We measured the concentrations of organochlorines (OCs) and trace elements in tissues and stomach contents collected from juvenile gray whales that were taken off their Arctic feeding grounds in the western Bering Sea during a Russian subsistence harvest. Blubber biopsy samples that were taken from gray whales off the California and Washington coasts were also analyzed for OCs; previously we measured these contaminants in tissues and stomach contents of gray whales that stranded along the U.S. west coast and Alaska. There were no differences in the concentrations (based on wet weight of tissue) of contaminants between female and male subsistence animals. The lipid content [48 (5)%] of blubber for animals from the Arctic feeding grounds was higher than that in the biopsy samples [9.4 (0.8)%] from free-ranging, apparently healthy whales. Concentrations on a lipid basis of the sum of polychlorinated

biphenyls (∑PCBs) in the juvenile stranded whales and the juvenile subsistence whales were significantly different [19,000 (14,000) and 680 (67) ng/g lipid, respectively]. The mean concentration of the ∑PCBs for the biopsy samples was 2,000 (280) ng/g lipid weight. We hypothesize that the higher concentration of ∑PCBs in the stranded animals may be due to the retention of OCs in blubber during fasting rather than to increased exposure to these contaminants. The concentrations of certain trace elements (e.g., cadmium) is some tissues, such as kidney, were also elevated in the stranded animals. Moreover, aluminum in stomach contents and tissues of the subsistence whales was high compared to other marine mammal species, which is consistent with the ingestion of sediment during feeding.

Agenda Section 4.2
4.3

POTENTIAL IMPACT OF OFFSHORE HUMAN ACTIVITIES ON GRAY WHALES

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Moore, S.E., and J.T. Clarke. In press. Potential impact of offshore human activities on gray whales. J. Cetacean Res. Manage. Special Issue 2.

Gray whale (*Eschrichtius robustus*) reactions to offshore human activities have been relatively well studied compared to those of other mysticetes. Studies of short-term behavioural responses to underwater noise associated with aircraft, ships and seismic explorations indicate a 0.5 probability that whales will respond to continuous broadband noise when sound levels exceed *ca.* 120dB[2] and to intermittent noise when levels exceed *ca.* 170dB, usually by changing their swimming course to avoid the source. Gray whales 'startled' at the sudden onset of noise during playback studies, but demonstrated a flexibility in swimming and calling behaviour that may allow them to circumvent increased noise levels. Whales may be 'harassed' by noise from large commercial vessels, especially in shipping lanes or near busy ports. Gray whales sometimes change course and alter their swimming speed and respiratory patterns when followed by whalewatching boats. Conversely, some whales swim toward small skiffs deployed from whalewatching boats in breeding lagoons, seemingly attracted by the noise of idling outboard engines. Reported gray whale reactions to aircraft are varied and seem related to ongoing whale behaviour and aircraft altitude. Whale response to research involving tagging and biopsy sampling appears to be short term. Gray whales were seen swimming through surface oil from the *Exxon Valdez* oil spill along the Alaskan coast and showed only partial avoidance to natural oil seeps off the California coast. Laboratory tests suggest that gray whale baleen, and possibly skin, may be resistant to damage by oil, but spilled oil or oil dispersant in a primary feeding area could negatively affect gray whales by contaminating benthic prey. Gray whales are sometimes injured or killed in collisions with vessels or entanglement in fishing gear. Concern about the cumulative long-term impact of offshore human activities is particularly acute in the Southern California Bight, where many activities are often concurrent.

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[2] dB re 1 μPa.

Agenda Section 4.3

BIO-ACOUSTICS OF THE GRAY WHALE (*ESCHRICHTIUS ROBUSTUS*)

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Dahlheim, M.E. 1988. Bio-acoustics of the gray whale (*Eschrichtius robustus*). Ph.D. Thesis, University of British Columbia. xiii+266 p.+appendices.

Gray whales (*Eschrichtius robustus*), while engaged in underwater signalling, circumvent noise in the acoustical channel by the structure and timing of their calls. Data yielding this conclusion were collected during an acoustical study on gray whales and their habitats (1981-84). Sonographic analyses of tape recordings were used to quantify the acoustical repertoire, the ambient noise characteristics of the area, and the relationship between the animals' calls and the environment. The acoustical responses of whales to artificially increased levels of noise were documented during playback experimentation in Mexico. Nine sound parameters were inspected and compared between control and experimental conditions: calling rates, call types, frequency range of signals (Hz), emphasized frequencies (Hz), received levels of sounds (dB re 1 μPa), call duration (sec), percentage of calls exhibiting frequency modulation, number of pulses per series, and repetition rates of signals. The observed surface behavior of gray whales in response to noise (i.e., dive durations, movements and abundance) was also investigated. Analyses yielded: a description of gray whale call types; a characterization of the acoustical habitats occupied by this species, including a list of sources contributing to the ambient noise and a profile of the propagation characteristics of the study area; a determination of the relationship between whale calls and their habitats; and the acoustical capabilities and strategies of whales in response to noise. The plasticity observed in the overall behavior of this whale is of adaptive significance when considering the dynamic nature of noise in the environment. Typically, the multiple strategies employed by the whales when faced with various noise situations enable them to minimize the detrimental effect that noise has on their underwater signalling. Gray whale responses varied with the sound source and may also differ relative to the geographical range and/or general behavior of the animal. It is concluded that ambient noise (both natural and man-made) has a profound effect on the behavior of this coastal species and that acoustical calling is modified to optimize signal transmission and reception.

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Agenda Section 4.4

GRAY WHALE ENTANGLEMENTS IN CALIFORNIA, OREGON/WASHINGTON, AND ALASKA, 1990-98

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Hill, P.S. 1999a. Gray whale entanglements in California, Oregon/Washington, and Alaska, 1990-98. Unpubl. doc. submitted to the Workshop to Review the Status of the Eastern North Pacific Stock of Gray Whales, 16-17 March 1999, Seattle, WA.

Total number of entanglements reported during 1990-98 along the west coast of the United States (values in parentheses indicate known mortalities and reports in which the status of the whale is unknown)

	1998	**1997**	**1996**	**1995**	**1994**	**1993**	**1992**	**1991**	**1990**
CA	4[1] (2)	6[1] (5)	5[2] (4)	4 (1)	4[2] (4)	1 (0)	4 (3)	4 (3)	5 (5)
OR/WA	0	0	0	2 (2)	0	0	0	1 (0)	2 (1)
AK	3 (3)	1 (1)	0	1 (0)	0	0	0	0	0
Total	7	7	5	7	4	1	4	5	7

Data provided by J. Cordaro (SWR), B. Norberg (NWR), and M. Sternfeld (AKR).

[1] May include 2 sightings of the same entangled whale.

[2] Includes an unidentified whale that was most likely a gray whale.

Agenda Section 4.5

A REPORT TO THE MARINE MAMMAL COMMISSION ON PROPOSED SALT PRODUCTION FACILITIES AT SAN IGNACIO LAGOON BAJA CALIFORNIA

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Mate, B.R. 1995. A report to the Marine Mammal Commission on proposed salt production facilities at San Ignacio Lagoon, Baja California. Unpubl. report to U.S. Marine Mammal Commission, Washington, D.C. 13 p.

Exportadora de Sal, sometimes referred to as ESSA, has been a business partnership between Mitsubishi, Japan (49%), and Mexico (51%) since 1954. It operates a salt production facility at the town of Guerrero Negro, midway along the Pacific Coast of Baja California. It is the world's largest solar evaporative operation and produces 6.5 million metric tons of salt per year from the adjacent Laguna Ojo de Liebre. ESSA is planning to expand its operation to San Ignacio Lagoon.

Laguna Ojo de Liebre and San Ignacio Lagoon are both in the Vizcaíno Desert Biosphere Reserve, Mexico's largest refuge administered by Secretaria de Desarrollo Social (SEDESOL), the Secretariat of Social Development. An Environmental Impact Assessment was completed in July 1994 and was reviewed by SEDESOL. The application was either denied or withdrawn in March 1995.

This report summarizes the activities of the current operation and the proposed activity based on interviews with company officials in January 1995 and a review of the Environmental Impact Assessment.

Agenda Section 4.5
4.6

CONSERVATION AND DEVELOPMENT IN THE GRAY WHALE LAGOONS OF BAJA CALIFORNIA SUR, MEXICO

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Dedina, S., and E. Young. 1995a. Conservation and development in the gray whale lagoons of Baja California Sur, Mexico. Final report to U.S. Marine Mammal Commission, Washington, D.C. NTIS PB96-113154. iii+56 p.

In this report we identify ongoing and possible future development and related activities that could have a negative impact on two of the three main calving/breeding habitats for the eastern North Pacific gray whale (*Eschrichtius robustus*) population in Baja California Sur, namely Laguna San Ignacio and Bahía Magdalena. We also identify steps that are being or could be taken to assess and to prevent or minimize activities that may have adverse effects. We provide: 1) a brief summary of the natural history, exploitation, protection, and current status of the gray whale population in Mexico; 2) a description of the physical and human geography of the study area; 3) a history of environmental conservation efforts in the study area; 4) an overview of the environmental management structure in the study area and the environmental impact review process in Mexico; 5) descriptions of past, existing, and planned development and commercial activities in the study area; and 6) descriptions of impediments to effective assessment and control of activities with potentially adverse impacts and possible means to strengthen current gray whale conservation.

This study is based on field research undertaken in Laguna San Ignacio and Bahía Magdalena. We also conducted background research and interviews in San Diego, California, La Paz, Baja California Sur, and Mexico City. The research included: 1) open-ended and semi-structured interviews with local residents, government officials and others with knowledge of the area and matters of interest or concern to this study; 2) participant observation of local residents' activities; 3) a review of archival sources on the history of the study area and gray whale conservation; and 4) a review of newspaper coverage of issues related to gray whale conservation in Baja California Sur. This enabled us to compare actual use and management of gray whale habitats with: how government officials think these areas are and should be used and managed; and how different user groups in the study area view regulations of their activities for gray whale habitat management.

Laguna San Ignacio is the only primary gray whale breeding/calving area in Mexico that remains superficially unaltered. In contrast, portions of Bahía Magdalena have been changed by industrial and mining activities, as well as part of the Vizcaíno Biosphere Reserve. Bahía Magdalena remains unprotected.

Three federal agencies are responsible for on-site protection of gray whales and regulation of human activities in Laguna San Ignacio and Bahía Magdalena. These are the National Institute of Ecology (INE), the Federal Attorney General's Office for Environmental Protection (PROFEPA), and the Secretariat of Fisheries (Pesca).

The greatest potential threats to the whales and their habitat are from: 1) the proposed development of a 52,150 ha salt production facility on the shore of Laguna San Ignacio; 2) a proposed tourist resort development at Bahía Magdalena; and 3) the growth of gray whale tourism in the North Zone of Bahía Magdalena. Strict review and monitoring of development and whale-tourism by INE, PROFEPA, and Pesca under existing environmental impact assessment regulations, and the review of project plans and tourism activities by non-governmental organizations, research institutions, and scientists familiar with gray whale habitat, could help to minimize potentially adverse impacts.

Agenda Section 4.5

SAN IGNACIO SALTWORKS:
SALT AND WHALES IN BAJA CALIFORNIA

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SEMARNAP (Secretaria de Medio Ambiente, Recursos Naturales y Pesca). 1997. San Ignacio saltworks: Salt and whales in Baja California. 25 p.

The desert-like central region of the Baja California peninsula has characteristics that are unique in the world. One notable facet of its rich wildlife is that some of its coastal waters are winter sanctuaries where the gray whale reproduces. A significant area of this region was declared a Biosphere Reserve in 1988 (El Vizcaíno, the largest in the country: more than two and a half million hectares).

In 1994, a company (Exportadora de Sal, S.A. de C.V.) entered into negotiations with the environmental authorities to considerably expand its salt extraction and marketing activities within the Reserve's buffer zone. In 1995, owing to insufficiencies in the Statement of Environmental Impact (MIA, acronym in Spanish), the authorities denied the corresponding permit. In view of the company's wish to reopen negotiations for the project, and in order to address the unusual complexity of the analysis, the authorities established a Scientific Committee made up of seven distinguished specialists of different nationalities. This Scientific Committee was entrusted with specifying the terms of reference necessary for a new MIA (July 1996). Mexico's environmental authorities also pledged to submit to the consideration of the Committee any new MIA that might be presented, and to respect its opinion in any decision taken. The establishment of such a significant Scientific Committee and its public performance in assessing environmental impact is without precedent in this country, and possibly in Latin America.

To date, no proposal based on the rigorous terms of reference agreed upon has yet been received.

Irrespective of the economic importance of the project, the Government of Mexico will not authorize any proposal that runs counter to current regulations and that could jeopardize conservation of the region's natural resources, and in particular, its biological richness, which is the heritage of all Mexicans.

Agenda Section 4.71

DESCRIPCIÓN Y DESARROLLO DE LAS ACTIVIDADES TURÍSTICAS DE OBSERVACIÓN DE BALLENA GRIS EN LAS LAGUNAS DE LA RESERVA DE LA BIOSFERA "EL VIZCAÍNO" Y BAHÍA MAGDALENA, BAJA CALIFORNIA SUR, MÉXICO, TEMPORADAS 1996 Y 1997

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Sánchez Pacheco, J.A. 1997a. Descripción y desarrollo de las actividades turísticas de observación de ballena gris en las lagunas de la reserva de la Biosfera "El Vizcaíno" y Bahía Magdalena, Baja California Sur, México, temporadas 1996 y 1997. [Description and development of tourist gray whale watching activities in the lagoons of the biosphere reserve "El Vizcaíno" and Magdalena Bay, Baja California Sur, Mexico, during the 1996 and 1997 seasons.] Boletín Pesquero CRIP-La Paz 7:8-18.

A description is given of the development and monitoring of gray whale watching in the lagoons of the biosphere reserve "El Vizcaíno" and Magdalena Bay in 1996 and 1997. Described are the operations of the tourist industry in each lagoon, the observation time, the number of vessels involved, and an analysis of the demand for services. The above is discussed in light of the rules that regulate whale watching activities in Mexico. The 4 lagoons were visited by 23,971 tourists to whale watch in 1996 and 28,484 in 1997. This activity was estimated to generate a total of $321,590 in 1996 and $453,300 in 1997 for whale watching trips alone. An estimation of the economic activity generated included all services and expenses incurred by tourists at their whale watching destination and while traveling.

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Agenda Section 4.72

DETERMINACION DE LA CAPACIDAD DE CARGA EN TERMINOS DEL NÚMERO MÁXIMO SIMULTÁNEO DE EMBARCACIONES EN LAGUNA OJO DE LIEBRE Y LAGUNA SAN IGNACIO AREAS DE OBSERVACIÓN DE BALLENA GRIS EN BAJA CALIFORNIA SUR, MÉXICO

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Sánchez Pacheco, J.A. 1997b. Determinacion de la capacidad de carga en terminos del número máximo simultáneo de embarcaciones en Laguna Ojo de Liebre y Laguna San Ignacio areas de observación de ballena gris en Baja California Sur, México. [Determination of the carrying capacity in terms of maximum simultaneous number of vessels in the Ojo de Liebre Lagoon and San Ignacio Lagoon gray whale observation areas in Baja California Sur, Mexico.] Boletín Pesquero CRIP-La Paz 7:19-25

The change in the direction of movement of whales is considered an indicator of disturbance. A procedure was defined to estimate the Maximum Simultaneous Number (NMS, acronym in Spanish) of vessels that can watch whales in an area without disturbing more than 50% of them. In this procedure, vessels followed selected whales, while observers recorded whale reactions and the distance between the vessel and disturbed whales. The procedure was applied in Ojo de Liebre Lagoon and San Ignacio Lagoon during 1995. The NMS was 6 vessels in each of two areas in Ojo de Liebre Lagoon and 13 vessels in San Ignacio Lagoon.

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Agenda Section 4.8

GRAY WHALE STRANDINGS IN CALIFORNIA, OREGON/WASHINGTON, AND ALASKA, 1990-98

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Hill, P.S. 1999b. Gray whale strandings in California, Oregon/Washington, and Alaska, 1990-98. Unpubl. doc. submitted to the Workshop to Review the Status of the Eastern North Pacific Stock of Gray Whales, 16-17 March 1999, Seattle, WA.

Total number of strandings (excluding dead stranded whales in which the cause of death was due to entanglement) reported during 1990-98 along the west coast of the United States

	1998	1997	1996	1995	1994	1993	1992	1991	1990
CA	30	9	10	12	15	11	14	15	9
OR/WA	3	3	3	8	3	2	3	13	13
AK	1	0	0	1	4	14[1]	13[1]	14[1]	27[1]
Total	34	12	13	21	22	27[1]	30[1]	42[1]	49[1]

Data provided by J. Cordaro (SWR), B. Norberg (NWR), and M. Sternfeld (AKR).

[1] 1990-93 data for Alaska include 26, 12, 12, and 13 whales, respectively, seen during aerial surveys. Thus, the 1990-93 data are not comparable to the data collected during 1994-98.

GRAY WHALES STRANDED IN MEXICO, 1975-99

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Pérez-Cortés Moreno, H. 1999. Gray whales stranded in Mexico, 1975-99. Unpubl. doc. submitted to the Workshop to Review the Status of the Eastern North Pacific Stock of Gray Whales, 16-17 March 1999, Seattle, WA.

Location/year	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987
Baja California	-	-	-	-	-	-	-	-	-	-	-	1	-
Guerrero Negro Lagoon	-	-	-	-	-	8	4	2	-	*	*	*	*
Outer Beach (Vizcaíno Bay)	4	-	-	-	-	23	10	21	3	*	*	*	*
Ojo de Liebre Lagoon	16	-	-	-	4	16	-	12	13	10	7	6	11
San Ignacio Lagoon	-	-	4	7	5	6	6	4	10	5	-	-	-
Outer Beach (San Ignacio area)	-	-	-	-	-	-	-	-	-	-	-	-	-
Bahía Magdalena	-	1	-	1	-	-	-	6	-	1	-	-	-
Outer Beach (Magdalena area)	-	-	-	-	-	-	-	-	-	-	-	-	-
Gulf of California	-	-	-	-	-	-	-	1	1	-	1	1	1
Total	20	1	4	8	9	53	20	46	27	16	8	8	12

Gray whales stranded in Mexico, 1975-99 (continued).

Location/year	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	**Total**
Baja California	-	-	-	-	-	-	1	-	-	-	-	-	2
Guerrero Negro Lagoon	*	*	*	*	*	*	*	*	-	-	1	3	18
Outer Beach (Vizcaíno Bay)	*	*	*	*	*	*	*	*	-	-	1	28	90
Ojo de Liebre Lagoon	12	21	16	45	22	8	5	13	-	-	1	40	278
San Ignacio Lagoon	-	3	-	-	-	-	-	-	3	7	3	5	68
Outer Beach (San Ignacio area)	-	-	-	-	-	-	-	-	-	-	-	5	5
Bahía Magdalena	-	-	-	-	1	-	-	-	-	1	1	20	32
Outer Beach (Magdalena area)	-	-	-	-	-	-	-	-	-	0	0	11	11
Gulf of California	1	6	-	-	-	-	-	-	-	-	-	2	14
Total	13	30	16	45	23	8	6	13	3	8	7	114	518

Data are as available from 1975 to 16 June 1999. Dashes indicate no data are available. Asterisks indicate that data from Guerrero Negro Lagoon and Vizcaíno Bay are summarized with the data for Ojo de Liebre Lagoon for the respective years.

Data Sources:
- Heyning and Dahlheim (in press).
- Sánchez Pacheco (1998).
- Urbán et al. (1998a).
- Unpublished data, Instituto Nacional de la Pesca, CRIP.

Agenda Section 4.8

GRAY WHALE MORTALITY AT OJO DE LIEBRE AND GUERRERO NEGRO LAGOONS, BAJA CALIFORNIA SUR, MEXICO: 1984-1995

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Sánchez Pacheco, J.A. 1998. Gray whale mortality at Ojo de Liebre and Guerrero Negro lagoons, Baja California Sur, Mexico: 1984-1995. Mar. Mammal Sci. 14(1):149-155.

During a study of gray whale strandings at Ojo de Liebre and Guerrero Negro lagoons, conducted from 1984 to 1995, a total of 191 whales was found. Length was determined for 176 whales, sex was determined for 146, and time of death was estimated for 117. Common stranding locations within and adjacent to the lagoons were identified. Most (77%) of the calf mortality occurred between 15 January and 15 February. Stranded whales were divided into three size/age classes based on the frequency distributions of their lengths: calves (3.4 to 6.5 m, $\bar{x} = 4.63$), yearlings (6.6 to 9.5 m, $\bar{x} = 8.13$), and 2 years and older (9.6 to 14.2 m, $\bar{x} = 11.94$). During 1990-1992, an extraordinary number of whales 2 years and older stranded in the study area, with a maximum of 37 in 1991. Differences in the average lengths between female and male neonates and yearlings were not statistically different, but females were longer than males at two years and older. It was possible to determine causes of death in only a few cases.

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Agenda Section 4.9

GRAY WHALE SHIP STRIKES IN CALIFORNIA, OREGON/WASHINGTON, AND ALASKA, 1990-98

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Hill, P.S. 1999c. Gray whale ship strikes in California, Oregon/Washington, and Alaska, 1990-98. Unpubl. doc. submitted to the Workshop to Review the Status of the Eastern North Pacific Stock of Gray Whales, 16-17 March 1999, Seattle, WA.

Total number of vessel strikes reported during 1990-98 along the west coast of the United States (values in parentheses indicate known mortalities and reports in which the status of the whale is unknown)

	1998	**1997**	**1996**	**1995**	**1994**	**1993**	**1992**	**1991**	**1990**
CA	3 (2)	0	0	3 (1)	n/a	n/a	n/a	n/a	n/a
OR/WA	0	0	0	0	0	0	0	0	1
AK	0	1 (1)	0	0	0	0	0	0	0
Total	3	1	0	3	-	-	-	-	-

Data provided by J. Cordaro (SWR), B. Norberg (NWR), and M. Sternfeld (AKR).
n/a indicates that data are incomplete for that year.

Agenda Section 5.1
5.2

RECORDS OF HARVESTED GRAY WHALES

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Quan, J. 1999. Records of harvested gray whales. Unpubl. doc. submitted to the Workshop to Review the Status of the Eastern North Pacific Stock of Gray Whales, 16-17 March 1999, Seattle, WA.

Level of aboriginal harvest: In 1997 the International Whaling Commission set an aboriginal subsistence quota. A total of 620 gray whales, not to exceed 140 annually, may be taken over the years 1998-2002.

5.1) **Russian take:** Over the years 1998-2002 the Russian Federation has agreed to take no more than 135 whales annually. From 1970 to 1998 an average of 139 gray whales were taken annually (Table 1).

5.2) **Alaskan take**: Currently there are no allocations for a gray whale harvest by Alaskan Natives and none have been in place since 1991. An incidental take of two gray whales by Alaskan Natives occurred in 1995 (Table 1).

Table 1 (Continuation of Agenda Sections 5.1 and 5.2). Numbers of Eastern North Pacific gray whales harvested (including whales that were lost) between1970 and 1998. Parenthetic numbers in the USSR/Russia column indicate alternate counts from other sources.

Year	USSR/Russia		USA	Totals
1970	146[1,2,3]		5[4]	151
1971	150[1,2,3]		3[4]	153
1972	181[1,2,3]		1[4]	182
1973	178[1]	(173)[2,3]		178
1974	181[1,2,3]		3[4]	184
1975	171[1,2,3]			171
1976	165[1]	(163)[2,3,5]		165
1977	186[1,2,3]		1[4]	187
1978	182[1,2,3]		2[4]	184
1979	178[1,2,3]		4[4]	182
1980	179[1,2,3]		3[4]	182
1981	136[1]	(135)[2,3,6]		136
1982	165[1,2,3]		4[6]	169
1983	169[1]	(168)[2,3]	2[7]	171
1984	169[1,2,3]			169
1985	169[1,2,3]		1[8]	170
1986	169[1,2,3]		2[9]	171
1987	158[1]	(154)[2,3]		158
1988	150[1,2,3]		1[10]	151
1989	179[1,2,3]		1[11]	180
1990	162[1,2,3]			162
1991	169[1,2,3]			169
1992	0[12]	(169)[2]		0
1993	0[2,3,12]			0
1994	44[2,3]	(42)[13]		44
1995	90[2,3]	(85)[14]	2[15]	92
1996	43[2]	(38)[3]		43
1997	79[16]			79
1998	122[17]			122

[1] Ivashin (in press): Table 2.
[2] Russian Federation (1997): Table 3; the number reported in 1992 (169) was later found to be inaccurate (see IWC 1995).
[3] Blokhin (in press d).
[4] Marquette and Braham (1982).
[5] IWC (1979).
[6] IWC (1984).
[7] IWC (1985).
[8] IWC (1987).
[9] IWC (1988).
[10] IWC (1990).
[11] IWC (1991).
[12] IWC (1995).
[13] IWC (1996).
[14] IWC (1997a).
[15] IWC (1997b).
[16] IWC (1999b).
[17] Meghan Donahue/Robert Brownell, Jr., Southwest Fisheries Science Center, NMFS, P.O. Box 271, La Jolla CA 92038-0271.

Agenda Section 5.3

MAKAH WHALING

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Gearin, P. 1999. Makah whaling. Unpubl. doc. submitted to the Workshop to Review the Status of the Eastern North Pacific Stock of Gray Whales, 16-17 March 1999, Seattle, WA.

The Makah Indian Tribe received a five-year quota from the International Whaling Commission (IWC) in 1997 to harvest 20 gray whales for ceremonial and subsistence purposes. The Tribe may harvest up to five gray whales per year from 1998 through 2002 with no more than 33 strikes. The IWC approved a combined 5-year quota of 620 gray whales for aboriginal subsistence whaling by U.S. and Russian aboriginals based on the aboriginal needs statement from each country. The U.S. government requested the quota on behalf of the Makah Tribe in acknowledgment of the Makah's explicit treaty right to whaling (Treaty of Neah Bay, 1855). The NMFS-Northwest Regional Office will monitor the hunt and work with the tribe to ensure that the hunt is conducted within IWC guidelines. In accordance with an agreement between NOAA and the Makah Tribe, the Makah whalers will limit their hunting to the Pacific Ocean areas to the west of the entrance of the Strait of Juan de Fuca. The Makah hunt has no commercial aspects; the meat will be used only for local consumption and will not be sold. The Makah Tribe will use traditional methods of harvest including use of a cedar canoe and hand-thrown harpoon. However, to ensure humaneness of the hunt, the tribe will use a .50-caliber rifle to dispatch the whale. Makah whalers struck and killed one gray whale on 17 May 1999 (Gosho[14]).

RECENT TECHNICAL MEMORANDUMS

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Review of Studies on Stock Identity in the Gray Whale (*Eschrichtius robustus*)

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Abstract

Eastern and western North Pacific gray whales should be managed separately because their ranges do not currently overlap, genetic analyses indicate that the two stocks are significantly different from each other, and the evidence that the former has made a recovery while the latter has not indicates no meaningful dispersal between the two. Data are lacking regarding stock structure within western North Pacific gray whales. Eastern North Pacific gray whales breed promiscuously and mix in their winter assembly areas (i.e., during migration and along coastal waters and within the lagoons of Baja California) making population structure within the nuclear genome highly unlikely. Because selection occurs primarily on the nuclear genome it is unlikely that there is structuring among this population that could result in evolutionary differences. However, there are data from photographic identification studies on some of the feeding grounds indicating site fidelity, but these data exist for only a small proportion of the gray whales' range. Therefore, current data cannot exclude either hypothesis that there are or are not separate feeding stocks that would require separate management within eastern North Pacific gray whales.

CONTENTS

1. INTRODUCTION

To develop a systematic process for defining stocks of large whales within the management regime of the International Whaling Commission (IWC), the Stock Identity Working Group (SIWG) of the Scientific Committee is examining case studies for individual whale species. These case studies should reveal how the different life history strategies of species affect population structure, as well as how they reveal the utility of various types of data for evaluating stock identity and structure within populations. Therefore, the current review provides a section by section overview of the life-history strategy and ecology of gray whales as a context for discussion of the species stock structure. In this review we use 'population' to refer to units where virtually no gene flow (less than one disperser) would be expected within a generation (approximately 20 years). Such a unit is sometimes called an evolutionarily significant unit (ESU) because gene flow is sufficiently low to allow meaningful differences to develop. 'Stock' refers to a unit with a level of gene flow greater than an ESU but still small enough to be demographically important for management. For purposes of clarity, we suppose this level to be less than one percent dispersal between units per year. See the introduction of the review of bowhead (*Balaena mysticetus*) stock identification paper (DeMaster *et al*, 2000) for further discussion of this terminology.

2. BACKGROUND

Within historic Holocene time, there were two allopatric populations of gray whales, one with a circum-North Atlantic distribution and the other with a circum-North Pacific distribution. During inter-glacial periods over the last 3 million years, the Arctic Basin formed a corridor between the North Pacific and North Atlantic and was possibly a dispersal route followed by the gray whale. In current times, gray whales are extinct in the North Atlantic (Mead and Mitchell 1984), but in the North Pacific this species exhibits a highly migratory behavior with distinct corridors down either side of the North Pacific Basin. The Quaternary (Pleistocene to Recent) distribution of gray whales was undoubtedly influenced by cyclical changes in sea level during four massive glacial advances and retreats (Gilmore 1978). Lowering of sea level of up to 100 m correlated with glacial cooling eliminated some continental shelf areas presumably utilized by gray whales, while sea level rises during warming periods are suggested to have increased continental shelf space (Berta and Sumich 1999). During periods of Pleistocene glacial maxima, the polar ice pack and emergent Bering Isthmus which replaced the Bering Sea would have excluded gray whales entirely from the Arctic Basin and undoubtedly pushed their summer distribution farther south than at present. The more recent 'little ice age' investigated by Overpeck, *et al.* (1997) suggests that Arctic-wide cooling and widespread glaciation within the last 400 years may have affected the distributions of populations. Such an ice driven southerly shift in the distribution of species could have facilitated the mixing of eastern and western gray whales in the North Pacific during these ice ages as described for bowhead whales (Dyke *et al.* 1996).

The Atlantic population is now extinct (Mead and Mitchell 1984). Of the two extant populations, the western North Pacific or Korean-Okhotsk population remains critically depleted while the eastern North Pacific or California-Chukchi population has recovered to what may be its pre-exploitation size after it was harvested to depletion by the 1850s. The species was afforded protection from commercial whaling in 1946 by the International Convention for the Regulation of Whaling. Currently, the IWC sets an annual quota allowing gray whales to be harvested from the eastern North Pacific population for aboriginal subsistence use. In spite of the persistent subsistence harvest, the eastern North Pacific population has recovered to an estimated 26,635 animals in 1997/98 (CV=10.06%; Hobbs and Rugh 1999), and is increasing at a rate of 2.5% per year (SE=0.3%; Buckland and Breiwick, In press) (*See Section 4.2 Distribution, Abundance, and Current Status*).

Management authorities currently regard both the eastern and western North Pacific populations as separate 'stocks' for management purposes. Research on the current status of the small western population has only recently begun (Weller *et al.* 1999). Therefore, nearly all of what is known about the biology and natural history of the gray whale results from research conducted on the eastern North Pacific population.

3. WESTERN NORTH PACIFIC POPULATION

3.1 History of Exploitation

The western North Pacific population was probably never as numerous as the eastern North Pacific population. It was intensively hunted during the past three centuries. Pre-exploitation numbers are unknown. By the time commercial whaling ceased in the 1960s, this population was reduced to only a fraction of its original size and was thought by some to be extinct (Bowen 1974).

Intensive whaling pressure from the Japanese hand-harpoon fishery was underway by the 16th century, and Japanese net whaling continued to take gray whales during the 17th to 19th centuries (Omura, 1984). Groups of Koryak natives lived in the northeastern Okhotsk Sea and hunted whales, perhaps even into the early 1900s (Krupnick 1984). European and American whalers operating in the western North Pacific and Okhotsk Sea took gray whales between the late 1840s and early 1900s. Russian steam whalers took gray whales in the coastal waters of the Far East at the end of the 1800s. Japanese and Korean whalers continued to hunt gray whales until as recently as 1966 (Brownell and Chun 1977). Kato and Kasuya (1993) reviewed the catch history of western gray whales by Japanese and Korean modern whaling during the 1900s and revealed a period of peak annual catch of 100-200 whales occurred in the 1910s. This was followed by a rapid decline of the catch in the 1920s and 1930s, dropping to 10-20 whales per year for over 40 years until the hunt ended in the 1960s. It is estimated that a minimum of between 1,800 and 2,000 gray whales were taken during the whaling period between 1891 and 1966 (Kato and Kasuya 1993). They concluded that this last phase of continuing small scale exploitation could have been a major factor in suppressing the recovery of this population.

3.2 Distribution

Historic sighting data and whaling records suggest that summer feeding grounds were in the Okhotsk Sea and that the whales migrated to presently unknown wintering areas suspected to be along the coast of Guangdong Province and around the nearby Hainan Island in southern China (Henderson 1990). The western population formerly occupied the northern Sea of Okhotsk in the summer, as far north as Penzhinskaya Bay, and south to Akademii and Sakhalinskiy Gulfs on the west and the Kikhchik River on the east (Yablokov and Bogoslovskaya 1984). Southbound whales migrated along the coast of eastern Asia from Tatarskiy Strait to South Korea to wintering areas. Records of gray whale sightings, strandings and catches from 1933 to 1996 suggest that western gray whales frequent the coastal waters of China during the winter months as far south as Gwangxi and Gwangdong provinces and around Hainan Island (Zhu and Yue 1998) . The southernmost record of a western gray whale was from the east coast of Hainan Island (Rice 1998). The long-held belief that the western Pacific gray whales spent the winter along the south coast of Korea was based on unsupported conjecture (Rice, 1998).

Formerly, another migration corridor ran along the east coast of Japan to postulated calving grounds in the Seto Inland Sea. Prior to the 20th century, gray whales migrated to the coastal waters of Japan: one group to the southern coast of Hokkaido and Honshu and another group to the west coast of Kyushu (Omura 1984). The former migrated along the east coast of Japan from the north and entered the Seto Inland Sea, a supposed calving ground. The latter group is believed to migrate along the east coast of Korea and then to southwest Honshu and northwest Kyushu. It is plausible that these groups represented two stocks within the western population each with distinctive migration routes and wintering grounds. Recent sightings of gray whales along the east coast of Japan (National Geographic 1993) suggest that these two groups may still exist but in very reduced numbers.

Soviet scientists reported sightings of gray whales in the Okhotsk Sea along the shallow-water shelf of northeastern Sakhalin Island near Piltun Lagoon. A joint American-Russian-Japanese research project began in 1995 to determine the status of the western population and to identify a means to mitigate ongoing threats to its survival. The seasonal site fidelity and annual return of previously identified whales to this area, including mothers with calves, suggest these animals may represent a discrete sub-population that consistently utilizes the northeastern Sakhalin Island feeding ground (Weller *et al.*1999).

The western North Pacific gray whale population is generally thought to be independent from the eastern North Pacific population because there is a distinct gap in distribution along the eastern shore of the Kamchatka Peninsula, between the Okhotsk and Bering Seas, at least as far east as the Commander Islands (IWC 1993; Fig. 1). Strandings of gray whales reported from the Commander Islands are believed to be from the eastern population, while gray whales reported along the western Kamchatka coast are believed to be from the western population.

3.3 Current Status

The western North Pacific gray whale population was considered to be extinct or nearly so during the 20th century but is known to survive today as a remnant population. Catch records for 67 gray whales taken from the Korean coast between 1948 and 1966 (Brownell and Chun 1977) indicated the continuing existence of this population. Four gray whales observed in the western Okhotsk Sea in 1967, the sighting of a female gray whale with a calf in Korean waters in 1968, and three gray whales observed feeding off the eastern coast of Japan in 1993 (National Geographic magazine 1993) confirmed these whales were not extinct. Today the western North Pacific gray whale population is considered one of the most endangered large-whale populations in the world. While pre-exploitation abundance is unknown, catch histories suggest that this population once numbered at least in the few thousands of animals (*See Section 3.2 History of Exploitation*). Current abundance has yet to be reliably estimated owing to a lack of data. The portion of the population that summers off northeastern Sakhalin Island is thought to be about 100 animals, based on initial results of photo-identification studies conducted 1994-98 which identified 69 individuals (Weller *et al.*1999).

3.4 Morphology and Morphometrics

Few studies have been done to compare the morphology and morphometrics of eastern and western North Pacific gray whales. Zimushko (1972 in Yablokov and Bogoslovskaya 1984) compared data collected by Andrews (1914) on the external morphology of these two populations and believed that differences may indicate the existence of two distinctive populations or 'sub-species'. Andrews (1914) examined fifty or more gray whales harvested at the Toyo Hogei Kaisha whaling station in Ulsan, South Korea. He made detailed descriptions of gray whale morphology and collected two complete skeletons. Zimushko (1972) reported that the distance from the tip of the rostrum to the base of the pectoral flippers, from the tip of the rostrum to the eye, the maximum width of the pectoral flipper, and the length of the baleen plates were statistically greater in the western gray whales, and that western gray whales had fewer baleen plates and fewer throat grooves. Unfortunately, the details of these analyses have not been published. A re-examination of these data may help determine whether these differences are sufficient to reliably assign skeletal remains to the eastern or western populations.

3.5 Other Data

Recent genetic analyses comparing western and eastern North Pacific gray whales indicates that the two populations are significantly different from each other (LeDuc *et al.* 2000), and along with additional information on morphology, parasites, etc. have the potential to resolve the relationship of the western North Pacific population to the larger eastern North Pacific population (*See Section 5.2 Genetics*). Analysis of chemical signatures (*e.g.*, heavy metals and organochlorines) as ecological tracers could potentially distinguish differences between western and eastern gray whales. Other animals that use inland Asian waters (*e.g.*, the North Pacific minke whales of the J-stock) have highly distinctive chemical signatures, which distinguish them from other animals within the same species (Nakata *et al.* 1999; Fujise, *et al.* 1999). Such information could be used to detect dispersers and new individuals that enter the population from other areas. Mark-recapture through photographic identification should be effective at determining the plausibility that the western population is 'closed' because of its small size and resultant high probability for re-sightings of individuals (Weller *et al* 1999). The high annual re-sighting rate of individuals in this population suggests that any new individuals will likely be detected if eastern North Pacific gray whales are dispersing into the western population.

The strongest evidence that the eastern and western gray whale populations are segregated is the lack of recovery of the western population through a period in which the eastern population has rebounded remarkably well. If there was dispersal of individuals from east to west, the western population would have been re-populated by now. If the eastern population is approaching carrying capacity, then some individuals might expand their range in search of new feeding grounds. The apparent small population abundance of the western population suggests that emigration from the eastern population is not occurring at any meaningful level. Considering the existing data, it is generally agreed that the western population of gray whales represent a geographically isolated population, and should be treated as a distinctive stock for management purposes.

4. EASTERN NORTH PACIFIC POPULATION

The eastern North Pacific or California-Chukchi gray whale population has made a remarkable recovery from depletion caused by commercial whalers. This population has become one of the best studied groups of baleen whales. Most whales in this population make an extensive migration each year between their primary summer feeding grounds in the Bering and Chukchi seas and their winter assembly areas in the near-shore waters of Southern California, the coastal waters, bays and lagoons of Baja California, and to some extent the lower Gulf of California (Fig. 1). Most of what is known about gray whale biology, life history, ecology and behavior results from research conducted on this population. Because of their predictable migrations along the west coast of the U.S., these whales have been easy to find and access, making them relatively convenient to study.

4.1 History of Exploitation

Eskimos hunted gray whales near the shores of the northern Bering and Chukchi Seas for thousands of years. Natives of the Chukotka Peninsula selected young gray whales that were killed by using toggle-headed harpoons attached to seal and walrus skin floats (Krupnick 1984). Up until 1928 several Indian tribes between the Aleutian Islands and California hunted gray whales as a part of their cultural and religious traditions. They hunted from boats made of skin or wood and used hand-held harpoons, often with poison enhanced tips. Stranded whales were also utilized by some of these tribes. These included the Alutes, Koniag, Chugash, Tlingit, Haida, Tsimshian, Nootka, Makah, Ozette, Quileute, Klallam and the Chumash (O'Leary 1984).

In northeastern Asia, aboriginal whaling diminished early in the mid-nineteenth century. This resulted from a decline in the aboriginal populations as well as from changes in cultural traditions following contact with westerners, particularly Yankee whalers. Commercial shore whaling took gray whales along the coast of the Californias from the mid 1850s to the early 1900s (Sayers 1984). Scammon (1874) defined shore whaling as the pursuit of a whale from a boat launched from the shore. When the whale was captured, it was towed back to shore where it was flensed and its oil and other by-products were processed for market. The first station was established on Monterey Bay in 1854, and over the next 45 years 15 stations were operated at various times from Crescent City, to Punta Eugenia, Baja California. The industry was profitable for approximately 40 years, but by the turn of the century, whales had become scarce along the coast, and shore whaling became obsolete.

From 1845 to about 1900, American whalers hunted gray whales on their winter grounds in Baja California as well as along their coastal migration routes and on their summer grounds in the subarctic (Scammon 1874; Henderson 1984). After whalers discovered the wintering areas in lagoons along the Pacific Coast of Baja California, they took whales by the hundreds outside the entrances and within the lagoon interiors (Henderson 1984). The gray whale earned the names of 'devil fish' and 'hard head' from their habit of attacking whaling skiffs when harpooned. Skiffs were frequently overturned and stoved in, and human lives were lost. Thus, the whalers preferred hunting gray whales from shallow waters along the edges of the lagoon channels where they were relatively safe from attacks by injured whales, particularly after harpooning calves in order to capture the accompanying adult. Because females congregate within the lagoon interiors in winter to rear their calves, these catches comprised mostly females and their calves. This whaling strategy drastically reduced the reproductive capacity of the population. By the turn of the century, whaling for gray whales was no longer commercially viable. Henderson (1984) estimates that between 1845 and 1874 approximately 11,300 gray whales were harvested throughout the eastern North Pacific, including approximately 3,200 from the lagoons and bays of Baja California. Estimates of likely population sizes in 1846 range from 12,000 to 15,000 animals (Reilly 1992) which was reduced to 4,000 to 5,000 or fewer animals by 1900 (Butterworth *et al.* 1990) (*See Section 4.3, Abundance and Current Status*). Clearly, nineteenth century whaling from ships and shore stations resulted in dangerous decline in the eastern North Pacific population.

Modern whaling for eastern North Pacific gray whales began around 1914 and was pursued by the United States, Japan, Norway and the Soviet Union (Reeves 1984). Modern whaling refers to the catching of whales through the use of deck-mounted cannons, explosive grenades, direct fastening to the whales and diesel, gas or steam-powered boats and ships (Mitchell and Reeves 1983). From 1914-46, an estimated 940 gray whales were taken by factory ships and/or fleet whalers working from the North Pacific to Baja California in all seasons (Reeves 1984). The catch of gray whales off the Chukotka Peninsula increased in the 1930s after commercial over-harvesting caused the decline of the bowhead whale (Yablokov and Bogoslovskaya 1984). From 1933-46, the Soviet whaling fleet took 623 gray whales in the

Bering and Chukchi seas (Sleptsov 1955 in Blokhin 1997b). In 1940, the Japanese factory ship *Tonan Maru* took 58 gray whales in the North Pacific. After 1937, Norway and the United States protected gray whales from commercial whaling, and after 1938 Canada protected them from commercial whaling.

Commercial whaling for gray whales was banned by the International Convention for the Regulation of Whaling in 1946. That agreement included the provision for the natives of Chukotka and Koryak to harvest gray whales for subsistence use, a provision that continues under IWC management. From 1948-54, Chukchi hunters took 182 whales, and from 1956-68, the catches increased to more than 100 animals annually (Zimushko and Ivashin 1980). Between 1959-69, 316 gray whales were killed under Special Permits off central California during the fall southward and spring northward migrations. This take was for scientific investigations to establish the status of the population (Rice and Wolman 1971). From 1969-98, Chukotka natives harvested an average of 140 gray whales annually. In 1997 the IWC set an aboriginal subsistence quota of 620 gray whales for 1998-2002, not to exceed 140 whales annually (IWC 1998): the Russian Federation is allowed to take up to 135 gray whales annually, and the United States is allowed to harvest up to 5 gray whales annually (IWC 1998).

Donovan (1991) noted that a management unit is defined such that specific management goals are met (*e.g.*, commercial or aboriginal subsistence harvests do not lead to local depletions or extirpation). It would be useful to know if harvests of gray whales occurred at specific times or seasons and at locations containing genetically distinct sub-groups of the eastern North Pacific population of gray whales. Preferential harvests from such sub-groups could have the potential to extirpate or deplete them and/or result in abandonment of portions of the populations' range as proposed for some species of whales (Clapham and Pasboll 1999, Clapham and Hatch 2000).

There is evidence that gray whales segregate by age and sex on their northern feeding grounds, as reflected in the Russian harvests. Gray whales begin to arrive along the Chukotka coast in May and June (depending on annual ice conditions) and remain until late-October or early-November (Blokhin 1998). Gray whales are harvested in this area from late-June to early-November in most years (Blokhin 1997a, 1997b). Analysis of the summer catches of gray whales from 1969-81 indicated that 69.8% were female and 30.2% were male, and that females and young whales were distributed in the shallow coastal waters while larger adult animals were found further offshore in waters up to 50-60 m deep (Yablokov and Bogoslovskaya 1984). Bogoslovskaya (1982) concluded that the majority of the newly weaned whales congregated in nearshore, shallow waters and lagoons along the coast.

In the last decade selective harvesting in the nearshore areas is indicated by the increase in the number of immature animals in the catches when 'traditional' small-scale nearshore whaling methods replaced the use of state-supported whaling ships capable of taking animals of any size further from shore and from a wider geographic area (Blokhin 1995). If the Chukotka natives consistently harvest whales near their villages, and if there exist genetically distinct sub-groups that return to these areas each summer, the continuation of harvests could result in local depletions and extirpations of unique sub-groups. Alternatively, if gray whales move seasonally through the harvest areas as they search for productive feeding sites and do not show site fidelity, harvests probably do not focus on any genetically distinct portion of the population. Although some data are available on assemblages of young gray whales that segregate in areas along the coast of Vancouver, B.C. (Darling *et al.* 1998), data on the habits of individual gray whales in the northern feeding areas are lacking. Examination of harvest records (especially locations of takes), genetic analyses of the harvested animals and photographic identification research could be used to address the issue of population structure and fidelity on the northern feeding grounds.

Similarly, if there were unique stocks or groups of whales using the lagoons of Baja California, the intense whaling conducted there over a century ago would have eliminated them. However, all of the primary lagoons where historical removals occurred continue to be utilized by gray whales today. Removals did not result in the abandonment of these lagoons and presumably did not result in the extirpation of any distinct sub-groups of the population (*See Section 4.3 Migration Timing and Segregation*). Previous reports of San Diego Bay being utilized by gray whales in the winter have never been substantiated.

4.2 Distribution

While most of the eastern North Pacific gray whale population summers on feeding grounds in the northern Bering and southern Chukchi Seas (Moore and Ljungblad 1984), gray whales in this population are distributed from California to the Arctic during the summer months. In the Beaufort Sea, gray whales have been seen as far east as 130°W in August (Rugh and Fraker 1981). In the East Siberian Sea, gray whales are found as far west as 174° E in late September (Reilly 1984, Berzin 1984). In fall the population migrates south along the coast to its winter range off the coast of Southern California, the west coast and lagoons of Baja California, and to a limited extent into the Gulf of California and the mainland coast of Mexico (Fig. 1) (Gilmore 1960, Swartz 1986).

Observations of gray whales in summer months in locations well south of their northern summer feeding areas are not recent occurrences, and have been documented during periods of low and high population abundance (Gilmore 1960 and 1976, Pike 1962, Rice 1963, Hattler and Darling 1974, Patten and Samaras 1977, Darling 1984, Nerini 1984, Mallonee 1991, Avery and Hawkinson 1992, Clapham *et al.* 1997, Calambokidis and Quan 1999, Sanchez-Pacheco *et al. In Press*). Often these animals are observed feeding in various locations along the migration route. Such occurrences may not be solely the result of range expansion in an increasing population, but may reflect the gray whales' predilection to forage widely for suitable prey species. A number of identifiable individual gray whales, termed 'summer residents,' have been observed to return each summer to the same areas in various locations from Southeast Alaska to Vancouver Island, Canada, and the states of Washington, Oregon and California (Hattler and Darling 1974, Darling *et al.* 1998, Darling 1984, Calambokidis and Quan 1999, Gosho *et al.* 1999) (*See Section 4.5, Feeding and Prey Species*).

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Gray whale *Eschrichtius robustus* population and stock identity

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ABSTRACT

1. In response to conservation and management concerns about gray whale *Eschrichtius robustus* population and stock structure, we provide an overview of the life history and ecology of gray whales as a context for discussion of population and stock structure within the species. Historically eastern and western North Pacific gray whales were managed separately because: (i) their ranges do not overlap; (ii) genetic analyses indicate that the two populations are significantly different; and (iii) eastern gray whales have increased in abundance over the past century while western gray whales have not.

2. Here, we review gray whale migration timing and segregation, feeding and prey species, and reproduction and reproductive behaviour. For the eastern and western gray whale, we review their distribution, history of exploitation, abundance and current status, although most of what is known is founded on the better studied eastern gray whale and only implied for the lesser known western gray whale. Methods to investigate population and stock identity are reviewed including genetics, morphology, chemical signatures, carbon isotopes, parasites, photographic identification and trends in abundance.

3. While the evidence indicates that there is at least some degree of mixing within each of the gray whale populations, no stocks or sub-stocks can be defined. Population structure is not evident in nuclear data, and because selection occurs primarily on the nuclear genome, it is unlikely that there is structuring within each population that could result in evolutionary differences. For western gray whales, there are insufficient data to assess the plausibility of stock structure within the population, owing to its extremely depleted state. Research on eastern gray whales has focused mostly on documenting changes in abundance, feeding biology and behaviour, and suggests separate breeding groups to be unlikely. Both males and females are promiscuous breeders lending little opportunity for the nuclear genome to be anything other than well mixed as is suggested by the high haplotypic diversity of the eastern population.

4. The available data strongly indicate that western gray whales represent a population geographically isolated from eastern gray whales and therefore that the western and eastern populations should be treated as separate management units.

Keywords: cetaceans, marine mammals, North Pacific Ocean, population structure, stock identity, wildlife management

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INTRODUCTION

Conservation of large whales has been an international concern ever since widespread commercial hunts severely depleted whale stocks, in many cases continuing to take whales until many species were too scarce to be an economic resource (see review in Reeves, 2002). The International Whaling Commission (IWC) was formed to assess the viability of whaling practices and the size of remaining whale stocks. To develop a systematic process for defining stocks of large whales within the management regime of the IWC, the Stock Identity Working Group of the Scientific Committee examined case studies for individual whale species. The objective of these case studies was to reveal how the different life history strategies of species affect population structure, as well as how the studies reveal the utility of various types of data for evaluating stock identity and structure within populations. In response to concerns about the conservation and management of gray whale *Eschrichtius robustus* population and stock structure, the current review provides an overview of their life history and ecology.

In this review, we use 'population' to refer to units where virtually no gene flow (less than one disperser) would be expected within a generation (approximately 20 years). Such a unit is sometimes called an evolutionarily significant unit (ESU) because gene flow is sufficiently low to allow meaningful differences to develop. 'Stock' refers to a unit with a level of gene flow greater than an ESU but still small enough to be demographically important for management (Taylor, 2005). For purposes of clarity, we suppose this level to be less than 1% dispersal between units per year. Each 'population' can be composed of one or multiple 'stocks'. See the introduction of the review of bowhead *Balaena mysticetus* stock identification paper (Rugh *et al.*, 2003) for further discussion of this terminology.

BACKGROUND

Gray whales are sufficiently distinctive relative to other cetaceans to be placed in their own family: Eschrichtiidae (Rice, 1998); however, recent molecular analysis has provided conflicting views regarding this taxonomy (Sasaki *et al.*, 2005). Although skeletal remains and sightings of live animals indicate that this species occurred historically in both the North Pacific and North Atlantic (Fig. 1), gray whales are believed to have been extinct in the North Atlantic since the early 18th century (Mead & Mitchell, 1984). It is possible that during interglacial periods in the distant past, e.g. massive glacial advances and retreats in the Quaternary (Pleistocene and Holocene), corridors were available across the Arctic, allowing for exchange of whales between the Pacific and Atlantic (Gilmore, 1978). During glaciations, sea levels dropped in the North Pacific exposing some or most continental shelf areas, which would have severely reduced gray whale habitat (as we currently know it) and eliminated their options to enter the Arctic basin, which was blocked at the time by the Bering Isthmus (Berta & Sumich, 1999). The more recent 'little ice age' investigated by Overpeck *et al.* (1997) suggests that Arctic-wide cooling and widespread glaciation within the last 400 years may have affected the distribution of the species in the North Pacific. Such an ice-driven southerly shift in their distribution could have facilitated the mixing of gray whales from the east and west sides of the North Pacific during these ice ages as has been suggested for bowhead whales (Dyke, Hooper & Savelle, 1996).

Of the two extant North Pacific populations, the western (also known as the Western North Pacific population or the Korean-Okhotsk population) remains critically depleted (Weller *et al.*, 2002) while the eastern (also known as the Eastern North Pacific population or the California-Chukchi population) has recovered from exploitation (Rugh *et al.*, 1999, 2005). The species began to receive protection from commercial whaling in the 1930s (see review in

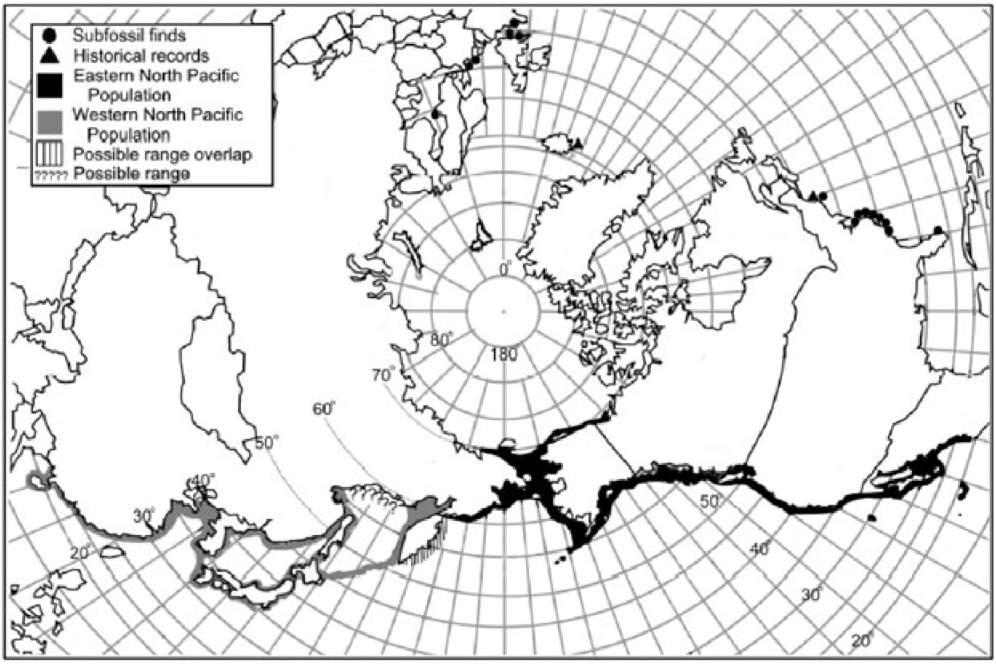

Fig. 1. The range of the gray whale, *Eschrichtius robustus*.

Reeves, 1984). However, hunting continued in the western population for many more years (Brownell & Chun, 1977). Currently, the IWC sets a quota allowing 169 gray whales to be caught annually from the eastern population for aboriginal subsistence use (IWC, 1998). In spite of the persistent subsistence hunt, the eastern population has recovered at a rate of 1.9% to a recent abundance estimate of nearly 20 000 animals (Rugh *et al.*, 2005). In contrast, the western population has shown no sign of recovery and may consist of only 100 whales (Weller *et al.*, 2002).

Management authorities, such as the US National Marine Fisheries Service and the IWC, regard both the eastern and western populations as separate management units (Rugh *et al.*, 1999; LeDuc *et al.*, 2002), and this division is supported by material presented in the current review. Under the US Endangered Species Act, these populations have separate listings as Distinct Population Segments, which are considered to be of evolutionary importance, and the populations are listed separately under the International Convention for the Conservation of Nature and Natural Resources, i.e. the IUCN (Baillie, Hilton-Taylor & Stuart, 2004). The objective of this document is to collate components of gray whale life history information (migration, feeding and reproduction), describe the two populations (relative to exploitation history, distribution and abundance), and note what tools are available for analysing population and stock differentiation (e.g. genetics, morphology and chemical signatures). Accordingly, this review will draw together a summary of what is known about population and stock structure of gray whales and provide a framework for management applications.

GENERAL BIOLOGY

Eastern North Pacific gray whales have been studied throughout their range for many years, which is not the case for the western gray whales. While many specific details of western gray whale life history are unknown, it can be expected that the general life history patterns are similar. Information on the general biology and life history, such as migratory routes, range and seasonal timing, provides a context for discussing possible population and stock differentiations or the lack thereof.

Migration timing and segregation

The migrations of most mysticete whales are thought to have arisen as an evolutionary response to the seasonal production of prey in polar regions (Lipps & Mitchell, 1976). Seasonally predictable sources of food shaped the life history of baleen whales into two periods: summers when whales feed in higher latitudes with abundant food and minimal sea ice; and winters when whales migrate to lower latitudes to escape inclement weather and to calve in warmer waters. Reduced predation by killer whales *Orcinus orca* in lower latitudes also may or may not have played a significant role in the evolution of migration of some mysticete whales (Corkerton & Connor, 1999; Clapham, 2001), but in gray whales it is unclear how this evolution is influenced by the predation that is known to occur during their northbound migration.

Gray whale migration has evolved into fall southward and spring northward migrations along the western North American coast for the eastern gray whale, and a similar seasonal migration along the eastern coast of Asia for the western gray whale. Comparatively little is known about the details of migration in the western population.

By late November, most eastern gray whales have started migrating south out of their Arctic summer feeding grounds (Rugh, 1984). The start of the migration coincides with the period of conception, which for most (but not all) gray whales occurs during a 3-week period centred in early December (Rice & Wolman, 1971). During this time, gray whales are concentrating in nearshore areas, improving opportunities for finding mates and for genetic mixing. Southward migrating gray whales are observed moving through coastal waters of the North Pacific from November to February (Rugh, Shelden & Schulman-Janiger, 2001). They begin arriving in their winter grounds as early as mid-December with peak numbers of whales passing the California coast in mid-January The southward migration for better-known eastern gray whale population generally ends in mid-February just as the northward migration begins, with the last of the southbound animals overlapping with the first northward migrants (Rugh *et al*., 2001). This overlap suggests that only a portion of this population is in the waters of Mexico during the winter, while the remainder are distributed in coastal waters of southern and central California (Swartz, 1986).

The southward migration of eastern gray whales is segregated by age, sex and reproductive status (Rice & Wolman, 1971); the first pulse is led by near-term pregnant females, followed by oestrous females and mature males, and the last phase includes immature animals of both sexes. Eastern gray whales reach maximum densities on their wintering grounds by mid-February (Jones & Swartz, 1984). While the majority of eastern gray whale calves are believed to be born within or near the coastal lagoons of Baja California, Mexico. Sightings of newborn calves migrating south past central and southern California in January and February have increased in recent years (Shelden, Rugh & Schulman-Janiger, 2004). Southward migration timing may be affected by how widely the population is distributed for foraging, and this is affected in part by the onset of winter and the extent of ice coverage in the Arctic.

As eastern gray whales arrive at the lagoons of Baja California, mainly in January, they segregated spatially and temporally such that their distribution, gross movements and timetable of lagoon occupation differ for each age–sex group (Jones & Swartz, 1984; Urban *et al*., 2003). Single whales (i.e. oestrous females and mature males) are found at highest densities near lagoon inlets and in adjacent coastal waters. By contrast, females with calves concentrate within the interiors of lagoons (Jones & Swartz, 1984). With the departure of adult whales without calves in late February, females with calves shift their distribution to lagoon inlets and adjacent coastal areas, essentially abandoning the inner lagoon nurseries (Jones & Swartz, 1984). This segregation of adult whales without calves from females with calves is an extension of the age and sex segregation seen during the spring and fall migrations (Rice & Wolman, 1971).

The spring northward migration of eastern gray whales occurs in two distinct phases segregated according to age, sex and reproductive condition (Poole, 1984; Swartz, 1986). The first phase centred in February includes newly pregnant females followed 2 weeks later by adult males and anoestrous females and another week later by immature whales of both sexes. The second phase consists of mothers with calves that begin to leave the lagoons after the first phase and are observed along the migration route from March to May, generally arriving on their summer Arctic feeding grounds from May to June

Feeding and prey species

Unlike more pelagic mysticete species that migrate and feed across deep ocean basins, eastern gray whales migrate along the western coast of North America where upwellings of nutrient-rich waters produce some of the world's most productive marine ecosystems and afford gray whales with a variety of potential prey species. Gray whales are primarily, although not exclusively, bottom-feeders. Their prey includes a wide range of benthic and epibenthic invertebrates such as gammaridean amphipods; these occur during the summer months in dense colonies on the continental shelf sea floor of regions like the Bering and Chukchi seas (Nerini, 1984). Limited feeding also occurs outside the primary feeding grounds, along their migration route and in some portions of their winter range (Oliver *et al.*, 1983; Nerini, 1984; Sanchez, Vasquez-Hanckin & DeSilva-Davila, 2001).

Reproduction and breeding behaviour

Gray whale females normally reproduce on a 2-year cycle, producing a single calf every other year, a cycle which is intimately tied to the whales' annual migrations and environmental conditions favourable for the early development of calves (Rice & Wolman, 1971; Swartz, 1986). Rice & Wolman (1971) examined 150 female gray whales during their migration near central California 1959–69, while the population was recovering from commercial exploitation. Their data showed that gray whale breeding is highly synchronous, with females coming into oestrus in a 3-week period from late November to early December; this coincides with the initiation of the southward migration out of the summering areas. If there is no conception, a second oestrus may occur 40 days later (Rice & Wolman, 1971) when the whales are in or near their winter grounds (Jones & Swartz, 1984; Swartz & Jones, 1984). Mating behaviour is observed during most seasons (Gilmore, 1960; Rice & Wolman, 1971; Jones & Swartz, 1984; Swartz, 1986; Berta & Sumich, 1999), but conception appears to be restricted to a fairly short period between late November and early January. Both female and male gray whales are promiscuous and copulate repeatedly with more than one mate (Jones & Swartz, 1984). With a gestation period of 13 months and a mean calving date around 10 January (Rice & Wolman, 1971), some calves are born during the southward migration (Shelden *et al.*, 2004). Calves stay with their mothers for 6–7 months and are weaned and independent while on the summer feeding grounds. Following weaning, adult females remain anoestrus for several months until they enter into a new oestrus cycle and are receptive to a new pregnancy in late autumn (Rice & Wolman, 1971). Mature male gray whales also have a marked seasonal cycle with a seasonal increase in testes weight and a peak period of spermatogenic activity that correlates closely with the time females come into oestrus (Rice & Wolman, 1971).

EASTERN POPULATION

Distribution

Although most of the eastern gray whale population summers on feeding grounds in the northern Bering and southern Chukchi Seas (Moore & Ljungblad, 1984), some whales in this population are distributed far to the east and west in the Arctic and along the coast as far south as California. In the Beaufort Sea, gray whales have been seen in arctic Canada (to 130°W) in August (Rugh & Fraker, 1981). In the East Siberian Sea, gray whales occur even west of Wrangel Island (to 174°E) in late September (Berzin, 1984; Reilly, 1984).

Observations of gray whales in summer months well south of Alaska are not recent occurrences and have been documented during periods of both low and high population abundance (Gilmore, 1960; Pike, 1962; Rice, 1963; Hatler & Darling, 1974; Patten & Samaras, 1977; Darling, 1984; Nerini, 1984; Mallonée, 1991; Avery & Hawkinson, 1992; Gosho *et al.*, 2001; Sanchez *et al.*, 2001; Calambokidis *et al.*, 2002). A number of identifiable individual gray whales, termed 'summer residents' or members of the 'Pacific Coast Feeding Aggregation', have returned to the same areas over the course of many summers in various locations from South-east Alaska to Vancouver Island, Canada, and off the states of Washington, Oregon and California (Hatler & Darling, 1974; Dahlheim, Fisher, & Schempp, 1984; Darling, Keogh, & Steeves, 1998; Gosho *et al.*, 2001; Calambokidis *et al.*, 2002). Photographic re-identifications suggest that these whales also range widely within other coastal areas as far south as northern California and north to Alaska, and these diverse movements could account for inconsistencies in year-to-year re-sightings of individuals at specific locations (Calambokidis *et al.*, 2002).

In the late fall/early winter, eastern gray whales migrate south along the eastern Pacific coast to their primary winter range along the west coast of Peninsula de Baja California (Fig. 1) (Gilmore, 1960; Swartz, 1986; Urban *et al.*, 2003) and along the Gulf of California (Findley & Vidal, 2002). Although there is repeated use of some lagoons, eastern gray whales do move between lagoons and spend some amount of the winter in waters outside of the lagoons (Urban *et al.*, 2003) and along the Baja California and southern California coasts.

History of exploitation

Eskimos have hunted eastern gray whales near the shores of the northern Bering and Chukchi Seas for thousands of years. Historically, Chukotka natives killed young gray whales (Krupnik, 1984), and until 1928, several Indian tribes between the Aleutian Islands and California hunted gray whales as a part of their cultural and religious traditions (O'Leary, 1984). Aboriginal whaling diminished in the mid-19th century caused in part by declines in gray whale abundance resulting from commercial hunting and native hunting and by changes in cultural traditions following contact with westerners (Krupnik, 1984). Commercial shore whaling took gray whales along the coast of California and Mexico from the mid-1850s to the early 1900s (Sayers, 1984). The first shore whaling station was established on Monterey Bay in 1854, and over the next 45 years, 15 stations were operated at various times from Crescent City (northernmost tip of California) to Punta Eugenia (Baja California); however, by the turn of the century, whales had become scarce along the coast, and shore whaling became economically unviable (Sayers, 1984).

From 1845 to about 1900, American 'Yankee' whalers utilized sailing ships that launched small oar-powered skiffs (i.e. longboats) to hunt gray whales on their winter grounds in Baja California as well as along their coastal migration routes and on their summer grounds in the sub-Arctic (Scammon, 1874; Henderson, 1984). Hunts in and near the lagoons greatly reduced the reproductive capacity of the population by killing the females with calves congregating there. By the turn of the century, whaling for gray whales was no longer commercially viable. Henderson (1984) estimates that between 1845 and 1874, approximately 11 300 gray whales were killed throughout the entire eastern Pacific.

Modern 'industrial' whaling (that utilized steam-powered catchers and explosive harpoons) for eastern gray whales around 1914 was pursued by the United States, Japan, Norway and the Soviet Union (Reeves, 1984). From 1914 to 1946, an estimated 940 gray whales were taken by factory ships and/or fleet whalers working in the North Pacific in all seasons (Reeves, 1984). With the signing of the International Agreement for the Regulation of Whaling in 1937, gray whales were protected from commercial whaling, at least by some countries (Reeves, 1984). That agreement included a provision for natives of Chukotka and Koryak to kill gray whales for subsistence use. Catches by Russians have averaged between 100 and 200 animals annually since 1948 (Zimushko & Ivashin, 1980; IWC, 1998). From 1959 to 1969, 316 gray whales were killed off central California under IWC special research permits to establish the status of the population (Rice & Wolman, 1971).

Abundance and current status

Scammon (1874) speculated that the eastern gray whale population numbered 30 000 in 1853–56, but by 1874, following commercial exploitation, the number did not exceed 8000–10 000 whales (Henderson, 1984). Henderson (1984) examined whaling records and made a qualitative conclusion that the population did not exceed 15 000–20 000 whales before the initiation of commercial exploitation in 1846. The most recent estimates of minimum population sizes following commercial exploitation are based on back-calculation analyses that utilize records of catch histories and a range of estimates of maximum sustainable yield rates. Reilly (1981) concluded that the most likely pre-exploitation size of the population was 24 000, which had been reduced to below 12 000 by the year 1900 as the result of commercial whaling. Minimum population size estimates range from 12 000 to 15 000 animals in 1846 at the beginning of commercial exploitation (Reilly, 1992) to only 4000–5000 or perhaps as low as 1500–1900 by 1900 (Butterworth, Korrûbel & Punt, 2002).

Direct estimates of current population size come from the analyses of systematic shore counts of southward migrating gray whales. These counts were initiated in 1967/68 near Monterey, California, where the majority of the population passes within 4 km of shore (Shelden & Laake, 2002). Abundance estimates from 1967/68 to 1997/98 showed a population increasing at an annual rate of 2.6% (S.E. = 0.28%), peaking at 30 000; however, in 2000/01 and 2001/02, the estimates dropped to about 18 000 (Rugh *et al*., 2005). The drop in abundance appears to indicate that this population is reaching carrying capacity (Wade, 2002).

Stock structure

Donovan (1991) noted that a management unit is defined such that specific management goals are met (e.g. commercial or aboriginal subsistence hunts do not lead to local depletions or extirpation). It would be useful to know if hunts of gray whales occurred at specific times or seasons and at locations containing genetically distinct stocks of the eastern population of gray whales. Preferential catches from such stocks could have the potential to extirpate or deplete those stocks and/or result in abandonment of portions of the popula-

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tions' range as proposed for some species of whales (Clapham & Palsbøll, 1999; Clapham & Hatch, 2000).

When most receptive for mating, females are not concentrated in a specific breeding 'area'; rather, they are distributed along the migratory route, mostly in Alaska (Rugh *et al.*, 2001). This concentration of whales along the narrow migratory corridor may play a key role in helping these animals find mates at a critical time, and provide opportunity for genetic mixing throughout the population. There is no current information available to suggest that distinct sub-components of the eastern population segregate in any specific breeding areas.

There is evidence that gray whales segregate by age and sex on their northern feeding grounds, as reflected in the Russian aboriginal subsistence catches (Yablokov & Bogoslovskaya, 1984), but no genetic data are available to gain further insight into stock structure. In general, data on the habits and genetic identity of individual gray whales in the more northern feeding areas are lacking. Historical samples are unavailable to assess whether stock structure within the lagoons existed in the past.

In recent years, about 200 identifiable individual gray whales have returned one or more summers to the same areas at various locations along the Pacific North-west coast, perhaps as a function of seasonal abundance of prey (Darling *et al.*, 1998; Gosho *et al.*, 2001; Calambokidis *et al.*, 2002). These individual whales are believed to constitute the 'Pacific Coast Feeding Aggregation' which may or may not represent a genetically distinct stock of eastern gray whales, or just a recurring temporal aggregation of individuals that frequent this portion of the migration corridor during the summer. No definitive evidence is available to suggest that this 'Aggregation' represents a genetically distinct stock of eastern gray whales.

Examination of eastern gray whale hunting records (especially locations of takes), genetic analyses of animals killed and photographic identification research could be used to address the issue of population structure and fidelity throughout this population's range.

WESTERN POPULATION

Distribution

Historical sighting data and whaling records indicate that summer feeding grounds of western gray whales were in coastal waters of much of the northern Sea of Okhotsk (Yablokov & Bogoslovskaya, 1984; Henderson, 1990). However, gray whale sightings are now limited to the shallow-water shelf on north-eastern Sakhalin Island, Russia (Weller *et al.*, 1999). Recent research in the region results from a US–Russian environmental agreement initiated in 1995 to determine the status of the western population and to identify a means to mitigate ongoing threats to its survival (Weller *et al.*, 1999). The seasonal site fidelity and annual return of previously identified whales to this area, including mothers with calves, make the habitat off north-eastern Sakhalin Island of considerable concern relative to the conservation of these animals (Weller *et al.*, 1999). To date, no other feeding ground has been identified for western gray whales, underscoring the importance and potential fragility of the Sakhalin habitat.

In autumn, western gray whales migrate south along several possible routes, including down the coast of eastern Asia along the Korean Peninsula or along coastal waters of Japan (e.g. Kato & Tokuhiro, 1997). Migratory routes potentially include the waters off the coast of eastern Asia from Tatarskiy Strait to south of Korea or through coastal waters of Japan (e.g. Kato & Tokuhiro, 1997).

Wintering areas are unknown, but sightings, strandings and catches from 1933 to 1996 suggest the whales may be along the coast of Guangxi and Guangdong Provinces and around the nearby Hainan Island in southern China (Wang, 1984; Henderson, 1990; Zhu, 1998). The southernmost record of a western gray whale was from the east coast of Hainan Island (Rice, 1998). The long-held belief that western gray whales spend the winter along the south coast of Korea was based on unsupported conjecture (Rice, 1998).

The western North Pacific gray whale population is believed to be geographically independent from the eastern population because there is an apparent gap in distribution along the eastern shore of the Kamchatka Peninsula, between the Okhotsk and Bering Seas, at least as far east as the Commander Islands (IWC, 1993; Fig. 1).

History of exploitation

Although pre-exploitation numbers are unknown, the western gray whale population was probably never as numerous as the eastern population. It was intensively hunted during the past three centuries, and commercial whaling for the western population ceased in the 1960s. This period of exploitation reduced the population to only a fraction of its original size, and it was thought by some to be extinct (Bowen, 1974).

Japanese harpooners may have taken gray whales as early as the 16th century, and Japanese net whalers continued to take western gray whales during the 17th to 19th centuries (Omura, 1984). Groups of Koryak natives lived in the north-eastern Okhotsk Sea and may have hunted gray whales, perhaps even into the early 1900s (Krupnik, 1984). European and American ‘preindustrial’ whalers operating in the western North Pacific and Okhotsk Sea took gray whales from sailing ships and oar-powered ‘longboats’ between the late 1840s and early 1900s. With the advent of ‘industrial’ whaling with steam-powered catch vessels, Russian whalers took gray whales in the coastal waters of the Far East at the end of the 1800s (Henderson, 1984; Weller *et al.*, 2002). Mizue (1951) shows a dramatic decline in gray whale catches after 1910, with much of the effort attributed to the adoption of modern ‘industrial-type’ whaling in 1903.

Kato & Kasuya (2002) reviewed the catch history of western gray whales by Japanese and Korean modern whaling during the 1900s and revealed a period of peak annual catches of 100–200 whales occurred in the 1910s. This was followed by a rapid decline of the catch in the 1920s and 1930s, dropping to 10–20 whales per year for over 40 years until the hunt ended in the 1960s. Japanese and Korean whalers continued to hunt gray whales until as recently as 1966 (Brownell & Chun, 1977). It is estimated that a minimum of between 1800 and 2000 gray whales were taken during the whaling period between 1891 and 1966; Kato & Kasuya (2002) concluded that this last phase of continuing small-scale exploitation could have been a major factor in suppressing the recovery of this population.

Since the signing of the International Agreement for the Regulation of Whaling in 1937, western gray whales have been protected from commercial whaling, and no catch quotas have been established (IWC, 1998).

Abundance and current status

Only very rough approximations can be made of the original abundance of western gray whales. While not specifying a period of time, Yablokov & Bogoslovskaya (1984) reviewed records that suggested grey and humpback whales *Megaptera novaeangliae* were common and even abundant in the coastal waters of the northern Okhotsk Sea. They estimated that there were 1500–10 000 prior to the impact of commercial whaling. Bradford (2003) quantitatively back-calculated abundance estimates of 1000–1200 whales in 1900, which coincides with the qualitative estimate by Berzin & Vladimirov (1981) of 1000–1500 whales in 1910. Both of these estimates applied to a period prior to intensive modern whaling but after the population had already been substantially reduced by centuries of pre-modern catches.

Western gray whales were considered to be extinct or nearly so (Bowen, 1974) until records of catches and post-whaling sightings indicated the continuing existence of this population (Brownell & Chun, 1977). The population was listed as *Critically Endangered* by the IUCN in 2000 (Hilton-Taylor, 2000; Baillie *et al*., 2004) and is considered one of the most endangered populations of large whales in the world. Current population size estimates indicate that the western population contains approximately 100 individuals (Wade *et al*., 2003; IUCN, 2005; Weller *et al*., 2005), and its continued ability to survive is of considerable concern (Weller *et al*., 1999).

Stock structure

It is not known if stock structure exists or existed within the western gray whale population. While the western population was previously thought to have multiple migration routes between its summer and winter grounds, insufficient information is available to determine what, if any, implications multiple migration routes may have had for stock structure. Given this population's current small size, knowledge of stock structure would not likely influence conservation and management strategies for its protection and continued recovery.

METHODS USED TO INVESTIGATE POPULATION AND STOCK IDENTITY

Background

The IWC defines a management unit as a grouping of whales that, if subject to regulated hunts, would be sustained and not depleted or extirpated; both a population and a stock can be considered a management unit (Donovan, 1991). Historically, the data used to define such management units included: (i) demographic information on catch and sighting distributions; (ii) discontinuities in the distribution of animals on their feeding and breeding grounds; (iii) differences in biological parameters; (iv) length distributions; and (v) mark and recapture data. The advent of genetic data allows the information about the degree of connectivity between stocks to be considered. Information on rates of exchange among presumed management units allows estimation of the amount of time required for an extirpated management unit to recover and 'recolonise' its former range. Taylor (1997) illustrated cases of metapopulation dynamics important to management. For example, if a defined management unit was incorrectly assumed to be part of a larger population, its exploitation could result in its depletion and extirpation, with time to recovery difficult to estimate without some measure of dispersal of new individuals from some other source. Alternatively, if the proposed management unit was linked to a larger population, the management unit and its removals could be sustained owing to emigration and genetic exchange from the parent population, provided that dispersal rates were adequate to compensate for removals. Thus, management units must be defined by evaluating similarities and/or differences in demographic aspects of a population; the evaluation should include rates and degree of mixing and genetic exchange within and among adjacent populations (Taylor & Dizon, 1999). There are several tools that can be used to help delineate management units. The most powerful tool is genetics because of its ability to quantify similarities or differences between whales and provide a timescale for potential divergence. Other tools include morphology, chemical signatures, carbon isotope ratios, parasites, contaminants, photographic identification and trends in abundance, as described below.

Genetics

Molecular genetic methods have proven useful in clarifying the relationships between members of controversial taxa (e.g. Hillis & Moritz, 1990). Although the application of genetic techniques to the study of gray whale populations is ongoing, differentiation between eastern and western gray whales has been found (LeDuc *et al.*, 2002; Lang *et al.*, 2005; detailed below). Genetic analysis of structure within the eastern population has also been conducted (Ramakrsihman & Taylor, 2000; Steeves *et al.*, 2001; Goerlitz *et al.*, 2003).

LeDuc *et al.* (2002) used samples from eastern ($n = 120$) and western ($n = 45$) gray whales to document genetic differentiation on the basis of *mt*DNA haplotype diversities. Recent analyses used both *mt*DNA sequences and alleles from six microsatellite loci amplified from eastern ($n = 126$) and western ($n = 108$) populations of gray whales; the results supported previous studies and indicated that the populations are significantly different from each other (Fst = 0.062, $P \leq 0.001$, *mt*DNA data; Fst = 0.005, $P = 0.009$, microsatellite data) (Lang *et al.*, 2005). Differentiation in *mt*DNA sequences was due to differences in haplotypic diversity (0.95 in the east and 0.77 in the west) and in differences in the relative frequencies of haplotypes within each population. Of the 33 haplotypes present in the eastern sample set, the two most common were found in 10.3% and 9.5% of sampled individuals, illustrating the fairly even distribution of haplotypes. On the other hand, the two most common haplotypes (out of 20) in the western sample set were found in 36% and 33% of sampled animals, while 15 haplotypes were found in only one or two individuals. The high haplotypic diversity found in the eastern population indicates that there was a minimal loss of genetic diversity resulting from the historical reduction in population numbers. In contrast, the relatively low haplotypic diversity of the western population may be the result of a recent population bottleneck or of a small population size being maintained over long timescales. The high number ($n = 20$) of haplotypes found in the western population is surprising given what is known of the population's size and history. For comparison, the critically endangered North Atlantic right whale population contains only five extant haplotypes (Malik *et al.*, 2000) among an estimated 300 animals (Knowlton, Kraus, & Kenney, 1994).

Genetic analysis using nuclear DNA illustrated a relatively high level of microsatellite diversity (He = 0.724) in the western population; this diversity was lower but comparable to that found in the eastern population (He = 0.759) (Lang *et al.*, 2005). Although the results from the study by Lang *et al.* (2005) supported genetic isolation between the two populations, higher levels of differentiation were documented when only the females of each population were compared (Fst = 0.016, $P \leq 0.001$), and estimates of microsatellite differentiation were not significant when only the males were compared (Fst ≤ 0.001, $P = 0.423$).

Structure within the eastern population's southern feeding grounds has been examined using mtDNA. These studies found no evidence of matrilineal fidelity to the Clayoquot Sound, British Columbia southern feeding area among animals believed to constitute the 'Pacific Coast Feeding Aggregation'. Photo-identification records indicate long-term fidelity of whale to the area (Hatler & Darling, 1974; Darling, 1984), raising the possibility that the southern feeding group represents a learned cultural behaviour, similar to that seen for the feeding grounds of North Atlantic humpbacks, where knowledge of preferred feeding grounds is believed to be passed down from mother to offspring as evidenced in differences in their mtDNA (Smith *et al.*, 1999). However, significant differences in mitochondrial haplotyopes between whales in the Pacific Coast Feeding Aggregation and the general population were not found (Steeves *et al.*, 2001), indicating that either the southern feeding group has not been extant long enough to differentiate genetically, or that the gray whales are more flexible than humpbacks with regard to their learned behaviour (i.e. matrilineal fidelity is less strict).

Future studies may be able to better characterize the genetic composition of the whales in the southern feeding area by increasing sampling across the range. Recaptures in the photographic identification studies have shown a mixing across a large area. Simulation studies have suggested that even a recent colonization of the southern feeding areas along the Pacific North-west coast and elsewhere could be detected by genetic testing given sufficient sample sizes (Ramakrsihman & Taylor, 2000).

Analysis of *mt*DNA has also been used to explore matrilineal fidelity of eastern gray whales to wintering lagoons in Baja California (Goerlitz *et al.*, 2003). Weak but non-significant genetic differences were found between calving females in Laguna San Ignacio and in Laguna Ojo de Liebre, suggesting some level of natal philopatry to wintering lagoons. Differences in haplotype frequencies between calving females within and outside lagoons, as well as between single females and females with calves within each respective lagoon, were used to suggest that fidelity to lagoons might also be influenced by reproductive status (Goerlitz *et al.*, 2003). While natal fidelity of calving females to lagoons indicates that some substructuring of the eastern population occurs on the wintering grounds, this substructure may not be affecting gene flow, given that the majority of females are thought to conceive early in the migration (Rice & Wolman, 1971).

Morphology

There have been few comparative studies of the morphology and/or morphometrics of gray whales. Rice (1998) summarized several studies that found no clear differences in skeletons of gray whales from the Atlantic Ocean and from the western and eastern Pacific populations. Rice & Wolman (1971) examined 316 gray whales collected from the eastern population during migration past central California. Zimushko (1972 in Yablokov & Bogoslovskaya, 1984) compared data collected by Andrews (1914) on the external morphology of western and eastern gray whale populations and suggested that differences were sufficient to indicate the populations were distinct. Andrews (1914) examined 145 western gray whales caught at a whaling station in Ulsan, South Korea. He made detailed descriptions of gray whale morphology and collected two complete skeletons. Zimushko (1972) reported that the distance from the tip of the rostrum to the base of the pectoral flippers, from the tip of the rostrum to the eye, the maximum width of the pectoral flipper, and the length of the baleen plates were statistically greater in the western gray whales, and that western gray whales had fewer baleen plates and fewer throat grooves. Unfortunately, the details of these analyses were never published. There have been no additional published comparisons on the morphology of gray whales relevant to an analysis of population and stock structure.

Chemical signatures

Analysis of chemical signatures (e.g. heavy metals and organochlorines) as ecological tracers could also distinguish differences between populations or stocks of gray whales. Other animals that use inland Asian waters (e.g. North Pacific minke whales) have highly distinctive chemical signatures, characteristics which have been used to distinguish stocks within the same species (Fujise *et al.*, 2000; Nakata *et al.*, 2000). Tilbury *et al.* (2002) examined chemical contaminants from samples of gray whales killed by subsistence hunters in Russia and samples from gray whales stranded along the west coast of the USA during the northbound migration. These authors found that polychlorinated biphenyl (PCB) concentrations in whales killed in Russia were significantly lower than in stranded whales. This type of analysis of contaminant signatures could be used to discriminate small aggregations of whales that feed in a limited area with a persistent pollution feature. If there was no mixing of gray whales in the general population, then a chemical signature could theoretically identify a group of whales.

Carbon isotope ratios

Reliance on prey species unique to specific geographical locations could be detected by examination of carbon isotope ratio signatures found in hard tissues (e.g. baleen) compared with those found in prey species and, by proxy, the phytoplankton supporting the prey species found in specific locations over many years. Schell & Saupe (1993) and Schell (1998) examined the isotopic record in baleen plates from Western Arctic bowhead whales and constructed a prey-location specific feeding record that extends from 1947 to 1995. A similar study conducted on gray whale samples from catches and stranded animals throughout their range could provide indications of the prevalent use of prey from certain areas and the significance of annual feeding at those areas and, by inference, the potential for a subunit of the population representing a genetically distinct stock.

Parasites

Gray whales are heavily infested with ectoparasites and epizoites including a host specific barnacle *Cryptolepas rhachianecti* and three species of whale louse *Cyamus scammoni*, *C. ceti* and *C. kessler*, but gray whales have few endoparasites (Rice & Wolman, 1971). It seems that ectoparasites take advantage of the gray whales' habit of swimming slowly through shallow coastal waters rich in nutrients, but endoparsite concentrations are low because of the whales' long period of fasting each year. Although parasites can be used theoretically to recognize groups of whales that do not interact with the general population, there have been no comparative studies of gray whale parasites that could have bearing on stock structure.

Photographic identification

Photographic identification data indicate high levels of annual return and pronounced seasonal site fidelity for most whales identified on the western feeding ground (Weller *et al.*, 1999, 2002). Photographic identification has also been used to evaluate abundance, range and movements of gray whales in the Pacific North-west (Darling, 1984; Calambokidis *et al.*, 2002) and in the lagoons of Baja California (Jones & Swartz, 1984; Urban *et al.*, 2003). A recent effort to locate and combine historical photographic data sets with more recent photographs of eastern gray whales has resulted in the creation of a database that includes over 5000 images of individually recognizable whales photographed in the lagoons from 1960s to 2005 (S. Swartz, unpublished data). Analyses of these photographs along with future contributions to the database may yield additional information on the fidelity of individual whales to specific lagoons and possibly provide insight concerning the potential for stock structure within the eastern gray whale population.

Trends in abundance

The strongest evidence that the eastern and western gray whale populations are segregated is the lack of growth in the western population through a period in which the eastern population has made an excellent recovery. If there was a dispersal of individuals from east to west, the western population would likely have been repopulated by now, unless any immigration was offset by a currently unknown source of mortality. Mizue (1951, p. 72) points out that the take and subsequent decline of gray whales in the east sea area of Korea 'indicate[s] that the stock of gray whales in our adjacent waters was but a small one existing, as it were, independently, having no intercourse with the stocks of other waters'.

DISCUSSION

Gray whales have experienced major changes in their distribution with the periodic closure of the Bering Sea during the Pleistocene ice ages, and ice-driven contact between eastern and western populations could have occurred as recently as 400 years ago (Overpeck *et al.*, 1997). These Arctic cold periods are relatively recent events in the evolution of cetaceans, and we should expect to see the evidence of such history in the genetic composition of North Pacific gray whales today. The dramatic declines in abundance of gray whales brought about by commercial whaling occurred on such a recent timescale that fixed or nearly fixed genetic differences – criteria often used to signify evolutionary significance – would not be expected. However, differences in gene frequencies – i.e. criteria used as evidence for population structure meaningful to management – are likely to have developed on these timescales (LeDuc *et al.*, 2002). Such differences were observed in a preliminary analysis of mtDNA and microsatellites from two bowhead whale populations (i.e. Bering-Chukchi-Beaufort and Okhotsk) that were greatly reduced in numbers by whaling. There were small but significant differences in their respective gene pools, suggesting that postglaciation separation has been sufficiently long for genetic differentiation to develop between these two allopatric populations (LeDuc *et al.*, 1998). Analyses of genetic samples from both Pacific gray whale populations did indicate that the populations are significantly different from each other (LeDuc *et al.*, 2002; Lang *et al.*, 2005). The apparent genetic differences, different coastal migratory corridors, feeding and breeding areas, and the recovery of the eastern but not the western population are evidence of allopatry and cause for concern. The available data strongly indicate that western gray whales represent a population geographically isolated from eastern gray whales and that the two populations should continue to be managed separately.

For western gray whales, there are not sufficient data to assess the plausibility of stock structure within the population, owing to its extremely depleted state. Despite there having been a great deal of research on eastern gray whales, most of that effort has gone to documenting changes in abundance, feeding biology and behaviour. Nevertheless, enough is known about breeding behaviour and biology for separate breeding groups to be unlikely. If, as it appears, both males and females are promiscuous breeders (Swartz, 1986), then there is little opportunity for the nuclear genome to be anything other than well mixed, as is indirectly suggested by the high haplotypic diversity of the eastern population (LeDuc *et al.*, 2002).

Relatively little is known about how individuals choose feeding grounds throughout their lives. Photographic data from the Pacific Coast Feeding Aggregation indicate that some individuals show site fidelity over periods of at least years while others at least appear regularly in the same areas at particular times (Calambokidis *et al.*, 2002). Data from Russian hunts show segregation by age and sex on the high-latitude northern feeding grounds (Reeves, 1984), which is also seen during migration (Rice & Wolman, 1971) and within the wintering areas (Jones & Swartz, 1984). However, the available data are from only the small portion of the whales' range where the catches occur, relative to the entire known summer feeding grounds utilized by gray whales. A better understanding of site fidelity and potential stock structure will be gained through continuation and expansion of photographic identification and satellite tagging research on the feeding grounds coupled with comparisons of genetic and pollutant/chemical samples from animals in these areas.

In conclusion, it is unequivocal that the western and eastern populations of gray whales should be treated as separate management units, and there is a strong case for treating all gray whales within each of these populations as belonging to a single unit. Although there are repeated concentrations of whales in some areas, as described for the Pacific Coast

Feeding Aggregation and the tendency of some whales to reuse certain lagoons in Baja California, there is also evidence that there is mixing within each of the respective general populations. However, it would be prudent to closely monitor small, localized feeding groups, and management should be adapted to detect and avoid adverse population changes that would result from excess mortalities in any specific habitat.

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Abundance estimates for western North Pacific gray whales for use with stock structure hypotheses of the Range-wide Review of the Population Structure and Status of North Pacific gray whales

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INTERNATIONAL
WHALING COMMISSION

SC/67b/ASI

Abundance estimates for western North Pacific gray whales for use with stock structure hypotheses of the Range-wide Review of the Population Structure and Status of North Pacific gray whales

Justin G. Cooke[1]

ABSTRACT

Abundance estimates are derived for western North Pacific gray whales *Eschrichtius robustus* that correspond to the various stock structure hypotheses developed by the IWC Scientific Committee's Range-wide Review of the Population Structure and Status of North Pacific gray whales (IWC 2018a), by fitting an individually-based population model to photo-id data and other data collected off Sakhalin, Kamchatka and Mexico. Abundance estimates are presented for the putative Western Feeding Group and Western Breeding Stock in 1995 and 2015. Abundance estimates for the Western Feeding Group in 2015 range from about 130 to about 300 whales (aged 1 yr and over) depending on stock structure hypothesis, while abundance estimates for the putative Western Breeding Stock are all less than 100.

1 INTRODUCTION

This paper presents abundance estimates for gray whales in the western North Pacific that correspond to the various stock structure hypotheses developed by the IWC Rangewide Workshops on North Pacific Gray Whales (IWC 2018a). Estimates corresponding to some further plausible stock structure hypotheses are also presented.

To derive the esitmates, an individually-based model is fitted to photo-id data collected during 1995-2016 from Sakhalin Island and Kamchatka Peninsula (Burdin et al. 2017; Yakovlev et al. 2013, 2017), supplemented with sex determinations from biopsies (Lang 2010), photographic matches with wintering grounds in Mexico during 2006-12 (Urbán *et al.* 2012; 2013), and satellite tracking of some tagged individuals from Sakhalin towards their wintering grounds (Mate et al. 2015).

The generic individually-based population model structure and the method of fitting to data is specified in Appendix I. The specific implementation choices used for western North Pacific gray whales are described in the Methods section.

2 METHODS

2.1 Stock structure hypotheses

The stock structure hypotheses developed by the 4th IWC Rangewide Workshop on North Pacific Gray Whales (IWC 2018a) which were still under consideration for consideration after the 5th Workshop (IWC 2018b) are hypotheses 3a, 3b, 3c, 3e, 5a, 6b listed in Table 6 (JCRM 19(Suppl.):528).

The hypotheses posit the existence of up to two breeding stocks: an eastern breeding stock (EBS) which winters off Mexico, and possibly a western breeding stock (WBS) which winters at one or more locations in Asian waters. The hypotheses also posit the existence within the eastern breeding stock of a western feeding group (WFG) which visits Sakhalin and Kamchatka in summer, and a northern feeding group (NFG) which feeds in the Bering and Chuckchi Seas and possibly also off SE Kamchatka.

Of these, hypotheses 3a, 3c, 3e posit only a single breeding stock, and are mutually indistinguishable with respect to the data collected on western North Pacific gray whales.

Hypothesis 6b posits a western breeding stock (WBS) but it only occurs in areas for which no data are available, and is therefore effectively invisible with respect to the available datasets. With regard to observed whales in the western North Pacific, 6b is indistinguishable from the hypotheses with just one breeding stock (3a/3c/3e).

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In order to implement the hypotheses, whales occurring off Sakhalin and Kamchatka were divided into four subgroups, whose numbers are to be estimated from the data:

Table 1. feeding subgroups defined for the purpose of implementing stock structure hypotheses

Subgroup	Description
S	Whales that visit Sakhalin but not Kamchatka
SK	Whales that visit Sakhalin and occasionally Kamchatka
KS	Whales that visit Kamchatka and occasionally Sakhalin
K	Whales that visit Kamchatka but not Sakhalin

The hypotheses and their definitions are listed in Table 2. In all the hypotheses considered by IWC (2018), whales seen off Sakhalin include WFG whales and possibly also WBS whales. Whales seen of SE Kamchatka include WFG whales and possibly also WBS and NFG whales. The hypotheses considered by IWC (2018) do not allow for the possibility that all whales seen off Kamchatka belong to the WFG. In view of the lack of evidence that any Kamchatka whales belong to the NFG, two further hypotheses were added (8 and 9) in which there are no NFG whales off Kamchatka.

Table 2. Definitions of stock structure hypotheses in terms of affiliations of feeding subgroups

Hypothesis	Description	WBS	WFG	NFG
3a/3c/3e	One breeding stock, some NFG in K		S, SK, KS	K
3b	Two breeding stocks, WBS in K	K	S, SK, KS	
5a	Two breeding stocks, some NFG in K	S, SK	S, SK, KS	K
8	One breeding stock, no NFG in K		S, SK, KS, K	
9	Two breeding stocks, no NFG in K	S, SK	S, SK, KS, K	

In each case, the initial population sizes of each feeding subgroup/breeding stock combination were modelled using a log-linear model with one intercept parameter with a uniform prior, plus a random effect term for the feeding subgroup/breeding stock combination.

2.2 Data

2.2.1 Photo.identification

Sampling with photo-identification was conducted in the summer feeding grounds off NE Sakhalin during 1995-2016 and off SE Kamchatka during 2004-12. There were two research teams working off Sakhalin and one off Kamchatka. Off Sakhalin, the Russian Gray Whale Project (RGWP, Pacific Geography Institute, Petropavlovsk, Kamchatka; a continuation of the former Russia-US project) has been collecting data since 1995 ((Burdin et al. 2017), and the Marine Biology National Research Center , (MBNRC, Vladivostok; formerly Institute of Marine Biology, IBM) has been collecting data since 2002 and cross-matched the results with photos from Kamchatka (Yakovlev et al. 2013, 2017).

A total of 287 distinct whales had been identified through the 2011 season, based on cross-matching of the individuals observed by each team. During 2012-2016, a further 56 whales were seen by the RGWP team and 73 whales by the MBNRC and Kamchatka teams, which have not been cross-matched.

Sampling also occurred in the wintering grounds off Baja California, Mexico. Because theses grounds are shared with the more numerous eastern North Pacific gray whales, only individuals matched with the western North Pacific were included in the analysis. Cross-matching was conducted between whales identified in Mexico during 2006-12 and all whales in the Sakhalin and Kamchatka catalogues up to 2011 (Urbán et al. 2012, 2013).

Because the matching rate in Mexico appeared to be strongly age-specific, only animals known to be at east 6yr old were considered as potentially samplable in Mexico, and only matches from those animals were used, for the reasons explained by Cooke (2016). Of 17 whales matched between Sakhalin and Mexico, 16 met this criterion. Of a further 4 whales matched between Kamchatka and Mexico, 2 met this criterion.

2.2.2 Additional features recorded

The additional features recorded for at least some identified animals were: sex; mother/calf status; breeding stock affiliation.

Sex. Sex was determined by biopsy for a total of 167 whales, including 156 by the RGWP project, 23 by the MBNRC project, and 12 by both projects. Of the 12 individuals sexed by both projects, 11 agreed with respect to sex. The one whale without agreement was deemed to be female, because it had been biopsied as female by the RGWP project on four separate occasions. Sex determination is assumed for modelling purposes to be 100% accurate.

Cow/calf status. Of 3,602 encounters of living whales off Sakhalin and Kamchatka (where "encounter" means an individual identified at least once by a team in a season) 205 were of cow-calf pairs and 71 were unaccompanied calves. It is assumed that all cow-calf pairs and accompanied calves were correctly identified by the RGWP team from 1995 and by the MBNRC team from 2003. The mother/calf status was not recorded by the MBNRC team in 2002. It is assumed that all unaccompanied calves were correctly identified by the RGWP team from 1995 and by the MBNRC team from 2007, which used the same criteria from this date. For the years 2003-06, MBNRC unaccompanied calf identifications were not used (they were treated as indistinguishable from other whales).

Of the 23 matching identifications from Mexico that were used in this analysis, 8 were of cows accompanied by calves, but the calf identifications were not available for this analysis.

Breeding stock affiliation

Three individuals sighted off Sakhalin were successfully tagged and tracked to the eastern North Pacific (Mace et al. 2015). It is assumed that the successful long-term tracking of an individual reveals its breeding stock affiliation (eastern or western). Individuals sighted in Mexico are also assumed to belong to the Eastern Breeding Stock (EBS).

2.3 Population model

The structure of the generic population model structure and the method of fitting to data is specified in the Appendix. The specific implementation choices used for western North Pacific gray whales are described here.

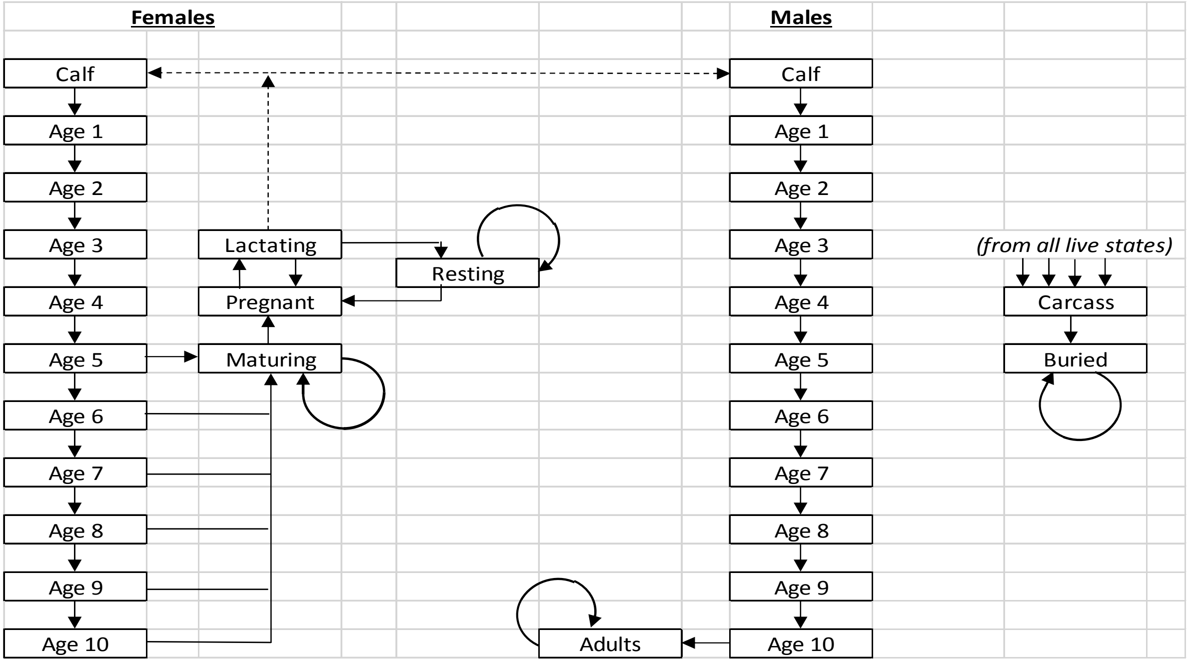
2.3.1 State space

The following attributes are represented in the state space:

- Life stage (sex, age and reproductive status, mortality status)
- Feeding subgroup affiliation
- Breeding stock affiliation
- Sampling availability (reflection of individual heterogeneity in capture probability)

The life stages and the possible transitions are shown in Table 3. Animals in any of these stages can die by entering a "carcass" state, where they have a (typically small) probability of being recovered and identified. From the following year they are assumed to be unobservable ("buried").

Table 3. List of living stages in the gray whale model



The youngest allowed age for a pregnant whale is 7 years and the youngest age for a lactating whale is 8 years. In the summer season, the "Age *x*" stage contains animals aged approximately x + ½ .

Feeding group and breeding stock affiliations are assumed to be maternally inherited and to remain constant throughout life.

Individual heterogeneity in availability was modelled using 1,3 or 5 availability classes. Each whale is born into a random class with equal probability. The individual availability class is assumed to be retained throughout life but not to be heritable. The purpose of including these classes is to reduce the bias in abundance estimation arising from capture probability heterogeneity.

2.3.2 Reproduction, mortality and other transitions

Each animal in the lactating stage has exactly one calf, assumed to be male or female with equal probability.

The calf mortality is modelled as a constant plus an optional annual random effect. The non-calf mortality rate is assumed to be constant.

The transition probability to the maturing class is assumed to be constant. The transition probability to the pregnant stage depends on the source stage (maturing, lactating or resting) plus an optional annual random effect.

2.4 Sampling model

2.4.1 Primary and secondary sampling occasions

The sampling in a season by a research team is treated as sampling occasion. Up to and including the 2011 season, each season of sampling by each team off Sakhalin and Kamchatka is treated as a primary sampling occasion (see Appendix section 2.1 for the definition). From 2012, two options were considered: (i) RGWAP team as primary team throughout, MBNEC and Kamchatka teams secondary from 2012; (ii) MBNRC and Kamchatka teams are primary throughout, RGWAP secondary from 2012.

Individuals sighted up to 2011 by a non-primary team only were treated as "identity lost" (see Appendix section 2.4) from 2012 onwards, because they might, unknown to the analysis, match whales seen by the primary team for the first time in 2012 or later. Sampling occasions in Mexico during 2006-12 are treated as secondary, because only whales matched with Sakhalin or Kamchatka were used.

2.4.2 Capture probability models

The capture probability model for the summer sampling includes a free parameter for each sampling occasion (team by year), and a parameter for each combination of feeding subgroup and location, where "location" means Sakhalin or Kamchatka. That is, each feeding subgroup may be differentially catchable in each location.

The summer capture probability model also contains optional random-effect terms for life stage, life stage × team interaction, and availability class. The life stages for this purposes were summarized into five stages: calves, subadults, lactating mothers, other mature females, and mature males.

The capture probability for the Mexican wintering grounds was estimated externally of this model, because the great majority of the animals there are eastern North Pacific gray whales. The average annual capture probability was estimated to be 0.054 (Cooke 2016).

Because only three identified carcasses were observed, a single value for the capture probability of carcasses was estimated. Unidentified carcasses were not used: each year, the observation of carcasses is treated as a secondary sampling occasion.

2.4.3 Additional features recorded

The additional features enter the likelihood through the Q factor in expression (A.13).

Sex is treated as a deterministically observed feature ($Q = 0$ or 1). Any gender bias present in the sampling of individuals is modelled through the capture probability model, which allows for sex-biased sampling.

The probability ($0 < Q < 1$) that a calf of the year was still with its mother when first sampled by a team in a season was modelled as a team-specific parameter, because the MBNRC team tended to observe the animals later in the season than the RGWP team, after more calves had been weaned.

Identifications of calves were assumed to be deterministic ($Q = 0$ or 1) in all years in which they were used (see above).

Individuals sighted in Mexico are automatically assigned belong to the eastern breeding stock (EBS), in the sense that the probability of sighting an animal from the western breeding stock (WBS) in Mexico is assumed to be zero ($Q = 0$).

Three individuals were successfully tagged and tracked to the eastern North Pacific were likewise assigned to EBS. It is assumed that, conditional on the location where they were originally sampled and tagged (in this case, Sakhalin) the probability of successfully tagging and tracking a sampled animal is independent of their breeding stock affiliation (that is, had the individuals been western breeding stock animals, this would have been verified).

2.5 Model selection

Model selection for the purpose of determining which nuisance covariates need to be included was performed with the AIC criterion applied to the large population approximation to the parameter likelihood (see Appendix, section 2.6.2). For this purpose, stock structure hypothesis 3a was used.

3 RESULTS

3.1 Model selection

The results of fitting various models are listed in Table 4 with the AIC criterion from the approximate parameter likelihood. The preferred model (F) includes the following factors: annual variability in calf survival and pregnancy rate; capture probability depends on: team/year interaction, stage effect and team/stage interaction, subgroup/location interaction and availability class (3 levels). Increasing the number of availability classes to 5 increased the AIC.

Fig 1 shows a comparison of the mean population trajectory using (a) the RGWP data; (b) the MBNRC data as the primary data set for the years 2012-16 (when no cross-matching was conducted). The difference in trajectories is seen to be negligible, and the RGWP data were treated as the primary data set for all other model fits.

3.2 Abundance and trends

Population trajectories for the aged 1+ population size for the WFG, the WBS and their sum, were extracted from the posterior distributions of the individual-based population trajectories for each stock structure hypothesis. The estimates of abundance for 1995 and 2015, and of the annual trend, are shown in Table 5. The reason for selecting years near the beginning and end of the data series is that the estimates for the two years have low covariance and together summarize the fitted population trajectories well. The mean abundance estimates for the western feeding group (WFG) in 2015 range from 132 to 287 depending on the stock structure hypothesis. The estimates for the western breeding stock (WBS) are all below 100. The estimate annual rate of increase from 1995-2015 is about 0.05 in all cases. Figs 2a-e show samples of population trajectories from the posterior distributions for each hypothesis.

Table 4. Results of model selection

Case	LogLike	Rank	AIC	Calf mortality	Pregnancy	Capture probability
A	-3806.9	60.0	7733.7	Constant	Stage	Team.Year + Subgroup.Location
B	-3773.9	64.1	7676.1	Constant	Stage	Team.Year + Subgroup.Location + Stage
C	-3697.2	71.6	7537.7	Constant	Stage	Team.Year + Subgroup.Location + Stage + Stage.Team
D	-3653.9	73.3	7454.2	Constant	Stage	Team.Year + Subgroup.Location + Stage + Stage.Team + AvailabilityClass
E	-3640.2	83.1	7446.5	Constant	Stage + Annual	Team.Year + Subgroup.Location + Stage + Stage.Team + AvailabilityClass
F	-3635.5	87.7	7446.4	Annual	Stage + Annual	Team.Year + Subgroup.Location + Stage + Stage.Team + AvailabilityClass

Table 5. Estimates of abundances and trends by stock structure hypothesis

			Abundance estimates (aged 1+)		
Year	**Hypothesis**	**Group**	Mean	SD	CV
1995	3a	WFG	74	4	0.05
1995	3b	WBS	33	6	0.17
1995	3b	WFG	75	4	0.06
1995	5a	WBS	27	6	0.24
1995	5a	WFG	47	7	0.16
1995	5a	WFG+WBS	74	4	0.05
1995	8	WFG	106	8	0.07
1995	9	WBS	27	6	0.24
1995	9	WFG	78	10	0.12
1995	9	WFG+WBS	105	7	0.07
2015	3a	WFG	200	6	0.03
2015	3b	WBS	86	11	0.13
2015	3b	WFG	202	5	0.03
2015	5a	WBS	67	14	0.20
2015	5a	WFG	132	14	0.11
2015	5a	WFG+WBS	199	6	0.03
2015	8	WFG	287	12	0.04
2015	9	WBS	67	14	0.20
2015	9	WFG	218	19	0.09
2015	9	WFG+WBS	285	14	0.05

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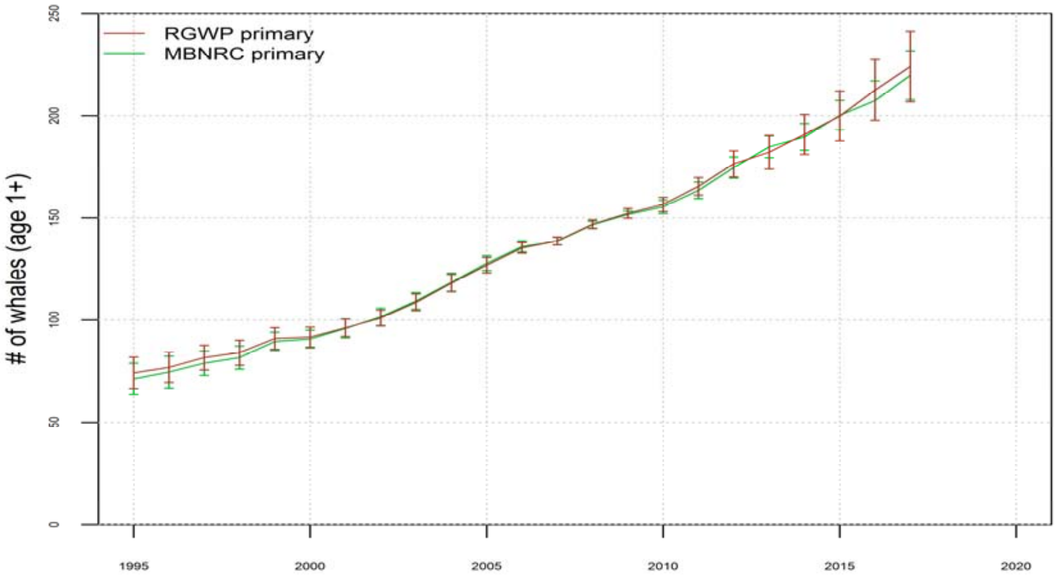

Fig. 1. Comparison of estimated population trajectories for Western feeding Group (WFG) for Hypothesis 3a using RGWP and MBNRC data sets as primary data sets during 2012-16.

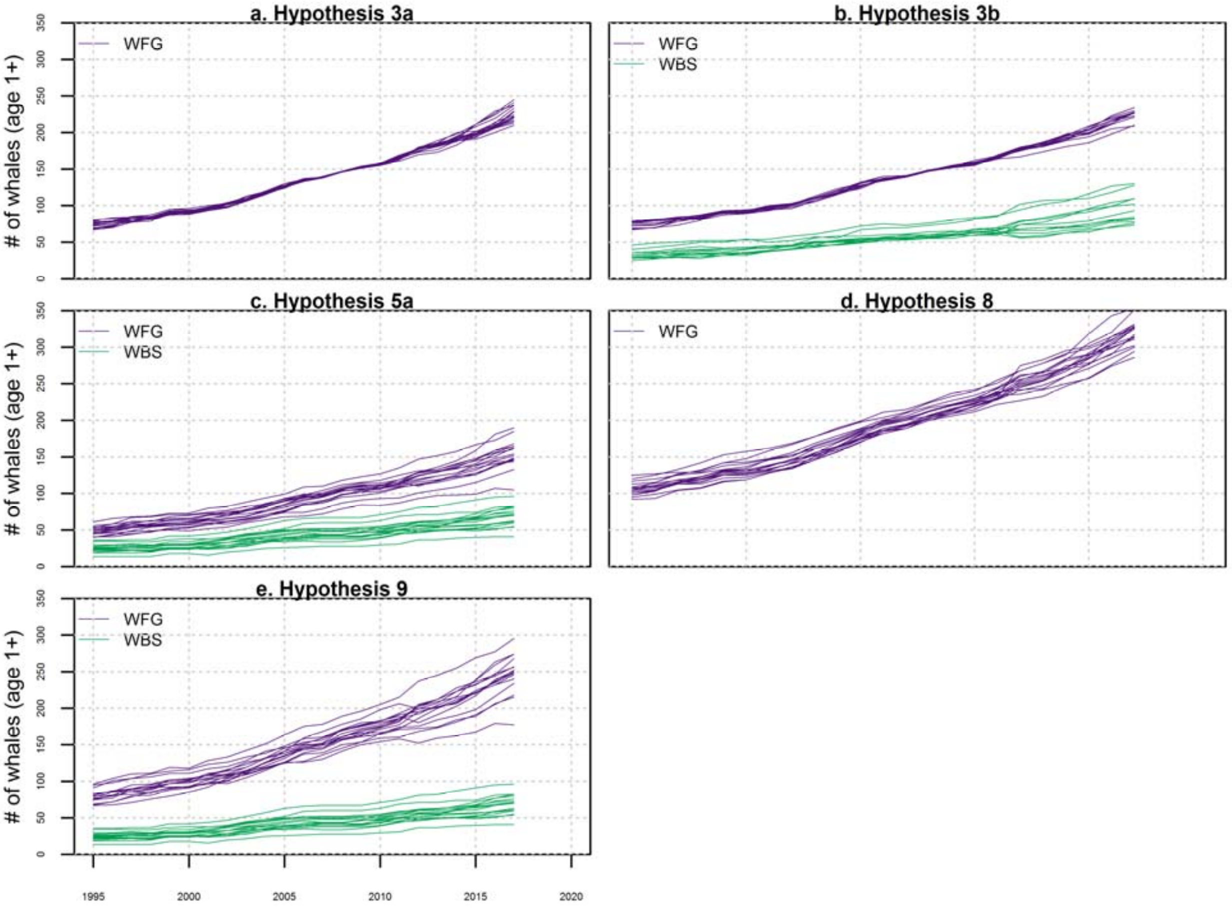

Fig. 2a-e. Posterior samples of population trajectories for WFG and WBS by stock structure hypothesis.

Appendix

Specification of the generic individually-based population model

This Appendix specifies the generic individually-based population model, applicable to any mammal population with seasonal breeding and litter size 1. The implementation choices for the specific application are noted in the main text. The generic model consists of a biological model and a sampling model.

1 BIOLOGICAL MODEL

1.1 State space representation

The biological model is a stochastic, individual-based model with a fixed time step, usually 1 year. At each time step, each individual is in one of n possible states. There are up to N individuals in total, where N is chosen large enough to accommodate any individual alive at any time during the era of interest, which runs from time $t = 0$ to $t_{\max}$.

Each row of the $N \times n$ matrix S represents an individual biography, where S_{it} is the state of individual i in year t ($i = 1, \ldots N$; $t = 0, \ldots, t_{\max}$). The matrix S as a whole represents the individual-based population trajectory.

If the state of an individual is characterized by r attributes, and the jth attribute can take n_j values, then the number of possible states is up to $\prod_{j=1}^{r} n_j$ but may be less if not all combinations of attribute levels are allowed.

The attributes reflected in the range of individual states include those that are relevant for the population dynamics (such as age, sex, health and reproductive status) and those that are relevant for the sampling process, such as migration habits, behavior etc. These two categories of attributes typically overlap. The attributes of an individual that define its state may or may not correspond to observable features of the individual. Some attributes remain fixed throughout life, such as sex, while others, such as reproductive status, may change each year.

The possible states of an individual include live states, dead states, and the unborn state (individuals which have not yet entered the population).

Because an unborn animal cannot be observed, only one unborn state need be recognized. All attributes of an individual, including inherited attributes, can, without loss of generality, be deemed to be acquired at birth or on entry into the population. The unborns include not only individuals which are literally unborn, but also immigrants prior to their immigration. All individuals count as unborn prior to $t = 0$.

Post-mortem states can be divided into one or more freshly dead “carcass” states where there is still some chance that the animal will be found and identified, and a terminal “buried” state where the animal has, for the purpose of the analysis, become permanently unobservable.

In order to limit the number of parameters to be estimated, individual variation in an attribute, such as migration behavior or reproductive output, is modelled by allowing individuals to belong to a fixed number of notional classes with respect to that attribute. The number of such classes is deemed sufficient when further subdivision has negligible effect on the results.

Some of the individuals will be individually identified at some point during the era of interest. Individuals which are identified at any time during the era of interest are termed “known”, while those which are never identified are termed “unknown”. At any given time t, individuals identified prior to that time are termed “identified” otherwise “unidentified”.

The value of N need not be fixed in advance. Only those individuals which are alive and/or identified at some time within the era of interest need be represented explicitly in the model. Unknown individuals remain mutually indistinguishable with respect to the model until they are born. Whenever an unknown individual is born or otherwise enters the population, it can be taken from a presumed unlimited source of unborn unknowns, and the value of N incremented by 1. Where a distinction is required, N denotes the number of individuals alive at some point during the era of interest, N^+ denotes the indefinitely large number of potential individuals, and N^- denotes the number of known individuals.

The description of the population trajectory is completed by defining a vector of parents π, such that π_i is the parent (mother) of individual *i*. By convention, π_i is set to 0 (parentage unspecified) for individuals which are already alive at time $t = 0$, or which enter the population other than by birth to a member of the population, such as by immigration.

1.2 Aggregate population trajectory

The aggregate population trajectory is given by the matrix *P* where P_{kt} is the number of individuals in state *k* in year *t*. The aggregate population trajectory is related to the individual-based population trajectory by:

$$P_{kt} = \sum_{i=1}^{N} I(S_{it} == k) \quad \text{(A.1)}$$

I is the indicator function (1 for true, 0 for false) according to the equality of its arguments.

To fit a population trajectory to individually-based data, such as photographic or genetic identification of individuals, the full individual-based trajectory is required. To fit to aggregate data, such as abundance and trends, where individuals are not distinguished, the aggregate trajectory is sufficient. Many different individual-based trajectories share the same aggregate trajectory.

1.3 Population aggregates

Arbitrary linear population aggregates are defined as required. The value of the *j*th population aggregate in year *t* is a weighted sum of individuals by state:

$$A_{jt} = \sum_k W_{jk} P_{kt} \quad \text{(A.2)}$$

where the weight matrix *W* defines the population aggregates. Population aggregates can serve as explanatory variables for density-dependent effects.

1.4 Dynamics

The dynamics of the population are determined by two (time-varying) matrices, the transition matrix *T* and the reproduction matrix *R*.

For $j > 0$, the transition matrix entry T_{jkt} is the probability that an individual in state *j* at time *t* transitions to state *k* at time t+1. Some of the entries of *T* are constants, while others depend on unknown parameters, whose values are to be estimated. Entries of *T* that correspond to inadmissible transitions, such as sex change, are zero.

For any given source state $j > 0$, the set of allowed direct destination states (the set of values of *k* for which the entries T_{jkt} are non-zero), is assumed to be time-invariant. Let n_j denote the number of possible destination states from source state *j*, and let the integer-valued matrix U_{jl} (j=1,…, n; l = 1, … n_j) denote the *l*th possible destination state from source state *j*. Let φ_{jlt} denote the transition probability from state *j* to state *Ujl* during time *t* to *t* +1, conditional on the individual not having transitioned to any of the states $U_{j,1}$, …, $U_{j,l\text{-}1}$. The ordering of the allowed destination states is significant and forms part of the model specification. By definition, $\varphi(j, n_j, t) = 1$, because there are no further allowed destination states remaining.

Transition probabilities that depend on unknown parameters are modelled with a logit-linear model:

$$\varphi_{jlt} = 1 / (1 + \exp(-\zeta_{jlt}) \quad (l = 1, \ldots, n_j - 1) \quad \text{(A.3)}$$

where the values of ζ are unconstrained (can take any values from -∞ to +∞) and are modelled as linear combinations of unknown parameters:

$$\zeta_{jlt} = \sum_k X_{jltk} \beta_k \quad \text{(A.4)}$$

where β is the vector of parameters where the entries of the data matrix *X* are either constants or values of population aggregates.

The entries $T_{0,k,t}$, where $k > 0$, have a special meaning. $T_{0,k,t}$ represents the expected total number of individuals to enter the population in state *k* at time *t*, for example through birth or immigration. For convenience in formulae, $T_{0,0,0}$ is set to 1.

For $j>0$ and $k > 0$, The reproduction matrix entry $R_{j,k,t}$ is the probability that a female in state j in year t bears a calf that is in state k. The entry $R_{j,0,t}$ is the probability that an animal in state j does not bear a calf in year t. Entries of R which depend on unknown parameters are modelled in a similar way to the entries of T.

The entry $R_{0,k,t}$ denotes the expected number of individuals that enter the population in state k at time t other than by birth to a member of the population, for example by immigration. Expected numbers of immigrants that depend on unknown parameters are modelled in the same way as the expected initial numbers by state.

From these definitions of T and R it follows that:

$$T_{0,k,t} = \sum_{i=0}^{N} R_{i,k,t} \tag{A.5}$$

1.5 Initial conditions

The initial conditions for the population are handled by taking the initial time sufficiently far before the era of interest that the results are insensitive to the choice of initial conditions.

Expected initial numbers that that depend on unknown parameters are modelled with a log-linear model:

$$T_{0,j,0} = R_{0,j,0} = \exp(\psi_j) \tag{A.6}$$

where the values of ψ are unconstrained (can take any values from $-\infty$ to $+\infty$) and are modelled as linear combinations of unknown parameters:

$$\psi_j = \sum_l Z_{jl}\beta_l \tag{A.7}$$

where β is the vector of parameters and the entries of the data matrix Z are constants.

2 SAMPLING MODEL

2.1 Sampling occasions

The sampling process involves a fixed number of sampling occasions. Each sampling occasion involves sampling individuals randomly, without replacement, with a probability that can depend on the state of the individual. Each sampling occasion is tied to a specific time step. Multiple sampling occasions associated with the same time step are treated for analysis purposes as occurring in a specified order, even if in reality they overlap in time.

Sampling occasions can be *primary* or *secondary*. All individuals encountered on a *primary* sampling occasion are eligible for use in the analysis, including individuals identified for the first time. Individuals encountered on a *secondary* sampling occasion are eligible only if they are previously identified. Secondary sampling occasions include, for example, samples taken in areas or at times where conspecifics of other populations (other than the populations of interest) are also present.

The matrix entry J_{ij} takes the value 1 if individual i is eligible for sampling on sampling occasion j, 0 otherwise.

2.2 Sampling probability

Let p_{jk} denote the probability that an eligible individual in state k is sampled on sampling occasion j. The entries p_{jk} typically depend on unknown parameters, whose values are to be estimated. Sampling probabilities that depend on unknown parameters are modelled using a complementary log-log-linear model:

$$p_{jk} = 1 - \exp\left(-\exp(\eta_{jk})\right) \tag{A.8}$$

where the values of η are unconstrained (can take any values from $-\infty$ to $+\infty$) and are modelled as linear combinations of unknown parameters:

$$\eta_{jk} = \sum_l D_{jkl}\beta_l \tag{A.9}$$

where the entries of the data matrix D are constants, usually 0 or 1.

2.3 Observed features

When an individual is sampled, features of the individual may be observed, depending on the nature of the sampling occasion. They are called *features* to distinguish them from the *attributes* defined in section 1.1. The observation of features is conditional on the sampling of the individual.

Some features may be observed deterministically. For example, with genetic capture-recapture, the gender may be determined with effectively 100% certainty once the genetic sample has been analyzed. Any gender bias that may exist in the chance of being sampled would be modelled through the sampling probabilities p.

The observation of some features may depend on probabilities. For example, if an animal is suckling a calf, the probability of seeing the calf when the animal is sampled may be appreciably less than 100%.

Let Q_{fjkl} denote the probability that feature f an individual in state k sampled on occasion j is observed to have level l. For each f, j, k we require $\sum_l Q_{fjkl} = 1$. For deterministically observed features, the corresponding entries of Q are 0 or 1. Where the probability Q depends on unknown parameters, a normalized log-linear model is used for Q:

$$Q_{fjkl} = \frac{\exp(\theta_{fjkl})}{\sum_l \exp(\theta_{fjkl})} \tag{A.10}$$

where the values θ_{fjkl} are unconstrained (can take any values from -∞ to +∞) and are modelled as linear combinations of unknown parameters:

$$\theta_{fjkl} = \sum_i G_{fjkli} \beta_i \tag{A.11}$$

where the entries of the data matrix G are constants, mostly 0 or 1. There is no explicit time-dependence in the entries of θ, but they may depend on sampling occasion and thereby on time.

2.4 Loss of identity

Loss of identity can occur if artificial or natural marks are lost. Effective loss of photographic or genetic identity can also occur if the study is continued by a new research group without the possibility for cross-matching with the previous records. Loss of identity of an individual is modelled by appearance of a new individual into the same state as the old individual ("cloning"), coupled with the simultaneous transition of the old individual into an unobservable "lost" state.

2.5 Data

The data consist of a list or catalogue of identified individuals and an associated sampling history of each individual. Associated with each occasion on which an individual was sampled is a list of observable features that were checked for that individual, and the recorded levels of each observed feature.

The meta-data include a list of sampling occasions and any relevant properties of those occasions, such as the time or the primary/secondary attribute, and the number and nature of observable features that were checked (for at least some sampled individuals) on that sampling occasion. Let $\mathcal{T}_j$ denote the time of sampling occasion j, and m_j denote the maximum number of observable features checked on that occasion.

The sampling histories form a matrix Y where Y_{ij} is 0 or 1 according to whether individual i was sampled on occasion j. The entries in the array K_{ijf} are 0 or 1 according to whether feature f was checked for individual i on sampling occasion j. The matrix L_{ijf} specifies the observed level of feature f for individual i on sampling occasion j, when that feature is checked, otherwise 0.

2.6 Likelihood

We distinguish between the trajectory likelihood and the parameter likelihood. The trajectory likelihood is the likelihood of a single individually-based population trajectory. The parameter likelihood is the sum of the likelihoods all possible trajectories given those parameters.

2.6.1 Trajectory likelihood

The trajectory likelihood is the product of the simulation likelihood and the data likelihood. The simulation likelihood is given by:

$$\Lambda_S = \exp\left(-\sum_{t=0}^{t_{\max}} \sum_{j=1}^{n} R_{0,j,t} \right) \prod_{i=1}^{N} \left(\frac{R(S_{\pi_i,\tau_i},\, S_{i,\tau_i},\, \tau_i)}{R(S_{\pi_i,\tau_i},\, 0,\, \tau_i)} \prod_{t=\tau_i}^{t_{\max}-1} R(S_{i,t},\, 0,\, t)\; T(S_{i,t}, S_{i,t+1},\, t) \right) \tag{A.12}$$

where τ_i is the year of birth or entry into the population of individual i,

The first factor accounts for the fact that N includes only individuals born or alive during the era of interest. The first sub-factor of the second factor ensures that the birth probability of each individual is included only once, even though it is an event in the life both of the parent and of the child.

The probability of the data collected on individual i at time t, given the state k of the individual at that time is given by:

$$\phi_{ikt} = \prod_{j:\, \mathcal{T}_j = t} p_{jk}^{\,J_{ij} Y_{ij}} (1 - p_{jk})^{J_{ij}(1-Y_{ij})} \prod_{f=1}^{m_j} Q(f, j, k, L_{ijf})^{J_{ij} K_{ijf} Y_{ij}} \tag{A.13}$$

where the first product sign is over the sampling occasions that occur in time step t. The first factor contains the probabilities that individuals are seen (captured) or not seen on each sampling occasion, while the second factor contains the probabilities that various features are observed on the occasions on which an individual is seen.

The data likelihood is then given by:

$$\Lambda_D = \prod_{i=1}^{N} \prod_{t=0}^{t_{\max}} \phi(i, S_{i,t}, t) \tag{A.14}$$

The trajectory likelihood is then given by: $\Lambda_T = \Lambda_S \bullet \Lambda_D$.

2.6.2 Parameter likelihood – large population approximation

The exact computation of the parameter likelihood as the integral of the trajectory likelihoods for the given parameter values is seemingly intractable. The model describes a hidden Markov process, which can, in principle, be solved by applying the forward-backward algorithm to the probability distribution over states (Eddy1996). However, the size of the population state space is approximately n^N, which is too large for computation of the probability distribution over states to be feasible.

An approximation to the parameter likelihood is obtained by computing the probability distribution over states separately by individual, on the assumption that population aggregates that affect the trajectory of an individual can be treated as independent of the state of the individual (the large population approximation). Population aggregates that affect an individual include, for example: (i) the breeding population, which drives the probability that an individual will be born in a given year; and (ii) the feeding population, which may have a density-dependent effect on the survival or reproduction probability of an individual.

Using the large population approximation, the probability distribution of the population state can be approximated by an independent distribution of each of N individuals over n states. This reduces the effective dimension of the state space from n^N to $n \times N$.

We take the notional individual $i = 0$ to represent unknown individuals, so that:

$$\phi_{0,j,t} = \prod_{l:\, \mathcal{T}_l = t} (1 - p_{lj}) \tag{A.15}$$

We define the array Φ_{ijt} recursively as follows:

$$\Phi_{i,j,0} = T_{0,j,0} \quad (0 \le i \le N^- \, ; \, 0 \le j \le n)$$

$$\Phi_{i,j,t+1} = \sum_{k=0}^{n} \Phi_{i,k,t} \, \phi_{i,k,t} \, T_{k,j,t} \quad (0 \le t < t_{\max}) \tag{A.16}$$

The probability of the observed data for a known individual *i*, summed over all possible trajectories consistent with those data is then given by:

$$\Psi_i = \sum_{j=1}^{n} \Phi_{i,j,t_{\max}} \tag{A.17}$$

assuming that no data are available for time $t = t_{\max}$.

The approximate log-likelihood for all individuals is then obtained by summing the individual log-likelihoods, treating them as independent:

$$\log\left(\Lambda_P\right) = \sum_{i=1}^{N^-} \log \Psi_i - E(N^-) \tag{A.18}$$

where the final term is the expected number of known individuals. It accounts for the large potential number of unknown individuals, each of which has a vanishingly small probability of being born and identified (Poisson limit of the binomial). The final term can be computed by:

$$E(N^-) = E(N) - \sum_{j=1}^{n} \Phi_{0,j,t_{\max}} \tag{A.19}$$

where:

$$E(N) = \sum_{j=1}^{n} \sum_{t=0}^{t_{\max}} T_{0,j,t} \tag{A.20}$$

2.7 Priors

Where probabilities are modelled using generalized linear models, each term in the model is an intercept term or a random effect term.

The prior for each parameter associated with an intercept term is chosen such that the prior for the corresponding probability would be uniform on [0,1] if the model only included that intercept term. Thus, the prior for an intercept parameter in the transition probability model (A.3) is $\exp(\zeta) \Big/ \left(1 + \exp(\zeta)\right)^2$. The prior for an intercept parameter in the sampling probability model (A.8) is $\exp(\eta - \exp(\eta))$.

The prior for an intercept in a feature observation model of the form (A.10) is $\exp(\theta) \Big/ \left(1 + \exp(\theta)\right)^2$.

The prior for a random effect term is $N(0,\sigma^2)$ where σ^2 is either estimated or fixed at 1. If σ^2 is estimated, then $\log \sigma^2$ has an $N(0,1)$ prior.

The use of proper (normalized) priors ensures that the posterior distribution of each parameter is normalizable.

Typically, the model for sampling probabilities will have at least an intercept term for each sampling occasion, while the remaining terms, if any, are modelled as random effects.

2.8 Fitting the model and model outputs

The primary output of interest is the posterior distribution of individual-based population trajectories. From this posterior distribution, posterior distributions of any population parameters of interest can be calculated. The posterior distribution of individual-based population trajectories is obtained from the prior distributions of parameters and the trajectory likelihood in the usual way.

The validity of the resulting trajectory posterior does not depend on the large population approximation. However, in order to enable reasonably efficient sampling of the trajectory posterior, the parameter likelihood is maximized as a first step, and an approximate posterior distribution of the parameter values is obtained using a quadratic approximation the likelihood. This approximate parameter posterior is then used for importance sampling of the trajectory posterior. A poor approximation to the parameter posterior would not invalidate the resulting trajectory posterior, but would reduce the efficiency with which it can be sampled.

The estimates of parameter values and their nominal variances obtained by maximizing the approximate parameter likelihood can also be used directly, but the interpretation of such parameter values is, in general, model-dependent. Furthermore, the nominal variances of parameter values derived from quadratic approximation to the likelihood can be rather inaccurate.

2.9 Model selection

Preliminary model selection proceeds using the large population approximation of the parameter likelihood. The model selection is based on the Akaike Information Criterion (AIC; Akaike 1973).

For model selection using the trajectory likelihood, the Widely Applicable Information Criterion (WAIC; Watanabe 2009) is used. The definition of the WAIC is:

$$\mathrm{WAIC} \;=\; -2\bar{L} \;+\; \mathrm{var}(L) \qquad \text{(A.21)}$$

where $\bar{L}$ is the posterior mean of the log-likelihood and var(L) is the posterior variance of the log-likelihood.

The WAIC does not depend on the notion of a parameter count, which is not well-defined for individual trajectories, because the discrete individual transitions do not correspond to continuous, real-valued parameters. The WAIC coincides with the AIC in cases were the latter is applicable (i.e. where all parameters are real-valued and unconstrained, and the log-likelihood function is quadratic). Although the formula for the WAIC is not explicitly dependent on the prior distributions of the parameters, the priors affect the posterior distribution of the log-likelihood and hence the value of the WAIC.

A disadvantage of the WAIC is that its computation is subject to sampling error, because it is computed from a finite sample of the posterior distribution of the likelihood. This can make it difficult to measure small differences in WAIC.

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Annex O

Report of the Sub-Committee on Cetacean Stocks That Are or Might Be the Subject of Conservation Management Plans (CMPs)

Members: Walløe (co-Convenor), Urbán-Ramirez (co-Convenor), Al Jabri, Arguedas, Baker, Baldwin, Bell, Bjørge, Bickham, Brandão, Brockington, Brownell, Burkhardt, Collins, Cooke, Crespo, de Freitas, de la Mare, Doherty, Donovan, Double, Enmynkau, Ferris, Fortuna, Frey, Fruet, Funahashi, Galletti Vernazzani, Gonzalez, Greig, Haug, Herr, Holm, Hubbell, Iñíguez, Isoda, Jackson, Jelić, Johnson, Kato, Kim, Konan, Lang, Langerock, Lauriano, Leaper, Lee, Leslie, A., Leslie, M., Litovka, Long, Lovell, Lundquist, Mallette, Mattila, Minton, Morita, H., Morita, Y., Moronuki, Nakamura, Nelson, Øien, Palka, Panigada, Parsons, Pierce, Punt, Redfern, Reeves, R., Reeves, S., Rendell, Reyes, Robbins, Rojas-Bracho, Rose, Rosel, Rosenbaum, Rowles, Santos, Scordino, Simmonds, Slugina, Stachowitsch, Stimmelmayr, Strbenac, Suydam, Sutaria, Thomas, Van Waerebeek, Vermeulen, Wade, Weinrich, Weller, Willson, Zerbini, Zharikov.

1. INTRODUCTORY ITEMS

1.1 Convenor's opening remarks

Walløe welcomed the participants. This is a new sub-committee this year. It will consider stocks (with a focus on progress with scientific work and information) that are:

(1) the subject of existing CMPs; or
(2) high priority candidates for a CMP.

It will also consider stocks that have previously been considered as potential CMPs, recognising that the Commission has stressed the need for Range States to support any IWC CMPs. Items related to the stock structure and abundance of these stocks are considered by the sub-groups on SD&DNA and ASI.

1.2 Election of Chair and Co-Chair

Walløe was elected Chair and Urbán-Ramirez was elected co-Chair.

1.3 Appointment of rapporteurs

Johnson was appointed to act as rapporteur.

1.4 Adoption of Agenda

The adopted agenda is given as Appendix 1.

1.5 Review of available documents

The documents available for discussion by the sub-committee included SC/67a/CMP01-03, SC/67a/CMP05-15, SC/67a/HIM14, SC/67a/HIM17, SC/67a/Rep04, SC/67a/NH03, SC/67a/NH11, SC/67a/SM04, SC/67a/SM12, SC/A17/GW07 and Gagnon (2016).

2. STOCKS FOR WHICH CMPS ARE IN PLACE

2.1 Southeast Pacific southern right whales

2.1.1 New information

SC/67a/HIM14 presented information on the entanglement and stranding of a southern right whale in February 2017 in southern Chile (for details see Annex J). The whale was first seen alive with clear scars caused by entanglement in fishing gear and a large number of cyamids with an abnormal distribution. Ten days later, the carcass stranded and was examined, where examiners concluded that although no ropes or nets were found on its body, the pattern of the marks observed suggested that the whale had been entangled and this was among the main factors causing its death. This is the third entanglement reported in Chile since 1986 and the second in the last two and a half years raising concerns about the negative impacts of entanglement to the recovery of this endangered population. The authors suggested that actions are needed to prevent further entanglements.

The sub-committee **reiterated** its previous advice that efforts should be made to avoid anthropogenic mortality for this stock, noting that this was a priority action for the CMP (see below).

SC/67a/CMP13 reported on progress made between December 2016 to April 2017 on the acoustic monitoring of eastern south Pacific southern right whales, first discussed in Suydam *et al.* (2016). The project, supported by the IWC Scientific Committee in 2016, proposed the use of moored hydrophones to investigate the seasonal distribution along the coasts of Chile and Peru. Additionally, a best-case scenario could inform the presence of breeding grounds using reproductive vocalisations (e.g. the 'gunshot' type). The potential information to be gained is crucial to facilitate the implementation of the CMP long-term monitoring programme. To date, a steering group and supporting staff have been established, consisting of experts on acoustics and right whales and governmental representatives and currently available data were reviewed. Consequently, the programme decided to first prioritise expanding temporal and spatial coverage of passive acoustic data and secondly the securing of funding for a postgraduate student to analyse current and future data sets. The project was presented to the CMP international coordination meeting (see Item 2.1.1) and the governments of Chile and Peru committed to supporting it within their capacities. Selection of deployment sites, including identification of existing and available moorings, is pending. Future work will include the selection and acquisition of acoustic devices, planning of their deployment and recovery, data analyses and training.

The sub-committee **welcomed** this information and the progress made. It was confirmed that the primary goal of the programme is to identify breeding areas of southeast Pacific southern right whales and the secondary goal is to use acoustic recordings to inform vessel-survey effort. Historically, vessel-survey effort has been allocated according to previous sightings, a method that has met with limited success.

The sub-committee **commended** the effort being put into finding the breeding grounds. It looks forward to future results from not only passive acoustic monitoring, but all research regarding this population. Furthermore, the sub-committee **thanked** the authors for coordinating work that spans international boundaries.

2.1.2 Progress with the CMP

SC/67a/CMP09 summarised results of the first international coordination meeting to implement the eastern south Pacific southern right whale CMP, held 7-8 March 2017 in Santiago, Chile. During the meeting, a Memorandum of Understanding between Peru and Chile to formalise co-operation on the CMP was agreed upon, a Bi-National Steering Committee for 2017-18 was established, priority actions were reviewed, an implementation strategy was proposed and a second meeting was scheduled for March-April 2018 in Peru. Short-term priority rangewide actions included the identification of a breeding area; increased photo-identification and genetic data; increased capacity regarding entanglement response; increased species identification capacity, with special emphasis on southern right whales; advice on whale watching regulations and the development of a strategy to raise citizens' awareness and increase the capacity of involved range states. Medium- to long-term actions were also discussed, but given the current level of available information, they continue to be difficult to implement, and therefore, they were postponed. The Steering Committee also identified and developed a list of stakeholders, associated experts for specific topics, agreed upon a co-ordination and reporting system, established an agenda of implementation with clear deadlines (Annex 4 of SC/67a/CMP09) and reviewed possible funding strategies in addition to the contributions made by IWC and range states.

The sub-committee **welcomed** this update on the work being undertaken within the CMP framework and the progress on scientific components such as the acoustic programme discussed under Item 2.1.1. It **commended** the work being undertaken and the international co-operation this entailed. It **stressed** its willingness to assist and provide advice on scientific matters.

2.2 Southwest Atlantic southern right whales

2.2.1 New information

SC/67a/CMP01 reported on aerial surveys conducted to estimate the relative abundance of southern right whales from the mouth of Chubut River (42°30') to Puerto Lobos (42°), with long-term efforts to document temporal changes in distribution by age and sex classes. The surveys were carried out along 350 n.miles (620km) of coastline using high-wing single-engine aircrafts (*Cessna B-182*), flown at an altitude of 500ft. A crew of four (pilot, recorder and two observers, one on each side of the plane) were used to cover an effective strip width of 1,500m, where the distance to the coast from the left-hand side of the plane was held constant at 500m. Sightings were recorded as: (a) cow-calf pairs; (b) solitary individuals; or (c) breeding groups, which usually included one adult female and several males. A number of models for the data were explored within the GLIM framework using various explanatory variables. In summary, the authors concluded that the data supports the increasing trend in abundance for southern right whales in the Península Valdés nursing area, while the rate of increase is decreasing. Additionally, it was noted that the rate of increase for calves is much smaller than previously reported and that the numbers of solitary individuals and breeding groups are no longer increasing, suggesting that whales are relocating within and out of the Península Valdés area.

For the discussion of this paper, carrying capacity with respect to the Península Valdés nursing area was defined as the capacity of the area to support whales during the breeding season in terms of space. The authors noted that once whales reach 2.5-3.0 per km^2 they begin to increase in density in less optimal habitat along the coast. Of the 620km of coast surveyed, whales mainly concentrated themselves in three areas, two located in the Golfo Nuevo and one in Golfo San Jose, but it remains unknown why. Feeding has been observed and could play a role. A similar phenomenon, though with higher densities, has been observed in the Auckland Islands, where cow-calf pairs are mainly found inside a sheltered bay and concentrations outside of the bay are mostly comprised of juveniles or cows without calves and additional bays remain unoccupied. Logbooks from whaling data can provide information on where whales used to be, but shifts in distribution have been noted in other areas and for other species, and, at this time, it may not be a fruitful effort to attempt to determine why whales shift in their distribution. Additionally, it was noted that documenting whales in all areas is currently not possible because of less than ideal survey conditions off of the outer coast and additional logistical limitations. Satellite tagging was proposed as a method to overcome these limitations.

The sub-committee **welcomed** this work and **recommended** that the aerial surveys continue noting the importance of long-term monitoring and recognising the value of investigating changes in distribution in the context of environmental and other variables.

SC/67a/CMP06 summarised information on southern right whales in San Matías Gulf, Argentina, from data on their distribution, abundance and social structure. The study area encompassed 354km of coastline from Puerto Lobos (42°00'S, 65°04'W) to the mouth of Río Negro (41°02'S, 62°47'W), in the Río Negro province of Argentina. Whales were observed from August to October, peaking in late August-early September, every year since 2007 during the annual aerial survey, with a maximum of 160 individuals recorded in early September 2015. Solitary whales were always the predominant group, but the proportion of breeding groups and cow-calf pairs typically increased in September and October, respectively. Non-social, active groups were present in every month in similar proportions. Whales were mainly found near the northwest coast of the San Matías Gulf, particularly from San Antonio Este to Caleta de los Loros. Since 2008, the areas in which whales were found concentrated along the coast of Rio Negro changed from mainly around Puerto Lobos (near Península Valdés) to the northern coast of the San Matías Gulf.

The presence, or lack thereof, of kelp gulls in areas utilised by these southern right whales was also discussed. The current kelp gull population abundance in the San Matías Gulf was unknown, but has been increasing. However, kelp gull harassment has not been recorded in areas outside Península Valdés.

SC/67a/CMP08 presented information on opportunistic sightings of southern right whales on the Patagonian shelf and shelf break off Argentina during austral summer, along with satellite-telemetry data from whales tagged off Península Valdés following the Committee's recommendation (IWC, 2017b). Encounter rates in the Patagonian shelf between 42°S to 46°S were substantially higher than south of 46°S and in the shelf break, which is consistent with satellite-telemetry data and indicated a probable feeding ground. The authors suggested that dedicated research efforts within the Patagonian shelf be increased to assess habitat use, estimate the availability and seasonality of food and exposure to biotoxins, pollution and infectious agents along the migratory and feeding grounds.

Traditionally, southern right whales have been photographed using aerial surveys and how to compare these photographs to photographs taken from research vessels was discussed. The authors noted that photographs were being analysed and they welcomed future discussions on how to reconcile these with aerial photographs.

The sub-committee **welcomed** future photo-identifications of whales from this area. Additionally, the sub-committee noted the paucity of biopsy samples from this area and **strongly encouraged** the collection of such samples. The sub-committee also **encouraged** the use and exploration of platforms of opportunity for data collection and **commended** the use of such platforms to collect data on this population, for which little is known.

The sub-committee was updated on actions developed during June 2016-April 2017 in Argentina for the southern right whale CMP for the southwest Atlantic (detailed in Appendix 2). Activities were proposed and carried out to: (1) ensure long-term monitoring of abundance, trends and biological parameters; (2) enhance existing stranding networks including the capacity for undertaking post-mortem examinations; (3) research movements, migration routes and the location of feeding grounds; (4) develop and implement a strategy to minimise kelp gull harassment; and (5) develop a strategy to increase public awareness.

The report highlighted telemetry studies, addressing (3), in particular for whales wintering near Península Valdés. The tagging programme was developed by a large group of collaborating organisations including NOAA, Cascadia Research, Wildlife Conservation Society, Aqualie, Fundación Patagonia Natural, Instituto de Conservación de Ballenas, University of California Davis and Laboratorio de Mamíferos Marinos-Centro Nacional Patagónico. Between 2014-16 ten location-only and six archival transdermal satellite tags were deployed on individuals of both sexes and different maturity/reproductive stages in Golfo Nuevo, Province of Chubut, Bahía San Antonio and Province of Río Negro (Zerbini *et al.*, 2015; 2016). Duration of fully-implanted tags varied between 10 and 237 days (mean=90 days). Data showed substantial individual and yearly variation, providing new insights regarding habitat use and the potential for connections with additional habitat along the coast of Argentina during the breeding and calving season. For instance, some tagged whales visited the outer Patagonian shelf east of Península Valdés, Southwest Atlantic Islands and the South Atlantic basin between 38 and 58°S within the same season. Nevertheless, state-space models suggested that the Patagonian shelf and the subtropical convergence and the continental shelf break around South Georgia Islands/Islas Georgias del Sur were of potential importance for foraging. Additionally, investigations of movement patterns relative to environmental data indicated that whales may be using oceanographic features (e.g. eddies) at the Subtropical Convergence for foraging. Diving profiles indicated potential differences in habitat use between juvenile and adult whales. Future studies are planned to continue the investigation of movement patterns off Península Valdés, with the ultimate goal of understanding their large-scale habitat use in the South Atlantic Ocean.

In discussion, it was noted that although six viable hypotheses have been proposed to explain the recent mortality event, to date, results remain inconclusive. The use of blow samples from drone data collection schemes were suggested as a method to assess health. Additional analyses will be available in 2018 with respect to relatedness of stranded individuals using multi-locus genotyping.

The sub-committee **acknowledged** the importance of the relevant CMP, as well as **recommended** the continued cooperation and collaboration between all research groups and stakeholders to build the knowledge needed to address mortality issues present in this population. The sub-committee **recommended** continuation of the work to understand habitat-use, dispersal and migratory patterns at different scales, in connection to overall population demography. The sub-committee **recommended** continued exploration of methods to encounter and observe live calves prior to death and to gather individual health information on both cows and live and recently deceased calves. The sub-committee **recommended** that more work be done to elucidate the differences between nutritional stress imposed on calves induced from the inability of cows to feed and other types of physiological stress resulting from open wounds (e.g. electrolyte and fluid loss and thermoregulation), energetic expenditure related to avoidance behaviours, and other stressors experienced by whales. Methods to advance such knowledge should include stable isotope analysis, nutritional condition and lipid content analyses, population genetic analysis, oceanography surveys, assessment of biotoxin presence and distribution and the continuation of behavioural observations and satellite tracking.

2.3 North Pacific gray whales

2.3.1 Rangewide assessment

Donovan presented a summary of SC/67a/Rep04, the fourth rangewide Workshop on the Status of North Pacific gray whales held from 27-29 April 2017 in La Jolla, California. This series of workshops originated in the need to consider new telemetry and photo-identification results indicating that the 'traditional' idea of two separate populations in the North Pacific ('eastern' and 'western') needed re-evaluation. The 2017 Workshop's primary focus was to review new information and build upon the excellent intersessional work undertaken by Punt since SC/66b.

The Workshop reviewed the new genetic and photo-identification information presented in the light of the stock structure hypotheses developed at previous workshops. It welcomed updated information on the analyses of whole genome sequences and SNPs presented last year (DeWoody *et al.*, 2016) and news that additional studies were ongoing to compare samples from Sakhalin Island and Mexico. New photo-identification data for PCFG whales was presented and the Workshop encouraged the development of a manuscript (including examples from PCFG and Sakhalin whales) related to affiliative behaviour on migration and potential implications for stock structure. The Workshop also reviewed new information on mixing rates for PCFG whales for use in the modelling framework. An important component of the discussion related to how to develop and include time series of bycatch (and ship strike) data in the assessment. Considerable progress was made and an approach was developed to capture and investigate the effects of the considerable uncertainty in such estimates. The Workshop received new abundance information and this was referred to the ASI working group for discussion at SC67a. Based upon the new information, the Workshop agreed to take four stock structure hypotheses forwards: 3(a), 3(e), 5(a) and 5(b). These are illustrated in fig. 1 and summarised in table 1 of the Workshop report. The revised trial structure is provided in Annex E to the report.

The Workshop agreed on an extremely ambitious workplan to try and provide results for consideration at SC/67a, recognising that this may not be possible given the short time between the close of the Workshop and SC/67a and the other commitments of the relevant scientists. In concluding his report, Donovan thanked Punt for his tireless computing work and Weller and the Southwest Fisheries Science Center for once again providing excellent facilities.

Donovan noted that not all aspects of the Workplan could be completed and Punt summarised the progress made on the modelling aspects of the workplan since the Workshop. He noted that the model specifications and associated code had been updated to treat entanglements and ship strikes separately, and to calculate survival rates for PCFG animals separately for animals that joined the population before and after 1999.

As noted above, the Workshop had referred new abundance estimates to the ASI Working Group (see Annex Q). Their conclusions are summarised briefly here and the estimates are included in the final abundance table in Annex Q. SC/A17/GW05 reported on abundance estimates based on mark-recapture modelling of photo-identification data for the period 1996-2015 for the PCFG gray whales. The estimates were endorsed and accepted for use in assessments. SC/A17/GW06 summarises abundance estimates for gray whales migrating southbound off the central California coast between December and February 2014/15 and 2015/16, using the counting and analytical methods described by Durban *et al.* (2015). The paper provided two new estimates of abundance for a time series starting in the mid 1960s. While suggestions were made of potential improvements to the models, the estimates were endorsed and accepted for use in assessments. SC/67a/NH11 provided abundance estimates using mark-recapture modelling of photo-identification data from Sakhalin Island and Kamchatka. The analytical approach has been updated from previous analyses (see Cooke, 2016). The estimates were endorsed and accepted for use in assessments but it was noted that the code will need to be verified formally for use in assessments.

In discussion, it was noted that integrating the abundance estimates provided in SC/67a/NH11 into the modelling framework would require some additional work for the stock structure hypotheses that assume that the southern Kamchatka sub-area is used by more than one feeding group and/or breeding stock. Within this sub-area, the existing SC/67a/NH11 estimates pertain to whales that feed predominantly in the Sakhalin sub-area and those that feed predominantly off southern Kamchatka, but do not explicitly address what proportion of the whales that feed off southern Kamchatka could be part of ‘other’ groups (e.g. northern feeding group whales in hypothesis 3a or Western breeding stock whales in hypothesis 3b). A small group discussed the issue and, subsequently, reported back that a method to address this issue had been identified and that modeling results incorporating the SC/67a/NH11 abundance estimates will be reported at the next rangewide Workshop.

Results of SC/67a/NH11 also have implications for inferring the extent to which the Sakhalin or the combined Sakhalin and southern Kamchatka feeding groups are reproductively closed. However, the modelling framework is not explicit with respect to mating between groups, and thus further reconsideration of hypotheses in light of this information was not warranted.

In discussion of the approach used to estimate bycatches and ship strikes, it was also noted that the mixing rates used in the model were informed by data from northwest Washington, and that these data do not represent a random sample of the North American west coast. It was suggested that telemetry data can assist in providing some inferences on residence time (although not in a direct quantitative manner) as can photo-identification data although they are limited to sampled areas. Recognising the difficulties of modelling bycatch and the associated uncertainty, the sub-committee agreed that the three scenarios agreed upon during the Workshop represented a reasonable way forward.

The sub-committee thanked the convenors and participants of the Workshop, especially Punt, for their effort and diligence in producing a report in such a short period. It welcomed the progress made and endorsed the report of the Workshop and its recommendations. It noted the endorsement of the abundance estimates and recommended that a 5th Workshop be undertaken with a view to completing the rangewide review at the 2018 Annual Meeting.

The sub-committee recognised that the results of the Workshop are relevant to the updating of the CMP in time for the stakeholder workshop planned to occur before the 2018 Commission meeting that had been endorsed last year. To facilitate this work the sub-committee **recommended** that a small drafting group meeting be held. The sub-committee also recognised the importance of the rangewide work to the ability of the SWG on the AWMP (Annex E) to provide informed advice on subsistence hunts for gray whales.

In recent years as part of the rangewide review, the Committee has recommended and encouraged the sharing of gray whale samples to better understand the stock structure of North Pacific gray whales. Japan kindly indicated its willingness to share samples collected by its scientists if a formal request was submitted (IWC, 2017a, p.24). The Data Availability Group (DAG) received and forwarded a request from the USA to Japan asking for gray whale samples for use in a genetic study extending work that was presented to the Workshop for Sakhalin and US samples. The request is now being reviewed by Japan. This sub-committee noted that such cooperation and collaboration is also facilitated through the Memorandum of Cooperation (MoC) ‘concerning conservation measures for the western gray whale population’ among the participating range states. The sub-committee **encouraged** the range states of other CMPs to follow this positive example of a MoC, noting the similar step of Chile and Peru noted under Item 2.1.2. In addition, the sub-committee encouraged the Russian Federation to continue to collect photo-identification data (including in Chukotka; see Annex E).

The sub-committee looks forward to receiving papers detailing analyses that incorporate the data from Japan, Russia and the USA.

2.3.2 Regional studies

2.3.2.1 RUSSIA

The sub-committee has had long-standing co-operation with the IUCN Western Gray Whale Advisory Panel (WGWAP) and there is a joint IUCN/IWC CMP for western gray whales. Reeves summarised activities and findings of the WGWAP since SC/66b (see Appendix 3). The Panel’s Noise Task Force met twice and focussed primarily on follow-up work related to monitoring and mitigation during Sakhalin Energy’s 2015 seismic survey off Sakhalin Island and development of a monitoring and mitigation plan for another large-scale seismic survey in 2018. The full Panel met in Moscow in November. Among the issues addressed at that meeting were: (a) the implications of an apparent long-term decline in amphipod biomass in the Piltun gray whale feeding area; (b) a proposal by Sakhalin Energy to increase speed limits for its crew-change vessels; (c) risks to gray whales of entanglement in salmon nets along the north-eastern Sakhalin coast; and (d) a document prepared for IUCN and submitted to the Russian Ministry of Natural Resources and Ecology entitled ‘Principles and Guidelines for the Monitoring and Mitigation of Impacts on Large

Whales from Offshore Industrial Activity in Russian Waters'. The sub-committee thanked Reeves for this update. It noted that a recommendation regarding the updating of the IUCN/CMP is included in the work plan (see Item 2.3.1).

SC/67a/NH03 reviewed findings from 2016 field studies conducted by the Russia Gray Whale Project (formerly the Russia-US Program) on gray whales feeding near Piltun Lagoon in the western North Pacific off Sakhalin Island, Russia. This research program has been ongoing since 1997 and represents the 20+ year time-series that has served as the foundation for the assessments of the population (see discussion of SC/67a/NH11 above). Photo-identification research in 2016 resulted in the identification of 56 individuals, including six calves and seven previously unidentified non-calves. No previously unidentified reproductive females were recorded in 2016, resulting in a minimum of 33 reproductive females observed since 1995. The general distribution of gray whales in 2016 was notably different to that in 2015, with most of the whales encountered south of the mouth of Piltun lagoon. The authors noted that potential impacts from nearby offshore oil and gas developments, including nearly annual seismic surveying, remain a concern for the wellbeing of the population (see Appendix to SC/67a/NH02). Additionally, the coastal salmon trap net fishery, which overlaps spatially and temporally with feeding gray whales during the summer and fall, continues to present considerable risk (SC/67a/HIM17) as is evidenced by the report of an entangled whale in September 2016. This fisheries-related risk is of particular concern because adult females and their calves show strong fidelity to this feeding area at a critical time when the females are recovering from pregnancy and lactation and the calves are being weaned.

There was a general discussion of the information from the Sakhalin and Kamchatka areas including the results of SC/67a/NH11. It was noted that the site fidelity of newly identified non-calves was confirmed to be relatively high. These newly identified individuals are typically assumed to be whales that were missed as calves rather than immigrants. In the model described in SC/67a/NH11, these animals enter the model with a probability distribution for their age depending on the current dynamics of the population. Cooke reported that future analyses will look at the model output to see which group new non-calves are predominately found within. It was suggested that biopsy samples from Kamchatka could provide valuable information to clarify the situation in this region. Additionally, it was suggested that survey work in the Kamchatka region be continued to determine if, for example, some individuals spend significant periods of time there in the summer and autumn feeding season and others just pass through.

The sub-committee commended the ongoing work in the region and recommended that studies in the Kamchatka area continue and if possible expand as they can provide valuable information for analyses regarding stock structure and status. The sub-committee noted the discussion of SC/67a/HIM17, discussed by the HIM sub-committee (see Annex J), that reviewed the available evidence of gray whale entanglements in the western North Pacific and reviewed the literature on gear types used in the Russian Far East that are known or suspected to catch gray whales. The Committee has previously expressed concern over the potential threat of fishing gear off Sakhalin (IWC, 2017a, p.38).

The sub-committee has recommended in the past that the two groups working off Sakhalin (the Russia Gray Whale Project and the Joint Programme of Sakhalin Energy and ENL) work together to develop a single publicly available photo-identification catalogue. This will improve analyses of abundance, movements and biological parameters and lead to a better understanding of the status of the animals there. Donovan provided a short report on efforts to facilitate the development of a single catalogue and related database, perhaps held under the auspices of the IWC. The sub-committee welcomed this news and **strongly encouraged** Donovan to work with the various data holders to facilitate the development of a single reconciled catalogue and database. Furthermore, the sub-committee **reiterated** the importance of the work of the Russian Gray Whale Project and recommended that it continue.

The sub-committee recalled that there had been a major seismic survey effort at Sakhalin in 2015 (IWC, 2017a). It noted that considerable monitoring data had been collected by two of the oil companies involved to enable analyses of potential effects of the surveys on gray whales in the area. The sub-committee was given to understand that such analyses were underway and noted that it would welcome presentation of the results of those analyses at a future meeting.

2.3.2.2 JAPAN

SC/67a/CMP02 reported on the recent status of conservation and research on gray whales in Japan. During the period May 2016-April 2017, no anthropogenic mortality has been reported while two opportunistic sightings of gray whales were made in Tokyo Bay on 22 February and 18-23 April. The Fisheries Agency promptly informed individuals of the occurrence and cautioned responsible local authorities to avoid entanglements of the animal(s) in fishing nets and prevent ship strikes. Fishermen are prohibited from capturing gray whales and set-net fishermen are asked to make their best effort to release any whales found in their nets.

Sightings from Izu archipelago and Shizuoka prefecture from 2015 to 2016 were identified as involving the same individual (Nakamura *et al.*, In press). Additionally, it was noted that Kato (TUMSAT) had been nominated as the coordinator of the Memorandum of Co-operation for Conservation of Western Gray Whales at the 2016 IWC Commission meeting.

In discussion, an additional report (sourced on Facebook) of a gray whale seen and photographed off Aogashima Island, Japan was noted. Whilst the photograph was clearly of a gray whale, the sub-committee noted that confirmation of the location can be more problematic in such cases unless the original source is contacted.

The sub-committee **welcomed** the information and especially that of the sightings off Japan. It **encourages** that sighting information continue to be collected. This can provide helpful information on the age classes using waters near Japan.

2.3.2.3 EAST CHINA SEA

The question of whether a western breeding stock is extant has been a key part of the discussions and hypotheses considered during the rangewide review. At the 2016 Commission meeting, Gagnon (2016) reported on recent acoustic detections made by the US Navy of what have been tentatively classified as gray whales in the East China Sea. These detections have been made on numerous occasions over the last six years (2011-16) using towed hydrophone arrays in mobile, high-precision acoustic monitoring systems (Surveillance Towed Array Sensor System-Low Frequency Active Sonar - SURTASS-LFA). Vocalisations were detected on multiple occasions in multiple years and were consistent in structure across years. Calls consist of a 55 Hz pulse about 1s in duration, which has multiple harmonics (110 and 165Hz strongest) and the calls are typically repeated two or three times by the same individual. These calls have been detected annually in relatively shallow waters between September and March. The whales remain in the same general areas for weeks at a time, but have generally been observed to be moving south in the autumn and north in the spring. These acoustic data have not yet been accompanied by visual observations to confirm species identification.

The sub-committee welcomed this information and expressed its appreciation to the author and the US Navy for bringing it forward. The author has expressed his willingness to collaborate with biologists familiar with gray whale calls with the goal of verifying species identification. If it is determined with high probability that these are gray whale calls, it will be important to develop a dedicated field-research effort to verify species identification with visual observations, photographs and biopsies.

The sub-committee endorsed the recommendation from the rangewide Workshop (SC/67a/Rep04) that every effort be made, in the first instance, to determine with high probability that the calls are from gray whales. If so a dedicated field effort should be launched to observe, photograph and biopsy the animals.

2.3.2.4 MEXICO

SC/67a/CMP11 presented the results of gray whale research conducted in the wintering lagoon of San Ignacio and the Bahía Magdalena complex. Overall, the number of gray whales and their seasonal occupation of the lagoons were slightly lower than seen in previous years, and the authors thought that this was probably due to cooler sea-surface temperatures. Conversely, the number of single animals observed in the Bahía Magdalena complex was notably higher in 2017. A total of 646 individual whales where identified in Laguna San Ignacio and 374 in Bahía Magdalena complex. In recent years, photographic re-captures of gray whales first photographed in Bahía Magdalena and subsequently photographed in Laguna San Ignacio during the same year, suggests that the direction of movement occurs south to north. Females can bear calves up to an age of at least 47 years.

The sub-committee also considered SC/A17/GW07 which had been presented at the intersessional Workshop. It provided an update and overview of results from shore-based counts of northbound eastern North Pacific gray whale calves conducted March-June from the Piedras Blancas Light Station on the central California coast each year from 1994-2016. Estimates of the total number of northbound calves displayed a high degree of inter-annual variability, ranging from 254 calves in 2010 to 1,528 calves in 2004. Calf production has been particularly high during the past 5 years (2012-16) with a total of >6,500 calves estimated during this period, including four of the highest years (>1,000 calves per year) since these calf counts began in 1994. The 2016 estimate of calf production (1,351) is about 5% of the reported total abundance (26,960; SC/A17/GW/06) for the eastern North Pacific population in 2016. A trend in median migration dates was observed, indicating that the midpoint of the migration is now occurring about a week later than it did in the mid-1990s.

The sub-committee **welcomed** the results of this long-term study, as had the Workshop. It **reiterated** the importance of such studies, particularly in light of analyses of abundance and calf production in conjunction with environmental factors. Such analyses can provide general as well as specific insights on the population dynamics of whales in response to environmental factors. The sub-committee looked forward to receiving additional analyses of these data in future years.

2.3.3 Other studies

SC/67a/CMP10 presented a study of steroid hormones in gray whales. Using the ELISA method, progesterone and testosterone were reported from biopsies of 14 western gray whales from Sakhalin Island including 2 immature males, 1 adult male, 2 males of unknown life-stage, 2 immature females, 1 adult female and 6 females of unknown life-stage. Progesterone concentrations ranged from below the limit of detection (8.57pg/mL) to 0.21 ng/g. Progesterone levels in pregnant gray whales have not yet been determined, but the female western gray whale progesterone values detected were below those reported in some non-pregnant mature individuals of other cetacean species, and it is likely that the female western gray whales in this study were not pregnant at the time of sample collection. Progesterone detected in male western gray whales was in the range reported in male humpback whales and bowhead whales. Testosterone concentrations ranged from below the limit of detection (5.67pg/mL) to 1.36ng/g. The values reported here are in the lower end of values reported in pubertal and immature male short-beaked common dolphins. This study also investigated the use of a nanoLC-MS/MS method to determine progesterone, testosterone, hydrocortisone, and cholic acid (as a surrogate internal standard) in blubber samples from 3 stranded eastern gray whales. Progesterone concentrations were detected in two of the three samples and were higher in the adult female than in the adult male. Testosterone concentrations were detected in both male blubber samples with the adult male having a higher testosterone concentration than the juvenile male. Future development of this work will include the addition of biologically relevant hormones, such as estradiol and other glucocorticosteroids.

The sub-committee welcomed these analyses and looks forward to future analyses and further validation of the method, noting that future work should include consideration of how health can be monitored using such data. Additionally, it was recommended that collaboration with field biologists be initiated to combine the laboratory findings with metadata to provide more accurate estimates of animal age and reproductive stage.

2.4 Franciscana

2.4.1 New information

SC/67a/SM04 provided a preliminary report on a project funded by the Government of Italy to assess characteristics of fisheries in Franciscana Management Areas Ia and Ib, two areas thought to have the smallest abundance. They are geographically disjoint from all other areas and thought to be subject to high levels of bycatch. Interviews of 76 fishers were carried out between May to September in 2016 and in March 2017 to evaluate the type of fisheries and fishing gear operating in the area. Of those fishers, 54 claimed to know of franciscana, but only 9 could accurately identify them based on illustrations. Five of these fishers reported having historically captured franciscana in bottom-set and floating gillnets, but the authors were unable to assess the relative proportion of franciscana in reported bycatch because of the difficulty in identifying bycatch to the species level. The authors plan on conducting additional interviews, funded by fisheries monitoring, and providing these results to SC/67b.

In discussion, it was noted that, typically, most fishers are able to identify franciscana in the field and that the improper identification of the species from photographs may have been an artefact of the photographs that were used or that fishers chose to falsely answer the question in the interest of securing access to fishing within these areas.

2.4.2 Progress with the CMP

SC/67/SM12 reported on the beginning of the implementation of the franciscana CMP (IWC/66/CC11) funded by the IWC CMP Voluntary Funds and WWF. A Steering Committee was initiated including representatives from Argentina, Brazil, and Uruguay, IWC Conservation Committee Chair, IWC Scientific Committee Chair, IWC CMP Standing working group Chair and IWC Head of Science, coordinated by Iñíguez and supported by an established panel of experts. The two main objectives of the CMP are to protect franciscana habitat and to minimise anthropogenic threats (e.g. bycatch) to the population. Consequently, the CMP includes seven actions of high priority, ranging from initiating public awareness to increasing capacity for activities such as research and mitigation. Specifically, the need to reduce bycatch was included, and the authors suggested that research be performed to assess the degree to which pingers could reduce bycatch of franciscana in the Buenos Aires gillnet fishery.

In discussion, it was highlighted that Brazil will be providing 1 million dollars for research and conservation work according to the National Action Plan of Franciscana in management areas II and III. Additionally, the authors noted that although initial efforts were initiated in areas in which they currently work, in the future, work will be conducted in additional range states.

The sub-committee **commended** the breadth of work that has been undertaken towards franciscana research and conservation and noted that this CMP is the first for a small-cetacean species and **welcomed** the development of more in the future, as appropriate. It also **commended** efforts being made to coordinate research across international boundaries and **recommended** that this collaboration continue, despite the difficulties involved.

The sub-committee **recommended** that it should conduct an in-depth review of franciscana soon, given that the last IWC review of franciscana was performed in 2004 (IWC, 2005). The review should include new estimates of franciscana mortality, as previously recommended by the Committee. Such estimates are still unavailable for Management Areas Ia and Ib.

Finally, the sub-committee **concurred** with need to investigate the possibility that pingers are suitable to reduce bycatches of franciscana.

3. PROGRESS WITH IDENTIFIED PRIORITIES

3.1 Humpback whales in the northern Indian Ocean including the Arabian Sea

3.1.1 New information

SC/67a/CMP14 summarised reports of humpback whales in the Persian Gulf from 1883 to 2017. In total, five specimens were recorded, but no sightings. The first record, from Bassore Bay, Iraq, is currently on display at the Paris Museum and is the holotype for *Megaptera indica Gervais* 1883. The remaining records included an individual potentially killed from ship strike at the port of Doha, Qatar, an individual struck by a ship's propeller in Kuwait, a juvenile entangled in a gillnet at Qeshm Island, Iran and a juvenile found floating near Akhtar, Iran. Initially, reports were assumed to be of rare stragglers from the Arabian Sea population, however, as additional records were accumulated, the authors hypothesised that perhaps humpback whales are normal visitors to the Persian Gulf, if not resident. The authors recommended that increased efforts be allocated towards systematic surveys in the Persian Gulf region.

The sub-committee **welcomed** this information. It **concurred** with the authors that additional systematic research be conducted within the Persian Gulf area to characterise the residency of whales reported in this area.

SC/67a/CMP05 reviewed published records of baleen whales (including blue whales, Bryde's whales and humpback whales) in Pakistan and an ongoing observer programme implemented in 2012. Prior to 2012, knowledge of whales in Pakistan included a limited number of sighting and stranding records and whaling data (Mikhalev, 1997; 2000; Minton *et al.*, 2015). In 2012, WWF-Pakistan implemented a programme to train the crew of tuna gillnet vessels to document sightings, entanglements and bycatch. Vessels are provided with a digital camera and are encouraged to photograph humpback whales. The programme now includes 75 vessels, and hundreds of bycaught animals have been released alive, including one humpback whale. Three humpback whales were photographed in 2014, and there were two confirmed sightings in 2015 and 12 in 2016.

In discussion, it was noted that the data is part of a larger dataset used to document bycatch by the Indian Ocean Tuna Commission, and that up until now observer reporting within this dataset has been poor for all areas, with Sri Lanka being an exception. Additionally, the cetacean data is stored in the regional archiving system available from the WWF.

The sub-committee **commended** the amount of work that has been conducted, work which has led to the availability of a large amount of data where previously there was none. The sub-committee **recommended** that this work be continued and be replicated, where possible, throughout the region, especially in regions where it is not feasible to conduct cetacean surveys.

SC/67a/CMP03rev1 summarised records of baleen whales from the Indian coast of the Arabian Sea from 2001 to March 2017. Previously, data were available only from the west coast of India (Sutaria *et al.*, 2016). Humpback whales were reported along the west coast, with most sightings occurring between February and May. Additionally, undocumented sightings were reported near the India-Pakistan border. In March 2017, at least one vocalising humpback whale was recorded off the Goa coast, and in prior years, vocalising whales were recorded near the Netrani islands, off the coast of Karnataka, in Kochi harbour in Kerala, and in offshore waters from Malvan-Sindhudurg in Maharashtra (Mahanty *et al.*, 2015). The authors recommended that efforts be made to conduct dedicated baleen whale surveys in Gujarat, Maharashtra, Goa and Karnataka and for the establishment of passive acoustic monitoring along the northwestern coast from Porbandarto the Netrani Islands. Additionally, they recommended an increased collection of samples from stranded whales, the establishment of a centralised repository for tissue samples and the enhancement of collaborative efforts with local regional authorities to facilitate in-depth analyses.

The sub-committee **welcomed** the report and its value to better understand this endangered population. The sub-committee **recommended** that further emphasis be placed on using acoustic methods to document cetaceans in these areas and other areas, particularly areas that are not safe to survey. Additionally, the sub-committee **recommended** that all documented entanglements and ship strikes be entered into the IWC database and that an enhanced effort be made to archive any tissue samples that are or become available in a central repository. No tissue samples are currently available for humpback whales. The sub-committee **thanked** the Government of India, Maharashtra Forest Department and the local office of the United Nations Development Programme for their support of this work.

SC/67a/CMP12 reported on the continuation of Oman-based satellite telemetry studies initiated in 2014. Telemetry data from nine whales showed whales spending 35% of their time in the Gulf of Masirah and 27% in Hallaniyat Bay. During a two-week survey in March 2017 no humpback whales were sighted in the Gulf of Masirah and only two individuals were encountered in Hallaniyat Bay, neither of which were tagged. The authors updated the sub-committee on the increasing threats to areas of critical habitat and high cetacean biodiversity, including increased numbers of gillnet fishing vessels in Hallaniyat Bay. Shipping traffic in the Gulf of Masirah is expected to increase in the next five years due to new investment and the further development of the port of Duqm and associated industrial area. The port in Duqm has supported and is currently supporting a management and mitigation plan, but continued effort is required to ensure research inform such plans. The authors noted that recent stranding records confirm the importance of addressing bycatch in this area.

The sub-committee noted that there is no specific management plan for marine resources within the area, although some vessels did abide by voluntary speed recommendations. The port actively disseminates mitigation information. Additional mitigation plans were discussed, including the use of the 'Whale Alert' system to act as a whale and shipping collision avoidance system for the port and to also aid in the collection of whale sightings in the area.

The sub-committee noted that satellite tagging offers a method to collect cetacean data in areas that can be constrained by inclement weather and piracy. It **recommended** that the work be continued noting its value in understanding the risk of animals to anthropogenic mortality recognising the increasing shipping activity within the two areas that the whales inhabited. Lastly, it was **recommended** that the collaborative efforts with industry shown in Duqm be adopted in other ports and harbours.

SC/67a/CMP15 reported on the use of an Ensemble Ecological Niche Modelling approach to predict humpback whale habitat throughout the Arabian Sea using vessel-sightings data and satellite-telemetry data (using a state-space modelling approach) from Oman. Ensemble models of both datasets predicted areas of suitability along the coast of Oman and Northern Arabian Sea between Iran and India for November to May. Model predictions fit well with historical locations of Soviet whale captures from the 1960s and co-occur with areas of high vessel-traffic density in the Northern Indian Ocean where container-shipping traffic increased threefold between 2004 and 2014 (Willson *et al.*, 2016). Telemetry data provided the most robust source of data, but models could be improved upon by incorporating data from other range states. The authors recommended that this work, together with recent blue whale modelling work (Redfern *et al.*, 2017), could help guide future research activities and mitigation efforts in the region through the use of a multi-species modelling approach.

In discussion, it was suggested that other sources of available data such as acoustic data also be included in the model, where additional data could allow the model to estimate habitat preferences specific to behaviour modes.

The sub-committee **welcomed** the work, and highlighted the immense amount of effort that was put forward to carry out such an analysis. The sub-committee **recommended** that the ensemble niche modelling presented in SC/67a/CMP15 be expanded to include data reported from Pakistan and India and be used to inform future research efforts, particularly where to concentrate efforts for passive acoustic research and to help determine where vessel-based surveys for photo-identification and biopsy work should be prioritised, when logistically possible. Additionally, it was **recommended** that ensemble niche modelling be applied to examine potential threats from shipping using AIS/Vessel traffic data, and fishing using any available data on fishing effort in the region.

3.1.2 Regional co-operation

SC/67a/CMP07rev1 summarised the progress of the Arabian Sea Whale Network (ASWN), an informal collaboration between researchers and conservation bodies working toward better understanding and the conservation of whales in the Arabian Sea. The document summarised the 12 reports prepared for SC/67a by ASWN members and colleagues working in the region, including contributions from Oman, India, Pakistan, Sri Lanka and the Persian Gulf. This represents an increase in the number of reports, the breadth of topics and the number of range states represented from the Arabian Sea presented to this meeting, demonstrating concrete progress toward increased awareness, data collection and capacity building in the region. Most recommendations proposed in 2015 (IWC, 2016) related to improved communication, awareness raising and capacity building have progressed adequately (e.g. ASWN infographics), but the raising of funds for shared regional-level projects has been challenging and limited to funds granted by the IWC and WWF. Progress was also made towards the implementation of regional online data platform, funded under IWC SH3B, where a contract between the IWC and the Emirates Wildlife Society (EWS)-WWF, who will host the project, was signed in February 2017. Co-funding from WWF and the Environment Society of Oman enabled EWS-WWF to sign a contract with Flukebook (a subsidiary of WildMe) allowing photo-identification data from Oman to be included in the online platform starting in June 2017. A fully functioning data platform with expanded capacity to archive and analyse sightings, strandings and genetic data, as well as photo-identification data should be ready to share at SC/67b.

The sub-committee **commended** the work performed by researchers in the Arabian Sea, noting the expansion of research topics and recognising the difficulty of establishing and maintaining such a network, which it recognised as important for the conservation and management of this highly endangered population. The sub-committee **recommend** further development of the online regional data archiving platform to facilitate regional analyses and the comparison of data between study sites and the identification of locations conducive to passive acoustic monitoring to inform directed effort for documenting basin-wide distributions. The sub-committee also **recommended** that the IWC Secretariat communicate the Committee's endorsement to the relevant range states. Lastly, the sub-committee repeated last year's **recommendation** to collect tissue sample where possible to facilitate the genetic identity of these animals.

3.1.3 Progress with international measures such as CMPs

The sub-committee was provided an update from the intersessional working group assigned to consider proposing the Arabian Sea as candidate for a CMP. To date, the working group has been unable to secure endorsement from range state members. Therefore, working group members initiated the regional ASWN as a way to build momentum

Table 1

Summary of the work plan for the sub-committee on Conservation Management Plans (CMP).

Item	Intersessional 2017/18	2018 Annual Meeting (SC/67b)
Southeast Pacific right whales	-	Review progress on scientific aspects of the CMP
South Atlantic right whales	-	Review progress on scientific aspects of the CMP
Gray whales	Workshop; CMP drafting group	Complete rangewide review
Franciscana	-	Prepare for in-depth review
Humpback whales in the northern Indian Ocean	-	-

Table 2

Summary of budget requests for the 2017-18 period. For explanation and details of each project see text.

Title	2018 (£)
Fifth Workshop on the rangewide review of the population structure and status of North Pacific gray whales	2,500
Drafting group to finalise the scientific components of the updated IUCN/IWC CMP for western gray whales	3,000
Total	**5,500**

towards the development of a regional CMP and to directly promote conservation initiatives in the region (SC/67a/CMP07). The IWC Scientific and Conservation Committees recently reiterated the value of an Arabian Sea CMP for this species (see Item 10.3.3 in IWC (2017a). It was suggested that the Convention on Migratory Species (CMS) may offer an alternative means of achieving more regional and inter-governmental collaboration towards whale conservation in the Arabian Sea.

The CMS has introduced a new mechanism with which to designate the status of species or populations as ‘Concerted Action’ (see CMS Resolution 11.13 in Convention on Migratory Species, 2014). Efforts are underway to draft and complete a proposal to obtain this recognition for Arabian Sea humpback whales during the next CoP of CMS parties in October 2017. It would be valuable if the IWC collaborates on this effort, following the model of the joint IWC-IUCN CMP for western gray whales. Efforts are also underway to obtain support from the relevant range states for this initiative, which, as a joint IWC-CMS initiative, would include all Arabian Sea humpback whale range states.

The sub-committee **reiterated** its serious concern about its status of the endangered Arabian Sea humpback whale population and the anthropogenic threats it faces. It **stressed** the value of regional initiatives and **encouraged** range states to explore the possibility of future collaboration either through a CMP or CMS ‘Concerted Action’ and encourages IWC co-operation in these initiatives. Finally, the sub-committee **stressed** the need for continued scientific efforts to improve the knowledge of Arabian Sea humpback whales to assist conservation efforts.

4. UPDATE ON PREVIOUSLY SUGGESTED POTENTIAL CMPS

No new information was provided for the following populations: (1) blue whales from the northern Indian Ocean; (2) sperm whales in the Mediterranean; and (3) boto in Amazonia. Donovan reported that efforts are underway to develop a CMP for fin whales in the Mediterranean by ACCOBAMS following the IWC model.

5. WORK PLAN AND BUDGET REQUESTS

5.1 Work plan and intersessional groups

The sub-committee work plan and intersessional groups are found in Table 1 and Annex W.

5.2 Budget requests

The sub-committee **recommended** the following two requests for funding (Table 2).

6. ADOPTION OF REPORT

The Report was adopted at 16:45 on 16 May 2017. The sub-committee thanked Walløe and Urbán-Ramirez for their excellent Chairmanship.

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Appendix 1

AGENDA

1. Introductory items
    1.1 Convenor's opening remarks
    1.2 Election of Chair and Co-Chair
    1.3 Appointment of rapporteurs
    1.4 Adoption of Agenda
    1.5 Review of available documents
2. Stocks for which CMPs are in place
    2.1 SE Pacific southern right whales
    2.2 SW Atlantic southern right whales
    2.3 North Pacific gray whales
    2.4 Franciscana
3. Progress with identified priorities
    3.1 Humpback whales in the northern Indian Ocean including the Arabian Sea
4. Update on previously suggested potential CMPs
    4.1 Blue whales (northern Indian Ocean)
    4.2 Fin whales (Mediterranean)
    4.3 Sperm whales (Mediterranean)
    4.4 Boto in Amazonia
    4.5 Topic-based or area-based CMPs (e.g. bycatch)
5. Work plan and budget requests
6. Other business
7. Adoption of Report

Appendix 2

SOUTHERN RIGHT WHALE OF THE SW ATLANTIC: AN UPDATE ON THE CMP ACTIONS IN ARGENTINA (2016-17)

M. Iñíguez, G. Caille, E. Crespo, V. Reyes Reyes, M. Sironi and A. Zerbini

The Conservation Management Plan for the southern right whale (SRW) Southwest Atlantic population was adopted in 2012 following the recommendations of the IWC and particularly considering the SRW die-off event in Península Valdés (PV) area, Argentina. This plan started to be implemented after the meeting held in 2013 in Buenos Aires (Thomas *et al.*, 2013).

The overall objective of the CMP is to protect southern right whales (SRW) habitat and minimise anthropogenic threats to maximise the likelihood that SRW will recover to healthy levels and recolonise their historical range.

This appendix summarises those actions developed in Argentina and related to the CMP for the period June 2016-April 2017.

ACTIONS

MON-01: Ensure long-term monitoring of abundance, trends and biological parameters

The Marine Mammal Lab of the Centro Nacional Patagónico (LAMAMA-CENPAT) conducted 65 aerial surveys between May 1999 to December 2000 and from June 2005 to November 2016. The results of its work support that the SRW population is still increasing in the nursing area around PV. In spite that the number of whales in the surveyed area is increasing, the rate is steadily decreasing. Density has been also increasing and whales have been expanding their distribution to deeper waters during the last decade, and mothers with calves are using the more protected areas near the coast. These responses are expected as density-dependence response to population increase (SC/67a/CMP01). It was also observed a geographic distribution change from the west to the north coast of San Matías gulf, especially in areas with high-quality habitat. Mother-calf pairs, breeding groups, non-social active groups and solitary individuals were observed in the area, the latter being the predominant group type along the entire coast (SC/67a/CMP06)

Aerial surveys of SRWs off the coast of PV were conducted in September 2015 and 2016 by the Instituto de Conservación de Ballenas (ICB) and Ocean Alliance (OA). The purpose of the surveys was to document the presence and distribution of SRWs along the perimeter of the Península

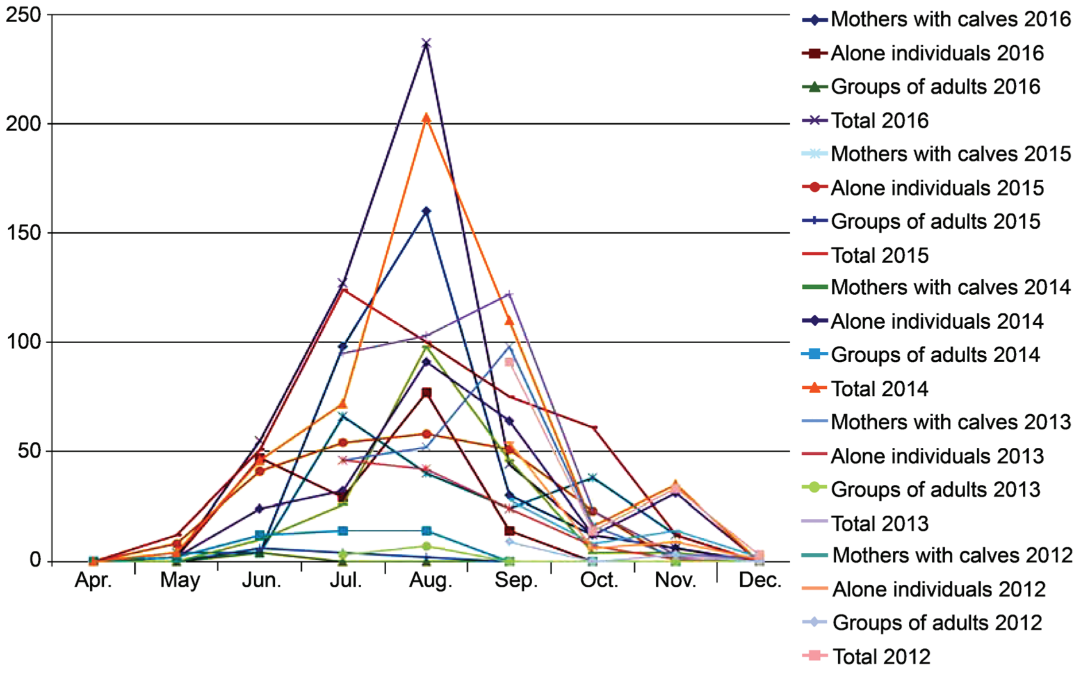

Fig. 1. Number of individuals (total and by category) registered for the 2012, 2013, 2014, 2015 and 2016 seasons.

Table 1

Analyses of photographs in the right whale catalogue of ICB/OA are available for the years 1970-2014. Number of individuals photo-identified: 3,100.

Date	Area	Mothers	Calves	Adults	Juveniles	Total
03/09/15	Golfo Nuevo	145	145	102	46	438
06/09/15	Golfo San José	48	48	8	7	111
06/09/15	Outer Coast	0	0	1	0	1
Total	**P. Valdés**	**193**	**193**	**111**	**53**	**550**
26/09/16	Golfo Nuevo	103	103	33	21	260
28/09/16	Golfo San José	57	57	7	3	124
Total	**P. Valdés**	**160**	**160**	**40**	**24**	**384**

by photo-identifying individuals from the callosity patterns on their heads and recording their locations and the presence of calves.

The following table summarises the basic results of the surveys each year.

Fundación Patagonia Natural (FPN) carried out 9 censuses on SRWs from the right whale observatory 'Punta Flecha', on the coasts of Golfo Nuevo (Chubut Province, Patagonia Argentina) in 2016. The total number of whales counted varied between a maximum of 237 individuals (24 August) and a minimum of 2 individuals (12 May) and 6 individuals (13 November). No whales were recorded in the first census (1 May) and in the last census (22 November). This seasonal data confirm that the months with the greatest number of SRWs, in the waters of the Golfo Nuevo front to the Natural Protected Area 'El Doradillo', cover July to September (3-4 months) and always with a predominance of mothers with calves.

MON-02: enhance existing strandings networks including the capacity for undertaking post-mortems

The Southern Right Whale Health Monitoring Program (SRWHMP) at PV began in 2003 with support from the US National Marine Fisheries Service. The Program is developing as collaboration between local NGOs, research centers, and governmental agencies. At present, the Program operates as a collaboration of the ICB, OA, University of California, Davis, University of Utah, Wildlife Conservation Society (WCS) and FPN, with funds from the member organisations and donations from private foundations and individuals.

Since its beginning in 2003, the Program has recorded 753 dead SRWs found on the shores of PV and surrounding areas, with an annual maximum of 116 dead whales in 2012 (McAloose *et al.*, 2016; Rowntree *et al.*, 2013; Wilson *et al.*, 2016). No other stranding research program in the world has documented such a high number of dead SRWs in one decade or created such complete database on the health of SRWs.

A Contact Network (CN) has been essential to the success of the Program. Members of the CN include: park rangers, fishermen, local people, whale watch companies, dive companies, tourism companies, nature guides, sailors, airplane pilots, artisanal fishermen, researchers, NGOs, and local authorities such as the Argentine Navy and the Argentine Coastguard. In addition to reports from the CN, the Program surveys the beaches in both gulfs in regions where the whales concentrate by land and air. Aerial surveys were opportunistic between 2006 and 2009, but have been systematic (minimum 6 and maximum 8 flights per season) since 2010. Regular aerial surveys encompass the entire perimeter of Golfo Nuevo and Golfo San José, and the external coast of the peninsula is added at least twice during the season.

In 2016, the Program studied and collected samples from a total of 16 stranded whales that died at PV and surrounding areas, including 14 calves (88%), 1 juvenile and 1 adult. The stranded whales included 9 females (56%), 6 males (38%) and 1 whale (6%) of unknown sex. Most whales (13) died in the southern gulf (Golfo Nuevo) followed by 2 whales in the northern gulf (Golfo San José) and 1 in Golfo San Matías, to the north of PV. They conducted post-mortem examinations on the stranded whales and when conditions permitted, biological samples were collected that will be analysed for infectious diseases, biotoxins, contaminants, nutritional

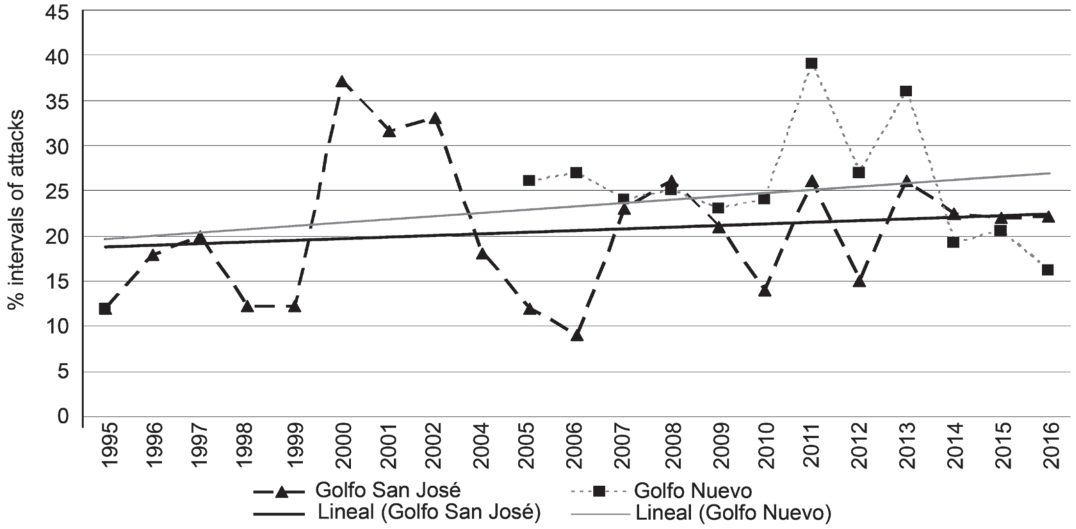

Fig. 2. Kelp gull attack frequency in Golfo San José and Golfo Nuevo, Península Valdés for the period 1995-2016.

status, foraging locations, diet, genetics, and other potential factors contributing to mortality. One live stranding was recorded in 2016: the individual in Golfo San Matías, which died after it, was found.

Among other observations and analyses, the Program's researchers quantified the number and size of kelp gull-inflicted lesions on dead whales through time to assess their potential systemic impacts on the whale's health and welfare. These data will help to develop and test novel diagnostic approaches to identify signs of stress, pain, dehydration and thermoregulatory effects of gull-inflicted wounds on whale calves. It is possible that increasing gull attack frequency and the level of physical and behavioural disturbance of SRW calves has reached a threshold in recent years that has led to the exceedingly high calf mortality levels observed between 2007 and 2014.

Two recent papers were published, Wilson *et al.* (2016) and McAloose *et al.* (2016).

RES-01: determine movements, migration routes and location of feeding ground(s)

Telemetry studies were conducted to assess movements and the location of the feeding grounds of whales wintering near PV. This project is developed by a large group of collaborating organisations including NOAA/Cascadia Research, WCS, Aqualie, FPN, ICB, University of California Davis, and LAMAMA-CONICET. Between 2014 and 2016, 10 location-only and six archival transdermal satellite tags were deployed in individuals of both sexes and different maturity/ reproductive stages in Golfo Nuevo, Province of Chubut, and in Golfo San Antonio, Province of Río Negro (Zerbini *et al.*, 2015; 2016). Duration of fully implanted tags varied between 10 and 237 days (average=90 days). Movement data provided new insights into habitat use within the gulfs and potential connections with other habitats along the coast of Argentina during the breeding/calving season. Migratory behaviour showed substantial individual and yearly variation. Tagged whales visited the outer Patagonian shelf east of PV and north of the Falkland Islands/ Islas Malvinas, the Scotia Sea near South Georgia Islands/Islas Georgias del Sur and the South Sandwich Islands/Islas Sandwich del Sur, and the South Atlantic basin between 38 and 58°S. In some cases, individuals visited these three regions within the same season. State-space models were used to estimate behavioural states and suggested areas of potential foraging importance in the Patagonian shelf (PS), the subtropical convergence and the continental shelf break around South Georgia Islands/Islas Georgias del Sur. An investigation of movement patterns relative to environmental data indicated that SRWs might be using oceanographic features (e.g. eddies) at the Subtropical Convergence for foraging. Dive profiles suggest potential differences in juvenile and adult whale habitat use and provide unprecedented information on diving behaviour of these animals. Future studies are planned to continue elucidating the movement patterns of PV SRWs with the ultimate goals of understanding their large-scale habitat use in the South Atlantic Ocean.

Line-transect visual observations were made by dedicated observers of Fundación Cethus on the Argentinean Shelf (including the PS) and shelf break during four surveys from two Argentinean Coast Guard's vessels used as platforms of opportunity: one in January, two in February, and one in December 2016. A total of 34 groups of SRWs were observed in the PS, totalising 58 individuals, and 4 groups in the shelf break, totalising 5 individuals, up to a depth of 970m. The highest encounter rate (ER) was estimated for the PS between 42° and 46°S in January. The estimated mean ER for the shelf was substantially lower than that from January in the northern area of the PS. Dedicated efforts of research within the PS should be made covering a wider area than already surveyed opportunistically including during different months of the year.

Since 2016 a systematic survey in Miramar, province of Buenos Aires, from April to November has been conducted by Fundación Cethus to establish the seasonality and habitat use of the species in the area. The peak of sightings occurred in August, with 194 whales, then declining towards November abruptly.

An aerial survey between Mar del Plata and Necochea to census and photo-identification SRWs was carried out. Thirteen whales in eight groups were sighted and many of them were photographed to create a SRW catalogue for the area.

MIT-02: develop and implement a strategy to minimise kelp gull harassment

Kelp gull (*Larus dominicanus*) attacks are a unique, increasing, and acute element of the life cycle of young SRW calves at PV. The physical injury of extensive gull lesions has been hypothesised to compromise the integrity and impermeability of a calf's surface layers and lead to dehydration, loss of thermoregulatory capacity, and an increased energy outlay to wound healing and metabolic stasis. Documented behavioural consequences of gull attacks include increased high energy reactive or flight behaviour and reduced time resting and probably nursing.

Researchers from the ICB and the OA have recorded the frequency of the attacks at different sites of PV annually since 1995 as a way to gauge the success of efforts to curb gull attacks. This is the longest database in the world on this parasitic behaviour (Maron *et al.*, 2015; Rowntree *et al.*, 1998; Sironi *et al.*, 2009).

ICB/OA monitored the attack frequency in September of 2015 and 2016. The following figure shows the annual frequency of gull attacks in Golfo Nuevo and Golfo San José since 1995.

A proposed hypothesis to guide the evaluation of the possible contribution of gull attacks to the ongoing calf mortality at PV states that 'high levels of harassment by kelp gulls that peck on a calf's exposed skin and then feed on the underlying blubber, cause significant physical injuries, energetically expensive avoidance behaviour, and reductions in suckling time. This syndrome may result in, *inter alia,* decreased food intake, increased energy expenditure, exhaustion, catabolism, dehydration, and thermoregulatory stress, with cumulative and cascading effects that can lead to calf death' (Thomas *et al.*, 2013). Gulls aim the vast majority of their attacks at newborn calves, which raises concerns about the impact that this parasitic behaviour has on the health and welfare of this highly sensitive age class.

Monitoring and controlling the gull harassment problem has become a joint initiative with NGOs and national research centers (CENPAT-CONICET) and government officials of Chubut Province.

Drone-derived measures of respiratory microbiome and girths: non-invasive indicators of right whale health

Understanding the relationship between health and environmental stressors is important for large whale conservation. However, robust measurements of health are challenging to acquire, but methodology to non-invasively assess the health of large whales is being developed. In 2015 we began a study to assess the health of SRWs at PV utilising drones to: (1) collect blow samples of the respiratory microbiome (the assemblage of microorganisms residing in the respiratory tract), which is the most common source of cetacean disease; and (2) acquire high resolution vertical images to assess body condition from girth (fat) levels and gull lesion markings. Using the drone APH-22 (Aerial Imaging Systems) with a high resolution still camera we took 1,220 vertical overhead images of 57 whales. The photographs will be used to take accurate measurement of length and width profiles for morphometric analyses, photo-identification and visual assessment of skin lesions. Using another drone (*Yuneec Typhoon/Tornado*) with sterile Petri dishes we collected 22 blow samples that were preserved in liquid nitrogen. Results of photographs and blow samples are still pending.

The study is a collaborative effort between ICB and the SRWHMP from Argentina and OA, Woods Hole Oceanographic Institution, NOAA SW Fisheries Science Center, and University of California, Davis from the USA.

PACB-01: develop a strategy to increase public awareness

On 20 and 21 April 2016 a responsible whale watching workshop was held promoting land-based whale watching in Miramar, province of Buenos Aires, as part of a joint project between Fundación Cethus and the Municipality of General Alvarado.

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Appendix 3

PROGRESS REPORT ON IUCN WESTERN GRAY WHALE ADVISORY PANEL (WGWAP) WORK FROM JUNE 2016 TO MAY 2017

R. Reeves, D. Weller, J. Cooke and G. Donovan

The Western Gray Whale Advisory Panel (WGWAP)[1], which is convened by the International Union for Conservation of Nature (IUCN), continued to provide advice to various parties, but particularly to Sakhalin Energy Investment Company (SEIC), concerning the gray whales that feed each summer off Sakhalin Island, Russia. Since SC/66b, there has been no major change in the Panel's composition and remit although a reduced budget has required scaling back the Panel's range of activities. Reeves and Donovan continue as Co-chairs and Cooke and Weller as members. IUCN and Sakhalin Energy have agreed to extend the WGWAP project for a third five-year tranche from 1 January 2017.

Three formal meetings took place between June 2016 and May 2017:

(1) 11th meeting of the Noise Task Force (NTF-11), November 2016 in Moscow, Russia;
(2) 17th meeting of the Panel (WGWAP-17), November 2016 in Moscow, Russia; and
(3) 12th meeting of the Noise Task Force (NTF-12), March 2017 in Gland, Switzerland.

Final reports of Panel and Noise Task Force (NTF) meetings are available on the WGWAP website. In addition, all recommendations made by the WGWAP and its predecessor IUCN western gray whale panels can be viewed on a searchable database[2].

The objectives of the 2016 and 2017 NTF meetings were: (1) review progress on analyses of data collected during the 2015 seismic survey; (2) receive updates on the proposed 2018 seismic survey and proceed with development of a Monitoring and Mitigation Plan (MMP); and (3) review non-seismic issues as time allowed. A major element of the NTF's work was a simulation analysis by Cooke of the implications of Sakhalin Energy's 2015 MMP to determine: (a) to what extent the mitigation measures contributed to reducing sonic exposure of gray whales; and (b) the effects on predicted exposure of the decisions that were made to relax certain measures that had been implemented in the company's 2010 seismic survey. The Panel recommended that Cooke carry out a similar analysis for the planned 2018 seismic survey once more details on timing, mode (streamer *vs* ocean bottom node) and other aspects are available.

The ongoing collaboration between the IWC and the WGWAP in 2016/17 led to further progress with model testing of gray whale stock identity hypotheses, updating and revision of scientific components of the IUCN/IWC Western Gray Whale Conservation Management Plan, and preparations for a western gray whale stakeholder workshop in early 2018.

Important new information was received at WGWAP-17 on gray whale observations in the western Pacific outside the Sakhalin feeding areas. There were reports of two dead gray whales in Japan in the spring of 2016 and a mother-calf pair of gray whales was photographed in Gizhiginskaya Bay (north-eastern Okhotsk Sea) in late June 2016. The Panel also received the report on acoustic data from the US Navy suggesting that small groups of gray whales are present annually in the East China Sea, moving southwards in the autumn and northwards in the spring that had been presented to the IWC Conservation Committee (Gagnon, 2016). Efforts are underway for independent confirmation of species identity by acoustic experts.

In its WGWAP-17 report, the Panel again emphasised the importance of regular updates to the population assessment and expressed appreciation for the work of the Russian Gray Whale Project (formerly the Russia-US Program), which has provided the long time-series of data used in Cooke's regular assessments. An updated assessment by Cooke is presented at this meeting (SC/67a/NH11).

The Panel expressed concern about an apparent long-term decline in amphipod biomass in the Piltun feeding area because of the implications for gray whale feeding. It recommended that the joint research programme of the two oil and gas companies (SEIC and Exxon Neftegas Limited) explore the nature and causes of this apparent decline in greater detail and provide a report on findings at the next Panel meeting.

In response to a proposal by Sakhalin Energy to increase the speed limit for its crew change vessels from 21 to 35 knots in areas outside the main feeding grounds, the Panel advised that from a conservation perspective, such an increase would be acceptable for a provisional period of 2 years, pending more refined estimation of the risk of ship strikes. The Panel recommended that within the provisional 2-year period, consideration be given to installing dashcams on each vessel that would monitor the sea surface area in front of the bows and that accelerometers be installed with continuous recording, or selective recording of large accelerations. The Company gave assurance that it would carry out the recommended monitoring to enable a risk analysis and also attempt to make the recommend installations on its vessels.

A collaboration between IUCN and the Project 'Mainstreaming Biodiversity into Russia's Energy Sector Practice and Policy' of the United Nations Development Programme (UNDP)/Global Environmental Facility (GEF)/ Ministry of Natural Resources and Ecology of the Russian Federation (MNR) resulted in a final document issued by UNDP titled 'Principles and Guidelines for the Monitoring and Mitigation of Impacts on Large Whales from Offshore Industrial Activity in Russian Waters'[3] for consideration by Russian authorities. This work was presented to Russian authorities immediately ahead of the November 2017 WGWAP meeting in Moscow.

Finally, the issue of gray whale entanglement in fishing gear continued to be a significant concern, as evidenced by a gray whale entangled in fishing gear (net and rope) sighted off Sakhalin in September 2016. An Associate Scientist (Vladimir Burkanov) was enlisted in 2016 to assist the Panel in preparation of a document for the attention of Russian fishery authorities and for submission to the Scientific Committee (see SC/67a/HIM17).

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[1] *http://www.iucn.org/western-gray-whale-advisory-panel.*

[2] *http://www.iucn.org/western-gray-whale-advisorypanel/recommendations.*

[3] *https://www.iucn.org/sites/dev/files/wgwap_17-28_final_undp_guidelines_clean_2016_en.pdf.*

SC/67B/AWMP/20 Rev1

Whaling in Chukotka from 2013 till 2017

Sergei V. Zagrebelnyy

INTERNATIONAL
WHALING COMMISSION

Whaling in Chukotka from 2013 till 2017

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ABSTRACT

During 2013-2017, whaling in Chukotka was conducted by sea-hunters from 9 communities (14 whaling settlements), but whaling only by people from 4 villages (Lorino, Inchoun, Lavrentiya, Uelen), which makes over 70% of the whaling limit. For the last 5 years the average catch per year is 123 gray and 1-2 bowhead whales. The average size of the gray whales from 2013 to 2017 varies from 9.4 up to 10.9 meters for females and from 9.4 up to 10.6 meters for males. Mostly young females are currently whaled – annually females make up 52% to 69% of the slaughtered animals. Whales caught on Chukotka's Arctic coast are statistically larger (by more than 1 meter) and fatter (by 30%) than the whales harvested on the eastern coast. The natives population of Chukotka has risen by 11% (in 2010 - 17,900; in 2015 - 19,140 people) since 2010 and also considering the biomass of the harvested whales being currently almost 2 times less than it was in the 1980s-1990s, so the needs of local people are not met.

KEY WORDS: gray whale, bowhead whale, whaling, Chukotka, traditional use, harvest

INTRODUCTION

At all times and under all circumstances, harvesting of marine mammals guaranteed survival and cultural continuity for Chukotka's indigenous people. Whale harvest in Chukotka has, at least, two thousand years of history. Thanks to traditional fishing and the use of whales and other marine mammals, Chukotka's natives were able to survive the economic collapse caused by Russia's transition to a market economy. However, this transition adversely affected the structure of the whaling industry.

In the 1980s and early 1990s (during the Soviet period), whaling was an integral part of the unified Soviet economy and was organized through state farms. Whaling itself was done from whaling ships (for example, vessel «Zvezdny»). The average weight of a whale in that period was nearly 18 tons. From 1991 to 1995, the government support was reduced to a minimum, state farms ceased to exist, people organized whaling brigades and communities, and turned to traditional methods of whaling using small boats (whaleboats and canoes; fig.1). All this accounted for the decrease in the average weight of the harvested whales by half (up to 8-9 tons), which continued until the early 2000s (Litovka, 2008). And the total biomass of the harvested whales before the decline in whaling in the 1990s was 2.7 times bigger than the biomass of the currently harvested whales (fig.2).

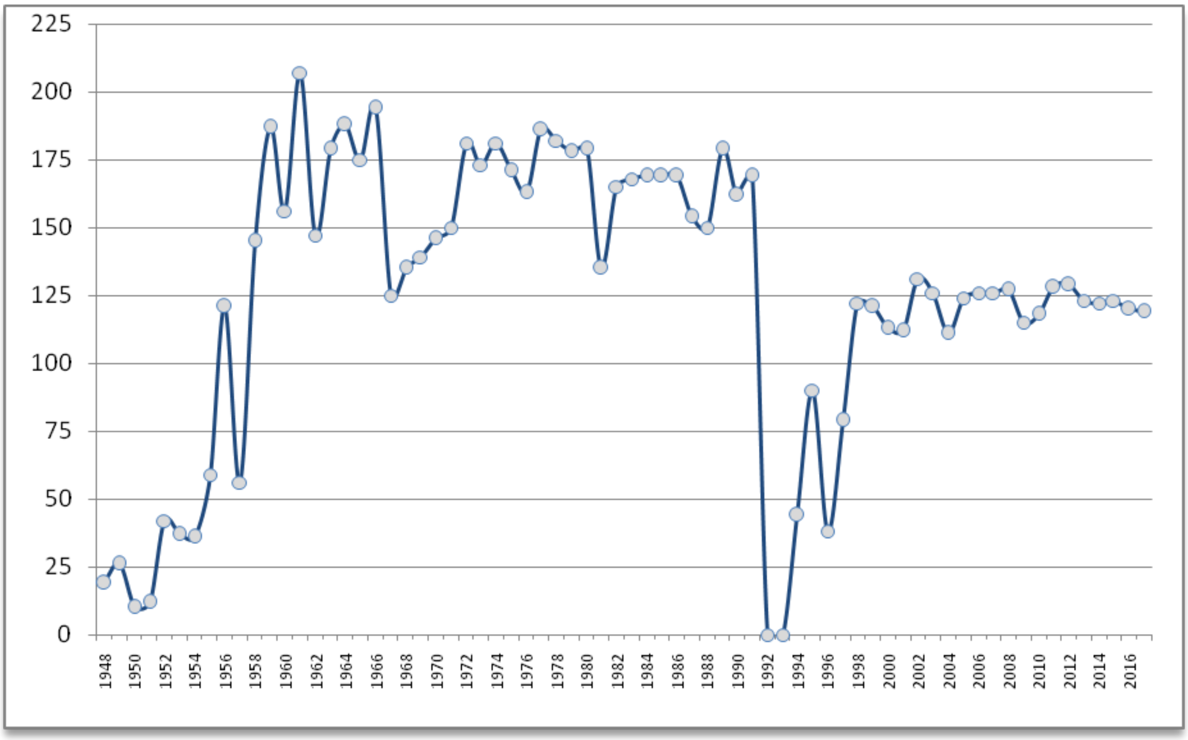

Figure 1. Total number of the harvested GW from 1949 till 2017

It is believed that the eastern (Californian-Chukchi) population of gray whales, inhabiting the Bering and Chukchi seas, has reached the optimum level. Despite this, the population size for as yet unexplained circumstances fell from 26,6 to 21 thousand individuals (Buckland et al., 1993; Gerber et al., 1999; Rugh et al., 2005; Blochin et al., 2011). According to the published data, the West-Arctic (Bering-Chukchi-Beaufort) population of bowhead whales is slightly more than 16,7 thousand individuals (Givens et al., 2013).

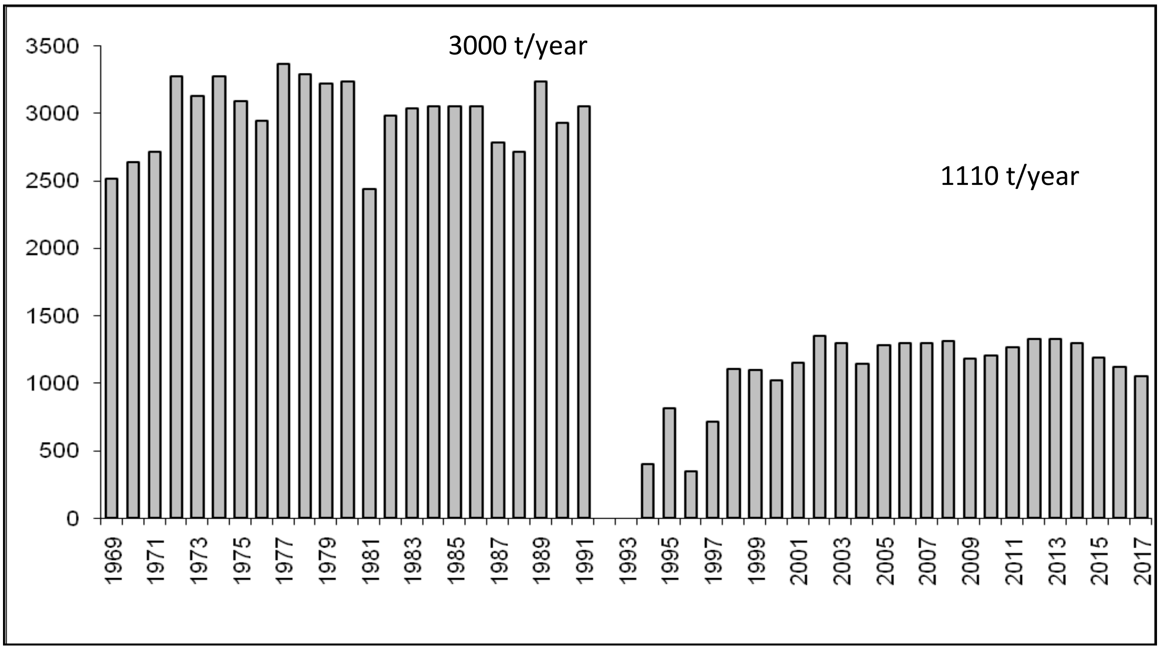

Figure 2. The total weight of the harvested gray whales

This is a total reserve of gray and bowhead whales shared by the Russian Federation and the United States. It serves as the basis for calculating the whaling ratio primarily to satisfy needs of Chukotka and Alaska’s natives.

In accordance with the decisions of the 65th Int.Whaling Commission’s session, the indigenous people of northern Russia (Chukotka Region) were given 6-year whaling quotas for the period of 2013-2018. The Russian share in the gray whales block quota is 135 heads per year (96.4%), 5 heads are given annually to the Maca tribe (Washington, USA). The Russian share of the bowhead whales is 5 heads per year (7.7%), and the US share is 60 bowhead whales. In total, Russia can harvest 720 gray and 30 bowhead whales within 6 years. As agreed by the Russian and American sites, it is possible to redistribute the quotas on gray and bowhead whales between them.

RESULTS

During 2013-2017, whaling in Chukotka region was conducted by sea-hunters from 9 communities (14 whaling settlements) in the traditional way: from canoes, whaleboats, and motor boats using rifles, American large-caliber darting guns, and rotary harpoons. Whaling was mainly done by people from 4 villages - Lorino (282 whales were caught during 5 years), Inchoun (60 whales), Lavrentiya (58 whales), Uelen (50 whales), which makes over 70% of the whaling limit. The other 10 settlements hunt from 1 to 7 animals per year each (fig.3).

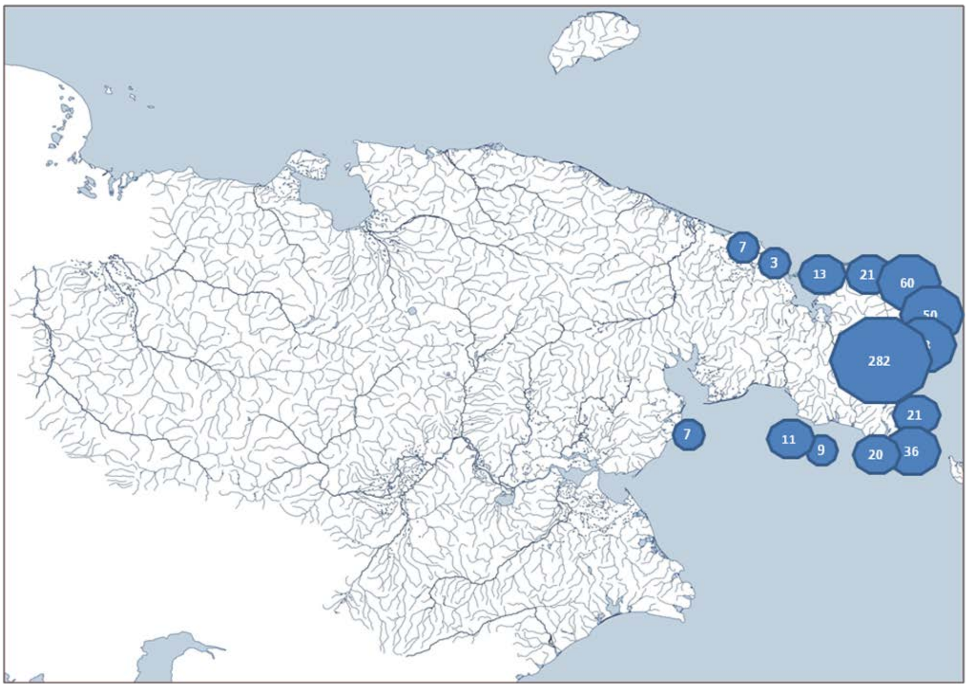

Figure 3. Gray whale harvest level

Until the early 1990s, more than 175 gray whales were harvested annually. For the last 5 years, it has been allowed to catch no more than 135 gray whales every year. Nevertheless, the average catch per year is 123 gray and 1-2 bowhead whales (not every year).

The annually harvested animals are mostly from 8 up to 10 meters long (fig.4, 5). The average size of the gray whales from 2013 to 2017 varies from 9.4 up to 10.9 meters for females and from 9.4 up to 10.6 meters for males.

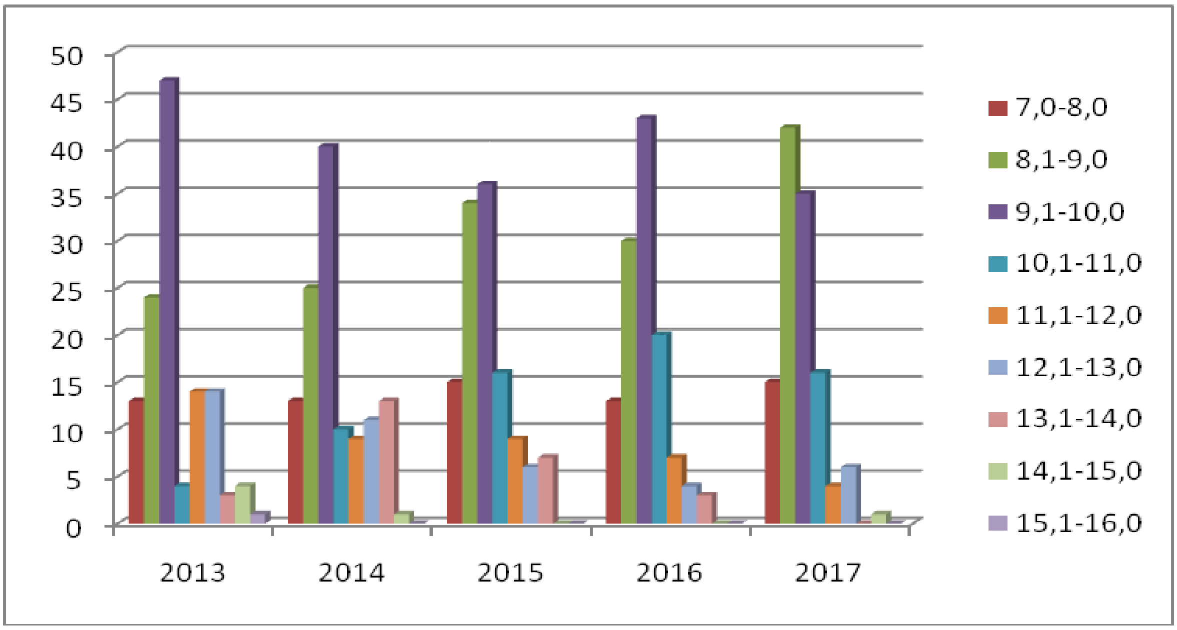

Figure 4. Length of harvested Gray whales

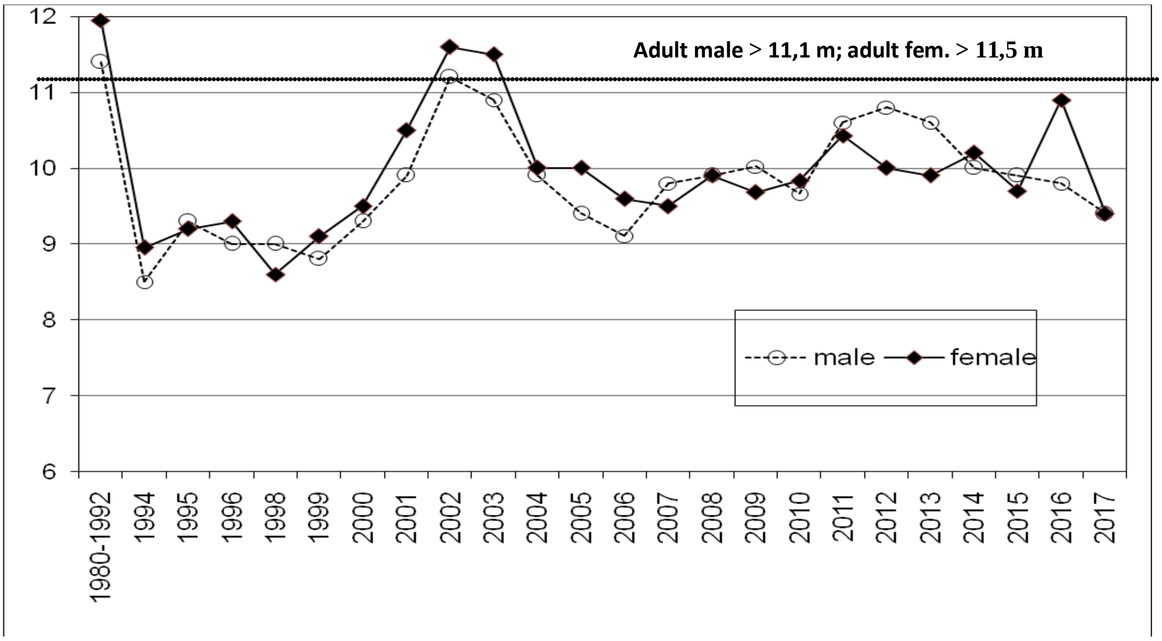

Figure 5. Average length of harvested gray whales

According to the data mentioned above, mostly young females are currently whaled – annually females make up 52% to 69% of the slaughtered animals. Adult animals (larger than 11 meters) constitute only a small part of the catch (fig. 6), and animals larger than 13-14 meters are rare (due to difficulty in whaling and transporting such large whales).

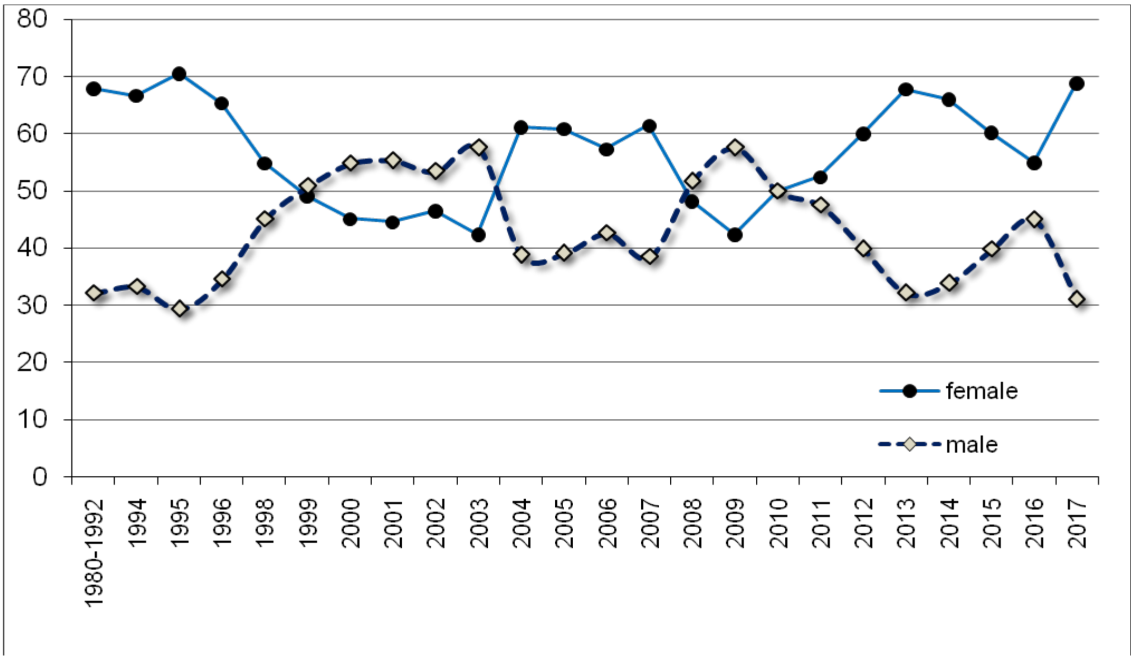

Figure 6. Sex ratio of harvested gray whales

Whales caught on Chukotka's Arctic coast are statistically larger (by more than 1 meter) and fatter (by 30%) than the whales harvested on the eastern coast (fig. 7). Probably, adult animals pass through the Bering Strait into the Arctic, and youngsters stay to feed near the eastern coast of Anadyr Bay.

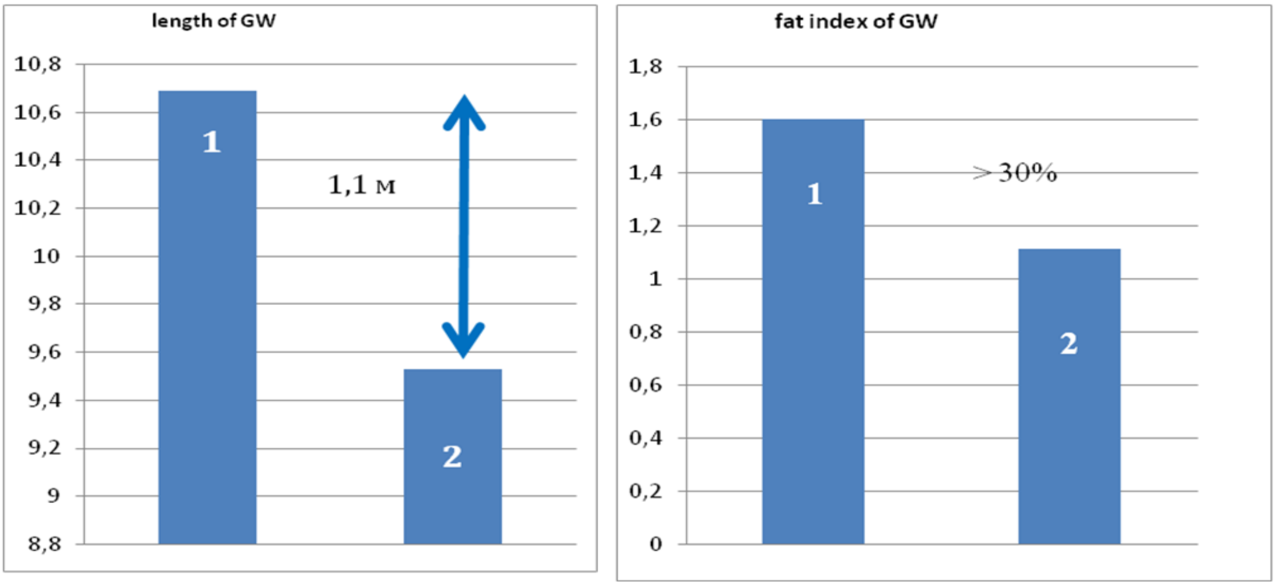

Figure 7. Average length and Fat Index of gray whales harvested in Arctic (1) and eastern shores (2) of Chukotka

Almost every year there are animals in the total catch of whales which are not taken into account in the quota (or subsequently excluded from the catch). These are animals lost due to aggressiveness or a sharp change in the weather during transportation of a whale ashore or because of their specific odor. In both cases, a relevant document is drawn (about the loss or disposal of the whale). From 2013 to 2017, five whales were lost and 4 harvested whales had specific odor.

From 2013 to 2017, four bowhead whales (2 females and 2 males) were harvested near Chukotka, mainly in Anadyr Bay. The average size of the whales was 14.5 meters (minimum 13.0, maximum 17.0 meters).

SUMMARY

- Despite planned whaling being over approximately 25 years ago, hunters continue to catch small, immature grey whales;
- basically immature female whales are harvested which suggests sex and age-based segregation of the grey whales group during the summer-fall period in the western Arctic;
- the size characteristics of the whales harvested on the Arctic coast of Chukotka are higher than of those caught on the eastern coast of the same region. It is quite possible that more mature whales migrate to the Arctic via the Bering Strait compared to those remaining in Anadyr Bay although we do not exclude the possibility of our mistake;
- the current grey and bowhead whales harvesting in Chukotka is below a maximum of the sustainable level recommended by the IWC Scientific Committee for both whale species. The natives population of Chukotka has risen by 11% (in 2010 - 17,900; in 2015 - 19,140 people) since 2010 and also considering the biomass of the harvested whales being currently almost 2 times less than it was in the 1980s-1990s. That is why subsistence needs of aboriginal population are not satisfied.

ACKOWLEDGEMENTS

We are grateful for the support and assistance provided by the Department of Natural Resources Chukotka Governments and members of the indigenous communities also.

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The Gray Whale

Eschrichtius robustus

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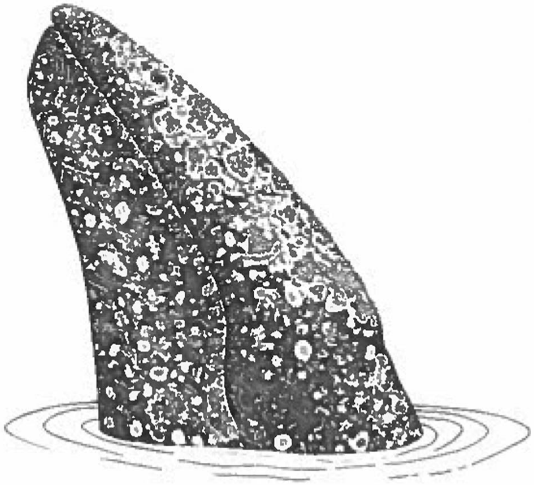

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24

Dive Characteristics and Movements of Radio-Tagged Gray Whales in San Ignacio Lagoon, Baja California Sur, Mexico

James T. Harvey and Bruce R. Mate

Introduction

The study of baleen whale biology has traditionally relied on collected specimens or observations of individual whales for short periods of time. Continuous long-term observations of whale behavior and activities are infrequent because individuals are difficult to identify, can travel long distances underwater without detection, and may remain at the surface only for short periods. Recent radio miniaturization and attachment techniques have provided an alternative mechanism for continuous (24-hr) tracking of specific whales traveling great distances.

Gray whales, *Eschrichtius robustus*, are excellent subjects for the attachment of radio tags because they travel near shore and may occupy confined embayments during

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winter. These animals tolerate large numbers of epizoic organisms and thus appear to be adapted to foreign objects in the skin. Additionally, in the breeding and calving lagoons of Baja California Sur, Mexico, some "inquisitive" gray whales can be closely approached (Gilmore, 1961). Gray whales, however, are less than ideal animals for radio-tagging studies because they rub against the seafloor while feeding and against each other during mating and raising of the young, thus increasing the chances of displacing an attached tag.

Recent studies of gray whales in Baja California have been conducted in Ojo de Liebre and Guerrero Negro lagoons (Rice *et al.*, 1981), San Ignacio Lagoon (Swartz and Cummings, 1978; Swartz and Jones, 1979, 1980, Chapter 14, this volume) and in Bahia de Magdalena (Norris *et al.*, 1977; Chapter 15, this volume). These studies did not concentrate on dive and surface patterns. Previous tagging efforts with gray whales involved the use of belly bands attached to restrained calves (Norris and Gentry, 1974) and a radio tag surgically sutured to a captive yearling (Evans, 1974; Sweeney and Mattsson, 1974).

The purpose of our study was to collect long-term information on the dive and surfacing characteristics and local movements of individual radio-tagged gray whales in San Ignacio Lagoon, Baja California Sur, Mexico.

Methods

San Ignacio Lagoon (26°50′N, 113°10′W) is a relatively small protected area and offers the possibility of closely approaching "inquisitive" whales, those which approach boats and often allow themselves to be touched. Two camps were established to monitor the activities of tagged whales. The base camp was located approximately halfway up the eastern shoreline of the lagoon, and the second camp was placed on Bronaugh Point on the north shore of the lagoon entrance (Fig. 1). The lagoon was arbitrarily demarcated from the ocean by a line between Bronaugh and Holcomb Points roughly approximating the position of the breaking surf.

The radio tag and its method of application have been described by Mate *et al.* (1983). The radio transmitters were 3.8 × 3.6 × 2.5 cm and transmitted pulsed signals between 148 and 149 MHz. Radio tags transmitted on one of six different frequencies with pulsed signals at one of six different rates. The tag was suspended from a tag applicator at the end of a 5-m pole; therefore, only whales within 3 m of the boat could be tagged. We only attempted to tag inquisitive whales because our previous experiences indicated it was difficult to closely approach other whales.

Tags were placed 1–2 m behind the blowhole on the middorsal line such that, at most surfacings, the tag's antenna was exposed and signals could be transmitted. Each tagged whale could be distinguished by its combination of signal frequency and transmission rate. A tagged whale could breathe without a signal being transmitted only when it raised its head vertically out of the water, which is a rare event.

From February 8 through March 20, 1980, radio-tagged whales were monitored

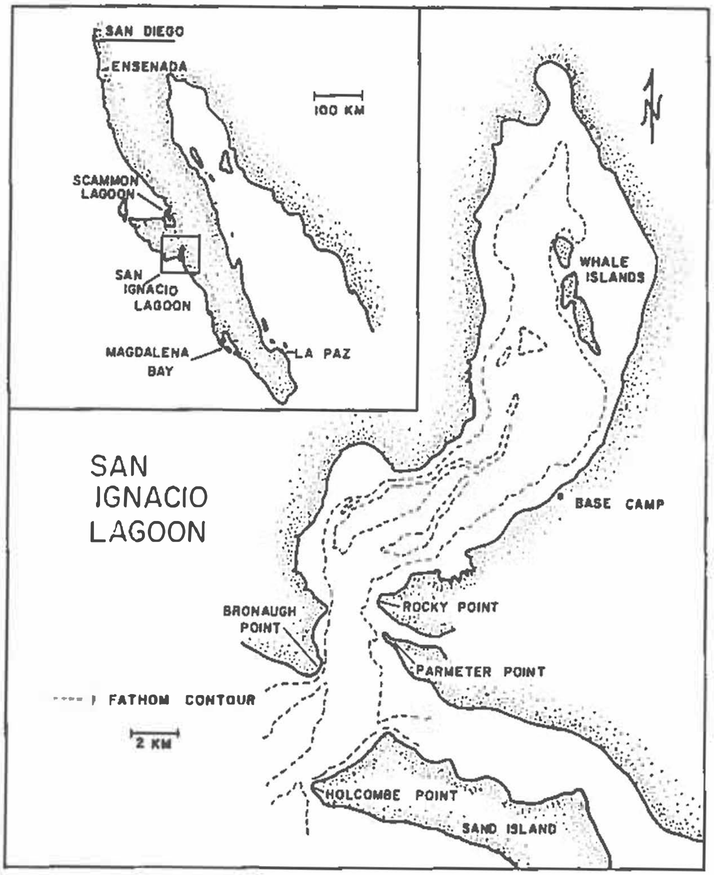

Fig. 1. *San Ignacio Lagoon, Baja California Sur, Mexico was the location of all tagging activities. A base camp and field camp at Bronaugh Camp were established to monitor radio-tagged whales. The lower lagoon was arbitrarily demarcated from the ocean by bearings originating from Bronaugh Point to Holcombe Point.*

from four platforms; base camp, Rocky Point, Bronaugh Point, and by boat. Rocky Point served as the monitoring location March 18–20 and Bronaugh Point was used from March 21 through the completion of the field season on April 29. At the base camp and Bronaugh Point, two 14-element yagi antennas were mounted perpendicularly to each other and separated vertically by 1 m on a 10-m mast. A switch box allowed reception from either antenna or both. Maximum reception range for these antennas was approximately 10 km. A direction finding (DF) antenna also was mounted on top of a 6-m mast and provided information on the bearing of the radio tags up to 10 km from camp. Handheld 2-element Yagi antennas and DF antennas were used for receiving signals while monitoring from boats. Each morning, afternoon, and evening, checks were made for tagged whales from the land camps. Weather permitting, daily boat surveys also were made to locate radio-tagged whales. During such times that a tagged whale was

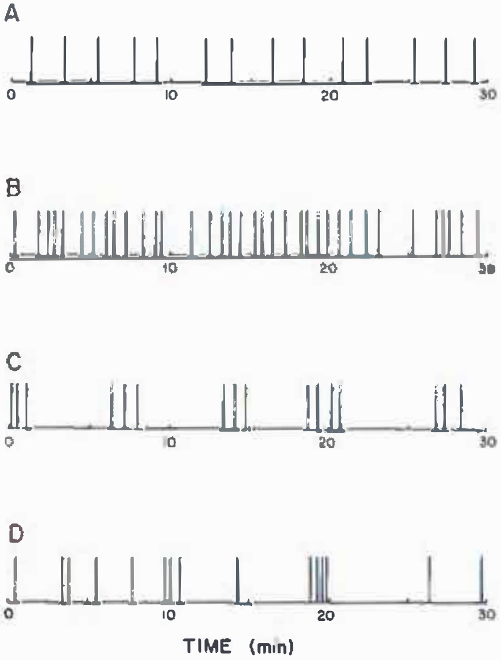

Fig. 2. *Examples of three dive patterns (from Whale 100R) which are typical of gray whales in San Ignacio Lagoon. (A) Regular–long, (B) regular–short; (C) clumped. The irregular or unpatterned dive series is shown in (D). Each vertical line represents a series of signals received when a whale surfaced.*

within monitoring range of the camps, nearly continuous data were collected on its activities.

As a whale surfaced, the times of the first and last signal received were recorded. Dive duration was defined as the time between the last audible signal during a surfacing and the first signal pulse upon resurfacing. Surface duration was defined as a period of continuous signal pulses. Relative signal strength was noted (strong, moderate, weak, or very weak). Records of very weak signals were not analyzed. The bearing of a tagged whale was determined approximately every 2 hr. Visual observations of tagged whales were made opportunistically from boats or 6-m observation towers at the shore camps.

Idealized diving and surfacing patterns were modeled (with the assistance of Fred Ramsey and Richard Hanlen) for each of three discernible patterns as a first-order Markov process, using transition matrices. The three patterns used were (1) "regular–long," regularly spaced dives greater than 1 min in duration; (2) "regular–short," dives less than 1 min in duration; and (3) "clumped," a long dive of greater than 1 min followed by two to six shorter dives of less than 1 min each (Fig. 2). W. Watkins (personal communication) has used the term "clustered" for a pattern similar to our "clumped." In addition, an irregular or unpatterned catch-all category was established for dives that did not fit the criteria of the other patterns. The dive pattern data were summarized from a series of seven dives at a time. A computer program calculated the probability that an observed series of dives fit a particular pattern by comparing the series of seven dives with the modeled, idealized dive patterns.

Results

DIVE AND SURFACE DURATIONS

Ten gray whales were radio tagged and tracked in San Ignacio Lagoon in 1980; three single adults (two females, one of undetermined sex) were tagged in early February, and the remaining seven whales were females with calves tagged between early March and mid-April (Table I). All remained in the lagoon at least 2 days. One female with calf (100R), tagged on March 19, lost her tag after 11 days (154.3 hr of monitoring). This animal was seen in the lagoon on 3 separate days subsequent to tag loss. Two other whales were monitored 4 and 5 days each during mid-March and early April. Seven of the tagged whales were later relocated along the Baja California and California coasts (Chapter 25, this volume), indicating that the tags had remained attached after the whales left the lagoon (Table I).

Duration of dives and surfacings were determined for radio-tagged gray whales monitored for a total 303.7 hr. Mean dive duration was 1.57 ± 0.02 min (SE) ($n = 11{,}080$ dives). Fifty-one percent (5,651) of these dives were less than 1 min duration, and 99% (10,969) were less than 6 min (Fig. 3). The mean dive duration for 5,455 dives longer than 1 min duration was 2.71 ± 0.03 min (Table II).

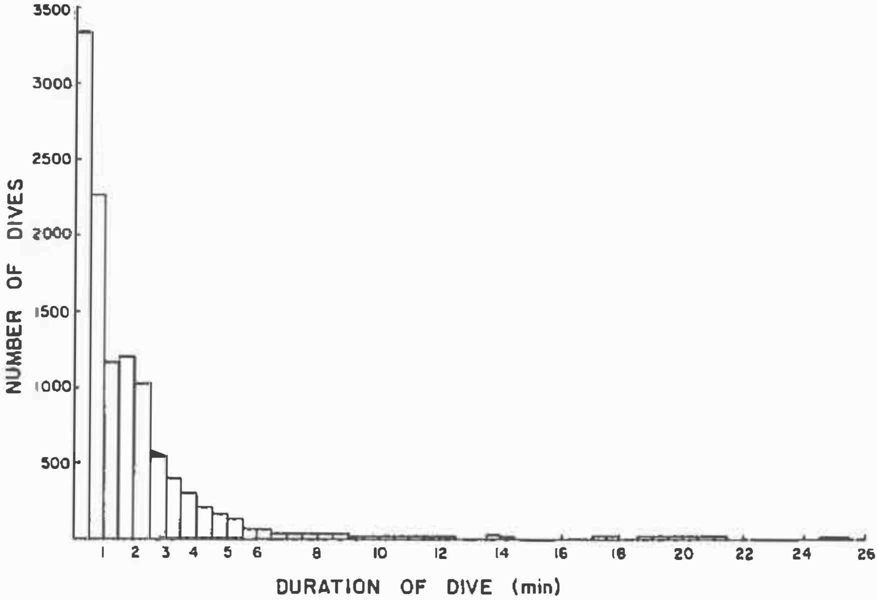

Fig. 3. *The frequency of distribution of 11,080 dive durations from 10 different radio-tagged whales monitored for 303.7 hr in San Ignacio Lagoon. The mean is 1.57 ± 0.02 (SE) min.*

Table I
Identification Number, Description, Radio Frequency, Tagging Date, Monitoring Time, and Duration of Tag Retention for 10 Gray Whales Radio Tagged in San Ignacio Lagoon, Baja California, Mexico (1980)

Whale I.D.	Whale description	Tag frequency (MHz)	Tagging date	Time monitored in lagoon vicinity (days)	Time monitored in lagoon vicinity (hr)	Known duration of tag retention (days)
50Y	Single adult	149.050	Feb. 8	2	8.0	7
80Y	Single female	149.080	Feb. 11	2	20.0	40
160Y	Single female	149.160	Feb. 11	1	1.6	50
50R	Female with calf	149.050	Mar. 18	5	29.6	19
100R	Female with calf	149.100	Mar. 19	11	154.3	13
120R	Female with calf	149.120	Apr. 5	4	47.2	4
140R	Female with calf	149.140	Apr. 9	1	3.1	1
50B	Female with calf	149.050	Apr. 11	2	7.1	16
160R	Female with calf	149.160	Apr. 11	2	10.9	20
80R	Female with calf	149.080	Apr. 14	2	21.6	13
				32	303.7	

Table II
Mean and Maximum Dive and Surface Durations for 10 Radio-Tagged Gray Whales in San Ignacio Lagoon[a]

Whale I.D.	Dive duration (min)			Dives > Min		Surface durations (min)		
	n	$\bar{x}$ ± SE	Maximum	*n*	x ± SE	*n*	x ± SE	Maximum
50R	1,066	1.63 ± 0.04	8.63	665	2.33 ± 0.05	1.091	0.04 ± 0.01	0.18
50B	444	0.96 ± 0.05	7.68	102	2.28 ± 0.13	450	0.02 ± 0.01	0.35
80Y	388	2.58 ± 0.21	25.88	160	5.74 ± 0.40	392	0.50 ± 0.20	51.62
80R	1.043	1.21 ± 0.04	8.83	433	2.27 ± 0.06	1,053	0.03 ± 0.01	0.40
50Y	276	1.69 ± 0.16	12.28	94	4.24 ± 0.34	278	0.05 ± 0.01	0.15
100R	5,788	1.51 ± 0.02	16.27	2,893	2.59 ± 0.03	5,862	0.08 ± 0.01	12.13
120R	1,595	1.74 ± 0.04	11.90	835	2.86 ± 0.05	1,615	0.04 ± 0.01	0.75
140R	93	1.95 ± 0.14	6.22	65	2.54 ± 0.14	95	0.03 ± 0.01	0.07
160Y	45	2.04 ± 0.21	5.70	35	2.43 ± 0.23	46	0.06 ± 0.02	0.97
160R	342	1.87 ± 0.10	11.27	173	3.20 ± 0.13	347	0.03 ± 0.01	0.07
	11,080	1.57 ± 0.02	25.88	5,455	2.71 ± 0.03	11,229	0.07 ± 0.01	51.62

[a] Including separate analysis of dives longer than 1 min.

Table III
Summary of Dive Data Collected from Whale 100R

Date	Time monitored (hr)	Total surface time (hr)	Total dive duration (hr)	n	Mean dive duration (min)	Time at surface (%)
Mar. 19	2.26	0.06	2.21	94	1.14	2.7
Mar. 20	9.56	0.35	9.21	349	1.58	3.7
Mar. 23	14.7	0.77	13.93	529	1.58	5.2
Mar. 24	12.3	0.36	11.99	457	1.57	2.9
Mar. 25	15.45	1.38	14.07	509	1.66	8.9
Mar. 26	16.00	0.92	15.08	657	1.38	5.8
Mar. 27	20.38	0.96	19.42	778	1.50	4.7
Mar. 28	16.49	0.84	15.65	675	1.39	5.1
Mar. 29	14.30	0.31	13.99	527	1.59	2.2
Mar. 30	13.79	0.56	13.23	536	1.48	4.1
Mar. 31	12.01	0.64	11.37	469	1.45	5.3
	147.3[a]	7.15	140.15	5580	1.51	4.9

[a] Does not include 7 hr of data collected during periods of less than 10 min duration.

Mean dive durations for individual whales ranged from 0.96 to 2.58 min with a maximum dive duration of 25.88 min (Table II). Means for dives longer than 1 min ranged from 2.27 to 5.74 min. Whale 100R, for which we have the most data, was monitored for 154.3 hr and had a mean dive duration of 1.51 ± 0.02 min. Mean daily dive durations for 100R ranged from 1.14 to 1.66 min (Table III). The mean dive duration for single whales (50Y, 80Y, and 160Y) was generally longer than that of females with calves. No significance was attached to these data because a model is currently being generated to analyze the skewed distribution of duration of dives.

The mean surface duration for all 10 tagged whales was 0.07 ± 0.01 min (or 4.4 ± 0.6 sec). The maximum continuous surface duration was 51.62 min (whale 80Y). Mean duration per surfacing for individual whales ranged from 0.02 min (whale 50B) to 0.50 min (whale 80Y) (Table II). Overall, tagged whales spent 4.5% of the time at the surface (i.e., percentage of total time monitored that the antenna was above the water's surface). The percentage of time spent at the surface varied from 1.5 (whale 140R) to 16.3% (whale 80Y).

The mean rate of surfacing for tagged whales was 35.6 ± 0.8 surfacings/hr (Table IV). These were quite variable among individuals and ranged from 19.4 to 62.5 surfacings/hr. Gray whales surfaced significantly more often during the day ($x = 37.1 \pm 1.3$ surfacings/hr) than at night ($x = 30.3 \pm 1.5$ surfacings/hr) [$t(.05, 200) = 4.33$, $p < .05$]. The variation in surfacing rate was great among all 10 animals, and mean surfacing rate was not significantly different between morning, midday, and afternoon (weighted ANOVA, $p > .05$).

SURFACING PATTERNS

Surfacing patterns were analyzed for tagged whales 100R and 120R. During 30.07 hr of analyzed surfacing patterns, whale 100R surfaced 1108 times. Forty-five percent of

Table IV
Mean Rate of Surfacing (±SE) for 10 Radio-Tagged Gray Whales at Different Times of the Day[a]

	Mean surfacings/hr (*n*)					
Whale I.D.	(0600–1900) day	(1900–0600) night	(0600–1100) morning	(1100–1500) midday	(1500–1900) afternoon	Total
120R	33.7 ± 0.6 (20)	31.6 ± 0.5 (14)	33.25 ± 1.4 (8)	34.7 ± 0.8 (8)	32.5 ± 1.2 (4)	32.9 ± 0.5 (34)
100R	36.5 ± 0.6 (81)	37.0 ± 0.9 (27)	37.1 ± 1.0 (26)	36.5 ± 1.2 (27)	36.1 ± 1.3 (28)	36.7 ± 0.5 (108)
100Y	—[b]	34.0 ± 1.0 (7)	—	—	—	34.0 ± 0.6 (7)
80Y	22.0 ± 0.5 (7)	16.0 ± 1.4 (9)	25.0 ± 0.7 (4)	—	18.0 ± 0.8 (3)	18.6 ± 0.7 (16)
80R	51.4 ± 1.3 (10)	43.8 ± 0.3 (5)	57.8 ± 2.5 (5)	49.0 ± 2.0 (2)	42.3 ± 0.7 (3)	48.9 ± 0.9 (15)
50R	38.3 ± 0.6 (6)	30.2 ± 0.8 (6)	38.3 ± 1.2 (4)	38.5 ± 1.3 (2)	—	34.3 ± 0.3 (12)
160R	33.3 ± 0.5 (3)	32.3 ± 0.2 (3)	—	—	33.3 ± 0.9 (3)	32.8 ± 0.3 (6)
50B	67.0 ± 1.7 (3)	36.0 (1)	—	—	67.0 ± 3.0 (3)	59.3 ± 1.6 (4)
	37.1 ± 1.3 (130)	30.3 ± 1.5 (72)	36.9 ± 1.8 (47)	36.9 ± 7.4 (39)	36.6 ± 12.9 (44)	35.6 ± 0.8 (202)

[a] Number in parentheses is the number of hour intervals.
[b] No data.

Table V
Amount of Time and Number of Surfacings for Specific Surfacing Patterns from Two Radio-Tagged Gray Whales in San Ignacio Lagoon[a]

	Surfacing patterns				
	Clumped	Regular–Long	Regular–Short	Unpatterned	Total
Whale 100R					
Time in hr*	8.72	6.62	1.20	13.53	30.07*
Surfacings**	321	211	111	465	1108**
Whale 120R					
Time in hr*	7.94	8.34	1.59	21.85	39.72*
Surfacings**	368	284	134	869	1655**

[a] The total time and number of surfacings for each whale is in parentheses.
*Significant difference ($\chi^2 = 31.43$, $p < .05$).
**Not significant ($p > .05$).

the time (42% of the surfacings) the surfacings did not fit one of the previously described patterns (Table 5). The "clumped" pattern (Fig. 2) was most frequently observed for this whale: 29% (321) of the surfacings and 29% (8.72 hr) of the total time were represented by this pattern. The "regular–long" pattern was the second most common pattern, occurring 22% (6.62 hr) of the time and representing 19% (211) of the surfacings. The "regular–short" pattern occurred only 4% of the time (1.20 hr), or 111 dives.

Whale 120R surfaced 1655 times during the 39.72 hr analyzed for surfacing patterns. Forty-four percent of these surfacings fit into one of the three recognized patterns. The "regular–long" pattern of surfacings was recorded 21% (8.34 hr) of the time, and the "clumped" pattern occurred 20% of the time (7.94 hr). As with whale 100R, "regular–short" surfacing patterns were only observed 4% of the time (1.59 hr) (Table V). There was a significant difference between whales for the amount of time spent in each pattern ($\chi^2 = 31.43$, $p < .05$), but no difference was found for number of surfacings per pattern ($p > .05$).

LOCAL MOVEMENTS

Movements of three tagged females with their calves were monitored for the 4,5, and 11 days, respectively, that each pair remained in the lagoon vicinity after tagging. Female 120R and her calf were monitored for 4 days. They moved out of the lagoon during darkness (between 0100 and 0500) on two separate occasions, for 40 and 7 continuous hr, respectively, before returning to the lagoon. Whale 50R was monitored for 5 days in the vicinity of the lagoon; this whale moved out of the lagoon twice at 0100, for 2 and 8 hr, respectively.

The greatest amount of movement information was collected from whale 100R, who was monitored for 11 days. This whale and her calf went outside the lagoon on 7 occasions (Table VI). Six of these exits occurred in darkness between 1800 and 2300, and six of seven returns to the lagoon occurred during daylight. This whale moved out of

Table VI
Location and Activities of Whale 100R within the Vicinity of San Ignacio Lagoon[a]

Date	Time	Tidal current	Locations, activities, and comments
Mar. 19	1200	Ebbing	Tagged near Parmeter Point; stayed in area of Rocky Point until 2400
Mar. 20	0220	Ebbing	Animal near mouth of lagoon
	0300	Ebbing	Moving toward lagoon mouth
	0900	Flooding	Moving up lagoon from lagoon mouth
	1000	Ebbing	Sighted near Rocky Point
	1700	Low tide	0.5 m north of Rocky Point
Mar. 21	—	—	—
Mar. 22	—	—	—
Mar. 23	0730	Ebbing	Animal near mouth of lagoon
	1115	Flooding	Moving up lagoon toward Rocky Point
	2300[b]	Low tide	Moved out of lagoon
Mar. 24	0910	Ebbing	Offshore, in vicinity of lagoon mouth
	1140	Low tide	Offshore
	1600[c]	Flooding	Entered lagoon
	1800	High tide	Sighted off Bronaugh Point
Mar. 25	0500	High tide	Near Rocky Point
	1200	Low tide	Approached our boat near Rocky Point
	1800	High tide	Near Rocky Point
	2245	Ebbing	Near Rocky Point
Mar. 26	0525[b]	High tide	Offshore, near lagoon mouth
	0750[c]	Ebbing	Between Sand Island and Bronaugh Point
	1700	Flooding	Moved north, near Rocky Point
	1900[b]	High tide	Offshore
	2350	Low tide	Offshore
Mar. 27	0700	High tide	Offshore
	1330[c]	Low tide	Moved into lagoon
	1400	Flooding	1 km offshore Bronaugh Point in lagoon
	1700	Flooding	Near Rocky Point
Mar. 28	0500[b]	Flooding	Offshore
	0800[c]	Ebbing	Moved into lagoon
	1600	Flooding	Near Parmeter Point
	1700	Flooding	Near Rocky Point
	2100[b]	Ebbing	Moved offshore just after high tide
Mar. 29	0150	Low tide	Offshore
	0500[c]	Flooding	Moved into lagoon
	1400[b]	Low tide	Offshore
	1900	Flooding	Offshore
Mar. 30	0800[c]	High tide	Inside lagoon, near mouth
	1140	Ebbing	Between Bronaugh and Parmeter Points
	2040	High tide	Near Rocky Point
Mar. 31	0220[b]	Low tide	Offshore
	0650[c]	Flooding	Entered lagoon
	1230	Ebbing	Near Rocky Point
	1344	Ebbing	Animal lost transmitter

[a] Selected times are presented to depict movements of the whale, although monitoring was often continuous.

[b] Movement out of the lagoon.

[c] Movement into the lagoon.

the lagoon against the tide 44% (three times) of the time. In general, there was no significant relationship between whale movements out of the lagoon and ebbing tides ($\chi^2 = 1.2$, $p > .05$).

Discussion and Conclusions

DIVE AND SURFACE DURATIONS

Wyrick (1954) and Evans (1974) reported maximum dive durations for migrating gray whales of 12 and 16.5 min, respectively. The maximum recorded dive duration for a gray whale tagged in San Ignacio Lagoon was 25.9 min. All dives longer than 12 min in the lagoon were associated with resting animals, typified by a whale floating at or slightly below the water surface for periods up to 51.6 min and then submerging for 12–26 min. These dive and surface durations are 2 to 250 times greater than those recorded for active whales and are not expected to be the same for traveling animals.

The average surfacing rates for tagged adult whales indicated a breathing rate of approximately 36 breaths per hr. Norris *et al.* (1977) recorded a breathing rate of 50 breaths/hr for one female gray whale with a calf in Bahia de Magdalena. Although tagged whales made from 16.0 to 67.0 surfacings/hr (Table IV), our large sample size of surfacings and the certainty of detection of tagged whale signals suggests that a breathing rate of 36 breaths/hr is representative of gray whale activities in the lagoon.

Surfacing rates and surface durations are useful statistics in developing sightability correction factors for surveys. Many factors affect the sightability of a whale, such as weather, area covered, speed of sighting platform, and whale species and behavior. One important factor in sightability is the amount of time a whale is visible; radio tags can be used to estimate this time.

Surfacing rates of tagged whales were generally consistent throughout the day. Lower surfacing rates (15–20 surfacings/hr) appeared to be associated with resting animals and not with animals actively diving for long times. Swartz and Jones (1980) reported a midday reduction in whale activity, based on movements of whales in front of their observation tower. Tagged whale activity was not reduced in the midday using surfacing rates as an index.

Radio tags attached to whales can provide information on their behavior. Long dive durations, extremely long surface durations, and low surfacing rates were observed for whales resting at the surface. Whale 80Y, which had the longest average dive duration (2.58 min) and lowest surfacing rate (18.6 surfacings/hr) was found to be resting for 7 of the 20 hours that this whale was monitored. Surfacing patterns for other whales indicated resting periods up to 4 hr duration. Short average dive and surface durations and high surfacing rates were indicative of directed swimming. Whale 50B swam at a moderate speed (4 km/hr) for 2 of 7 hr monitored; he/she had an average dive duration of 0.96 min and a surfacing rate of 59.3 surfacings/hr. In the future, additional visual observations of behavior with data collected from radio tags attached to whales may allow further correlations between whale behavior and signal patterns from tags. The signal patterns from radio tags on whales then may allow continuous collection of behavioral information day and night, in bad weather, and when the whale is out of view.

SURFACING PATTERNS

The clumped surfacing pattern described in this study has been documented for migrating gray whales (Wyrick, 1954; Gilmore, 1961; J. Sumich, personal communication) and for whales occupying the breeding and calving lagoons (Norris *et al.*, 1977; Swartz and Jones, 1979). The regular pattern, however, has not been previously reported. This pattern occurred approximately 20% of the time and was observed almost as frequently as the clumped pattern. The regular surfacing pattern was probably a consequence of the behavior associated with lagoon residency. Whales in the lagoon, especially females with calves, spent many hours milling within the lagoon oriented into the current and remaining fairly stationary or resting. The regular surfacing pattern may therefore be a product of this inactive period.

LOCAL MOVEMENTS

Swartz and Jones (1980) observed gray whale movements from a tower positioned at Rocky Point in San Ignacio Lagoon. They reported a preponderance of whales moving northward into the upper lagoon areas in the morning; the predominant direction of travel in the afternoon was southward toward the lagoon entrance. These observations were made approximately 6 km from the lagoon entrance, so the observors could not determine if the whales actually moved out of the lagoon. Our study supports their observations; radio-tagged whales generally left the lagoon during the night and returned in the morning hours. Swartz and Jones (1980) also found that gray whales moved with the direction of the tide, especially in the shallow upper lagoon. The movement of radio-tagged whales out of the lagoon did not significantly coincide with tidal flow. They did, however, move with more often than against the tide.

The reason for nighttime movements of gray whales out of the lagoon is not known at this time. Swartz and Jones (1980) suggested that aggregations of shrimp, which occur near the lagoon mouth at night, may provide a food source for whales. Examination of two stranded yearling gray whales in the lagoon did not reveal evidence of shrimp predation, however (J. Harvey, unpublished data).

LAGOON RESIDENCY

Tagged whales in general did not remain in the lagoon for extended periods of time. Seven tagged whales were later located by radio signals along the Baja and California coasts, indicating the tags had remained attached beyond monitoring periods in the lagoon. The short residence time for single tagged whales was expected, because single animals appear to be somewhat transitory and use the upper lagoon only infrequently (Swartz and Jones, 1979). The peak abundance of females with calves in the lagoon occurs from mid-March to early April (Swartz and Jones, 1980). The three tagged females with calves, which remained in the lagoon for the longest time, were tagged during this period. By April, whales begin to leave the lagoon and move northward. The last four whales tagged (April 9–14) left the lagoon after 1–2 days, presumably commencing their northward migration.

The short residence time in the lagoon and daily movements for many of the tagged whales suggest that there is a considerable turnover in the lagoon population. Estimates of whale abundance in San Ignacio Lagoon fluctuated between consecutive daily counts (Swartz and Jones, 1980). This implies that some whales may be continuously moving out of the lagoon while others replace them. Estimates of the total number of whales using a particular lagoon, therefore, cannot be made simply from visual counts. Further tagging studies may help in developing turnover rates, which will allow the number of whales using a lagoon to be calculated based on visual surveys.

Radio tags attached to whales can provide a large amount of information on whale behavior that can be very difficult or impossible to collect using other techniques. The potential data which can be gathered is expanded to include 24 hr (continuous) observations during bad weather and when the whale is out of visual range. The coupling of visual observations of whale behavior with reception of radio-tag signals can be used to develop profiles of surfacing behavior for whales throughout the day. Additionally, radiotelemetry can collect physiological and hydrographic data as long as the tags remain attached.

Dive and surface durations and surfacing rates may be used to calculate sightability correction factors for cetaceans. Knowledge of time spent at the surface and the rate of surfacings may provide better estimates of whale abundance.

Summary

Ten gray whales, *Eschrichtius robustus*, were radio tagged and monitored in San Ignacio Lagoon, Baja California Sur, Mexico, from February 9 to April 15, 1980. Mean duration of dive for individual whales varied from 1.0 to 2.6 min ($\bar{x}$ = 1.6 ± 0.02 min). Ninety-nine percent of the 11,080 dives recorded were less than 6 min and 49% less than 1 min in duration. The longest dive was 25.9 min. Tagged whales averaged 4.4 ± 0.6 sec at the surface per surfacing. Eight of the tagged whales averaged less than 2.9% of the time at the surface (range, 1.56–16.3%). The tagged whales averaged 35.6 surfacings per hr. Three surfacing patterns were documented (regular–long, regular–short, and clumped) which accounted for approximately one-half of all dive sequences analyzed for two whales. Three radio-tagged whales were monitored for 4, 5, and 11 days, and moved into the ocean on 2, 2, and 7 occasions, respectively. Most oceanic movements were at night and 40% were against the tide. Seven of the tagged whales did not remain in the lagoon for more than 2 days.

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REACTIONS OF HUMPBACK WHALES TO SKIN BIOPSY SAMPLING ON A WEST INDIES BREEDING GROUND

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Abstract

Reactions of humpback whales, *Megaptera novaeangliae,* to the taking of skin biopsies and to associated activities were studied on one of their principal West Indies breeding grounds on Silver Bank (Dominican Republic). Results were in some cases different from those reported from a similar study of this species in a high-latitude feeding area. Almost half (44.1%) of 565 biopsied whales showed no immediate reaction to a hit, while a further 22.5% showed only low-level reactions. A total of 375 (87.8%) of 427 misses involved no reaction. Only one strong reaction was recorded. Behavior changes were recorded following 31 (5.5%) of 569 hits, and 18 (4.5%) of 404 misses. Evasive behavior related to vessel approach was exhibited prior to 72 (12.0%) of 598 hits and 100 (24.1%) of 415 misses. Mothers showed significantly fewer reactions to hits than other whales, and a similar frequency and type of behavior changes, although they tended to be more evasive before a shot was made. Presumed males in competitive groups also showed significantly fewer reactions to shots, and very few behavior changes. Overall, this study supports the belief that the biopsy itself has little effect on a whale and that, if the associated vessel approach is conducted with care, samples can usually be taken with minimal disturbance to the target animal. However, approaches may affect the probability of obtaining fluke photographs for individual identification.

Key words: biopsy sampling, genetics, humpback whale, *Megaptera novaeangliae.*

In recent years the application of molecular genetics to studies of cetaceans has produced significant insights into the biology and behavior of several species (summarized *in* Hoelzel 1991). Since such techniques potentially provide answers to questions that in many cases cannot be addressed by other means, they represent an invaluable investigative tool for studies concerning both the biology and conservation management of endangered species. Samples for such analyses are obtained in the form of either skin biopsies (Lambertsen 1987) or as sloughed skin left behind in the water (Whitehead *et al.* 1990, Amos *et al.* 1992, Clapham *et al.* 1993). Skin biopsies are typically taken using a dart fitted with a sampling tip and fired from a crossbow (Lambertsen 1987, Palsbøll *et al.* 1991).

Reactions to the biopsy procedure have been studied in three species of baleen whales. Brown *et al.* (1991) described reactions of right whales (*Eubalaena glacialis*) as minimal and short-lived, a characterization similar to that given by Mathews (1986) for responses of gray whales (*Eschrichtius robustus*). Weinrich *et al.* (1991, 1992) concluded that for humpback whales (*Megaptera novaeangliae*) in the southern Gulf of Maine a biopsy represented a momentary painful or surprising stimulus that typically caused only short-term behavioral disturbance. To date, no study of this type has been published for humpback whales in their breeding range. In this report we summarize data on the behavioral responses of North Atlantic humpback whales to approximately 1,000 biopsy attempts (both successful and unsuccessful) and associated vessel approaches made on this population's principal breeding and calving ground in the West Indies. This study provides further support for the belief that, if conducted with appropriate care, the biopsy procedure represents a minimal intrusion into the life of an animal and has no long-term effect on behavior.

MATERIALS AND METHODS

Study area and sampling methods—In February and March 1992, as part of the large-scale project known as Years of the North Atlantic Humpback (YONAH), several hundred biopsies were obtained from humpback whales on Silver Bank, a limestone platform reef off the Dominican Republic's northern coast. Silver Bank represents the most important mating and calving area for North Atlantic humpbacks (Balcomb and Nichols 1982, Mattila *et al.* 1989), with as many as two or three thousand individuals present during the peak of the season.

Biopsies were taken using a 68-kg draw crossbow and modified bolt fitted with a stainless steel sampling tip (similar to designs described in Palsbøll *et al.* 1991); the tip is 4 cm long with a diameter of 9 mm. Tips were cleaned thoroughly between each sampling event and were sterilized by immersion in ethanol. Darts were fitted with a 2.5-cm diameter stop to ensure recoil after penetration of the whale, and with flotation for easy retrieval from the water. A retrieval line was not used. Biopsies were preserved in a saturated sodium chloride solution with 20% dimethylsulfoxide as described by Amos and Hoelzel (1991).

Whales were approached for sampling from inflatable boats which varied in length from 4 to 5.5 m, and which were powered by a single 25-hp or 30-hp outboard engine. Each boat was crewed by a driver, a photographer, and an archer. Virtually all sampled whales were photographically identified using variations in ventral fluke pattern (Katona *et al.* 1980) and in the shape, size, and scarring of the dorsal fin.

Definitions and categorization of responses—In this report the term "sampling procedure" refers to the entire process of obtaining, or attempting to obtain, a

Table 1. Reactions of all whales to hits and misses.

	Total recorded	None	Low	Moderate	Strong
Hits	565	249	127	188	1
Percent	100	44.1	22.5	33.2	0.2
Misses	427	375	28	24	0
Percent	100	87.8	6.6	5.6	0
Total	992	624	155	212	1
Percent	100	62.9	15.6	21.4	0.1

skin biopsy from a humpback whale. This includes both the vessel approach and the firing of the dart from the crossbow. The firing event is referred to here as a "shot," and includes both hits (where the dart struck the target animal) and misses.

Reaction: the term "reaction" refers solely to the immediate response of a whale to a shot (whether hit or miss). Reactions were categorized hierarchically as follows: (1) none: the whale exhibited no observable response; (2) low: the whale reacted with either a brief startle (a flinch), or a quick submergence, or both; (3) moderate: the whale reacted with one or two tail flicks; or (4) strong: the whale reacted with multiple tail flicks and/or lateral tail thrashes, and/or with high-energy behavior. The latter was defined as one or more instances of a breach, a tail breach, a lobtail, or a flipper slap. This categorization is similar to that employed for a study of southern Gulf of Maine humpbacks by Weinrich *et al.* (1991).

Behavior change: while we were unable to allocate time to a standardized control period prior to vessel approach, observers attempted to categorize the behavior of target animals when first encountered in order to assess whether this behavior changed as a result of the sampling procedure; in all cases, behaviors were categorized by individuals having many years of experience with humpback whales on a breeding ground. A difference between the behavior recorded before a shot and that noted afterwards is termed a "behavior change." Changes from non-curious to curious behavior (in which the animal approached and investigated the vessel), or from evasive to non-evasive behavior, were classified as "positive." All other behavior changes (*e.g.*, from travel to evasive) were considered negative. We did not include fluking to non-fluking as a behavior change; this was dealt with separately (see below).

Because animals exhibiting evasive behavior prior to a shot would not have been classified as showing a behavior change if they remained evasive afterwards, we have also reported the number of cases in which evasiveness was observed before a shot was made, irrespective of the subsequent behavior. Because multiple approaches were sometimes made to the same animal, a behavior recorded *before* a particular shot was taken may also have *followed* a preceding shot. An evasive behavior is defined as that in which the animal actively attempted to move away from the vessel, or exhibited decreased surface time, or both. Evasive whales often dove for shorter periods than in pre-approach behavior; consequently, a whale exhibiting shorter dive times and other evasive behavior was recorded as evasive but not as also showing a shorter dive. Behavior changes described here as "shorter dives" or "longer dives" involved no evidence of evasion but simply a pronounced modification of previous diving behavior, defined as the dive time changing by five minutes or more.

Class definitions—In order to test whether group size or behavior role affected the reactions of whales to hits and misses, each animal was assigned to one of the following categories: singleton (a lone whale), member of a pair, member of a non-competitive trio, mother, calf, escort to a mother/calf pair, or participant in a competitive group. The latter category was further divided according to the whale's role within the group, according to definitions given by Clapham *et al.* (1992): Nuclear Animal, Principal Escort, Challenger, or Secondary Escort. Nuclear Animals are generally female, while other participants in competitive groups are invariably male (Tyack and Whitehead 1982, Clapham *et al.* 1992). The Nuclear Animal category does not include lactating females in competitive groups; these were classified as mothers for the purpose of analysis.

RESULTS

Reactions to shots—Table 1 summarizes data on reactions to a total of 992 hits and misses. Almost half (44.1%) of 565 biopsied whales exhibited no detectable reaction to a hit, while a further 22.5% showed only a low-level reaction. A total of 375 (87.8%) of 427 misses involved no reaction by the target whale. Only one instance of a "strong" reaction was recorded: this involved a Nuclear Animal who reacted with two tail flicks followed by several lateral tail thrashes, after which she resumed her previous behavior in the group.

Variation in reactions by class—Figure 1 shows the frequency of reactions of different classes to hits. Chi-square tests were used to test these differences. In general, mothers were characterized by fewer reactions than any other class; with the exception of Nuclear Animals, competitive group members were also notably less reactive to being struck than were other whales (except mothers). Specific results were as follows ($\alpha = 0.05$, df = 2 except where noted):

(1) Competitive group members reacted significantly less to being struck than all other classes combined ($\chi^2 = 11.386$, $P < 0.005$), but significantly more than mothers ($\chi^2 = 11.599$, $P < 0.005$, Nuclear Animals excluded). Within competitive groups, Nuclear Animals reacted significantly more than Principal Escorts, Challengers, and Secondary Escorts ($\chi^2 = 18.071$, $P < 0.001$). Pairwise comparisons of the latter three categories revealed no significant difference (df = 1) in reactions. The reactions of Nuclear Animals were not significantly different from those of singletons, pairs, trios, escorts and calves, combined.

(2) Mothers reacted significantly less to being struck than all other classes combined ($\chi^2 = 46.025$, $P < 0.001$), and less than all other classes excluding Principal Escorts, Challengers, and Secondary Escorts ($\chi^2 = 70.814$, $P < 0.001$).

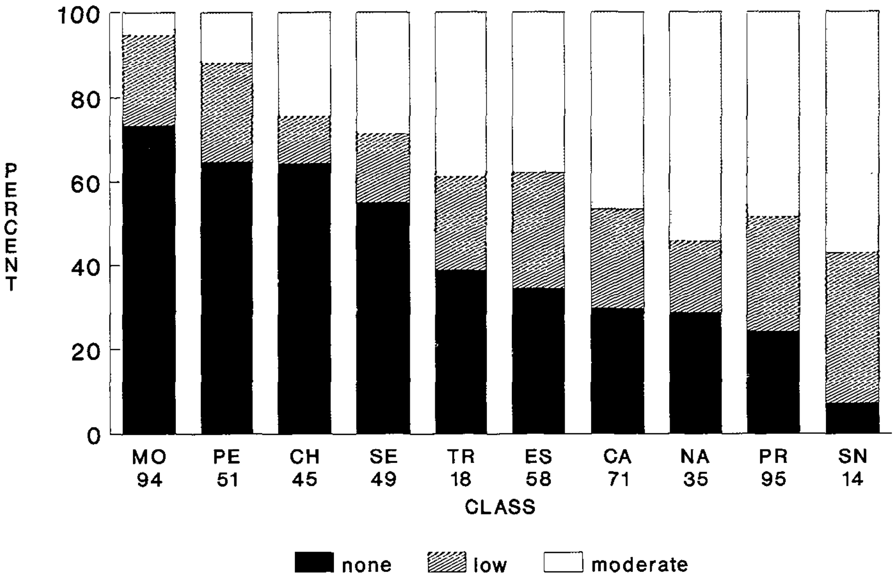

Figure 1. Reactions of different classes to hits. Abbreviations: MO mother; PE Principal Escort; CH Challenger; SE Secondary Escort; TR member of a trio; ES escort to a mother/calf pair; CA calf; NA Nuclear Animal; PR member of a pair; SN singleton. The single strong reaction recorded (by a Nuclear Animal) is not included.

(3) Calves reacted significantly more than all other classes combined, including mothers ($\chi^2 = 9.538$, $P < 0.01$). However, when mothers, Principal Escorts, Challengers, and Secondary Escorts were removed, there was no significant difference between the reactions of calves and those of the remaining classes combined.

(4) Pairwise comparisons showed no differences among the following classes (df = 1): pairs, trios, calves, Nuclear Animals, or escorts to mother/calf pairs. The sample size (n = 14) for singletons was too small to test against the other categories.

Unlike with observed reactions to hits, chi-square tests showed no differences between any of the classes in reactions to misses.

Behavior changes and evasiveness—Behavior both before and after a shot was recorded for a total of 973 hits and misses. A behavior change was recorded following 31 (5.5%) of 569 hits, and 18 (4.5%) of 404 misses. Table 2 summarizes the types of behavior change recorded. Three (9.7%) of the 31 changes after hits, and three (16.7%) of the 18 changes following misses, were classified as positive.

Behavior preceding a hit or a miss was recorded in 1,013 cases. Of these, 172 (17.0%) involved evasion, specifically 72 (12.0%) of 598 hits and 100 (24.1%) of 415 misses. No pre-shot evasive behavior was recorded for singletons (n = 55 approaches), non-lactating Nuclear Animals (n = 54), Principal Escorts (n = 78), Challengers (n = 65), or Secondary Escorts (n = 69). Evasive behavior before a shot was recorded for pairs (8.4% of 191 approaches), trios (8.3% of

Table 2. Observed behavior changes following hits and misses.

	Hit	Miss
Total recorded events	569	404
Total observed changes	31	18
Percent of total	5.5	4.5
Positive		
Curious (from non-curious)	1	2
Non-evasive (from evasive)	2	1
Negative		
Not curious (from curious)	5	0
Evasive (from non-evasive)	8	7
Shorter dive	2	3
Longer dive	4	1
Not singing (from singing)	1	1
Not logging (from logging)	2	0
Not travelling (from travel)	5	2
Travel to milling	1	1

36 approaches), escorts to mother/calf pairs (30.7% of 101 approaches), and mother/calf pairs (33.5% of 364 approaches).

Effect on fluking rate—Data on the rate of fluking on terminal dives were recorded prior to, and during or after (we did not distinguish between the two), approaches to 20 whales of various classes. Whales fluked on 28 (50.0%) of 56 terminal dives before an approach was made, but on only 17 (23.0%) of 74 terminal dives during or after the sampling procedure. This difference is significant ($\chi^2 = 4.909$, $P < 0.05$, df = 1).

Stuck darts—In ten cases on Silver Bank, the dart stuck in the target whale, eventually falling out after periods ranging from 2 to 45 min. Reactions associated with stuck darts ranged from none ($n = 4$), to low ($n = 4$) to moderate ($n = 2$).

Discussion

The results reported here provide further support for the belief that the biopsy sampling procedure, if properly applied, does not result in significant behavioral disturbance to humpback whales. The frequency with which target animals reacted to both hits and misses was considerably lower than that reported by Weinrich *et al.* (1991) for humpbacks on a feeding ground in the southern Gulf of Maine. In the latter area, 11.6% and 64.2% of animals showed no reactions to a hit and a miss, respectively; this compares to 44.1% and 87.8% from the present study. The difference is probably attributable in large part to the low frequency of reactions on the part of certain classes of whales in the breeding range, notably mothers and whales engaged in competitive groups. The latter primarily consist of mature males fighting for access to a female (Tyack and Whitehead 1982, Clapham *et al.* 1992); such groups are often fast-moving and violent, and it is therefore not surprising that the minimal stimulus of a skin biopsy goes unnoticed by animals who are presumably already in a high state of arousal, and who are expecting tactile stimuli. The lower frequency of reactions among mothers may be related to the fact that they are continually being touched by nursing calves and are therefore less likely to be surprised by a tactile stimulus.

The greater number of reactions to hits than misses observed in whales of all classes is hardly surprising given the tactile nature of a hit. That whales reacted in similar ways to many misses suggests that a large component of any reaction (hit or miss) is a startle response; whales may simply be surprised at the sudden stimulus (whether tactile in the case of a hit, or auditory in a miss) and react accordingly.

As more studies of this type are conducted, it is becoming clear that the various components of the sampling procedure elicit different levels of response. In particular, the actual biopsy is less likely to elicit a behavior change than the associated approach of the vessel. This was most noticeable in mothers, who showed little reaction to being struck, but who were consistently more evasive than other classes of whales. Weinrich *et al.* (1991) noted that mother/calf pairs in the southern Gulf of Maine did not differ significantly from other classes in their response to the sampling procedure, and our own work on this same feeding ground supports this (unpublished data). It is not surprising that mothers on the breeding grounds are more sensitized to vessel approach given that their calves are younger by weeks or months than those encountered in high latitudes. Furthermore, humpback whales in the Gulf of Maine are arguably more habituated to vessel approach than those of any other population (Watkins 1986). By contrast, many whales in the West Indies come from areas such as West Greenland which have little boat traffic and where they may still be hunted.

For all classes except competitive groups, the manner in which a vessel approaches a group of whales has a major influence on the probability that a negative response will be elicited. Again, this proved to be particularly true with mother/calf pairs. We experimented with many different approaches during this study, and it was clear that a slow, patient approach to groups (including those containing a calf) produced less evasion and yielded a higher probability of sampling success than more aggressive techniques. While individual variation guarantees that some whales will be unapproachable no matter how careful the boat driver, most whales (even mothers) seem to habituate to the presence of a vessel given sufficient time. This, in combination with the results of this study, strongly suggest that, for both efficacy of sampling and the well-being of the animals, such a careful approach is warranted, notably to mother/calf pairs in the breeding range. If conducted in this manner with experienced, trained personnel (this is essential), biopsies can be obtained from mothers and their calves with little effect on the animals; this is gratifying, since samples from related pairs are of particular importance in genetic analyses. It is likely that the high frequency of evasive behavior on the part of escorts to mother/calf pairs is a result of evasiveness on the part of the latter to any vessel approach, with the escort following the movements of the mother. Escorts are invariably males who are believed to associate with a lactating female in order to enhance their probability of mating with her.

This study also suggests that aggressive approaches can decrease the probability that a whale will fluke when diving, thus making it more difficult to obtain photographs for the purpose of individual identification. We would therefore recommend that, where possible, fluke photographs be obtained prior to the initiation of the sampling procedure. Our sample size was too small to allow us to test whether the observed change in fluking rate differed significantly among classes; if it does, this would be of particular concern since if not taken into consideration it would introduce the bias of heterogeneity of capture into estimates of population numbers. It is possible that whales may begin to fluke again after all approaches have ceased, but because we generally abandoned groups shortly after sampling we could not determine whether an additional investment of time would result in successful photographic capture of such individuals.

The virtual absence of strong reactions to shots is similar to observations made by Weinrich *et al.* (1991), who noted that the few cases where such reactions were observed involved either fouling with a retrieval line or a stuck dart. We did not use a retrieval line, and the ten cases in which a dart stuck in a whale produced no strong reactions. As noted above, the sole instance of a strong reaction during this study involved a Nuclear Animal in a competitive group. The only other strong reaction that we have observed in the West Indies involved a logging (resting) whale in Samana Bay (unpublished data), which presumably was awakened by the biopsy. This individual breached three times when struck, after which it resumed its previous resting behavior.

The occurrence of six instances of what we have termed "positive" responses (curious from non-curious, or non-evasive from evasive) following a shot is interesting, although we stress that the term "positive" is a label assigned by us and may not reflect the experience of the whale. As noted by E. Mathews (personal communication), responses such as curiosity may be somewhat negative for the whale in that they may detract from more critical behaviors such as nursing or courtship.

We have not attempted to assess the long-term effects of biopsying on individual humpbacks. There is good evidence that the procedure has no influence on rates of either within-season resighting or annual return (Weinrich *et al.* 1991), and the resighting of several biopsied animals during our studies in the West Indies supports this belief.

Overall, we conclude that the taking of skin biopsies has no significant effect on the animals concerned, although particular care should be taken in approaches to mother/calf pairs. Furthermore, regional differences in habitat use (*i.e.,* feeding versus breeding) produce different frequencies of short-term responses, notably among mother/calf pairs and whales engaged in breeding-related behavior.

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BEHAVIORAL RESPONSE OF FOUR SPECIES OF BALAENOPTERID WHALES TO BIOPSY SAMPLING

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ABSTRACT

Behavioral responses to biopsy sampling of four species of northwestern Atlantic balaenopterid whales summering in the estuary and Gulf of St. Lawrence, Quebec, from 1990 to 1995 were studied to determine if this technique was an important disturbance to the whales. A total of 447 biopsy samples were taken using a small punch-type biopsy tip fired from a crossbow. Biopsies were successfully taken from 91.2% of the whales approached. Whales displayed no reaction to 45.2% of the successful biopsy attempts. Whales that responded to biopsy sampling typically resumed their normal behavior immediately or within a few minutes. Most humpback whales displayed a hard tail flick, and the majority of fin and blue whales submerged following biopsy sampling. Significantly different frequencies and intensities of responses were found between whale species. Minke and humpback whales were found to be more sensitive to biopsy sampling than fin and blue whales. Response frequencies were similar between females and males for all species, with the exception of fin whales where females had a higher response frequency than males. Biopsy sample length, *i.e.,* penetration depth, did not explain variations in response intensity but may influence response frequency to biopsy sampling. Group size, geographical region, and number of biopsies taken per whale were not factors that explained variation in behavioral responses. The biopsy technique was found to be an efficient method for obtaining high-quality whale skin and blubber samples with limited behavioral disturbance to balaenopterid whales.

Key words: balaenopterid, biopsy, behavior, response frequency, intensity of response.

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Biopsy sampling is a method for obtaining very small cores of skin and underlying blubber from free-ranging cetaceans with a modified crossbow or gun. This method has been successfully used on both mysticetes and odontocetes (*e.g.*, Winn *et al.* 1973; Mathews *et al.* 1988; Whitehead *et al.* 1990; Brown *et al.* 1991, 1994; Kasamatsu *et al.* 1991; Palsbøll *et al.* 1991; Weinrich *et al.* 1991, 1992; Clapham and Mattila 1993; Barrett-Lennard *et al.* 1996).

DNA extracted from skin biopsies has been used to obtain information on gender, lineage, social organization, identity of stocks and individuals, and genetic variation between stocks (*e.g.*, Amos and Hoelzel 1990; Baker *et al.* 1990, 1991, 1993; Pasbøll *et al.* 1992). Skin biopsies have also been used for determination of mixed function oxidase (MFO) activity (Fossi *et al.* 1992). Blubber portions of biopsy samples have been used for analysis of persistent lipophilic contaminants (Aguilar and Nadal 1984, Woodley *et al.* 1991, Marsili and Focardi 1996, Gauthier *et al.* 1997) and of feeding habits through analysis of fatty acids (Borobia *et al.* 1995).

An important consideration is to minimize disturbance to whales, while obtaining a satisfactory sample for research. Biopsy sampling has become widely used, yet studies on the behavioral effects of this technique have been largely limited to humpback whales (*Megaptera novaeangliae*) (Weinrich *et al.* 1991, 1992, Clapham and Mattila 1993, Brown *et al.* 1994). This study provides information on the effects of biopsy sampling on three other balaenopterid species and on interspecific comparisons using the same methodology. This study also provides novel information on the effect of biopsy sample length on the frequency and intensity of response in balaenopterid whales.

Frequency, intensity, and category of immediate response to biopsy sampling of minke (*Balaenoptera acutorostrata*), fin (*Balaenoptera physalus*), blue (*Balaenoptera musculus*), and humpback whales were determined according to species, sex, group size, geographical region, number of biopsies taken per whale, and length of biopsy sample.

METHODS

Study Area and Biopsy Sampling Conditions

Biopsy samples were taken from free-ranging whales in summer and fall from 1990 to 1995 (23 biopsies in 1990, 78 in 1991, 121 in 1992, 106 in 1993, 76 in 1994, and 43 in 1995). Whales were biopsied on their feeding grounds in the St. Lawrence estuary and Gulf of St. Lawrence, Quebec (Fig. 1). Whales were approached with a 5- or 7.5-m hard-bottom inflatable boat with a 70- or 90-hp outboard motor, respectively. To reduce the chances of biopsying the same individual twice, fin, blue, and humpback whales were photographed according to procedures described by Sears *et al.* (1990), and morphological features and natural body marks were recorded to aid in the photoidentification of individuals. Minke whales were not photoidentified because their surface times were too short to allow time for both photoidentification and biopsy sampling using the procedures in this study. When pos-

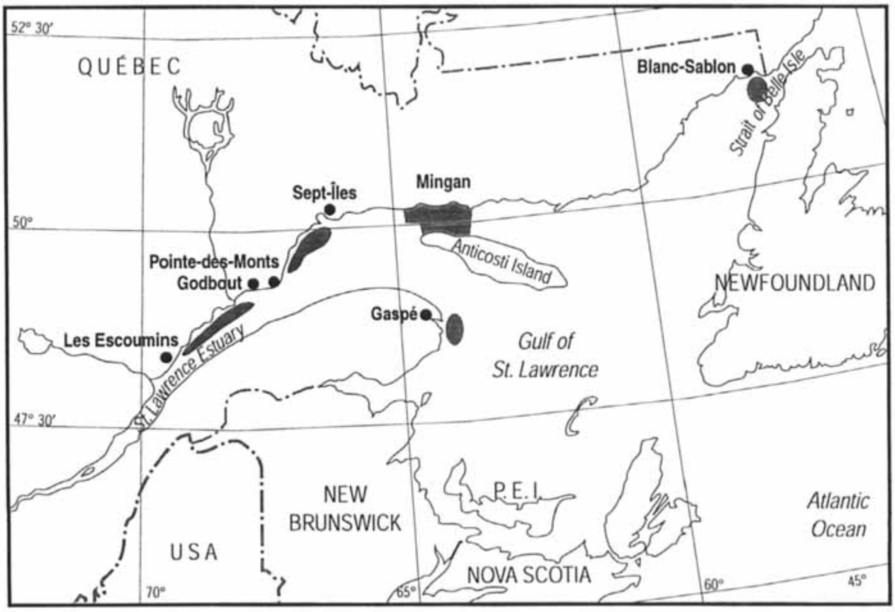

Figure 1. Map of study area showing balaenopterid whales summering in St. Lawrence estuary and Gulf of St. Lawrence, Quebec, biopsied in five different regions (shaded). Samples sizes in each localized geographical region for minke, fin, blue, and humpback whales, respectively, are: Mingan = 23, 109, 21, and 64; Strait of Belle Isle = 0, 0, 0, and 141; Godbout to Escoumins = 2, 3, 56 and 0; Sept-Îles to Pointe-des-Monts = 0, 1, 18, and 0; Gaspé = 0, 0, 8, and 1.

sible, group size was recorded. In this study, a group was defined as a concentration of whales of the same species inside an approximate diameter of 50 m. Although these groups may be associated with a larger and more-dispersed group, more-distant whales were not included in the analyses.

According to our criteria, a whale responded to biopsy sampling when it immediately modified its behavior observed before the biopsy attempt. These immediate reactions were recorded by constantly observing the selected whale with the naked eye, usually by two observers, throughout the entire sequence: the approach, the pursuit, and the pre- and postbiopsy periods. Observations were ended when the whale resumed its initial behavior or was out of sight. Individual behavior categories, such as a flipper flick, flipper slap, lobtail, startle, tail flick, hard tail flick, tail rise, tail slash, and trumpet blow, have been defined by Weinrich *et al.* (1992), Brown *et al.* (1994) and Lambertsen *et al.* (1994). In this study, tail flicks were either categorized as 'tail flicks' or 'hard tail flicks'. Tail flicks were light in intensity and caused little spray, while hard tail flicks were higher in intensity and produced much spray. Flipper rises are analogous to tail rises as described by Weinrich *et al.* (1992). Other individual behavior categories are described as follows:

Acceleration—Whale increased its speed if it was initially traveling, or otherwise swam rapidly away from boat for a short time period (quick burst of speed).

Breach—Whale emerged sideways from the water, rotated a half-turn, and landed on its back, producing a large splash.

Change in direction—Whale changed its traveling course in any direction different from that in which it was initially traveling without increasing its speed during otherwise normal swimming behavior.

Defecation—Whale defecated at the water surface without any other observable change in behavior.

Dive—Whale rapidly arched its back in a typical diving posture, with or without bringing its flukes above the surface. Although diving may have occurred regardless of biopsy attempt, it was assigned as a response only if it occurred immediately after the event or within a series of closely time-related reactions after the event, in the case of combined responses.

Forceful breath—Whale blew loudly during exhalation at or just below the surface, but without the wheezing sound produced by a trumpet blow.

Roll—Whale turned on its right or left side, either towards or away from the boat, during otherwise normal swimming behavior.

Submerge—Whale slowly submerged parallel to the water surface without arching its back, during otherwise normal swimming behavior.

Tail sweep—Whale moved tail laterally once on the water surface producing light water frothing. This movement was lighter in intensity than the tail slashes described by Weinrich *et al.* (1992).

Tail wave—Whale lifted tail out of the water and waved it laterally with light intensity.

In order to compare our results with those of other studies, the intensity of the response to biopsy sampling for each whale was classified according to Weinrich *et al.* (1991) or Clapham and Mattila (1993) as either no response or low-, moderate- or strong-level response, as follows:

No response—Whale continued its prebiopsy behavior with no observed reaction.

Low-level—Whale modified its prebiopsy behavior with brief and relatively mild responses (*i.e.*, change in direction/defecation/dive/flipper flick/flipper rise/roll/submerge/startle/tail flick/tail rise/tail wave).

Moderate-level—Whale modified its prebiopsy behavior in a more forceful manner, but gave no prolonged evidence of behavioral disturbance (*i.e.*, acceleration/forceful blow/hard tail flick/tail sweep/trumpet blow).

Strong-level—Whale modified its prebiopsy behavior to a succession of forceful activities (*i.e.*, numerous trumpet blows) or to high energy behavior (*i.e.*, breach/flipper slap/lobtail/tail slash).

Response categories cited for each level were either observed singly (individual responses) or in combination (combined responses). Combined responses which included responses from different levels were assigned to the strongest level (*e.g.*, submerge + hard tail flick = moderate level).

Biopsy Technique

Biopsy samples were taken using a small stainless-steel punch-type biopsy tip fired from a 76-cm, 1.8-kg Barnett WildCat crossbow. Draw weight of the bow was either 57 or 68 kg. The crossbow and biopsy tip were similar to the Barnett-type bow and tip described by Palsbøll *et al.* (1991), but no retrieval line was used. The arrow was kept afloat after it became dislodged from the whale's blubber with a buoyant, highly visible, cone-shaped stop collar designed to limit the penetration of the biopsy tip.

The approach process for biopsy sampling was similar to the method described previously by Sears *et al.* (1990), and target distance was 6–20 m. All biopsy attempts were carried out by the same four archers. Most biopsies were obtained at an angle perpendicular to the back of whales forward of the dorsal fin. This was the desired sampling location, in order to avoid the head and tail area and to increase the chances of a successful biopsy if the whale suddenly dove. Nineteen samples were obtained from the caudal peduncle, usually taken at a 30°–45° oblique angle. More skin but less blubber were obtained from these caudal-peduncle samples. The tip was cleaned with ethanol after each shot to minimize wound infection and bacterial contamination of the sample. Skin was cut from the blubber and placed in dimethyl sulphoxide (DMSO)/saturated saline solution and stored at 4°C. Skin samples were flown to Denmark for sex determination by Per Palsbøll and Martine Bérubé at the University of Copenhagen using the polymerase chain reaction (PCR) with SRY gene primers (5′CAT TAT GTG CTG GTT CTT TTC TG 3′ and 5′GTA TTT CTC TCT GTG CAT GG 3′) (Palsbøll *et al.* 1992). Blubber samples were frozen and used for organochlorine contaminant analysis and fatty acid determination. When possible, length and weight of blubber samples were recorded on thawed tissue.

Statistical Analysis of Data

Chi-square analyses (Minitab Software Inc., version 8, State College, PA) were used to compare behavioral responses in relation to species, sex, geographical region and group size. Chi-square analyses were conducted if the average expected frequency (n/rc, where n is the total of expected frequencies, c is the total number of columns and r is the total number of rows of the contingency table) was at least 6.0 when testing for $\alpha = 0.05$ (Roscoe and Byars 1971, Zar 1996). A regression was done to verify if the length of samples (blubber core length) was a good indicator of the size of the biopsy sample (Minitab Software Inc., version 8, State College, PA). The non-parametric Kruskal-Wallis test (Systat Inc. software, 1990, Evanston, IL) was used to compare blubber core length (mm) of the biopsy sample to the intensity of response. All statistical analyses were tested for $\alpha = 0.05$.

Table 1. Summary of unsuccessful and successful biopsy attempts on balaenopterid whales sampled in the St. Lawrence estuary and Gulf of St. Lawrence.

Attempt	Minke	Fin	Blue	Humpback	Total
Miss (hit water)	2	2	1	5	10
Hit/no sample (hit whale)	0	7	9	17	33
Hit/sample	25	113	103	206	447
Total	27	122	113	228	490

RESULTS

Relative Success of the Biopsy Technique

In 490 attempts on 443 whales, 447 biopsy samples were obtained (91.2% success rate) (Table 1). Of 447 biopsies, 433 yielded both skin and blubber and 14 only skin.

Ten arrows (2.0%) missed the whale and hit the water, and 33 attempts (6.7%) struck a whale but resulted in no sample (Table 1). In 39 of the 43 cases, a second biopsy attempt was successful. A third attempt was successful for three of the four whales which were unsuccessfully biopsied in the second attempt. A fourth attempt was successful for the remaining whale. Behavioral responses were recorded for 20 (9 misses and 11 no-samples) of the 43 unsuccessful attempts. For nine missed attempts, no reaction was observed for one minke, two fin, one blue and four humpback whales, and one fin whale dove when the arrow hit the water. Out of 11 hits which did not yield a sample, four did not elicit any response from fin and blue whales, and five were followed by a low-level response from one blue and four humpback whales, one by a moderate-level and one by a strong-level response from two humpback whales. These responses included hard tail flicks, flipper flicks, diving, changes in traveling direction, trumpeting, and rolling towards the boat. Repetitive attempts to biopsy a whale resulted in responses of similar or reduced intensity, with the exception of one humpback whale that responded by a low-level reaction at the first missed attempt and by a moderate-level reaction at the second and successful attempt.

On five occasions the biopsy tip stayed lodged in the blubber of humpback whales and this resulted in a reaction for four of the five whales. Two of these tips stayed lodged in the whale's blubber for 6 and 13 min, respectively, and resulted, in both cases, in strong-level responses which lasted until the tip was freed.

Photoidentification of whales indicated that certain whales were inadvertently biopsied more than once during the course of the study (Table 2). Most of these whales were biopsied in different months or years, but five fin, three blue and one humpback were biopsied twice within a week. Intensity of the behavioral response appeared to be similar at first and subsequent biopsy for the three species. Chi-square analyses were not conducted because the average expected frequency was smaller than 6.0 for all species.

Table 2. Intensity of response of balaenopterid whales inadvertantly biopsied more than once (*i.e.*, 2–4 times) during the course of the study.

		First				Second				Third				Fourth			
Species	*n*	NR	L	M	S	NR	L	M	S	NR	L	M	S	NR	L	M	S
Fin	11	6	4	1	0	7	3	1	0	1	1	0	0	0	0	0	0
Blue	14	11	3	0	0	9	5	0	0	1	0	0	0	0	0	0	0
Humpback	21	7	9	4	1	10	7	3	1	2	2	0	0	1	0	0	0

NR = no response, L = low-, M = moderate-, and S = strong-level responses.

Analysis by Species and Sex

Response frequency—Response frequencies to biopsy sampling for each species are presented in Table 3. No reaction to biopsy sampling was observed in 45.2% of cases. Minke whales responded the most often (84.0%), followed by humpback (65.5%), fin (50.4%), and blue (31.1%) whales. When data were analyzed using a 2 × 2 chi-square contingency table, response frequencies between all combinations of species were significantly different (minke and fin: $\chi^2_1 = 9.38$, $P = 0.002$, minke and blue: $\chi^2_1 = 23.23$, $P < 0.001$, fin and blue: $\chi^2_1 = 8.35$, $P = 0.003$, fin and humpback: $\chi^2_1 = 6.94$, $P = 0.008$, blue and humpback: $\chi^2_1 = 32.84$, $P < 0.001$), except between minke and humpback whales ($\chi^2_1 = 3.47$, $P = 0.06$).

Sex was determined for 400 of the 443 biopsied whales. Response frequencies by sex for each species are presented in Table 4. Only in fin whales were the response frequencies significantly different between sexes ($\chi^2_1 = 4.48$, $P = 0.03$), with females (65.7%) having a higher response frequency than males (44.2%).

Intensity of response—Analysis by 2 × 3 or 2 × 4 chi-square contingency tables of the intensity of response (no-, low-, and moderate-level with or without strong-level) for all combinations of whale species showed significant differences in all cases (minke and fin: $\chi^2_3 = 14.70$, $P = 0.002$, minke and blue: $\chi^2_3 = 34.58$, $P < 0.001$, fin and blue: $\chi^2_2 = 11.24$, $P = 0.004$, fin and humpback: $\chi^2_3 = 21.96$, $P < 0.001$, blue and humpback: $\chi^2_3 = 52.24$, $P < 0.001$), except between minke and humpback whales ($\chi^2_3 = 5.77$, $P = 0.123$). Blue and fin whales most frequently showed no-level responses and minke and humpback whales most often displayed moderate-level responses (Table 3). Strong-level responses were observed at low frequencies only in minke and humpback whales. Only three humpback whales had prolonged strong responses to biopsy sampling and two of these cases were related with retention of the biopsy dart in the whale. Whales typically resumed their normal behavior immediately or a few minutes after biopsy.

Differences in intensity of response between females and males were significant in fin whales ($\chi^2_2 = 8.13$, $P = 0.02$), but not in blue and humpback whales ($\chi^2_2 = 0.03$ and $\chi^2_3 = 4.19$, $P = 0.983$ and 0.123, respectively). However, differences between female and male fin whales reflected only the greater frequency of low-level responses compared to no-level responses in

Table 3. Frequency and intensity of response to successful biopsy attempts of balaenopterid whales.

Species	*n*	Response frequency			Intensity of response		
		No response	Response	% response	L	M	S
Minke	25	4	21	84.0%	9	11	1
Fin	113	56	57	50.4%	34	23	0
Blue	103	71	32	31.1%	25	7	0
Humpback	206	71	135	65.5%	38	87	10
Total	447	202	245	54.8%	106	128	11

L = low-, M = moderate-, and S = strong-level responses.

Table 4. Frequency and intensity of response to successful biopsy attempts of female and male balaenopterid whales.

			Response frequency			Intensity of response		
Species	Sex	*n*	No response	Response	% response	L	M	S
Minke	♀	20	2	18	90.0%	9	9	0
	♂	5	2	3	60.0%	0	2	1
Fin	♀	35	12	23	65.7%	17	6	0
	♂	77	43	34	44.2%	17	17	0
Blue	♀	44	30	14	31.8%	11	3	0
	♂	50	34	16	32.0%	13	3	0
Humpback	♀	88	33	55	62.5%	12	38	5
	♂	81	26	55	67.9%	21	29	5

L = low-, M = moderate-, and S = strong-level responses.

females since frequencies of moderate-level responses were similar between sexes. Chi-square analyses were not conducted for female and male minke whales because the average expected frequency was smaller than 6.0.

Response categories—Submerging (15.0%), combinations of two reactions (11.0%), tail flicks (8.9%), and hard tail flicks (8.3%) were the most frequently observed responses (Table 5). Humpback whales mainly displayed hard tail flicks. Most blue and fin whales submerged after the biopsy attempt. Breaching, flipper slapping, lobtailing, tail slashes, tail waving, and trumpet blows were observed only in humpback whales, tail sweeps only in minke whales and defecation and flipper flicking only in fin whales. Two biopsied fin whales and seven biopsied humpback whales were identified as calves. Three of the humpback whales and all the fin whale calves did not react to biopsy sampling, and the other four humpback calves responded by either a slight acceleration, a hard tail flick, or a combination of an acceleration and a tail flick.

Minke and humpback whales often showed combined reactions to biopsy sampling, which accounted for 32.0% and 17.5%, respectively, of their reactions (Table 5). Response categories which made up combined responses were similar to behaviors observed individually, except that no breaching, defecation, flipper flicks, or lobtails were observed. However, flipper slapping and tail waving were observed only within combined responses in humpback whales. Combined responses observed in minke whales consisted mostly of hard tail flicks (27.8%), diving (22.2%), acceleration (16.7%), and submerging (11.1%). Behaviors displayed during combined responses in fin whales were mainly hard tail flicks (22.2%), rolling (19.4%), submerging (16.7%), and diving (13.9%). Blue whales displayed few combined responses and these comprised mostly submerging (35.7%), acceleration (28.6%), and diving (21.4%). Trumpeting was an important component of combined responses in humpback whales (20.0%), but hard tail flicks (22.4%), diving (16.5%), and submerging (11.8%) were also frequently observed.

Effect of Group Size and Geographical Region

Group size was recorded for 223 of the 447 biopsied whales and categorized as singles, small groups (two–four) or large groups (five or more) (Table 6). No statistical differences were found in response frequencies for different group sizes in fin, blue, and humpback whales (χ^2_2 = 0.08, 1.13, and 0.006, P = 0.962, 0.568, and 0.997, respectively). Chi-square analyses were not conducted for minke whales because the average expected frequency was smaller than 6.0.

Biopsy samples were obtained from whales in regions of Mingan (217 biopsies), Strait of Belle Isle (141), Godbout to Les Escoumins (56), Sept-Îles to Pointe des Monts (24) and Gaspé (9) in the St. Lawrence estuary and Gulf of St. Lawrence, Quebec (Fig. 1). Response frequencies to biopsy sampling of humpback whales sampled in the Mingan (70.3%, n = 64) and in the Strait of Belle Isle (63.1%, n = 141) regions were not statistically different (χ^2_1 = 1.01, P = 0.316). No differences were found between blue whales sampled

Table 5. Frequency of response categories displayed following biopsy sampling by species and sex. Sex determined for 400 of 443 biopsied whales. Sex unknown for 1 fin, 9 blue, and 37 humpback whales. Categories within combined responses are described in text.

	Minke			Fin			Blue			Humpback		
Response category	♀	♂	total*	♀	♂	total*	♀	♂	total*	♀	♂	total*
No response	2	2	4	12	43	56	30	34	71	33	26	71
Acceleration	5	0	5	0	1	1	0	1	1	3	1	5
Breach	0	0	0	0	0	0	0	0	0	1	0	1
Change direction	1	0	1	0	0	0	0	0	0	0	1	1
Defecation	0	0	0	1	0	1	0	0	0	0	0	0
Dive	1	0	1	0	0	0	1	0	1	0	1	1
Flipper flick	0	0	0	1	0	1	0	0	0	0	0	0
Flipper rise	0	0	0	0	0	0	0	0	0	0	1	1
§Flipper slap	0	0	0	0	0	0	0	0	0	0	0	0
Forceful blow	0	0	0	0	0	0	1	0	1	0	1	1
Lobtail	0	0	0	0	0	0	0	0	0	1	1	3
Roll	0	0	0	0	1	1	0	0	0	0	0	0
Startle	0	0	0	1	0	1	0	0	0	0	0	0
Submerge	2	0	2	10	13	23	10	12	24	7	7	18
Tail flick	1	0	1	4	6	10	0	0	0	9	11	29
Hard *tail* flick	1	1	2	1	2	3	0	0	0	13	12	32
Tail rise	0	0	0	1	1	2	0	0	0	2	1	3
Tail slash	0	0	0	0	0	0	0	0	0	1	0	1
Tail sweep	1	0	1	0	0	0	0	0	0	0	0	0
§Tail wave	0	0	0	0	0	0	0	0	0	0	0	0
Trumpet blow	0	0	0	0	0	0	0	0	0	2	1	3
Combination of 2	5	1	6	3	6	9	2	3	5	11	15	29
Combination of 3	1	1	2	1	3	4	0	0	0	4	1	5
Combination of 4	0	0	0	0	1	1	0	0	0	1	0	1
Combination of 8	0	0	0	0	0	0	0	0	0	0	1	1
Total	20	5	25	35	77	113	44	50	103	88	81	206

§ Flipper slaps and tail waves were observed only within combined responses.
* Total within each species = females + males + whales of unknown sex.

Table 6. Response to biopsy sampling of balaenopterid whales within groups* of different sizes. Data are frequencies of whales that did not respond (NR) versus whales that did respond (R) by group size and species.

	Group size							
	single		small group (2–4)		large group (≥5)		Total	
Species	NR	R	NR	R	NR	R	NR	R
Minke	5	4	0	2	4	11	9	17
Fin	2	2	10	13	7	8	19	23
Blue	24	15	9	9	3	1	36	25
Humpback	7	9	25	32	9	12	41	53
Total	38	30	44	56	23	32	105	118

* See Methods for definition.

in regions of Godbout to Les Escoumins (25.0%, n = 56), Sept-Îles to Pointe-des-Monts (50.0%, n = 18), Gaspé (25.0%, n = 8) and Mingan (38.1%, n = 21) ($\chi^2_3 = 4.48$, $P = 0.214$).

Effect of Biopsy Sample Size

Blubber portions of biopsy samples had a diameter of 6 mm and, for 42 measured biopsies, the blubber core length ranged from 5 to 30 mm and the sample weighed between 0.035 and 0.582 g (mean = 0.25 g). Core length was found to be a good predictor of sample weight ($P < 0.001$) according to the regression equation: weight = 0.0062 + 0.0139 length (r^2adj. = 54.3%). Therefore, core length was used as the criterion for comparing response frequency and intensity of response with biopsy sample size.

Mean core length ranged from 14.6 to 21.8 mm (Table 7). Blubber cores with a greater length than average taken from minke whales (mean = 21.8 mm) may have contributed to the high response frequency in this species. Humpback whales appear to be particularly sensitive to biopsy sampling, since

Table 7. Sample size, mean, range (in parentheses), and standard deviation about mean for length of total blubber portions of 42 biopsy samples and response frequency to biopsy sampling for each species.

		Length (mm)		
Species	n	Mean (range)	S.D.	Response Frequency*
Minke	13	21.8 (14–30)	6.2	100%
Fin	19	17.8 (5–27)	5.9	68.4%
Blue	3	17.3 (6–21)	0.5	33.3%
Humpback	9	14.6 (5–20)	3.7	88.9%
Total	42	17.6 (5–30)	6.3	67.1%

* Calculated only for whales for which data were available on biopsy blubber core depth.

relatively short blubber cores (mean = 14.6 mm) were associated with a high response frequency (88.9%). In all species, no significant differences were found in blubber core length for the different response levels (P = 0.367–0.456).

DISCUSSION

The biopsy sampling technique used in this study was an efficient method for obtaining skin and blubber samples from four species of balaenopterid whales. Success rate for first biopsy attempt in this study (91.2%) was similar to or higher than reported for humpback and killer (*Orcinus orca*) whales (57.0%–85.0%: Weinrich *et al.* 1991, 1992; Clapham and Mattila 1993; Brown *et al.* 1994; Lambertsen *et al.* 1994; Barrett-Lennard *et al.* 1996).

Response frequencies to biopsy sampling of blue, fin, humpback, and minke whales were 2- to 5-fold greater than for right whales, *Balaena glacialis* (17.6%, Brown *et al.* 1991). However, blue whales appeared to have a low response frequency compared to other balaenopterid species. Response frequencies of minke, fin, and humpback whales were within the range previously reported for humpback whales (41.4%–85.9%, Weinrich *et al.* 1991, 1992; Clapham and Mattila 1993; Brown *et al.* 1994). Intensity of response was lower in both blue and fin whales compared to minke and humpback whales, which reacted with intensity similar to that for humpback whales sampled by Weinrich *et al.* (1991, 1992) and Clapham and Mattila (1993).

Individual fin, blue, and humpback whales reacted with similar intensity when biopsied more than once during this study, which may indicate that response to biopsy has a large individual component. A response may reflect general sensitivity of an individual or species to an unknown stimulus, including biopsy sampling. Small mammals have higher relative metabolic rates and usually react more strongly to stress than large mammals (Peters 1983). The susceptibility of reaction to an unknown stimulus, such as biopsy sampling, may be inversely related to size. The smaller minke (~8 m, 7 tons) and humpback (~15 m, 30 tons) whales responded two–three times more frequently to biopsy sampling than did blue whales (~25 m, 100 tons). Other morphological factors such as thickness and innervation of skin and blubber thickness may play a role in the differential sensitivity of species or individuals, but no quantitative data are available.

Compared to interspecific differences, most intraspecific factors had little or no effect on the response to biopsy sampling. Frequencies and intensities of response to biopsy were similar in female and male blue and humpback whales, which is comparable to results for humpback whales sampled on their feeding grounds by Weinrich *et al.* (1991). Although female fin whales showed greater response frequencies to biopsy than males, this was due mostly to differences between frequencies of no-level and low-level responses. Group size was not a factor that determined response to biopsy sampling for fin, blue, and humpback whales. Similar results were obtained for humpback whales sampled from different group sizes by Weinrich *et al.* (1991) and Brown *et al.* (1994). Although different geographical regions could have reflected differences in familiarization of whales to close boat traffic, blue and humpback whales sampled in different regions showed similar response frequencies to biopsy sampling.

In general, whales in this study demonstrated a similar range of behavioral responses as previously recorded for sperm (*Physeter macrocephalus*), right, and humpback whales (Whitehead *et al.* 1990; Brown *et al.* 1991; Lambertsen *et al.* 1994; Weinrich *et al.* 1991, 1992). While humpback, right, and sperm whales typically responded with tail flicks or hard tail flicks, fin and blue whales responded most often by submerging. Tail flicks may be a reflex response to biopsy, but have also been observed in non-reflexive contexts (Weinrich *et al.* 1992, Lambertsen *et al.* 1994). Defecation was observed in one fin whale and this behavior may be typical of startled sperm whales (Whitehead *et al.* 1990, Watkins and Tyack 1991). The tail slashes and trumpet blows observed only in humpback whales are thought to be aggressive behaviors in response to harassment (Norris and Reeves 1977, Baker and Herman 1984, Watkins and Wartzok 1985). However, many of the behaviors observed after biopsy have also been displayed in the study area by whales that were not approached for biopsy or photoidentification. This was also reported by Weinrich *et al.* (1992) for humpback whales biopsied in the Gulf of Maine.

Whales that responded to biopsy sampling typically resumed their normal behavior immediately or a few minutes after the response. This has also reported by other authors (Winn *et al.* 1973; Whitehead *et al.* 1990; Brown *et al.* 1991, 1994; Weinrich *et al.* 1991, 1992; Lambertsen *et al.* 1994; Barrett-Lennard *et al.* 1996). Repetitive attempts to biopsy a whale usually resulted in a response of similar or decreased intensity. As indicated by the short duration of the response and the apparent acclimation by some whales to repeated biopsy attempts, reaction to the tip may be due more to the element of surprise to an unknown sensation, rather than to pain. Implantation of radio tags into the muscle layer have mostly elicited no response or mild reactions in large baleen whales, including fin and humpback (Watkins, 1981, Watkins and Tyack 1991). Moreover, the absence of changes in response intensity for fin, blue, and humpback whales inadvertently biopsied more than once during this study suggests the lack of long-term effects of biopsy sampling.

Nevertheless, only immediate surface responses were recorded, and it must be considered whether other undetected effects were caused by biopsy. Also, the presence of strong responses indicates that certain individuals may be very sensitive to biopsy sampling. Biopsy tips which remained lodged in the whale's blubber usually resulted in a strong response, which subsided only when the tip was dislodged from the whale's body. Similar findings were observed by Brown *et al.* (1991) and Weinrich *et al.* (1991, 1992). It is more likely that the tip will remain lodged in the whale's blubber if deep cores are taken. Although no significant relationship was found between intensity of whale response and sample core length, the high response frequency of minke whales may be due in part to the relatively long biopsy samples (14–30 mm) obtained from individuals of this species, but a greater sample size is needed to verify this. Very small blubber samples (5 mm) weighing as little as 0.035 g can be used to quantify low concentrations of lipophilic organochlorine contaminants found in balaenopterid whales (Gauthier *et al.* 1997). Blubber samples measuring 11–22 mm were shared for fatty acid analysis and contaminant analysis, indicating that such small samples can be used in cooperative research projects.

In conclusion, species was the most important factor governing response to biopsy sampling. Interspecific comparisons in response of balaenopterid whales biopsied using the same methodology showed that blue and fin whales may be less sensitive to biopsy than the smaller minke and humpback whales. Results from this study also show that the biopsy technique is a relatively non-invasive method for obtaining high quality samples from balaenopterid whales with limited behavioral disturbances, as has been previously shown for humpback whales.

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GRAY WHALES ALONG THE OREGON COAST IN SUMMER, 1977-1980

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ABSTRACT—Gray whale (*Eschrichtius robustus*) distribution and relative abundance along the Oregon coast were studied during the summers of 1977-1980. Shore-based observations along the entire Oregon coast were made in 1977. In 1978-1980, detailed studies of whale distribution, activities, and body size were made along the central coast only; they were supplemented with observations from aircraft.

Over 1200 summer sightings were made within 0.5 km of shore. Numbers of sightings varied considerably from day to day and from year to year, with whale abundance estimated at 0.2-0.3 whales/km of shoreline for a 100 km portion of the study area. Over one-half the whales were presumed to be feeding; the remainder were traveling, usually parallel to shore. Body length was determined for 42 whales photogrammetrically. The majority of these summer whales were evidently subadults; calves and yearlings accounted for approximately 50% of the total.

The annual migration of the gray whale, *Eschrichtius robustus*, along the western shores of North America links summer feeding grounds in the arctic with their winter breeding, calving, and assembling grounds along the coast of Baja California and nearby mainland Mexico. Gray whales occupy their principal feeding grounds north of 60° N latitude, especially the Bering Strait region, from late May into November when the southward migration begins. Commencing in late December, gray whales arrive in their winter lagoons and remain there for a few weeks to several months. The northward migration has been described by Poole (1984) and by Herzing and Mate (1984) as two separate migratory pulses, the second composed chiefly of lactating females and their calves.

Not all northward migrants leaving their winter grounds in Mexico proceed directly to the Bering Sea. Pike (1962) reported that a few gray whales remained as summer residents along the British Columbia coast. Rice and Wolman (1971) listed six summer sightings between Baja California and British Columbia. Additional published reports (Hatler and Darling 1974, Patten and Samaras 1977, Sprague et al. 1977, Sullivan et al. 1983, Darling 1984) and numerous unpublished reports indicate that summer occurrences of gray whales along much of the west coast of North America are more common than previously assumed. In 1976, gray whales were reported as sighted or stranded during summer in at least 24 coastal locations in California and Oregon (Sumich, unpubl. data). Subsequent studies of summer gray whales in 1977-1980 along the Oregon coast are the subject of this paper.

METHODS

Summer sightings are defined as those occurring between 1 June and 15 September in coastal waters. Beginning in June 1977, fortnightly ground-based searches for summer gray whales were conducted from elevated observation sites approximately 20 km apart between the Columbia River and the Oregon-California border (a distance of 450 km). Visual searches for whales (aided by 7 × 35 binoculars) were made from each site. The date, time, apparent activity, direction of travel, and number of whales seen were recorded. Body size estimates were made when possible. These observations were supplemented with opportunistic sightings made by Coast Guard personnel, park rangers, commercial and sports fishers, and other cooperators. The counts were adjusted to discount possible repeated sightings of the same whale(s) on the same day. No corrections for visibility or observer effort have been attempted.

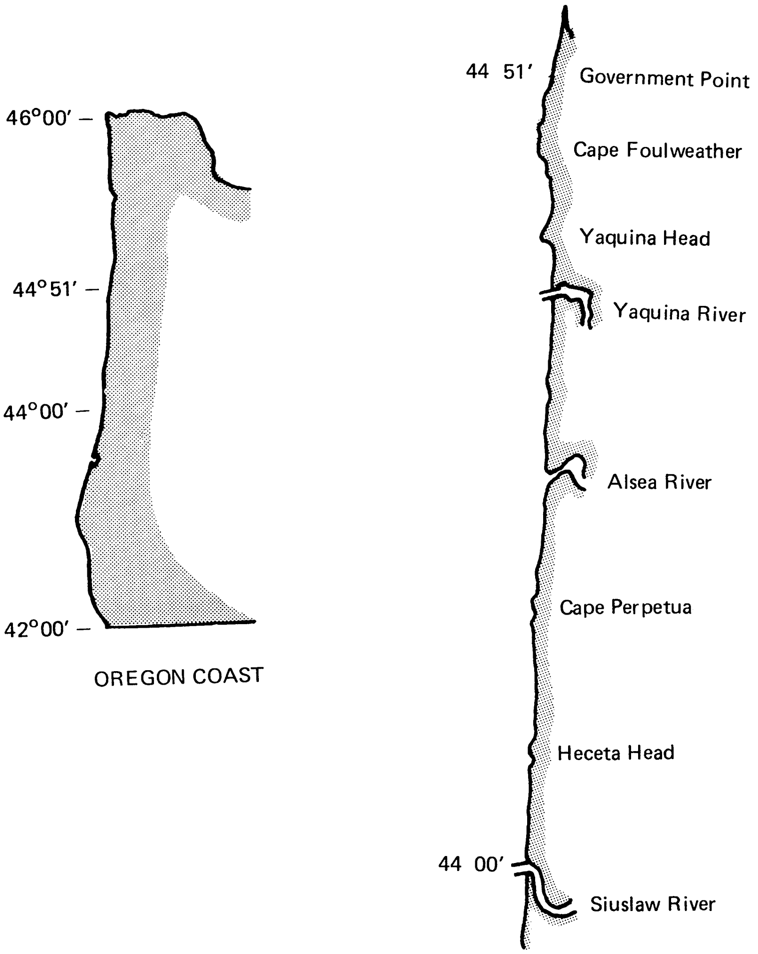

FIGURE 1. The 1977 (left) and 1978 (right) Oregon summer gray whale study areas.

The scope of the summer study area was narrowed in 1978 to 100 km of the Oregon coastline between the Siuslaw River (44°00' lat.) and Government Point (44°51' lat., Fig. 1) to obtain detailed information on site utilization, identification of individual whales, body length, and activities. Ground surveys in 1978 and 1979 were concentrated along the 25 km northern portion of the study area between Yaquina Bay (44°37' lat.) and Government Point, where several coastal bluffs and headlands (named in Fig. 1) provided elevated observation sites for complete visual coverage. Cape Foulweather (44°46' lat.) with an elevation of 140 m was especially suitable for monitoring behavior and for obtaining information on size and identification of individual whales. Ground surveys were discontinued in 1980.

During summer months of 1978, 1979, and 1980, aerial flights were made along portions of the Oregon coast. Helicopters of the U.S. Coast Guard (equipped with radar altimeters) or fixed wing aircraft were utilized as observation platforms. Determinations of body length were made from photographs taken from known distances with 35 mm high speed black and white film, 230 mm telephoto lens, and polarizing filter. Whales were usually photographed vertically from altitudes between 200 and 300 m when they surfaced to blow. For oblique photographs, the angle deviation from vertical was measured with a hand-held inclinometer and the correct camera-whale distance was calculated.

Additional photographs, using the same procedure, were taken from Cape Foulweather. Film

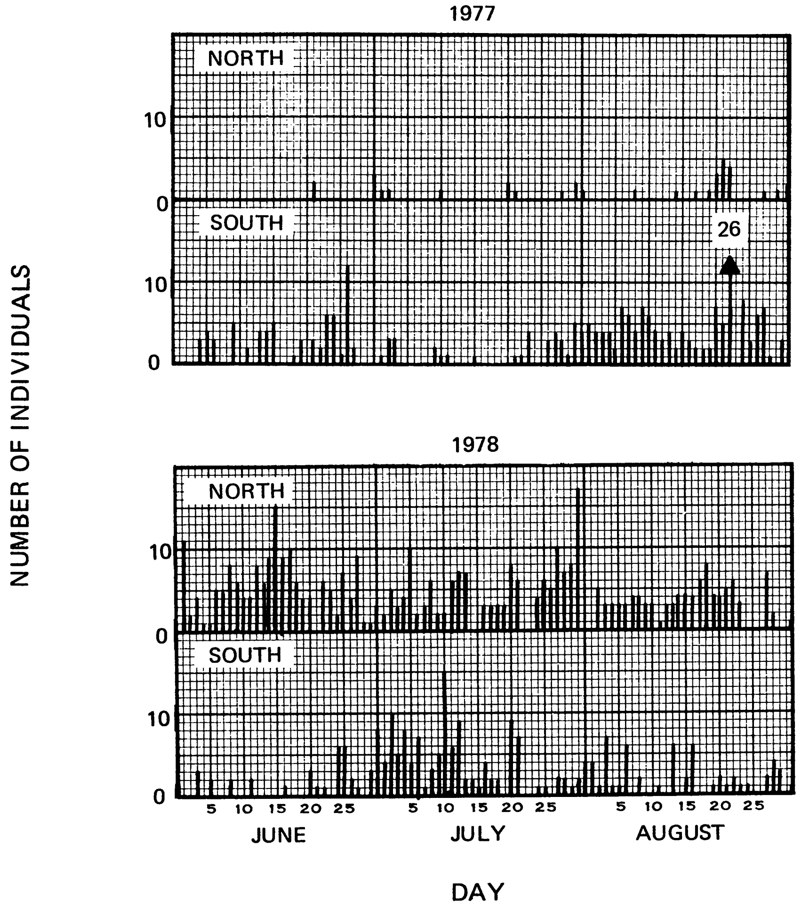

FIGURE 2. Daily numbers of summer gray whales reported from all sources in 1977 and 1978 for the northern (44°51′–44°25′ lat.) and southern (44°25′–44°00′ lat.) halves of the 100 km study area. Each small vertical division represents one whale.

negatives were examined under a 7× microscope. The standard length of the whale image was measured to the nearest 0.01 mm with an ocular micrometer. Body length was calculated with the following formula:

$$L = \frac{I \times D}{F}$$

where L = body length, m
I = whale image size on film, mm
D = whale to camera distance, m
F = camera lens' focal length, mm.

When a whale was photographed more than once, the lengths calculated from each photograph were averaged.

The relationship between body length and age of gray whales has been unresolved for some time (Zimushko 1970, Rice and Wolman 1971, Zimushko and Ivashin 1980), principally because most studies are of large, sexually mature whales. A re-examination of the age:body-length relationship of young gray whales (Sumich, unpubl. ms.) indicates that calves in their first summer are shorter than 8 m, and yearlings are between 8 and about 9.5 m.

TABLE 1. Results of 10 acceptable ground surveys between Yaquina River and Government Point, Oregon, in 1978 and 1979.

Date	Calves	Others	Total	Whales/km
1 Jun 78	2	5	7	0.28
17 Jun 78	1	5	6	0.24
5 Jul 78	4	7	11	0.44
11 Jul 78	3	3	6	0.24
13 Jul 78	3	3	6	0.24
1978 totals:	13	23	36	
25 Jun 79	0	0	0	0.00
6 Jul 79	1	9	10	0.40
8 Jul 79	3	4	7	0.28
3 Aug 79	0	2	2	0.08
6 Aug 79	1	1	2	0.08
1979 totals:	5	16	21	$\bar{x} = 0.23$
TOTALS:	18 (32%)	39 (68%)	57 (100%)	

On 20 July 1978, a study was conducted to test the value of aerial surveys along more extensive reaches of coastline. Seven shore observers were positioned on vantage points along a 25 km long portion of the study zone (Yaquina River to Government Point). Concurrently with the observations from shore, seven sequential flights of approximately ten minutes duration each were made over the zone with a Cessna 180 carrying a pilot and an observer. Flight speed was 180 km/h at 500 m altitude. The observation strip was 1 km wide, established with calibrated marks on the wing strut. Four flights were made to the south over the shoreline (observed strip extending from shore seaward 1 km); and three flights were made to the north 1 km offshore (observed strip extending from the line of flight to shore).

RESULTS

Over 1200 sightings of summer gray whales were reported from all sources along the Oregon coast between 1 June 1977 and 15 September 1980. Sixty percent of the 460 summer whales reported in 1977 were along the 100 km of coastline from the Siuslaw River to Government Point just north of Depoe Bay (latitude 44°00′ to 44°51′, Fig. 1), suggesting that they were either more numerous or were more easily seen there than along other portions of the Oregon coastline. Therefore, the 1978 shore surveys were limited to that region. Figure 2 illustrates the daily number of gray whale sightings from all sources between 1 June and 31 August of 1977 and 1978 for the northern (44°51′-44°25′ lat.) and southern (44°25′-44°00′ lat.) halves of that 100 km study area.

Observer effort and weather conditions affecting whale visibility were not necessarily equivalent for 1977 and 1978, and statistical comparisons of the two summers cannot be made. However, the data in Fig. 2 do suggest that summer gray whales occurred more frequently in the northern half of the study area in 1978 than in 1977. The largest single-day count in 1977 (August 22) was 30 for the 100 km study area; in 1978, it was 19 (on July 30), yielding a maximum observed occurrence of 0.2-0.3 whales/km of coastline.

Ten complete shore surveys were made along the 25 km coastal section from Yaquina River to Government Point in 1978 and 1979 during half-day periods of acceptable visibility (at least 5 km) and sea state conditions (Beaufort 3 or less). All 10 surveys were conducted by the same observer. Whale counts for those surveys are listed in Table 1. During June and July, calves remained close to their mothers and were easily recognized. As summer progressed, calves wandered farther (often more than 200 m) from their inferred mothers, were seen alone more frequently, and thus were more difficult to identify as calves without independent estimates of their body lengths. Accordingly, the relative number of calves listed in Table 1 (32% of the whales sighted) is considered a conservative estimate, particularly for the latter part of the summer. The mean ob-

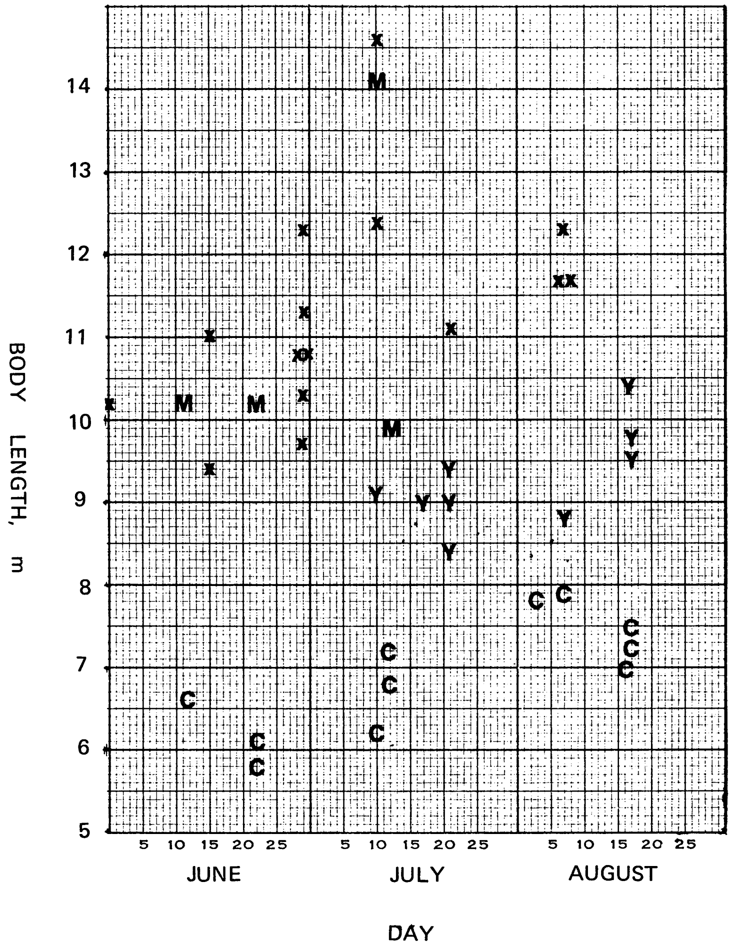

FIGURE 3. Body lengths of 42 summer gray whales photographed 1978–1980, plotted at dates of length determination. Age class assignment based on Sumich, unpubl. ms. (C = calf, Y = yearling, M = inferred mother with calf, x = other).

served occurrence of 0.23 whales/km compares well with the highest occurrences (0.2–0.3 whales/km) seen along the 100 km section of coastline in 1977 and 1978.

During the 20 July simultaneous ground/air study, the shore observers sighted 6 whales within the 25 km study zone during the aerial observation period. Four of the 6 whales were within 100 m of shore, and all 6 were located in surf or foam lines. No whales were seen from the air on any of the three flights 1 km offshore. Of the four flights over the shoreline, 0, 1, 3 and 1 whales were seen on successive passes ($\bar{x} = 1.25$ whales/pass; SD = 1.26).

In conditions of good visibility, 5 km was considered a practical maximum distance that gray whales could be reliably seen with binoculars under ideal conditions. Most of the sightings mentioned to this point were made within 500 m of shore. However, 14 reports of 27 whales 5 to 80 km offshore were received from Coast Guard personnel and fishing boat operators during 1977 and 1978. Water depths of these locations ranged from 50 to 2700 m. After 1978, efforts to contact these observers were discontinued.

Body lengths of 42 gray whales (Fig. 3) were determined using the photogrammetric technique. The precision of this technique was tested on a small whale photographed repeatedly from Cape Foulweather on 3 August 1979. Five film negatives showed the entire animal clearly. From these, body lengths were calculated ($\bar{x} = 7.78$ m; SD = 0.11 m). Twelve of the 42 whales (29%) measured were less than 8 m and were judged to be calves. This percentage is very close to the 32% calves observed in ground surveys (Table 1). Eight additional whales (19%) were considered yearlings (Fig. 3).

DISCUSSION

In the past decade, summer gray whale sightings have increased appreciably at several locations along the west coast of North America. The large variation in observed abundance along the Oregon coast described here may, in part, reflect varying observer effort. Sightings were never common north of Lincoln City (45°10′ lat.), where strategic headlands are fewer. Reliable estimates of whale numbers along inaccessible stretches of coastline could not be obtained from the air, because nearshore whales are extremely difficult to detect against their typical backdrop of surf and sea foam.

The numbers of summer whales at any one coastal site varied considerably from day to day and from one year to the next and showed no defined time of maximum occurrence to compare with other areas along the west coast. Due to the limitations of weather, sea state, and coastal terrain on the visibility of summer whales, the abundances reported in this study (0.2–0.3 whales/km) along the central Oregon coast are thought to represent fewer than the true number of whales in the study area. In another study of gray whales along a 40 km portion of the west coast of Vancouver Island, Darling (1984) found a maximum occurrence of 0.3 whales/km in July 1974 and 1976. In spite of the similar numbers of summer gray whales found for the Oregon and Vancouver Island locations situated over 500 km apart, it is premature to extrapolate these numbers to other west coast locations known to be frequented by summer whales. Consequently, it is not yet possible to indicate what fraction of the total whale population does not migrate to arctic waters in summer.

Although the principal activity of summer whales appears to be feeding, their prey is unknown. Gray whales in arctic feeding grounds forage on benthic infauna, particularly gammarid amphipods (Pike 1962, Rice and Wolman 1971). These organisms occur in the Bering and Chukchi Seas in densities to 24,000 animals/m^2 (Zimushko and Lenskaya 1970). The offshore sightings are intriguing in that eight of the 14 occurred at sites where water depths exceeded 100 m, and three were in depths of 400 m or more. Gray whales seldom feed in arctic waters deeper than 70 m (Nerini, pers. comm.). The presence of summer whales in deep water suggests that, if they are feeding, they are feeding on pelagic rather than benthic organisms, and thus they are exploiting a range of prey species broader than previously supposed.

Reilly (1984) estimated the annual gray whale birth rate to be no more than 14%, and the average annual mortality rate for all immature whales, 10%. However, it appears that mortality is much higher among calves (40%) and yearlings (27%) than for older immature animals (Sumich and Harvey, unpubl. ms.). Complications at birth, predation by sharks and killer whales, and severe storms may all contribute to high calf and yearling mortality (Morejohn 1968, Rice and Wolman 1971, Baldridge 1972). Thus, no more than 10% of the gray whale population during summer months would be expected to be calves, and 8%, yearlings. A Chi-square test indicated that the expected frequencies of calves (10%), yearlings (8%), and others (82%) were significantly different from those actually observed (29%, 19%, and 52%) ($\chi^2 = 57.30$, 2 df, $p < 0.001$).

Both calves and yearlings contribute significantly more to the counts of summer gray whales along the Oregon coast than would be expected from a random sample of the entire population. The numbers of calves suggest, by association, the presence of comparable numbers of lactating females, at least prior to weaning in late summer (Rice and

Wolman 1971). Moreover, approximately one-half of the whales in Fig. 3 larger than yearlings, including 3 of the 4 inferred females in the company of calves, are smaller than the mean length at sexual maturity (slightly over 11 m; Rice and Wolman 1971). Thus, Oregon summer whales are predominantly immature or atypically small mature animals.

Summer whales may gain energetic benefit by cutting short their northward migration and foraging in Oregon rather than colder arctic waters. Also, summer feeding can commence earlier and continue later prior to the southward autumn migration. These benefits may be particularly crucial for calves and their mothers, as pregnant females are the first to leave the arctic feeding grounds at the end of summer (Rice and Wolman 1971). Moreover, with their calves, they are the last to migrate north in spring (Sullivan et al. 1983, Poole 1984, Herzing and Mate 1984).

The benefits of a shortened northward migration hinge on the availability of adequate sources of prey in temperate southern waters. Where food resources are available well south of their principal feeding grounds, some whales can be expected to exploit them for energetic advantage. Thus, the shallow inshore portions of the Oregon coast, at least, should be considered as supplementary summer feeding grounds of the gray whale.

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Behaviour of gray whales (*Eschrichtius robustus*) summering off the northern California coast, from Patrick's Point to Crescent City

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MALLONÉE, J. S. 1991. Behaviour of gray whales (*Eschrichtius robustus*) summering off the northern California coast, from Patrick's Point to Crescent City. Can. J. Zool. **69**: 681–690.

This study quantifies basic dive characteristics and behaviour patterns of undisturbed gray whales (*Eschrichtius robustus*) observed summering at four northern California locations: the Big Lagoon – Patrick's Point area, Orick, Klamath River mouth, and Crescent City. Observable behaviours were limited to several locomotions (swim slow, swim moderate, swim fast, and floating) seen in different behavioural contexts (milling, circling, pluming, and transit). Sixteen behaviours were observed and they fit naturally into locomotive–context categories (i.e., swim-milling, swim slow – circling, etc.). Each behaviour was described using behavioural observations and dive characteristics. Behaviours that did not appear goal oriented or directed, i.e., milling and floating, had highly variable dive characteristics. More specific behaviours, such as circling and pluming, were less variable. Some specific and less directed behaviours appeared functionally related and usually occurred together. Apparent bottom feeding was observed and the Big Lagoon – Patrick's Point area appeared to be a favoured feeding site, as evidenced by mud plumes and repetitive circling of surfacing animals. Feeding was composed of at least three observable behaviours: circling, circling with pluming, and milling with pluming. Locomotive–context categories are useful in refining broad behavioural definitions and quantifying basic behaviour patterns. This approach can enhance the interpretation of observable surface behaviours.

MALLONÉE, J. S. 1991. Behaviour of gray whales (*Eschrichtius robustus*) summering off the northern California coast, from Patrick's Point to Crescent City. Can. J. Zool. **69** : 681–690.

Les caractéristiques de base de la plongée et les variations du comportement ont été étudiées chez des Baleines grises (*Eschrichtius robustus*) de Californie dans leurs territoires d'été au large de quatre points sur la côte, dans le nord de la Californie : site de Big Lagoon – Patrick's Point, Orick, embouchure de la rivière Klamath et Crescent City. Les comportements observés semblent restreints à divers types de mouvements (nage lente, nage modérée, nage rapide et flottement) reliés à des situations diverses (déplacements erratiques, déplacements circulaires, rejets de boue et déplacements d'un endroit à un autre). Seize comportements ont été observés et ils correspondent tout naturellement à des catégories de contextes de locomotion (i.e., nage lors de déplacements erratiques, nage lente lors de déplacements circulaires, etc.). Chaque comportement est décrit, tenant compte à la fois des observations du comportement lui-même et des caractéristiques des plongées. Les comportements qui ne semblent pas avoir de direction ou de but précis, par exemple les déplacements erratiques et les flottements, sont reliés à des caractéristiques de plongée extrèmement variables. Les comportements plus spécifiques, tels les déplacements circulaires et le rejet de boue, sont moins variables. Certains comportements spécifiques moins orientés semblent avoir une relation fonctionnelle et se produisent ordinairement en même temps. Les baleines semblent se nourrir sur le fond de l'eau et le site de Big Lagoon – Patrick's Point est apparemment un site d'alimentation de prédilection, du moins à en juger par le rejet de boue et les déplacements circulaires répétés des animaux qui refont surface. L'alimentation suppose au moins trois comportements différents : déplacements circulaires, déplacements circulaires avec rejet de boue et déplacements erratiques avec rejet de boue. Les catégories de contextes de locomotion sont des outils commodes pour raffiner les définitions trop vagues de certaines comportements et pour quantifier les comportements de base. Cette approche offre la possibilité d'une interprétation plus juste des comportements de surface observés.

[Traduit par la rédaction]

Introduction

The migratory pathway of gray whales (*Eschrichtius robustus*) extends from calving lagoons in Baja California, Mexico, along the west coast of North America to feeding areas in the Bering, Chukchi, and (occasionally) Beaufort seas (Rice and Wolman 1971; Rugh and Fraker 1981). However, detailed information about individual migratory patterns, coastline utilization, and summertime distributions is usually not available (Pike 1962; Rice and Wolman 1971; Wilke and Fiscus 1961). Censuses conducted at Unimak Pass, Alaska (Hall et al. 1977; Rugh and Braham 1979; Rugh 1984), indicate that by summer, the majority of gray whales end their migration at these northern feeding grounds. Groups of summering whales, however, have been observed in many coastal areas along the migratory pathway. Summertime sightings have occurred off British Columbia, Washington, Oregon, and California (Darling 1978, 1979, 1984; Dohl et al. 1981; Gilmore 1960; Pike 1962; Rice and Wolman 1971). Small groups of whales (six to eight per group) reside in at least four northern California locations during the summer months: the St. George Reef offshore from Crescent City, at the Klamath River mouth, in the Big Lagoon – Patrick's Point area, and in waters adjacent to the Farallon Islands (Dohl et al. 1983). The presence of summering whales in these areas offers an opportunity to observe identified individuals (using natural markings as described in Darling 1984) over extended time periods. Such observations are usually not possible for animals in the inaccessible northern seas or migrating far offshore.

Few detailed behavioural observations and dive characteristics have been reported for summering gray whales and the available literature deals mainly with feeding activity. Thus, behaviours such as bottom feeding by summering whales (Hatler and Darling 1974; Oliver et al. 1983; Oliver and Kvitek 1984) must usually be inferred from the muddy plumes of surfacing animals or resultant bottom depressions (Nerini 1984). Using indirect evidence of feeding, Guerrero (1989) reported that significantly different patterns in the apparent feeding behaviour of summering gray whales were related to the patchiness and mobility of two different benthic prey items.

Some gray whale behaviours are defined broadly and could

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reflect behavioural contexts rather than specific actions. For example, several specific behaviours may occur during "feeding," each having different dive characteristics. Taken together, these behaviours represent a feeding context rather than a specific feeding behaviour. Noting only that an animal is "feeding," therefore, may not accurately reflect the actions of that animal. Dive characteristics can be obtained by monitoring respiratory blows of surfaced whales (Sumich 1983; Würsig et al. 1986) and have been described by Harvey and Mate (1984) using radio-tagged animals. Combining visual observations of gray whales with their corresponding dive patterns can enhance the interpretation of many broadly defined behaviours, but this practice has been limited to only a few studies (Guerrero 1989; Harvey and Mate 1984; Murison et al. 1984; Oliver et al. 1984; Würsig et al. 1986). Admittedly, individual variability exists among whales exhibiting these behaviour patterns. This study, however, attempts only to describe observable behaviours common to most of the study animals rather than specify the behaviours of each individual.

Before this study, I observed undisturbed (from boat traffic, planes, divers, fishing operations, etc.) summering gray whales in the Big Lagoon – Patrick's Point area, California, during 1979 and 1980. These whales exhibited different behavioural contexts such as transit between areas, milling, and apparent feeding. Locomotions, ranging from floating to fast swimming, were noted throughout the observations and they did not occur with equal frequency in each behavioural context. All observable behaviours could be naturally grouped into locomotive–context categories (i.e., swim slow – milling, swim fast – transit, etc.). These categories showed that it was possible for many of the swimming movements to have different meanings or functions dependent upon the context in which they occurred. The meaning of some animal behaviours is known to change in different contexts (i.e., Smith 1965). Noting the context in which specific behaviours occur can improve the interpretation of those behaviours.

Locomotive–context categories offer a new approach to understanding gray whale behaviour by refining broad behavioural definitions. Much informal knowledge of gray whale behaviour exists, but little of it has been quantified. Swartz and Jones (1980) stated that in their study, much of the gray whale behaviour was anecdotal and requires additional study for quantification. This indicates that in general, gray whale behaviour needs additional quantification and a need exists for additional descriptions of base-line behaviours. Using the locomotive–context approach, this study will quantify some basic dive characteristics and base-line behaviour patterns of undisturbed gray whales that spend the summer off the northern California coast.

Methods

Four northern California locations served as observation sites: the Big Lagoon – Patrick's Point area, Orick, the Klamath River mouth, and Point St. George in Crescent City (Fig. 1). These sites afforded unobstructed views of the coastline and ranged from 6 to 50 m above the water surface. Observations were made 2 days each week from September 1986 through October 1987, and May 1988 through August 1988. The 1st year of observations provided information as to whether the summering whales migrated, and if so, their approximate departure and arrival times. Beginning in May 1987, observation time at each site was distributed approximately equally through the daylight hours so that daily behavioural changes could be observed. Each site was visited once or twice daily, 2 days a week, in the morning, afternoon, or evening. My previous sightings in 1979, 1980, and 1986 indicated that approximately 70% of sightings occur within the 1st hour of observation time. A 60-min minimum waiting period was therefore established before abandoning the site. When a sighting occurred, observations continued until the whale left the area. The remaining sites were then sampled as time permitted.

During a sighting, data used for calculating dive characteristics were recorded on respiration, location, locomotion, and general behaviour of each visible whale. A time, direction, compass bearing, and distance were noted for every surfacing. Because the whales were close to the shoreline, their distance offshore was estimated subjectively using offshore landmarks where distances were predetermined using a topography map. A similar technique of estimating distance subjectively has been used successfully by Poole (1984). Instead of a topography map, Poole used a surveyor's transit to determine the distance of offshore landmarks. He then estimated subjectively the distance offshore of migrating gray whales.

Observations were limited to behaviours at or above the water surface. Changes of direction in successive surfacings, however, were assumed to occur underwater. Surfacings with visibly exhaled water vapour were noted as blows. Remaining surfacings were noted as no-blows. When the animals dove after a surfacing, it was noted if the flukes were raised completely or partially above the water surface, or not at all. Visible flukes may indicate when the whales begin a long dive (sounding) and could be useful in determining their next surfacing. Whales were generally 100–500 m from shore and could be individually identified from scars and pigmentation patterns on the back, head, and sides (i.e., Darling 1984).

Previous observations determined that dive durations could be naturally grouped into surface–dive sequences of long and short dives. A surface–dive sequence was defined as one long dive (≥60 s) followed by a variable number of shorter surface respirations. A locomotive pattern and the context in which it occurred were assigned to all the observed surface–dive sequences. The surface–dive sequences were placed in locomotive-context categories and divided into duration of long dive, blow interval, number of blows per surfacing, and duration of surfacing. Dive characteristics were obtained for each categorical division by calculating the mean and standard deviation. Significant differences between categories were determined by using analysis of variance and *t*-tests.

When observing the summering whales prior to this study, I noted that at least three distinct swimming speeds could be observed. Approximate swimming speeds, therefore, were calculated in an attempt to quantify observable changes in speed. Because offshore distance was estimated subjectively, calculated swimming speeds were never intended to be extremely accurate. Instead, these swimming speeds were grouped into six gross categories of locomotion (Table 1).

Swimming speeds were determined by plotting the compass bearings onto topography maps and calculating the time and distance between surfacings. Based on the topography map scale, with 100 m as the smallest division, accuracy could have been within ±10 m for the distance between surfacings. Offshore distances, however, were estimated subjectively, which probably reduced accuracy by an unknown amount. Accuracy, therefore, was greater than ±10 m, but in my estimation, probably less than ±50 m (one-half of the smallest division). The whales were always observed within one of the following contexts: transit, milling, circling, and pluming. Contexts and locomotions are defined in Table 1.

Results

Summering whales were observed during 29 sightings at all observation sites between the dates of September 1 and October 31, 1986; May 1 and October 31, 1987; and May 1 and August 31, 1988. Whales sighted between the beginning of May and the end of October were considered summering whales. These animals remained close to shore and never appeared to be migrating. A total of 50 summering whales (representing a smaller number of resighted individuals) were observed. Thirty-one animals were observed at the Big Lagoon – Patrick's Point

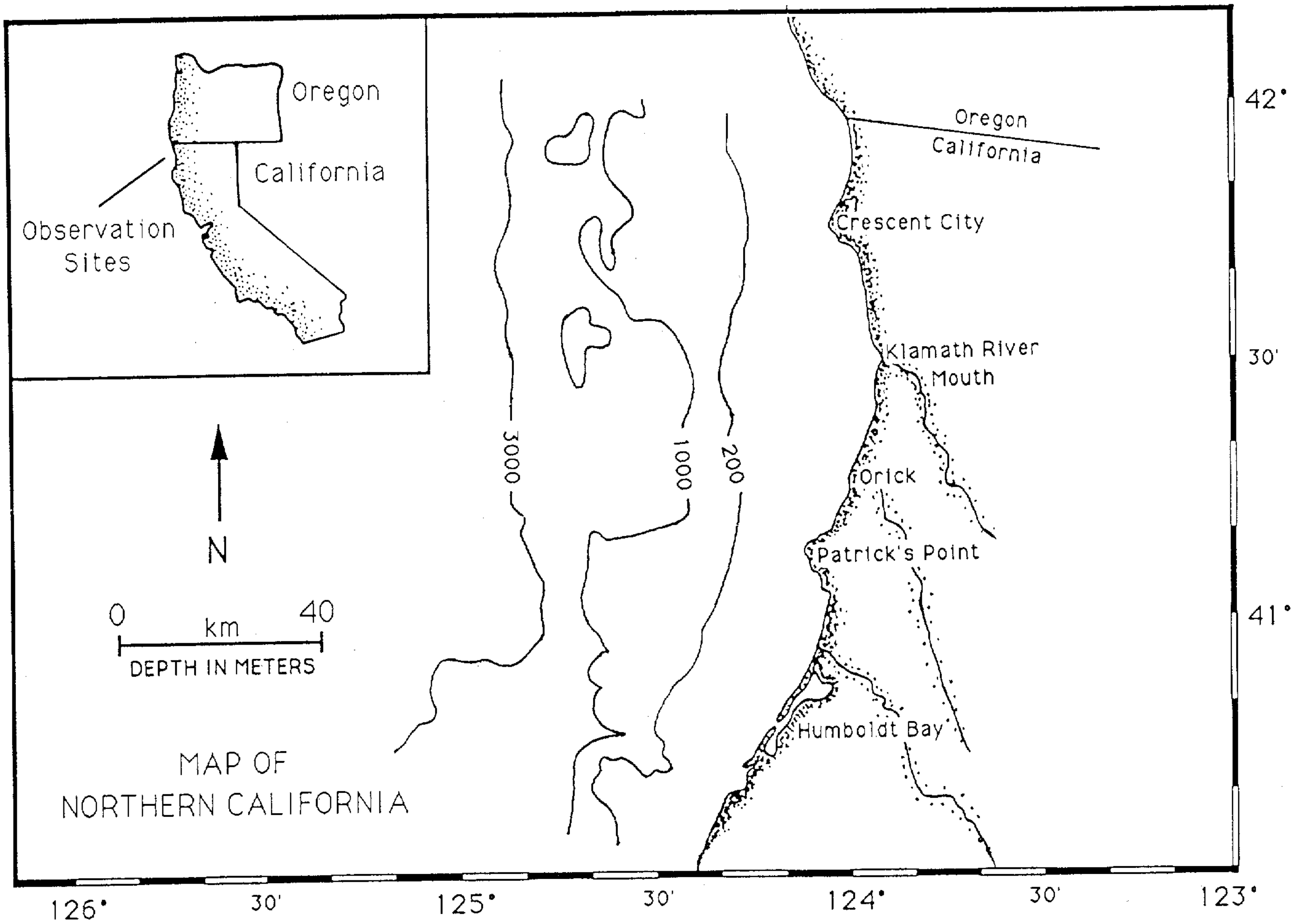

FIG. 1. The four observation sites used to observe gray whales summering off the northern California coast: Crescent City, Klamath River mouth, Orick, and Patrick's Point.

TABLE 1. Definition and probable function of the four behavioural contexts and six locomotions observed in gray whales summering off the coast of northern California

Term	Definition	Probable function
Context		
Transit	Forward movement from area to area	Travel
Milling	Forward and numerous directional changes in movement within a restricted area	Searching
Circling	Constant directional changes in movement within a restricted area	Bottom feeding
Pluming	Sea floor disturbance resulting in surface mud patches and plumes	Bottom feeding
Locomotion		
Swim slow	Minimal forward progress (0.5–1.0 km·h^{-1})	Bottom feeding
Swim moderate	Constant forward progress (3.0–4.0 km·h^{-1})	Travel
Swim fast	Rapid forward progress with occasional white water (7.0–8.0 km·h^{-1})	Unknown
Float	No forward movement	Resting/orientation
Float then swim slow	—	Searching
Float then swim fast	—	Searching

area. Three to five whales were observed at each of the remaining observation sites, including opportunistic sightings at Crescent Beach (three whales) and Dry Lagoon (three whales). The majority of whales were seen at the Big Lagoon – Patrick's Point area because fog and rain severely reduced observation time at Point St. George and the Klamath River mouth. All observed summering whales were judged to be "adults" and usually were sighted as individuals with occasional groups of two or three animals.

Because many whales were in transit and swam out of view before specific behaviours could be noted, behavioural analysis was limited to 13 sightings and a total of 12 different whales. One whale (identified by distinct natural markings) was observed in 3 of the 13 sightings, once with another whale and

TABLE 2. Number of observed surface–dive sequences per behaviour (locomotive–context category) seen during the 13 sightings

	Context					
Observed locomotion	Circling	Circling with pluming	Transit	Milling	Milling with pluming	None
Swim slow	38 (2)	9	2 (1)	92	15	*
Swim moderate	4 (4)	0	41 (11)	16 (16)	0	*
Swim fast	1 (1)	0	2	1 (1)	0	*
Float	5 (4)	*	*	*	*	14 (6)
Float then swim slow	6	*	*	*	*	2
Float then swim fast	1	*	*	*	*	0

NOTE: The numbers in parentheses represent the contribution made by one whale in the two sightings not used in statistical analysis.

*Behaviours that cannot take place. For example, a whale cannot simultaneously float and transit.

twice alone. To avoid repeated observations of the same whale (which would bias statistical analysis), two of these sightings were not included in the statistical analysis, which was limited to 11 sightings and 12 different whales. Six locomotive behaviours were seen across five behavioural contexts resulting in 16 observable behaviours (locomotive–context categories) (Table 2). The division of long and short dives was determined by inspecting the frequency distribution of all observed dive durations. An apparent break in dive duration occurred at 60 s and correlated well with the observed behaviours.

Locomotive behaviours

These behaviours ranged from variable speeds of forward movement to floating at the water surface (Tables 1 and 2). Swim slow was minimal forward movement seen in animals milling and apparently feeding. Slow swimming comprised 62.7% ($n = 156$) of observed surface–dive sequences. The swim moderate behaviour was also used while milling but rarely seen during apparent feeding. The majority of swim moderate surface–dive sequences were observed during transit when an animal would move from one area to another. Of observed surface–dive sequences, 24.5% ($n = 61$) were during swim moderate. Swim fast was observed rarely and never during apparent feeding (i.e., circling and pluming). Only 1.6% ($n = 4$) of observed surface–dive sequences were swim fast.

Floating was also observed, in which the animals remained just below the water surface. Because floating required no forward movement, it was seen rarely during the observed behavioural contexts. Instead, floating was observed by itself or in combination with another locomotive behaviour during apparent feeding. These feeding surface–dive sequences began with the animal floating near the surface and ended with the whale swimming slowly in a semicircle. Floating was seen in 11.2% ($n = 28$) of observed surface–dive sequences.

Behavioural contexts

Throughout each sighting, the whales were always observed to be in one of four behavioural contexts: transit, milling, circling, and pluming. Transit involved forward movement from one area to another, usually in a straight line. A beeline course was altered only when the animals were rounding a headland or avoiding an obstacle. Otherwise, the shortest distance was taken between two areas. Of observed surface–dive sequences, 18.1% ($n = 45$) were transit. When the new area was reached and transit ended, either the milling or the circling context would begin. Pluming was never observed immediately after transit.

Milling occurred in 43.8% ($n = 109$) of observed surface–dive sequences and involved swimming back and forth within a restricted area, usually a few 100 m in diameter. These areas were located approximately 50–500 m from rocky headlands, in the middle of bays, and occasionally at the Klamath River mouth. Milling usually involved only one or two animals. Six whales, however, were observed for 2 consecutive days at Patrick's Point milling near shore. During milling, the whales would swim throughout the area making many directional changes both above and below the water surface. Since individual whales would sometimes dive in one direction and surface in another, it was clear that directional changes occasionally took place underwater.

Some surface swimming patterns were repeated before diving. Within this context, the whales would swim in a semicircle before diving and then surface where the semicircle began, completing a circular route. The pattern would then be repeated numerous times with half the circle occurring at the surface and the other half apparently underwater. The majority of these circular patterns were in a clockwise direction (61.4%, $n = 35$) and never more than approximately 100 m in diameter. Circling comprised 22.1% ($n = 55$) of observed surface–dive sequences.

Occasionally, surface mud patches and plumes were seen during milling and circling. Mud patches about 20–25 m in diameter were present before the animals surfaced during milling. While at the surface, the whales never swam back or dove through the mud patches. If new mud patches were formed in succeeding dives, they would form near previous patches but never in the same location. During circling, mud patches formed semicircles before the animals surfaced and occasionally a whale surfaced with mud streaming from its mouth, forming mud plumes. Mud patches and plumes occurred in 6.0% ($n = 15$) of observed surface–dive sequences during milling and 3.6% ($n = 9$) during circling. Most sightings of mud patches and plumes involved one whale. If two animals were present, each formed mud patches or plumes independently of the other in different but nearby locations (approximately 100–300 m apart).

Behaviours (locomotive–context categories)

Table 3 provides descriptions of the most frequently observed behaviours. A frequent behaviour was defined to be a loco-

TABLE 3. Description of the most frequently observed behaviours (locomotive–context categories)

Behaviour (locomotive–context category)	Description	%*	*n*
Swim slow – milling	Most frequent behaviour. Tendency to surface facing the same direction. Constant positional changes for individual whales, ranging from 0 to 60°. Positional changes did not occur in a straight line, therefore constant directional changes occurred.	36.9	92
Swim slow – milling with pluming	Similar to swim slow – milling but involved the formation of mud patches and plumes. Tendency to surface facing the same direction. Occurred within smaller areas (0–14°) than swim slow – milling.	6.0	15
Swim slow – circling	Tendency for clockwise circling (63.2%, $n = 24$, of these observed surface–dive sequences). Surfaced facing different directions. Small positional changes (<10°). Occasional no-blows.	15.3	38
Swim slow – circling with pluming	Similar to swim slow – circling but involved the formation of mud patches and plumes. Clockwise circling in 57.1% ($n = 4$) of these observed surface–dive sequences.	3.6	9
Swim moderate – transit	Constant positional and distance changes. Always visible blows and surfaced facing the same direction.	16.5	41
Swim moderate – milling	Observed only in one whale. Similar to swim slow – milling but positional changes were smaller (0–15°). Occasional no-blows. Tendency to surface facing the same direction.	6.4	16
Swim moderate – circling	Observed only in one whale. Position never changed and surfaced facing the same direction. Occasional no-blows.	1.6	4
Float	Occurred at or near the water surface. Animals always faced the same direction. Numerous no-blows.	5.6	14
Float–circling	Same as float but whales' direction changed gradually with each succeeding respiration. They rotated (clockwise and counterclockwise) between 45 and 180° by the end of each surface–dive sequence. Numerous no-blows.	2.0	5
Float then swim slow – circling	Occasionally, floating preceded swim slow – circling within a surface–dive sequence. Respirations were visible and surfacing directions were always different.	2.4	6

*Percentage of all observed surface–dive sequences.

TABLE 4. Percentage of frequently observed behavioural surface–dive sequences in which the flukes or partial flukes (arched peduncle) were raised above the water surface before a long dive

Behaviour (locomotive–context category)	Flukes		Arched peduncle		
	%	*n*	%	*n*	Total %
Swim slow – milling	43.5	40	7.6	7	51.1
Swim slow – milling with pluming	53.3	8	6.7	1	60.0
Swim slow – circling	42.1	16	15.8	6	57.9
Swim slow – circling with pluming	66.7	6	—	0	66.7
Swim moderate – transit	14.6	6	—	0	14.6
Swim moderate – milling	50.0	8	—	0	50.0
Swim moderate – circling	100.0	4	—	0	100.0
Float	35.7	5	—	0	35.7
Float–circling	60.3	3	—	0	60.0
Float then swim slow – circling	50.0	3	—	0	50.0

motive–context category that was observed in a total of four or more surface–dive sequences. These behaviours occurred during swim slow, swim, float, and across most behavioural contexts. The majority of frequently observed behaviours were seen when the animals were swimming slowly within a restricted area.

When the animals completed a dive or surface respiration during swim slow – milling or swim slow – milling with pluming, they had a tendency to surface facing the same direction. For example, a whale that surfaced facing north did so during all of its swim slow – milling surface–dive sequences. The surfacing direction was different for each animal but usually remained constant throughout that animal's surface–dive sequences. The position or compass bearing, however, changed throughout the surface–dive sequences, indicating that directional changes occurred during swim slow – milling. Because a whale surfaced facing the same direction, changes in direction occurred underwater during the dive.

Occasionally, when the animals sounded (beginning of a long dive) at the end of a surface–dive sequence, the peduncle area became arched severely or the flukes were lifted entirely out of the water. The percentage of surface–dive sequences in which this occurred is listed in Table 4 for each frequently observed behaviour.

The majority of observed surface–dive sequences were of whales swimming slowly. Fewer surface–dive sequences and behaviours were observed when the locomotion was swim moderate. Most of the swim moderate surface–dive sequences

TABLE 5. Summary statistics for dive characteristics seen in the 11 sightings (12 different whales) used for statistical analysis

	Duration of dive (s)			Blow interval (s)			No. of blows/ surfacing			Duration of surfacing (s)		
	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*
Locomotion												
Swim slow	208.02	92.34	146	16.62	9.21	372	3.49	1.82	142	41.65	33.12	142
Swim moderate	145.41	64.17	29	30.12	13.54	57	3.07	1.75	27	62.44	65.28	27
Swim fast	156.50	50.20	2	19.33	7.02	3	2.50	0.71	2	29.00	24.04	2
Float	269.18	100.49	17	20.42	6.46	26	3.71	2.93	7	61.38	63.95	8
Context												
Milling	207.52	101.77	91	16.13	9.83	176	2.95	1.71	87	31.75	29.77	87
Transit	145.16	61.95	32	28.40	13.59	68	3.23	1.99	30	63.33	64.95	30
Circling	208.94	75.26	35	17.30	8.56	115	4.09	1.50	35	54.57	31.14	35
Pluming	213.63	75.45	19	16.40	8.41	73	4.53	1.71	19	57.16	27.40	19
Behaviour (locomotive–context category)												
Swim slow – transit	115.00	—	1	19.50	11.70	8	9.00	—	1	156.00	—	1
Swim slow – milling	207.52	101.77	91	16.13	9.83	176	2.95	1.71	87	31.75	29.77	87
Swim slow – milling with pluming	229.00	61.80	10	17.30	8.84	46	4.33	1.37	12	57.17	26.64	12
Swim slow – circling	208.94	75.26	35	17.30	8.56	115	4.09	1.50	35	54.57	31.14	35
Swim slow – circling with pluming	196.56	88.81	9	14.85	7.53	27	4.86	2.27	7	57.14	30.85	7
Swim moderate – transit	145.41	64.17	29	30.12	13.54	57	3.07	1.75	27	62.44	65.28	27
Swim moderate – milling*	225.00	133.20	16	18.00	7.95	49	4.13	1.68	15	54.27	33.54	15
Swim moderate – circling*	204.75	55.98	4	21.35	11.92	17	5.25	1.89	4	90.75	24.62	4
Swim fast – transit	156.50	50.20	2	19.33	7.02	3	2.50	0.71	2	29.00	24.04	2
Swim fast – milling*	166.00	—	1	18.00	—	1	2.00	—	1	18.00	—	1
Swim fast – circling*	242.00	—	1	12.67	2.29	9	10.00	—	1	114.00	—	1
Float	315.71	132.32	7	21.57	5.95	23	3.67	3.20	6	65.14	68.11	7
Float – circling	233.00	—	1	11.67	1.53	3	4.00	—	1	35.00	—	1
Float then swim slow	260.50	27.58	2	18.75	12.24	8	5.00	1.41	2	75.00	32.53	2
Float then swim slow – circling	238.00	72.16	6	16.52	7.27	29	5.83	2.23	6	79.83	49.08	6
Float then swim fast while circling	184.00	—	1	22.67	8.50	3	4.00	—	1	68.00	—	1

*Behaviours seen in repeated observations of only one whale. To avoid data bias, the remaining behaviours displayed by this animal were not incorporated into the other summary statistics.

were seen during transit in which the animals were usually passing through the immediate area. Less time, therefore, was spent observing animals in the swim moderate locomotion. Swim moderate was never seen during pluming and was observed only in transit, circling, and milling.

Floating, in one form or another, was seen in 11.2% ($n = 28$) of observed surface–dive sequences. Five variations of floating were observed, three of which were considered frequent behaviours. It was obvious when the animals were floating because the distance from shore and position never changed. The animals remained just under or at the water surface. They always remained low in the water and little of their bodies could be seen. During floating, many surfacings occurred with no visible blow and were therefore recorded as no-blows. When no-blows occurred, they were lumped together in particular surface–dive sequences. The remaining surface–dive sequences consisted mostly of visible respirations with occasional no-blows.

Surfacing and respiration characteristics

Although the aim of this study was to describe whale behaviour that occurred near or at the water surface, it was also possible to quantify these activities (Table 5). Surface–dive sequences for locomotion, context, and locomotive-context categories were analyzed for duration of dive, blow interval, number of blows per surfacing, and duration of surfacing. Frequency distributions of these four divisions are presented in Fig. 2. The distributions were skewed positively but when transformed into logarithms, they became approximately normal. The use of parametric statistics, therefore, was appropriate.

Using ANOVA (99% confidence intervals), significant differences were found between contexts for duration of dive ($F = 5.67$, $p = 0.001$), blow interval ($F = 24.71$, $p = 0.0001$), and number of blows per surfacing ($F = 8.28$, $p = 0.0001$). No significant differences were found among contexts for duration of surfacing. Duration of dives was significantly longer during milling ($t = 3.52$, df = 121, $p < 0.001$), circling ($t = -3.65$, df = 65, $p < 0.001$), and pluming ($t = -3.33$, df = 49, $p < 0.002$) than during transit. When transit occurred, the blow interval was significantly longer than that seen during milling ($t = -8.01$, df = 242, $p = 0.0001$), circling ($t = 6.54$, df = 181, $p = 0.0001$), and pluming ($t = 6.39$, df = 139, $p = 0.0001$). During apparent feeding (circling and pluming), the number of blows per surfacing was significantly higher than during nonfeeding activities (milling and transit). Circling had more blows per surfacing than did milling ($t = -3.86$, df = 120, $p < 0.001$) and transit ($t = -2.83$, df = 63, $p < 0.007$). Pluming also showed an increase in the number of blows per surfacing over milling ($t = -3.48$, df = 104, $p < 0.001$) and transit ($t = -2.79$, df = 47, $p < 0.008$).

Significant differences were also observed among locomotions (at the 99% confidence interval) for duration of dive ($F = 8.32$, $p = 0.0001$) and blow interval ($F = 28.00$, $p = 0.0001$). Dive duration was significantly longer when the whales swam

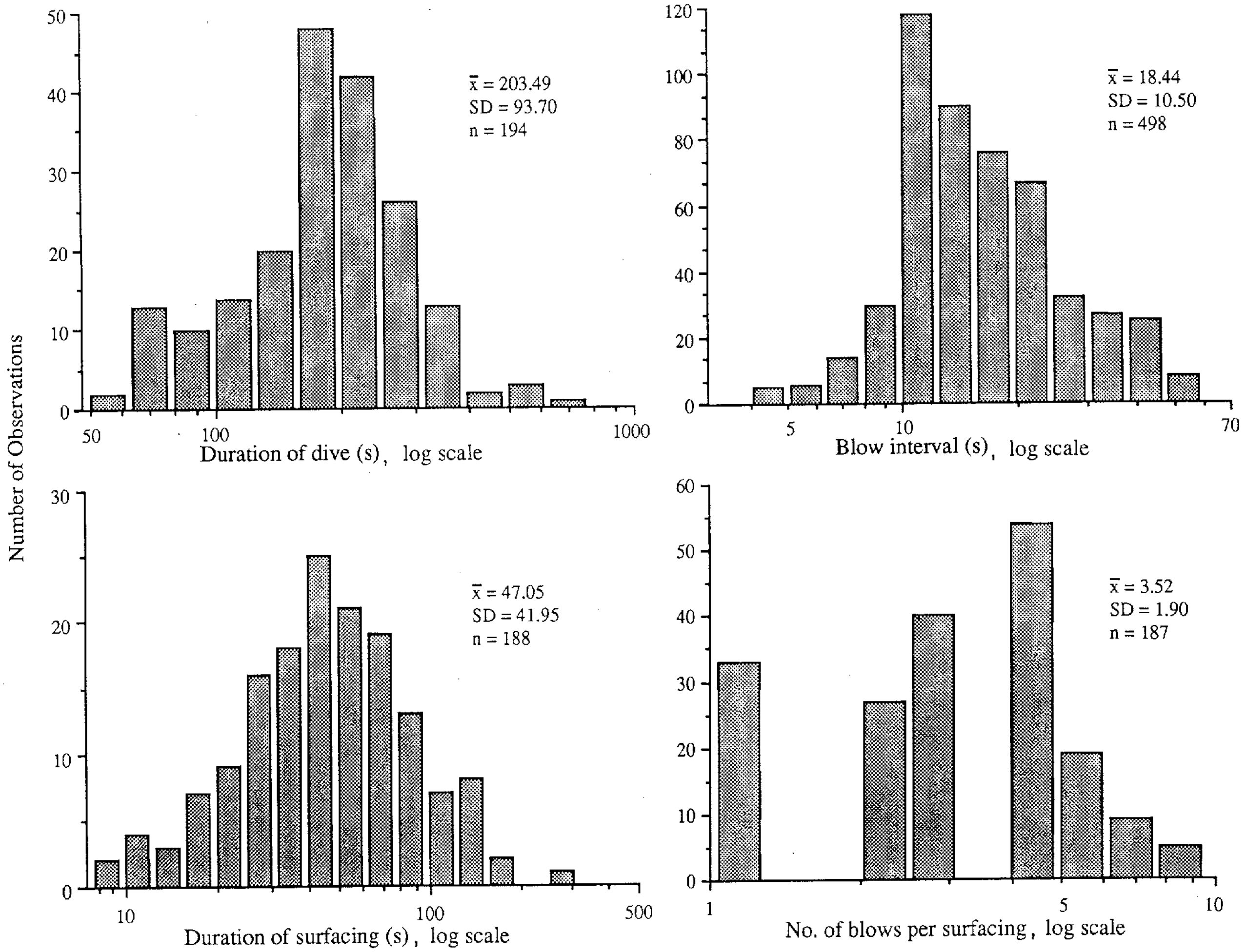

FIG. 2. Frequency distributions of the dive, respiration, and surfacing divisions. The $\bar{x}$ and SD are the observed measurements and are not log transformed numbers.

slowly rather than moderately ($t = 3.91$, df = 173, $p = 0.0001$). During float, dive duration was longer than that of swim moderate ($t = -4.81$, df = 44, $p = 0.0001$) and swim slow ($t = -2.47$, df = 161, $p < 0.02$). The blow interval during swim moderate was longer than the blow intervals in float ($t = 2.91$, df = 81, $p < 0.005$) and swim slow ($t = -8.77$, df = 427, $p = 0.0001$). While floating, however, the whales had longer blow intervals than they did during swim slow ($t = -2.95$, df = 396, $p < 0.004$). Sample sizes for swim fast were too small for statistical analysis in all four divisions. For duration of surfacing, float sample sizes were also too small for analysis and there was no significant difference between swim slow and moderate. No significant differences were found among locomotions for number of blows per surfacing.

Discussion

A dive pattern of one long dive followed by a surfacing sequence of one or more shorter dives (blow intervals) was constant throughout all the observed behaviours. There was undoubtedly a real distinction between long and short dives. This distinction becomes apparent by inspecting the frequency distribution of all observed dive durations. An apparent break in dive duration occurred at 60 s. This break could have been a chance sampling effect, but it correlated well with the observed behaviours. This study, therefore, used 60 s as the division between long and short dives. In Harvey and Mate's (1984) study of gray whale diving patterns, they also used 60 s as the division between long and short dives. After a long dive, the whales produced a sequence of blows separated by short, and doubtless, shallow dives. It is the overall duration of this surface sequence that is summarized in the duration of surfacing column in Table 5. It appears that gray whales must conform to a respiratory pattern of one long dive followed by one or more shorter dives and that the observed variability in respiration patterns can be correlated with the behaviours. Although the respiratory patterns observed in this study were those of summering gray whales, they appear to correspond with the "clumped" dive patterns observed by Harvey and Mate (1984) in gray whales wintering in Mexican lagoons, between southward and northward migrations.

For most frequent behaviours, locomotions, and contexts, coefficients of variation indicated that behavioural variability was high. This may reflect individual variability in behaviour patterns; nevertheless, some behaviours and contexts appeared more variable than others. For example, milling and floating did not appear goal oriented or directed and had the highest overall variability in respiration patterns. The more specific and directed behaviours like circling and pluming were less variable. Circling and pluming had extremely similar numbers in all four dive characteristic divisions. Both had the lowest overall behavioural variability of any locomotion or context. Their similarity reflects that these observations are probably the same and were only separated into different contexts because mud was not always visible.

While observing the whales, distinguishing between the different contexts and locomotions was not difficult. It was obvious when the whales were in transit, since they swam in a straight line and out of view. Circling and milling also appeared different from one another. Aside from significant differences in the number of blows per surfacing, it was obvious when the whales were circling as opposed to milling. During milling, the whales surfaced facing numerous directions, which they did not do during circling, and they also utilized a much wider area. Floating was also obvious because the whales did not move forward. In addition, significant differences in dive duration and blow interval were observed between swimming slowly and moderately.

My observations indicated that behaviours could be split naturally into two different groupings: context and locomotion (locomotive–context categories). Statistically significant differences between contexts were found for measures of dive duration, blow interval, and number of blows per surfacing; significant differences among locomotions were found for duration of dive and blow interval. Since I was unable to compare my observations with those of a second observer working independently, the reliability of the behavioural groupings needs to be established. Nevertheless, I believe that the differences between the various context and locomotive categories are real and provide a more refined and biologically meaningful view of previously defined behaviours (i.e., feeding).

Some specific behaviours and less goal-oriented behaviours appeared to be functionally related and usually occurred together. The best example was swim moderate – milling and swim moderate – circling. These two behaviours were seen numerous times as shown by one whale (Table 5). Although swim moderate – milling could happen alone, swim moderate – circling always occurred during swim moderate – milling. Swim moderate – milling had the highest variability in dive duration times of any behaviour. Swim moderate – circling had the second lowest dive duration variability. Duration of surfacing was also more variable during swim moderate – milling than during swim moderate – circling. When these behaviours occurred together, the whale would mill for five or six sets within a restricted area and then spend one or two sets circling at a specific location. This pattern of highly variable milling sets followed by a short series of less variable circling behaviours was repeated by this whale, sometimes for hours. Five other whales exhibited the same behaviour pattern using similar paired behaviours. Three of these whales used swim slow – milling with swim slow – circling and the remaining two used swim slow – milling (occasionally with pluming) with swim slow – circling with pluming. In all cases, the duration of dives and surfacings were more variable during milling than circling. From this behaviour pattern, it can be hypothesized that during milling, the whales appeared to be searching for a specific feeding site or object. When the feeding site was located, the whales began to circle and dive at this location. When pluming was observed, the whales were probably feeding. Even if mud was not observable, the whales still could have been feeding or perhaps verifying that this was an appropriate feeding site.

During circling, circling with pluming, and milling with pluming, the whales were apparently feeding. True feeding could not be verified and instead apparent feeding was divided into the three observable contexts. Pluming is a strong indication that the whales were bottom feeding and is associated with two of the feeding contexts. Mud patches and plumes have been reported during apparent feeding activity (Dohl et al. 1983; Harrison 1979; Hatler and Darling 1974; Norris et al. 1977; Wilke and Fiscus 1961), but most behavioural descriptions are general and do not include dive times. Two exceptions are Oliver et al. (1984) and Würsig et al. (1986), both of whom observed summering gray whales producing mud plumes and apparently feeding. The number of blows per surfacing, duration of surfacing, and dive duration were recorded. The locomotion and swim patterns were described as milling; circling was never mentioned. The dive times for these animals, therefore, could have reflected both milling and circling. Nerini (1984), in a review of gray whale feeding activities, concluded that whales feeding during migration or summering usually consume benthic resources, such as several species of amphipods and isopods. Because pluming has been associated with bottom feeding, the apparent feeding observations in this study support Nerini's conclusions and the summering gray whales observed pluming were probably bottom feeding. Feeding, however, may also take place without obvious pluming.

Circling (without pluming) was also associated with feeding. Although the whales appeared to be feeding exclusively on benthic organisms, it is possible that during circling they may have been feeding near the surface or thoughout the water column. Guerrero (1989) described the significantly different surface behaviours observed in gray whales feeding on benthic amphipods (*Ampelisca agassizi*) and free-swimming mysids (*Neomysis rayii*). The whales feeding on benthic amphipods dove and surfaced for longer periods and respired more times during surfacings than the whales feeding on swarms of mysids. In addition, respiratory patterns of mysid-feeding whales did not differ greatly from those engaged in nonfeeding activities, i.e., travel. The whales in this study exhibited similar respiratory patterns during apparent feeding activities, including circling (without pluming). There was a tendency for their dives and surfacings to be longer, with an increased number of blows per surfacing during apparent feeding activities than during nonfeeding activities. Guerrero also reports that during feeding on mysids, the whales she observed would initiate dives by rolling onto the side and exposing only one fluke. This did not occur with the whales feeding on benthic amphipods nor with the whales in this study. The feeding activities of the whales in this study, therefore, were probably oriented towards the sea floor rather than throughout the water column.

Although swim moderate – circling was observed only four times in one whale, on average this whale spent three times longer at the surface during swim moderate – circling than other whales did during swim slow – milling. Circling was observed to be associated with sea floor disturbances (swim slow – circling with pluming) and has been observed during feeding in other gray whales (Nerini 1984; Pike 1962; Sund 1975). The increased time spent at the surface during this behaviour may reflect the need to manipulate (i.e., swallow, spit out, sort out, etc.) the material obtained from the seabed. (It may also reflect individual variability in behaviour.) Although pluming was not associated with swim moderate – circling, the ingestion of food was still possible. A more likely possibility is that dives during swim moderate – circling may be more strenuous than those of swim slow – milling. A longer recovery period could be needed at the surface before another attempt is made at circling. Würsig et al. (1986) reported similar findings in feeding gray whales, which had longer dive and surface durations and more blows per surfacing than nonfeeding whales. Duration of surfacings and dives and the number of blows per surfacing have also been found to be correlated positively with water depth not only in gray whales (Würsig et al. 1986) but also in bowheads (*Balaena mysticetus*) (Würsig et al. 1984) and humpbacks (*Megaptera novaeangliae*) (Dolphin 1987*a*, 1987*b*). In this study, however, water depth was not measured and the whales did not show an increase in dive duration or number of blows per surfacing during apparent feeding.

Except for apparent feeding behaviours, almost all the remaining behaviours were seen at each observation site. Circling and pluming, however, were seen only in the Big Lagoon – Patrick's Point area. Hatler and Darling (1974) suggest that significant feeding grounds for gray whales may not exist south of Vancouver Island. Milling and apparent feeding, however, were the majority of behaviours observed at Patrick's Point, and of the four observation sites, Patrick's Point appeared to be a bottom feeding area for the summering gray whales.

The areas chosen as observation sites for this study were reported by Dohl et al. (1983) to be occupied by small groups of summering gray whales. The groups were indeed small and only once did I see more than two to three individuals during a sighting. This resulted in a low but adequate sample size. Opportunistic sightings between observation sites indicated that the whales transit between these areas and may utilize a large portion of the coastline rather than only a specific area. I am currently photographically identifying the summering whales to see if they utilize more than one area and if the same individuals return each year. One individual whale was sighted during each of the three summers I collected data and at different observation sites (twice at Patrick's Point – Big Lagoon area and once near Point St. George). This indicates that some whales may not only return to their previous summering grounds but also utilize a large portion of the coastline.

During transit, surface time was highly variable (Table 5). The whales were observed making a consistent forward progression and a high surface time variation was not expected for such a steady pace. The dive characteristics indicated that transit was not as directed as it appeared during observation. Transit may be undirected because all that is required is travelling from point A to point B. How the whales accomplish this may not be a specific process. Transit was associated with near-shore travel along the coastline and occasional observation of terrestrial landmarks may aid the animals in navigation. An increase in surface time variability would be expected under these circumstances, but behaviours such as spy hopping, which may increase long distance viewing of terrestrial reference points (Daugherty 1972; Pike 1962; Walker 1971), were never observed. The observation sites, however, were high bluffs and headlands that could be seen easily if the whales were looking for landmarks.

All calculated swimming speeds were grouped into three gross categories: swim slow ($0.5–1.0\,\mathrm{km \cdot h^{-1}}$), swim moderate ($3.0–4.0\,\mathrm{km \cdot h^{-1}}$), and swim fast ($7.0–8.0\,\mathrm{km \cdot h^{-1}}$). (Floating and its variations have been omitted here; see Table 1.) During observations, the different speed categories were easily distinguishable. Because distance from shore was estimated subjectively, the calculated swimming speeds are only estimates. They indicate, however, that the speeds of each category are different from one another, a difference that could be appreciated visually. Although many gray whales probably do not limit their swimming speeds to these categories, a tendency may exist for gray whales to utilize only certain ranges of speed. Mate and Harvey (1984) reported that gray whales average $127\,\mathrm{km \cdot day^{-1}}$ ($5.3\,\mathrm{km \cdot h^{-1}}$) during the last 29 days of the northward migration. During most of the migration, however, the whales average $85\,\mathrm{km \cdot day^{-1}}$ ($3.5\,\mathrm{km \cdot h^{-1}}$), which is within the swim moderate category range. Gray whales appear to swim faster during the southward migration at an average speed of $2.0\,\mathrm{m \cdot s^{-1}}$ ($7.2\,\mathrm{km \cdot h^{-1}}$) (Sumich 1983). The summering whales in this study displayed behaviours not usually associated with migration, but their swimming speeds could be categorized into distinct groups with swimming speeds similar to those observed in migrating animals. Why gray whales would swim within certain speed ranges is unknown. Perhaps swimming metabolism is more efficient at certain speed ranges and the whales tend to stay within them.

During the past observations of summering gray whales, I observed that their flukes would occasionally be lifted above the water surface as the animals began a long dive. This behaviour is common in migrating gray whales (Leatherwood et al. 1982). Observations of flukes raised above the water surface were recorded and found to be a reliable indication of when a surface–dive sequence ended (the beginning of a long dive). When raised flukes occurred, they were always at the end of a surface–dive sequence. The whales, however, did not always lift their flukes before a long dive. Occasionally, the flukes did not come out of the water completely and instead a severely arched peduncle was observed at the end of a surface–dive sequence.

Flukes were seen most frequently during apparent feeding and floating behaviours but almost never during transit. When the flukes were lifted above the water, the animals appeared to be entering a steep dive in which their bodies became almost perpendicular to the sea floor. W. J. Richardson (personal communication), however, observed similar behaviour in bowheads where raised flukes were seen when they dove in water only 4–5 m deep, less than half their body length. Raised flukes, therefore, may not be indicative of deep and near vertical dives in gray whales. Raised flukes, however, seem appropriate during feeding but unusual for floating animals. Float surface – dive sequences occurred independent of apparent feeding and tended to occur in a series. Flukes were seen rarely, indicating that the animals were actually resting. The frequency of flukes observed in float–circling and float then swim slow – circling, however, was the same as in apparent feeding behaviours. These two floating behaviours occurred occasionally during apparent feeding and never in a series. Under these conditions, the whales appeared inactive but were probably engaged in apparent feeding activities. Because transiting animals rarely show their flukes, they probably take shallower and most certainly less inclined long dives than during apparent feeding. Making shallow dives is consistent with whales that seem intent on travelling from one area to another.

In summary, locomotive–context categories, in conjunction with dive characteristics, has helped refine broad behavioural definitions and quantify several basic gray whale behaviour patterns not reported before this study. (*i*) Behaviours that did not appear goal oriented or directed, i.e., milling and floating, had highly variable dive characteristics. More specific behaviours, such as circling and pluming, were less variable. (*ii*) Some specific and less goal-oriented behaviours appeared functionally related and usually occurred together, i.e., swim slow – milling and swim slow – circling. (*iii*) Feeding was composed of at least three observable behaviours: circling, circling with pluming, and milling with pluming. Even an obvious behaviour such as floating had several variations. (*iv*) The Big Lagoon – Patrick's Point area appeared to be a main feeding site for many gray whales summering off the northern California coast.

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Foraging patterns of gray whales in central Clayoquot Sound, British Columbia, Canada

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ABSTRACT: Gray whales *Eschrichtius robustus* forage in parts of Clayoquot Sound on several prey species in different habitats. Between June and September in 1996 and 1997 we carried out analyses of the density, biomass, and other measures of their primary prey species, and of whales' movement patterns in response to prey characteristics. The prey base consists of hyper-benthic mysids (family Mysidae), pelagic porcelain crab larvae (4 spp. of family Porcellanidae), benthic amphipods (family Ampeliscidae) and benthic ghost shrimp *Callianassa californiensis*. Whales foraged primarily for mysids, switching to porcelain crab larvae in August, and then to amphipods even later in the season when these organisms increased in body size. In 1997, whales rapidly switched from feeding on planktonic to benthic prey during mid-August. Sampling indicated low numbers of mysids and crab larvae at that time. Selection of amphipod prey was based on high biomass and a high proportion of individuals ≥6 mm in length. In parts of the study area gray whales did not return to forage on benthic amphipods when this size criteria was not met. A single whale departed from a ghost shrimp feeding ground because its search time for food was long, it achieved only a low biomass removal rate, and it was not able to find sufficient food each day. We show that gray whales are dynamic and selective foragers that switch prey and foraging tactics rapidly to take advantage of short-term availability of energy.

KEY WORDS: Gray whale · *Eschrichtius robustus* · Prey selection · Prey-switching · Plankton · Benthos · Clayoquot Sound

INTRODUCTION

The primary foraging strategy of baleen whales is to locate dense concentrations of prey, since they cannot obtain their daily caloric requirements by feeding in areas of average food abundance (Nemoto 1970, Brodie 1977, Murison & Gaskin 1989). The foraging strategy of gray whales *Eschrichtius robustus* is similar. This species is predominantly a high-Arctic migrant which takes advantage of rich benthic amphipod beds. Numerous observations of gray whales along their migration route between Baja, Mexico and the western Arctic seas report opportunistic foraging along the west coast of North America (Howell & Huey 1930, Walker 1949, Pike 1962, Pike & MacAskie 1969, Rice & Wolman 1971, Hudnall 1983, Norris et al. 1983, Oliver et al. 1983, Murison et al. 1984, Nerini 1984, Sumich 1984, Guerrero 1989, Calambokidis et al. 1991, Weitkamp et al. 1992, Duffus 1996).

Apart from the more recent reports, these studies considered such opportunistic foraging events to be sporadic and transitory. However, as the total population of gray whales reaches estimated historic levels, more whales are at least temporarily abandoning their migratory habit and foraging in habitats along their migration route, taking advantage of whatever prey they encounter that is energetically 'profitable'. When feeding aggregations of whales become large stable associations with many individuals returning to spe-

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cific sites, these groups are equivalent to populations, but not with the same demographic status as biological populations, since they are unlikely to comprise distinct breeding entities. Short-term spatio-temporal grouping may be the most important focus for management. Human activities that affect gray whales, such as whale-watching, hunting by aboriginals and contamination, occur on scales much more applicable to the summer aggregation of whales described in this paper than to the larger Baja to Bering unit typically considered.

The consideration of smaller spatial units in the management of gray whales requires more detailed understanding of their ecology on the same scale. Thus, our objective was to document and analyze at least a part of the 'normal' ecology of gray whales *Eschrichtius robustus* on the west coast of Vancouver Island, Canada. In this region, aggregations of gray whales spend the boreal summer months feeding on an assemblage of invertebrate prey throughout central Clayoquot Sound. Since gray whales feed on a wide variety of prey items, important aspects of gray whale foraging behavior include prey choice, prey-switching, and the resulting habitat use patterns. While certain aspects of gray whale prey are known, such as abundance (Pike 1962, Moore et al. 1986), patchiness (Clarke et al. 1989) and availability (Gill & Hall 1983, Moore & Ljungblad 1984, Clarke et al. 1989), there is little information on prey-switching behavior or habitat use of gray whales feeding in Clayoquot Sound (Duffus 1996).

In this paper, we document those characteristics of their prey that affect whales' prey choices, their subsequent switching between prey items, and their use of prey habitats. We describe whale use of 5 prey habitats located in central Clayoquot Sound. The predominant prey types are hyper-benthic mysids (family Mysidae), pelagic porcelain crab larvae (family Porcellanidae), benthic amphipods (family Ampeliscidae) and benthic ghost shrimp *Callianassa californiensis*. We employed a quantitative sampling regime to estimate prey density, biomass and size in the various prey habitats. Estimates of these characteristics are linked to observations of whales' foraging patterns in the different prey habitats. By quantifying prey characteristics and whale observations simultaneously, we identified which specific characteristics of the prey caused whales to actively select them.

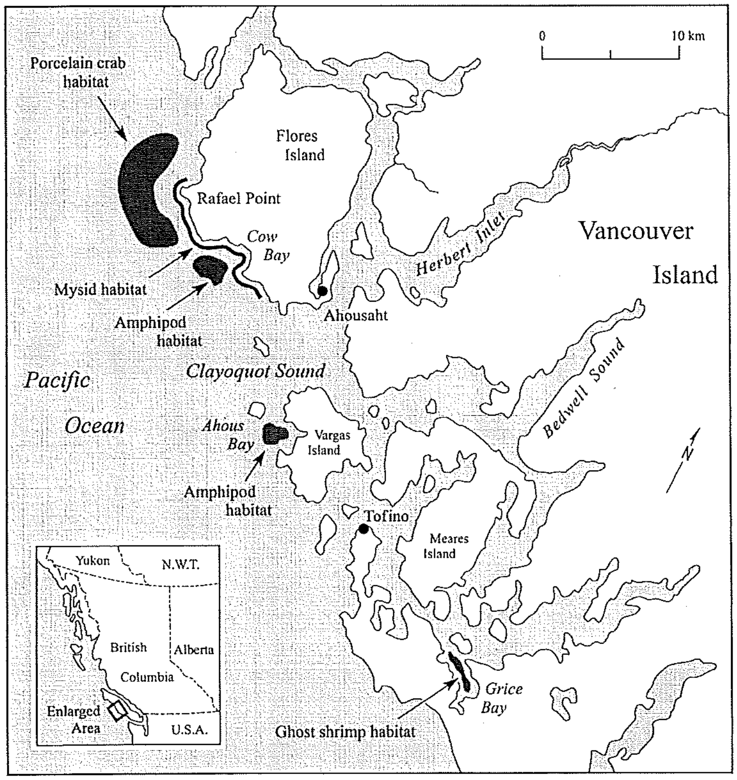

Fig. 1. Habitat of the gray whale *Eschrichtius robustus* and its prey in central Clayoquot Sound

METHODS

Study area. We classified 5 gray whale prey habitats in central Clayoquot Sound, British Columbia, based on observations from 1987 to 2000. The study area is a discrete unit bounded on each side by open deeper water and non-productive areas that are rarely, if ever, used by foraging gray whales. Prey habitats are distinguished according to distance from shore, type of substrate, and depth. Free-swimming porcelain crab larvae were collected >1 km from shore, over boulder substrate around Rafael Point (Fig. 1), in water depths between 10 and 30 m. Mysids were collected <1 km from shore near kelp beds and rock reefs on the south-southwest side of Flores Island, in water 0 to 15 m deep. Amphipods were collected from the sandy substrate that covers about 10 km^2 of the bottom of Cow Bay, in water 0 to 35 m deep. Amphipods were also collected from the fine-sandy substrate that covers about 8 km^2 of the bottom of Ahous Bay, in water 0 to 25 m deep. Ghost shrimp *Callianassa californiensis* were collected from littoral sand/mud flats in Grice Bay, in water <3 m deep.

Whale distributions. The number of gray whales observed foraging in the study area was recorded daily, and individual whales were identified in order to minimize the possibility of individuals being counted twice. In 1996, prey habitats were visited when sampling was conducted, when detailed whale respiration data were recorded, or when we were in transit between sampling sites. In 1997, a transect route was established along the southern and western shorelines of Flores Island. The transect passed through the mysid habitat along the shoreline of Flores Island, the amphipod habitat in Cow Bay, and the porcelain crab larvae habitat near Rafael Point. Vessel speed was constant (15 to 20 km h^{-1}) along the transect route. A minimum of 4 observers covered the 360° viewing area. In both years, we covered the entire study area daily, weather permitting, with the exception of the amphipod habitat in Ahous Bay and the ghost shrimp habitat in Grice Bay, which were not included in the transect route. We relied on periodic checks in both these bays and information collected by the local research coordinator Rod Palm (Strawberry Isle Research, Tofino) for dates of entry and departure of whales from the bays. Whale observations are standardized by the number of observation days.

Grice Bay is a shallow bay that enabled us to make detailed observations of whale foraging tactics and link them to prey characteristics. Feeding pits (n = 36) in Grice Bay were measured when they were exposed at low tide; only well defined pits with distinct edges were measured. Pit length (l) and width (w) were measured to the nearest 5 cm. Pit area was calculated as the area (a) of an ellipse, given by; $a = \pi\,[0.5\,(l) \times 0.5\,(w)]$. Foraging behavior was recorded as follows. The time from emergence of the pectoral fin as the whale rolled onto its side until the fin dropped down again as the whale righted itself was recorded as the time required to excavate a feeding pit. After the whale respired, it normally swam around for a short period of time until it again rolled onto its side to excavate another feeding pit. The time spent swimming after each ventilation until the whale stopped and rolled onto its side was defined as searching behavior.

Gray whales observed foraging in a particular habitat were assumed to be utilizing the prey type characteristic of that habitat. This assumption was based on analyses of whale feces, opportunistic and systematic plankton tows, core samples, SCUBA surveys, and underwater video records collected between 1993 and 2000. Crab larvae carapaces were collected in fecal samples. Both plankton samples taken near foraging whales and visual observation confirmed prey identity. Amphipods were the dominant organisms collected in benthic samples. Small amphipods were also collected in the sediment plumes of whales foraging in the amphipod habitat. Tows in the water column over these sandy bottom bays collected very little plankton. Clams and ghost shrimp constituted ≥98 % of the benthic biomass in Grice Bay, where there is little else upon which whales can forage.

Prey sampling. Prey sampling coordinates were determined using the Canadian Hydrographic Service Field Sheet No. 3603 (1996). Each prey habitat was divided by lines whose intersections created a minimum of 100 possible sampling coordinates. From these coordinates, 6 to 8 sampling sites were randomly chosen before each sampling period. In the field, a GPS was used to navigate the research vessel to each sampling site. During the 2 field seasons, each prey habitat was sampled at consistent time intervals between mid-June and early September. In 1996 samples were obtained semi-monthly, resulting in 5 sampling periods during the field season; in 1997 samples were obtained every 4 to 6 wk, resulting in 3 sampling periods. We collected samples adjacent to foraging whales in an opportunistic fashion. Foraging whales were defined as whales which remained within a restricted area of a particular habitat and exhibited constant directional changes in movement (Mallonée 1991).

We collected plankton samples with a 2 × 20 cm diameter bongo-style plankton net, 80 cm long, with 500 µm mesh size. A mechanical flowmeter (General Oceanics, Miami, FL, Model 2030R) determined the volume of water (m^3) to calculate standardized density and biomass estimates for the invertebrates. We collected porcelain crab larvae by towing the plankton net from the sea floor to the surface (max. depth = 30 m) in oblique tows through the water column. We collected mysids by towing the net horizontally along the bottom. Large samples were subdivided using a Folsom plankton splitter.

We used a 0.06 m^2 core sampler (WILDCO Ogeechee Sand Pounder) to collect benthic amphipods in Cow Bay and Ahous Bay. Sediment from each sample was rinsed through a 1 mm mesh screen to remove amphipods and other invertebrates. Amphipods were categorized into one of 2 size classes: individuals 0 to 5.9 mm in length were designated 'small' and individuals 6 to 11 mm 'large'. This classification follows with Rice & Wolman's (1971) analysis of the stomach contents of gray whales, where prey items measured >6 mm in length.

On July 15, 1996, we sampled 5 well-defined excavations created by 1 gray whale foraging in Grice Bay in order to quantify the density and biomass of ghost shrimp inside and outside feeding pits. We collected ghost shrimp with a section of PVC tubing 17 cm long and 10 cm in diameter. The tubing was pushed into the sediment and the core and sampler removed with a shovel. We removed 2 samples from inside and outside each feeding depression. Sediment removed from the depressions was rinsed through a 1 mm mesh screen on site, and ghost shrimp were retained. Two samples of sediment were retained to estimate the volume of sediment sampled.

We fixed all invertebrates in formaldehyde and stored them in 70% ethanol. Small individuals and species that were not known to be potential gray whale prey and that contributed very little to the overall biomass were not identified or counted. Biomass was measured to 0.001 g blotted wet weight.

We use both parametric and non-parametric tests to analyze our data. Significantly skewed data sets (Kolmogorov-Smirnov test, $\propto = 0.05$) were analyzed with non-parametric statistical tests.

RESULTS

Significantly fewer *Eschrichtius robustus* observations were made in the study area in 1996 (n = 171) than in 1997 (n = 363) ($\chi^2 = 69.03$, df = 1, $p < 0.05$; Fig. 2). In 1996, there were 2 d (August 10 and 11) on which no whales were observed and 19 d in which only 1 whale was observed (Fig. 2a). In 1997, whales were observed each day throughout the field season; on 2 d (July 28 and 29) only 1 whale was observed (Fig. 2b). Whales foraging on each specific prey type are discussed below.

Mysids

Mysids were the most consistently eaten prey during the 2 field seasons (Figs. 3a & 4a). In 1996, whales generally foraged for mysids between Cow Bay and Dagger Point on the northwestern margins of the study area; only on July 4 were 2 whales observed feeding near Fitzpatrick Rocks on the eastern margin of the study area. In contrast, in 1997, whales were consistently observed at Fitzpatrick Rocks between June 15 and July 19. Whales also foraged at Kutcous Point on the extreme eastern end of the study area between July 10 and 18; no whales were observed there in 1996. After July 19, whales suddenly abandoned the eastern sectors and moved to forage for mysids near Rafael Point.

The mean number of whales observed feeding in the mysid habitat at any one time was 2.6 in 1996 and 4.3 in

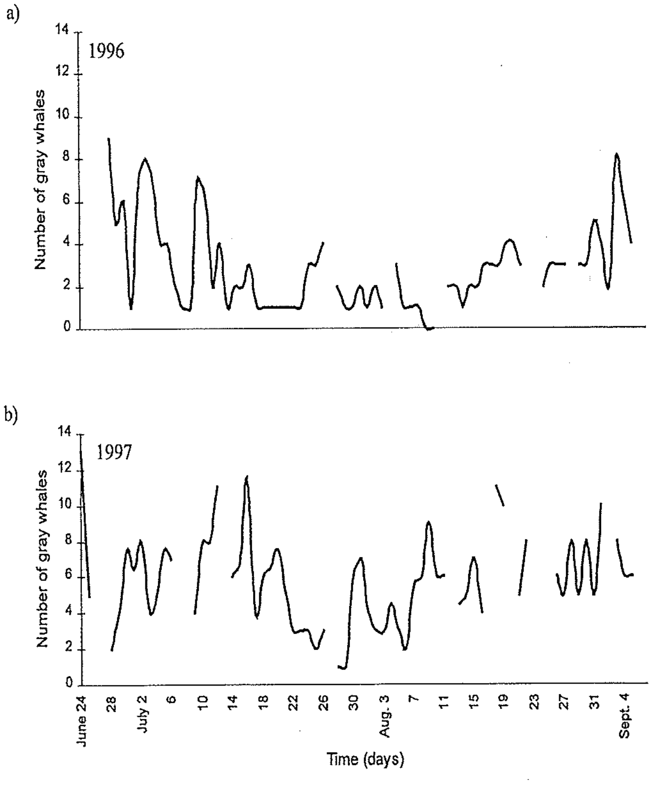

Fig. 2. *Eschrichtius robustus.* Daily numbers of gray whales observed throughout the study area in central Clayoquot Sound in 1996 and 1997. Breaks in lines are days on which no observations were made due to poor weather conditions

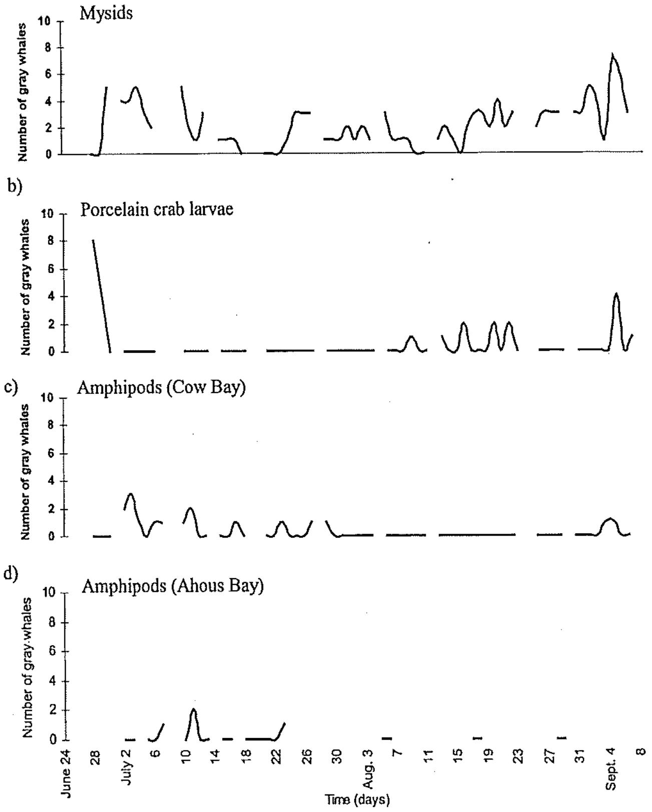

Fig. 3. *Eschrichtius robustus.* Daily observations of gray whales foraging in each of the 4 prey habitats in central Clayoquot Sound in 1996

1997 (Table 1). Results of our sampling tows suggest that mysid swarms were not as widely distributed along the shoreline of Flores Island in 1996 as in 1997. Mysid density was significantly lower in 1996 than in 1997 (Mann-Whitney *U*-test, $Z = -3.32$, $n = 59$, $p = 0.00$; Table 2).

When mysids were abundant, whales were present in larger numbers. The largest biomass of mysids (22.6 g m^{-3}) collected in the 2 field seasons was obtained on July 4, 1997. A larger number of whale observations ($n = 151$) were recorded around this date (between June 24 and July 23) than during the entire 1996 field season ($n = 131$) or after July 23 in 1997 ($n = 109$). Between June 24 and July 23, 5 to 6 whales (up to 10 individuals in 1 d) were observed each day foraging for mysids. The larger numbers of whales observed in the study area in 1997 foraged primarily for mysids (Fig. 4a).

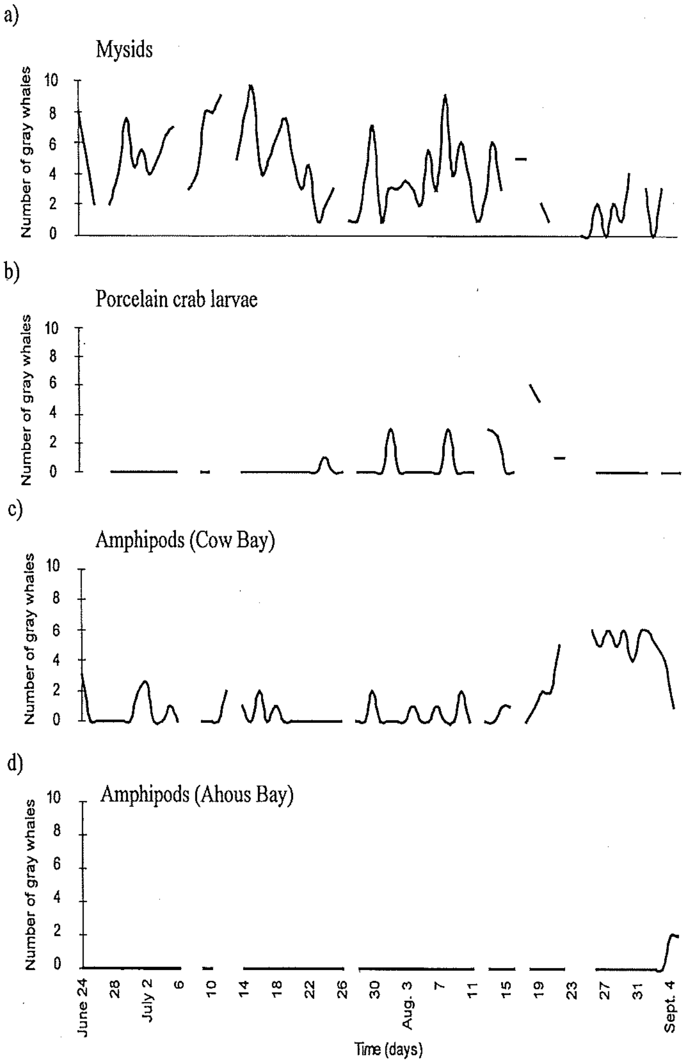

Fig. 4. *Eschrichtius robustus*. Daily observations of gray whales foraging in each of the 4 prey habitats in central Clayoquot Sound in 1997

Porcelain crab larvae

Gray whale presence in the porcelain crab larvae habitat was similar during the 2 field seasons. The proportions of whales foraging for crab larvae were similar in 1996 (17%) and 1997 (15%: Table 1) and the total number of whale observations ($n = 28$) made in crab larvae habitat in 1996 was similar to the number ($n = 26$) made in 1997 ($\chi^2 = 0.12$, $df = 1$, $p > 0.05$). The mean number of whales observed in the crab larvae habitat during each foraging episode in both years was identical (2.8 whales: Table 1). Crab larvae biomass was similar in 1996 and 1997 ($Z = -1.52$, $n = 25$, $p = 0.13$; Table 2), although density was significantly higher in 1997 ($Z = -2.16$, $n = 25$, $p = 0.03$; Table 2).

In 1996, 7 whale/crab larvae foraging episodes were recorded (Fig. 3b). Eight whales were observed foraging for crab larvae on June 28, falling to 4 individuals on June 29. On June 29 we obtained the highest density (10520 m^3) and biomass (16.7 g m^{-3}) of crab larvae collected in 1996. No whales were observed foraging for crab larvae between June 30 and August 8. During this period, crab biomass estimates ranged from 0 to 0.59 g m^{-3}.

In 1997, 6 whale/crab larvae foraging episodes were recorded (Fig. 4b). The maximum number of whales that foraged in the crab larvae habitat was 6 whales on August 18. On this date, the highest density (13198 m^3) and biomass (20.6 g m^{-3}) of crab larvae were obtained. No whales were observed foraging for crab larvae between June 24 and July 23 and after August 25. During these periods porcelain crab larvae biomass estimates ranged from 0 to 0.07 g m^{-3}.

Table 1. *Eschrichtius robustus*. Observations of gray whales foraging in each prey habitat in central Clayoquot Sound in 1996 and 1997. % of days: % of days whale(s) observed foraging in each prey habitat; no. observed: mean (±SD) no. of whale(s) observed foraging simultaneously

Prey	1996 (Jun 28–Sep 9)		1997 (Jun 24–Sep 7)	
	% of days	No. observed	% of days	No. observed
Mysids	85	2.6 ± 1.5	94	4.3 ± 2.3
Porcelain crab larvae	17	2.8 ± 2.1	15	2.8 ± 1.8
Amphipods in Cow Bay	18	1.4 ± 0.7	47	2.9 ± 1.9
Amphipods in Ahous Bay	13	1.3 ± 0.6	3	2.0 ± 0.0
Ghost shrimp	34	1.0 ± 0.0	0	0.0 ± 0.0

Table 2. Planktonic prey density and biomass near feeding *Eschrichtius robustus*. Data are means ± SD, and median inter quartile range [IQR] for 1996 and 1997

Prey	1996		1997	
	Density (m^3)	Biomass (g m^{-3})	Density (m^3)	Biomass (g m^{-3})
Mysids	10 [53] (n = 25)	0.32 [1.56] (n = 12)	175 [746] (n = 34)	1.43 [6.00] (n = 36)
Porcelain crab larvae	3006 ± 3718 (n = 17)	4.61 ± 6.09 (n = 17)	4726 ± 4598 (n = 8)	6.16 ± 7.54 (n = 8)

In general, whales foraged sporadically and for short periods of time on crab larvae. Observations of feeding whales indicated that crab larvae swarm in densities sufficient to attract whales for 2 to 3 d at a time. Gray whales generally foraged for crab larvae during August in both years (Figs 3b & 4b).

Proportions of the Zoea I and II larval stages determined for each sampling date in both years indicated that reproductive events for porcelain crabs occurred in August, at least in 1997. There was a large increase in the number of crab larvae in the Zoea I larval stage at the end of July, and a concomitant increase in the number of individuals in the Zoea II larval stage during the last 2 wk of August (Fig. 5). Reproductive events of *Pachycheles* spp. and *Petrolisthes* spp. at the beginning of August may have provided sufficient biomass to have attracted foraging gray whales throughout the month.

At particular times, gray whales were observed foraging in mysid and crab larvae habitats concurrently. In every case but one, not all whales left the mysid habitat to feed in the crab larvae habitat when crab larvae were sufficiently concentrated: whales normally spread out among the 2 food sources to forage. Mysid biomass (n = 36) in 1997 was similar to porcelain crab larvae biomass (n = 25) in 1996 and 1997 near foraging whales ($Z = -1.25$, $p = 0.21$; Table 2). In addition, maximum biomass estimates for mysids and crab larvae in both years were similar (22.6 and 20.6 g m^{-3} respectively). This suggests that when crab larvae were concentrated in patches a comparable amount of food was available for whales from the 2 prey types.

Only on June 28, 1996 did all 8 gray whales in the study area forage exclusively on crab larvae. The largest biomass estimate we collected during the 2 yr study was obtained on June 29, so there may have been an unusually large food source available during those 2 d.

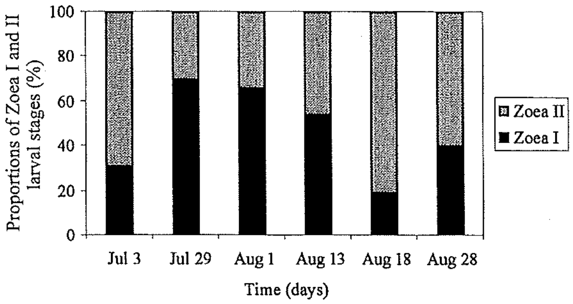

Fig. 5. Seasonal occurrence of Zoea I and II stage porcelain crab larvae, in central Clayoquot Sound, in 1997

Although quantitative sampling of the 2 types of planktonic prey indicate that there were comparable amounts of prey available to the whales, observations of the number and locations of feeding whales suggest that mysids were generally a more prevalent and consistent prey source than porcelain crab larvae (Table 1, Figs 3 & 4a,b).

Benthic amphipods

Between June 28 and September 9, 1996, we only occasionally observed gray whales foraging on the bottom in Cow Bay and Ahous Bay (Fig. 3c,d). In Cow Bay, no whales were observed foraging benthically between July 30 and September 3 (Fig. 3c). Whales that were observed in the bay did not remain for long periods of time; only on 2 occasions (July 2 and 3 and September 4 and 5) were whales observed foraging benthically for 2 consecutive days. In Ahous Bay, 1 or 2 whales were observed on July 7, 11 and 23, but these whales did not remain for more than 1 d in the bay (Fig. 3d).

In 1996, amphipod populations in Cow Bay and Ahous Bay were similar in terms of density ($Z = -0.79$,

Table 3. Characteristics of amphipods at sites where no *Eschrichtius robustus* were observed in 1996. Data are means ± SD

Characteristics	Cow Bay (n = 47)	Ahous Bay (n = 54)
Density (m^2)	16121 ± 20187	10654 ± 11741
Biomass (g m^{-2})	48 ± 54	36 ± 46
Length		
0–5.9 mm	3.4 ± 0.7 (n = 1257)	3.5 ± 0.8 (n = 870)
6–11 mm	7.9 ± 1.2 (n = 83)	7.7 ± 1.2 (n = 119)
Proportion		
0–5.9 mm	94	88
6–11 mm	6	12

n = 68, p = 0.43) and biomass ($Z = -1.04$, n = 67, p = 0.30; Table 3). 'Small' (0 to 5.9 mm) amphipods had similar mean lengths in both bays ($Z = -1.63$, n = 2127, p = 0.10), as did 'large' (6 to 11 mm) amphipods (Student's t-test, t = 1.17, df = 180, p = 0.24). Both bays had a high proportion of small amphipods and a corresponding low proportion of large amphipods (Table 3).

Table 4. *Eschrichtius robustus.* Gray whales observed foraging in each prey habitat before and after August 22, 1997. Total observation period was from June 24 to September 7. % of days: % of days whale(s) observed foraging in each prey habitat; no. observed: mean (±SD) no. of whale(s) observed foraging simultaneously

Prey	% of days		No. observed	
	Before Aug 22	After Aug 22	Before Aug 22	After Aug 22
Mysids	100	67	4.6 ± 2.3	2.3 ± 1.0
Porcelain crab larvae	17	8	3.1 ± 1.7	1.0 ± 0.0
Amphipods in Cow Bay	33	100	1.6 ± 0.7	4.8 ± 1.4
Amphipods in Ahous Bay	0	?	0.0 ± 0.0	2.0 ± 0.0
Ghost shrimp	0	0	0.0 ± 0.0	0.0 ± 0.0

Consistent bottom-foraging behavior by gray whales was only observed in Cow Bay in 1997. From June 24 to August 21 (49 observation days), between 1 and 3 whales were observed on 17 different days (approximately 1 in every 4 d) bottom-feeding in Cow Bay (Fig. 4c). However, on August 22 and 23, there was a rapid increase in the number of whales foraging on benthic prey in the bay. Between August 22 and September 4, 4 to 6 whales foraged continuously in Cow Bay on amphipods (Fig. 4c, Table 4). The maximum number of whales observed simultaneously feeding on benthic prey was 6.

Amphipod density (26 260 ± 23 716 m^{-2}) and biomass (73 ± 51 g m^{-2}) estimates (n = 34) obtained in 1996 from water depths ranging between 16 and 25 m were compared to density (11 054 ± 4151 m^{-2}) and biomass (113 ± 28 g m^{-2}) estimates (n = 21) obtained in 1997 from similar depths (between 18 and 24 m) near feeding whales. Although amphipod density was significantly higher in 1996 ($Z = -2.91$, n = 55, p = 0.00), biomass was higher in 1997 ($t = -3.28$, df = 53, p = 0.00).

Amphipod size changed as summer progressed. In 1996 in Cow Bay, amphipod density (ANOVA, F = 1.75, df = 31, p = 0.17), as well as biomass (F = 1.05, df = 31, p = 0.40), was similar between June 29 and September 2 (Table 5). 'Small' amphipods increased in length by 1 mm as the summer progressed (Kruskal-Wallis, χ^2 = 400.63, n = 1257, df = 4, p = 0.00; Table 5), but 'large' amphipods were not significantly larger over time (F = 1.47, df = 73, p = 0.22; Table 5). During the 2 field seasons in Cow Bay, amphipod density and biomass did not change between late June/early July and late August/early September. However, amphipod size did increase as summer progressed in both years: 'small' amphipods increased in size in 1996, whereas 'large' amphipods increased in size in 1997.

Amphipods also displayed size changes over time in Ahous Bay. In 1996, amphipod density was similar (F = 0.63, df = 35, p = 0.65), as well as biomass (F = 0.52, df = 34, p = 0.72), between July 2 and August 29 (Table 6). 'Small' amphipods increased in length by 1 mm as the summer progressed (χ^2 = 219.70, n = 870, df = 4, p = 0.00). In contrast, 'large' amphipods were not significantly larger (F = 0.41, df = 107, p = 0.80). In 1997, amphipod density (t = 2.02, df = 8.58, p = 0.08) and bio-

Table 5. Characteristics of amphipods in Cow Bay in 1996 and 1997. Data are means ± SD and median inter quartile range [IQR]. Percent: percentage of amphipods in that size class

Characteristics	1996					1997		
	Jun 29 (n = 7)	Jul 21, 22 (n = 10)	Aug 3, 4 (n = 10)	Aug 16 (n = 10)	Aug 31, Sep 2 (n = 10)	Jul 2 (n = 19)	Jul 16, 31 (n = 7)	Aug 20, 21 (n = 10)
Density (m^2)	38 258 ± 39 747	8996 ± 8580	5764 [23 200]	10 889 ± 9331	16 139 [32 278]	10 951 ± 5241	11 445 ± 3076	10 721 ± 6065
Biomass (g m^{-2})	55 ± 51	29 ± 25	17 [78]	33 ± 29	59 [124]	90 ± 36	123 ± 21	132 ± 84
Length								
0–5.9 mm	3.0 ± 0.6 (n = 428)	3.4 ± 0.7 (n = 154)	3.3 ± 0.6 (n = 231)	3.9 ± 0.6 (n = 152)	3.9 ± 0.6 (n = 292)	4.2 ± 1.3 (n = 159)	4.5 ± 1.3 (n = 52)	3.9 ± 0.8 (n = 38)
6–11 mm	8.2 ± 1.5 (n = 6)	7.3 ± 0.9 (n = 21)	7.9 ± 1.1 (n = 28)	7.8 ± 1.5 (n = 6)	8.2 ± 1.3 (n = 220)	7.0 ± 1.0 (n = 180)	7.1 ± 0.9 (n = 89)	7.9 ± 1.1 (n = 139)
Percent								
0–5.9 mm	99	88	89	96	93	47	37	21
6–11 mm	1	12	11	4	7	53	63	79

Table 6. Characteristics of amphipods in Ahous Bay in 1996 and 1997. Data are means ± SD and median inter quartile range [IQR]. Percent: percentage of amphipods in that size class

Characteristics	1996					1997	
	Jul 2, 3 (n = 10)	Jul 19, 20, 22 (n = 10)	Aug 6 (n = 11)	Aug 18 (n = 12)	Aug 29 (n = 11)	Jul 9,10 (n = 19)	Sep 2 (n = 10)
Density (m^2)	12784 ± 10358	8069 [19021]	6917 [12335]	5187 ± 4981	6917 [24821]	16880 ± 11087	7493 ± 5272
Biomass (g m^{-2})	22 ± 16	39 ± 41	30 ± 24	34 ± 36	12 [102]	89 ± 54	58 ± 55
Length							
0–5.9 mm	3.0 ± 0.6 (n = 203)	3.5 ± 0.8 (n = 141)	3.4 ± 0.6 (n = 175)	4.0 ± 0.8 (n = 103)	3.7 ± 0.8 (n = 248)	3.2 ± 1.0 (n = 498)	3.6 ± 1.0 (n = 63)
6–11 mm	7.4 ± 1.5 (n = 8)	7.8 ± 1.5 (n = 15)	7.6 ± 0.9 (n = 22)	7.8 ± 1.1 (n = 41)	7.5 ± 1.2 (n = 33)	6.8 ± 0.7 (n = 154)	7.0 ± 0.9 (n = 75)
Percent							
0–5.9 mm	96	90	89	72	88	76	46
6–11 mm	4	10	11	28	12	24	54

mass (t = 1.07, df = 12, p = 0.31) remained similar between July and September (Table 6). 'Small' amphipods were larger by 0.4 mm in September (Z = −4.56, n = 561, p = 0.00). In contrast, 'large' amphipods were not significantly bigger between the 2 sampling periods (Z = −0.42, n = 218, p = 0.68; Table 6). Therefore, during the 2 field seasons in Ahous Bay, amphipod density and biomass did not change significantly between early July and September. However, 'small' amphipods were larger later in the summer of both years.

Amphipod size may be important in determining gray whales' choices of benthic foraging grounds. Amphipod density (F = 0.20, df = 37, p = 0.82) and biomass (F = 1.78, df = 37, p = 0.18) at sites where whales were present in Cow Bay were similar to those at sites where whales were absent in Cow Bay and Ahous Bay (Table 7). However, amphipod sizes were significantly different between areas in which whales did and did not forage. 'Small' amphipods were significantly larger in Cow Bay, especially where whales foraged, than in Ahous Bay (χ^2 = 105.74, n = 879, df = 2, p = 0.00), and also 'large' amphipods were significantly larger in Cow Bay than in Ahous Bay, particularly in areas of Cow Bay where no whales were initially observed (χ^2 = 25.68, n = 671, df = 2, p = 0.00). Where gray whales foraged in Cow Bay, there was a higher proportion (61%) of large amphipods compared to similar-sized amphipods in Ahous Bay (29%; Table 7).

Table 7. Characteristics of amphipods at sites where *Eschrichtius robustus* foraged or did not forage in 1997. Data are means ± SD. Percent: percentage of amphipods in that size class

Characteristics	Foraging whales present	No whales present	
	Cow Bay (n = 21)	Cow Bay (n = 19)	Ahous Bay (n = 29)
Density (m^2)	11054 ± 4151	10332 ± 6704	12186 ± 9659
Biomass (g m^{-2})	113 ± 28	97 ± 80	74 ± 55
Length			
0–5.9 mm	4.3 ± 1.3 (n = 157)	4.1 ± 1.2 (n = 155)	3.3 ± 1.0 (n = 561)
6–11 mm	7.1 ± 1.0 (n = 246)	7.5 ± 1.2 (n = 207)	6.9 ± 0.8 (n = 229)
Percent			
0–5.9 mm	39	43	71
6–11 mm	61	57	29

No gray whales were observed bottom feeding in Ahous Bay until September 4 (Fig. 4d). Two whales remained in the bay for at least 2 d, but we do not know whether they remained there for a longer period of time. Amphipods were, on average, smaller in Ahous Bay than in Cow Bay in July (Z = −8.99, n = 874, p = 0.00) and near the end of August/beginning of September (Z = −7.06, n = 266, p = 0.00). Not until September did amphipods in Ahous Bay attain the sizes that amphipods in Cow Bay had reached in July (Z = −1.01, n = 367, p = 0.31; Table 8).

Ghost shrimp

In 1996, a single gray whale foraged in Grice Bay. Seven days before this whale departed from the bay, significantly more ghost shrimp were collected outside (1170 shrimp) than inside (405 shrimp) feeding pits (paired t-test, t = −3.64, df = 9, p = 0.01), indicating a

65% removal rate by numbers. Ghost shrimp biomass was 30 g m^{-2} outside and 19 g m^{-2} inside feeding pits, indicating a 37% removal rate of biomass. This removal rate estimate, however, is not significant (paired *t*-test, $t = -0.98$, df = 9, p = 0.35). The mean dimension of feeding pits made by the whale was 2.9 ± 0.4 m long (mean ± SD), 2.0 ± 0.3 m wide, encompassing an area of 4.6 ± 1.0 m^2 (n = 36). An average of 54 g of shrimp were removed per pit. Ghost shrimp sizes inside (18 ± 18 mm) and outside (17 ± 17 mm) the feeding pits were not significantly different (Student's *t*-test, $t = 0.81$, df = 62, p = 0.42).

Grice Bay mud flats were only accessible to the whale during high tide. Generally, the tide level was high enough for the whale to forage approximately 12 h each day. It is unknown whether it foraged at night, but we assume that the whale could forage for 12 h each day. A whale requires between 400 (Nerini 1984) and 1200 kg (Zimushko & Lenskaya 1970) of prey each day. If 54 g of ghost shrimp biomass were removed from each feeding pit, then the whale would have had to create 7407 to 22222 pits in 12 h to attain the consumption 'estimates above', assuming that ghost shrimp are not an exceptionally high-yield prey. This means that the whale would have had to excavate a new feeding pit every 2 to 6 s.

The clam *Cryptomya californica* was so prevalent throughout Grice Bay that we thought this organism, in addition to ghost shrimp, might provide an important source of energy to the whale. If clam biomass was included in the whale's intake, then 302 g of clam biomass removed from each feeding pit would be added to the 54 g of ghost shrimp biomass, making a total ghost shrimp and clam biomass removal from each feeding pit of 356 g. In this scenario, the whale would have had to excavate between 1124 and 3371 pits in 12 h, meaning that a new feeding pit would have had to be created every 13 to 38 s to achieve the above consumption estimates.

To compare expected pit-making times, we made detailed observations of the whale on July 1, 21 d before its departure from the bay. The time required for the whale to excavate a feeding pit was 25 ± 11 s (n = 11). In general, 54% of the entire time period in which the whale was observed involved searching behavior, while 46% was spent feeding and breathing. This suggests that 34% of the whale's foraging time or 4.1 h per day was spent actively making feeding pits. Thus, the whale had time to excavate 598 feeding pits in 12 h, which equals one pit every 72 s.

Table 8. Comparison of amphipod lengths (means ± SD) in Cow Bay and Ahous Bay in 1997

Cow Bay		Ahous Bay	
Date	Length (mm)	Date	Length (mm)
Jul 2	5.4 ± 1.7 (n = 339)	Jul 9, 10	4.1 ± 1.8 (n = 652)
Aug 20, 21	7.1 ± 2.1 (n = 177)	Sep 2	5.4 ± 1.9 (n = 138)
Jul 2	5.4 ± 1.7 (n = 339)	Sep 2	5.4 ± 1.9 (n = 138)

Benthic-pelagic prey-switching

Before August 22 in 1997, we observed gray whales foraging in planktonic prey habitats, primarily for mysids (Fig. 4a; Table 4). After August 22, the number of whales observed feeding in pelagic prey habitats decreased and the number of whales observed feeding in the benthic prey habitat in Cow Bay increased. More whales had not simply entered the study area to feed benthically; rather whales which had previously been feeding on planktonic prey switched to benthic prey (Table 4).

Reasons for gray whales switching from planktonic to benthic prey are either substantial increases in amphipod populations and biomass, or decreases in planktonic organism populations and biomass. Our data indicate there were no substantial changes in amphipod populations in Cow Bay as the summer progressed. Amphipod density ($F = 0.04$, df = 35, p = 0.96) and biomass ($F = 2.48$, df = 35, p = 0.10) were similar between July 2 and August 21 (Table 5). 'Small' amphipods did not increase in length as the summer progressed ($\chi^2 = 3.98$, n = 249, df = 2, p = 0.14). Only 'large' amphipods were significantly bigger (by 0.9 mm) in August ($\chi^2 = 66.54$, n = 408, df = 2, p = 0.00). Also, a higher proportion of 'large' amphipods was collected in August than in July (Table 5). Amphipod size, therefore, was the only variable that changed significantly as the summer progressed.

We believe decreased abundance of planktonic prey items played a bigger part than subtle changes in amphipod size to induce gray whales to feed on amphipods in 1997. No mysids were found in 12 plankton samples collected between August 19 and 31 at sites near Fitzpatrick Rocks where mysids had previously been sufficiently abundant to attract foraging whales. Whales had already abandoned this area when these samples were collected; however, several individuals were observed foraging in the mysid habitat about 10 km away at Rafael Point. The smallest number of whale observations (n = 18) was recorded in the mysid habitat between August 22 and September 7. In addition, crab larvae biomass was low (0.01 to 0.07 g m^{-3}) in samples taken on August 28. No whales were observed foraging in the porcelain crab larvae habitat after August 25 (Fig. 4b).

In contrast, during August and September in 1996, gray whales were observed foraging in planktonic rather than in amphipod prey habitats. Whales may have avoided amphipod habitats because mysids and, to a lesser extent, porcelain crab larvae were abundant during August and September. The maximum density of mysids (326 m^{-3}) collected during the 1996 field season was on September 1. Density of crab larvae collected on September 5 near 4 feeding whales was estimated to be 2776 ± 1761 m^{-3}.

DISCUSSION AND CONCLUSIONS

Mysids were the prey most extensively foraged by gray whales *Eschrichtius robustus* in central Clayoquot Sound between June and September. Although specific locations where mysids were collected changed, these invertebrates were always available at some sites along the shoreline of Flores Island. Since kelp forests fringe much of the gray whales' migration route south of the Bering Sea, mysids may be the most important prey in tertiary feeding grounds for these whales (Kim & Oliver 1989). Moreover, when their main feeding grounds were absent (Johnson & Nelson 1984) or inaccessible (Nelson et al. 1974, Hall 1980, Kim & Oliver 1989), the significance of mysids and invertebrates other than benthic amphipods to the gray whale diet was probably higher.

The occurrence of crab larvae has both life-history and spatio-temporal components (Knudsen 1964). Porcelain crab larvae may comprise more abundant or better-quality prey in nearshore waters at particular times, partially due to the hatching rhythms of *Pachycheles* spp. and *Petrolisthes* spp. Hatching increased for both genera of crabs between the end of July and mid-August. At first, the Zoea I larval stage was numerous in plankton samples. Then, 3 wk later, the larger Zoea II larval stage was more numerous. The 2 stages of *Pachycheles rudis* and *P. pubescens* last between 24–25 d (Knight 1966) and 34–40 d (Morris et al. 1980) respectively. Small-scale oceanographic events such as current and upwelling may also have served to concentrate these swarms in our study area at specific times.

Greater numbers of gray whales were consistently observed foraging at sites where planktonic prey was present in high densities and biomass. Whales were observed foraging for both mysids and porcelain crab larvae concurrently, indicating that they spread out between the 2 sources of food. This behavior is similar to Fretwell's (1972) ideal free-distribution concept, whereby competitors adjust their distribution in relation to habitat quality so that each individual enjoys the same rate of acquisition of resources (Krebs & Davies 1987).

The absence of gray whales from benthic prey habitats is usually explained by the availability of other prey such as mysids (Oliver et al. 1984, Kvitek & Oliver 1986, Guerrero 1989, Duffus 1996). In 1996, no benthic foraging was observed in late August/early September. At this time, planktonic prey were abundant and benthic biomass was generally low. In 1997, whales rapidly switched from planktonic to benthic prey in mid-August, at a time when planktonic prey were less abundant.

While prey density and biomass are linked quite distinctly to whale foraging, the predictability of prey may also be implicated. Distributions of planktonic organisms are less predictable in time and space than those of benthic organisms. It may be beneficial for whales to capitalize on planktonic species first, and forage on these ephemeral organisms when they are encountered. Whales may leave amphipod communities relatively undisturbed until planktonic prey are no longer abundant.

Like other predators, gray whales change their prey preference in response to their own estimate of the densities and profitability of each prey type (Sabelis 1990). Whales observed sporadically bottom feeding in the early summer months may have been exploring and sampling different prey habitats in order to assess the overall quality of food items available.

Size of benthic invertebrates may be an important variable controlling prey-switching behavior in gray whales. It may be beneficial for whales to forage for amphipods later in the summer because these organisms may improve as a food source as the summer progresses. Highsmith & Coyle (1990, 1992) found that the weight and caloric contents of Arctic amphipods increased during the summer, suggesting that energy-rich storage compounds such as lipids are accumulated in preparation for winter. We found that amphipods in Clayoquot Sound also increased in size as the summer progressed, but do not know whether their caloric content changed concurrently.

Since amphipod density and biomass were similar in Cow Bay and Ahous Bay in 1997, amphipod size may be the principal reason why gray whales initially did not bottom-feed in Ahous Bay. Amphipod size differed in 4 ways between Cow Bay and Ahous Bay: (1) there were more small amphipods in Ahous Bay; (2) their mean size was smaller than in samples collected near feeding whales and at other locations in Cow Bay; (3) there were fewer large amphipods in Ahous Bay than in Cow Bay where gray whales foraged; (4) large amphipods were smaller in Ahous Bay than in Cow Bay. Prey size and the mechanical limitation imposed by baleen 'mesh' size are important aspects of foraging decision-making by gray whales.

It is unclear which variables have more influence on prey-switching behavior in gray whales—characteristics of benthic prey populations such as biomass and individual size, or a decline in planktonic prey abundance. In 1997, whales had the opportunity to bottom-feed in Cow Bay throughout the summer, but generally foraged on planktonic instead of benthic prey. When whales switched to bottom-foraging behavior, amphipod density and biomass were not significantly different from those earlier in the summer; amphipod size was the only variable that had changed significantly during the season. These observations indicate that substantial changes in the benthic community were not a likely reason for gray whales switching between planktonic and benthic prey. Rather, the abundance of planktonic prey seemed to drive whales' prey choices.

Sabelis (1990) stated that prey quality is likely to be the ultimate cause of any behavioral change with respect to prey selection. However, differences in the quality of gray whale prey are difficult to measure because other variables are involved, including the energetic costs associated with capturing these prey organisms. Energetic costs are a function of diving depth and costs of specific foraging tactics. Gray whales are consistently characterized as benthic specialists, and in the high latitudes this may be so (Braham 1984). Animals spending the summer in Clayoquot Sound are predominantly pelagic foragers.

The solitary gray whale may have abandoned the ghost shrimp feeding ground in Grice Bay because 4 critical criteria which define foraging success were no longer fulfilled: (1) the length of time the whale had to search for food was too long; (2) it achieved only a low biomass removal rate; (3) ghost shrimp failed to supply the whale's minimum daily energy requirements; (4) the prey species preferred by the whale was no longer abundant.

Whale foraging in Grice Bay has aspects that require more study. This bay was not used by gray whales between 1984 and 1994; then, it was intensively used in 1995 by 5 whales, and sporadically in 1996 and 1997 by a single individual. Grice Bay is not easily reached; whales must traverse several narrow channels and intertidal mudflats to enter it. The small clam *Cryptomya californica* is abundant in the bay. Should this clam prove a useful energy source for whales, then this would make a significant contribution to the bay's attractiveness. Finally, the bay is shallow and whales do not have to dive for benthic prey, meaning lower energy expenditure; this may partly explain the discrepancy between the observed and the expected pit-making times.

The gray whales observed in central Clayoquot Sound were highly opportunistic foragers which preyed on concentrations of mysids, porcelain crab larvae, amphipods and ghost shrimp that were present in high density and biomass. Although mysid foraging predominated from June to September, porcelain crab larvae foraging was frequently observed during August. Benthic prey were also utilized by whales; amphipods fell prey to many whales, especially in 1997, whereas ghost shrimp were an important source of food for 1 whale only during the duration of this study.

Prey-switching behavior and prey-habitat selection in gray whales is probably influenced by 2 factors: a decline in the abundance of planktonic prey, and an increase in amphipod size which leads to a high proportion of the amphipod population being >6 mm in length. Data indicate that abundance of planktonic prey may be more important than benthic prey size in governing prey-switching behavior in gray whales.

While we can provide no insight into the decision-making mechanism of gray whales without more detailed experiments, our study indicates that less predictable (on the basis of availability) prey are preferred over more predictable prey. An ocean forager using very patchy resources (like most baleen whales) would be expected to be highly opportunistic and less selective; however, this small area within their range may provide an opportunity for whales to exhibit more complex foraging strategies. These strategies are an important aspect of the whales' presence in Clayoquot Sound and probably elsewhere in tertiary feeding grounds. With its return to pre-whaling levels, the eastern Pacific gray whale population has once again become a major resource for the recreational whale-watching industry and aboriginal hunters. Scientific management of these activities will require studies on the same scale as the present report to understand, and possibly predict, the spatio-temporal behavior of gray whales.

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Gray Whale Research in the Usual and Accustomed Fishing Grounds of the Makah Tribe

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ABSTRACT

Hunting of whales has for over 1500 years been central to the identity, culture and subsistence of the Makah Indian Tribe. It was so important to the Tribe that when it ceded its aboriginal lands to the United States Government in the 1855 Treaty of Neah Bay, tribal leaders insisted that the right to harvest whales be protected for all time. Makah whale hunts continued until the mid-1920s, when commercial whaling operations had decimated the population. After the gray whale was delisted as an endangered species in 1994, the Makah Tribe announced that they intended to resume hunting whales. From the beginning, the Makahs' effort to exercise its right to whale has been met with much opposition. In addition to the resumption and revival of whaling, the Makah Tribe has, in conjunction with the National Oceanic Atmospheric Administration's (NOAA) National Marine Mammal Lab (NMML), studied gray whales in the Tribe's Usual and Accustomed fishing grounds (U&A) to increase understanding of whales feeding in the U&A during the summer and fall when most of the Eastern North Pacific stock is in the Bering, Beaufort or Chukchi Seas. During surveys in the U&A, gray whales were frequently observed at an average depth of 10 m in rocky habitats and were observed to shift distribution in mid fall from feedings sites in both the Pacific Ocean and Strait of Juan de Fuca to predominately the Strait. The number of gray whales observed per hour of survey effort is dynamic by year and season. From 1993 to 2009, 189 unique whales were seen in the Makah U&A. An average of 12.7 new whales were seen in the Makah U&A survey area during each year. Of these an average of 5.6 individuals returned and were observed in subsequent years. On average, whales seen in the Makah U&A survey are seen for a short duration in terms of years observed and time span of observations within a year. The duration of time a whale was observed within the Makah U&A was positively correlated with the probability that the whale would be seen in the next year.

INTRODUCTION

The Makah Tribe resides on the Makah Indian Reservation which is located on the northwestern tip of Washington State. Unlike other Tribes of the Pacific Northwest which were located near productive salmon rivers, villages of the Makah Tribe were located near marine waters abundant in marine mammals. The Makah Tribe utilized marine mammals as a source of food, economy, fuel, and building materials for at least 4,500 years (MCRC, 2006). Archeological findings show the Makah Tribe has harvested whales for at least 1,500 years before present; the primary species of harvest was gray and humpback whales (Renker, 2007). It is possible that the Tribe harvested whales for a longer period of time, but hunting tools made from wood and shell in earlier years have decayed too much to show definitive evidence of hunting. Marine mammals are central to the culture of the Makah Tribe and, as such, are highly revered species (Huelsbeck, 1988; Renker, 2007).

In 1855, the Makah Tribe signed the Treaty of Neah Bay with the United States Government. Treaties were a means for tribal governments to protect or reserve rights most important to them while ceding land and other rights to the United States. Sealing and whaling were so important to the Makah Tribe for their economy, sustenance, and culture that leaders made sure such rights were reserved. The Makah Tribe is the only tribe in the United States with explicitly protected rights to harvest marine mammals. Whale hunts were suspended in the 1920s due to the severe impacts of commercial whaling on gray and humpback whale stocks despite the great importance of whale hunting to Makah culture and subsistence (Renker, 2007).

The US Government removed the gray whale from the Endangered Species List in 1994 after concluding the population was robust and neither in danger of extinction or likely to again become endangered in the near future (Rugh *et al.* 1999). With the recovery of the gray whale population, the Makah Tribe decided to resume exercising its whaling rights. The US Government asked the Tribe to delay its hunts until an aboriginal subsistence quota could be obtained from the International Whaling Commission (IWC). At the 1997 annual meeting, the IWC approved a shared gray whale quota for the United States and Russia to meet the needs of the Chukotkan Natives of Russia and the Makah Tribe.

Domestic animal welfare groups claimed that despite centuries of hunting in the U&A, a Makah hunt could disproportionately impact gray whales that feed in the vicinity of the Reservation during the summer and fall when most of the Eastern North Pacific stock is in the Bering, Beaufort or Chukchi Seas. The gray whales utilizing feeding sites on the Pacific Coast have been referred to under many names, including summer resident and Pacific Coast Feeding Aggregation, but are now officially recognized by the IWC as the Pacific Coast Feeding Group (PCFG) (IWC, 2010). Whales considered part of the PCFG presently include animals that feed during the summer and fall months from northern California to southeastern Alaska. In the 1990s the US government initiated research to assess the potential impact of a tribal hunt on these whales. In 1993 and 1994 NOAA Fisheries' National Marine Mammal Laboratory (NMML) photographed gray whales incidental to harbor porpoise and Steller sea lion studies. In 1996, NMML started rigorously monitoring the gray whales around the Makah Reservation on an annual basis through photo-identification research; staff of Makah Fisheries Management often assisted this research. These efforts were aided by the involvement of Cascadia Research

Collective (CRC) which contracted to review photos collected by NMML and other collaborators to compare to their catalogue of gray whales photographed south of Alaska.

Using data collected by NMML, the Makah Tribe established time and area closures to minimize the potential that PCFG whales would be harvested. In 1999, the Tribe harvested its first gray whale in over seventy years. Domestic legal challenges from 1999 through 2004 put the hunt on hold until NOAA analyzed the impact of the hunt on the PCFG whales and granted a waiver under the Marine Mammal Protection Act. That administrative process is ongoing. In 2004 the Makah Tribe hired a marine mammal biologist to research gray whales in the U&A. Since 2004, the marine mammal biologist has conducted surveys both independently and cooperatively with NMML biologists. Research has been focused on whales from June through November, but research activities are conducted throughout the year. Presented in this paper is a summary of findings from research of gray whales in the Makah U&A from 1993 to 2009 with an emphasis on sightings between 1 June and 30 November.

METHODS

Study Area

The Makah U&A is located on the Northwest tip of Washington State, United States of America. The boundaries of the U&A were adjudicated in a US court based on historic fishing practices and not marine mammal hunting (*United States v. Washington).* Whaling crews were known to travel 50 to 100 miles (80 to 161 km) offshore and spend multiple days on the water (Morse, 1897). If the Makah U&A boundaries had been determined by marine mammal harvest then they would be much different than the U&A boundary in Figure 1. However, the Makah whale hunt is limited to its U&A based on historic fishing locations.

The Makah U&A is encompassed by two bodies of water: the Strait of Juan de Fuca and the Pacific Ocean. The rocky shorelines are interspersed with sandy beaches. Rocky habitats are dominated by kelp forests of bull kelp for waters 5-15 meters of depth. The confluence of currents from the California Current and the drainage of Puget Sound through the Strait of Juan de Fuca make the Makah U&A very biologically productive.

Survey Methodology

Gray whale surveys of the Makah U&A were generally conducted over two back-to-back survey days. One day of surveys travels to the east of Neah Bay along the shores of the Strait of Juan de Fuca to Sekiu Point, approximately 25 km from Neah Bay. The other survey day travels west along the shores of the Strait of Juan de Fuca to Cape Flattery and then south following the shoreline of the Pacific Ocean down to Sea Lion Rock (47°59.58'N, 124°43.45'W). The total distance covered in the southbound survey is approximately 60 km. Sea Lion Rock is located south of the southern border of the Makah U&A (48°02.25'N). Surveys for gray whales were generally conducted within one to two kilometers of shore since gray whales summering in the Makah U&A often congregate around 10 meters of depth. Portions of the survey in the Pacific Ocean, particularly south of Cape Alava, are conducted further from shore due to poorly charted submerged rocks. Surveys were conducted with a 21 ft (6.5 m) rigid hull inflatable and a 24 ft (7.3 m) aluminum cabin cruiser made by Almar.

Surveys were attempted on a bi-weekly basis in the summer and fall as weather and ocean conditions allows. Surveys were also conducted in the spring and winter with lower frequency; results of this survey period are not included in this report.

During surveys, observers periodically note location, weather, sea state, and other variables that may influence the probability of sighting a whale. When gray whales are sighted, their location, depth, and activities are recorded. Observers then attempt to take photographs of both lateral flanks as well as the flukes if the whale is diving deep. Photographs are taken using a Nikon Digital SLR camera with a 70-300 mm lens (35 mm film cameras were used during the early years of this project). The lens magnification allows photo-documentation of unique coloration patterns on the lateral sides and flukes of the whales (Darling, 1984). The frame numbers from photographs taken are recorded on the field data sheet with the aforementioned sighting information.

Photo-Identification Methodology

All photographs of gray whales and field data are provided to CRC. The CRC research team identifies photographed whales as described in Calambokidis *et al.* (2010) and then sends the results of the identifications back to Makah and NMML researchers.

Mapping

ArcGIS version 9.0 was used to map all sightings of gray whales in the Makah U&A from Makah or combined NMML-Makah surveys from 1 June to 30 November of 2004 through 2009. The time period 1 June to 30 November marks the end of the northbound migration and beginning of the southbound migration, respectively. Data were filtered to facilitate mapping of sightings during each month (all years included) and for each year (all months included). Graduated symbol sizes were used to document the number of gray whales seen during each sighting.

Data exploration

Key data elements explored included several parameters related to gray whale counts and sightings of uniquely identified gray whales. CRC provided identification numbers for all gray whales identified from photographs taken by NMML and the Makah Tribe between 1993 and 2009 in a database that also included the date and location for each observed whale. NMML provided data on research effort from 2000 to 2009; NMML research effort from between 1996 and 1999 was determined from summary tables in Gosho *et al.* (2001). Survey effort and sighting locations and counts were maintained in a database for all Makah Tribe and combined NMML-Makah Tribe surveys. These data were used to analyze: 1) whales per hour of effort from the total effort in a given month and year and the number of whales observed in the same time period; 2) monthly and yearly sighting histories of identified whales to assess fidelity to the survey area; and 3) "minimum residency time" for each identified individual by year using the length in days between the first and last day a whale was seen during surveys from 1996 to 2009. The residency time estimate may be a minimum because it was possible that a whale was present before the first day (or after the last day) it was sighted during a given year. This estimate may also overestimate residency time because whales could have left the survey area for some unknown length of time between the first and last sighting of the year.

RESULTS/DISCUSSION

Research teams of NMML and the Makah Tribe combined for 487 dedicated surveys of the Strait of Juan de Fuca and 270 surveys of the outer coast of northern Washington from 1996 to 2009 (Table 1). In addition, earlier opportunistic surveys and collections of gray whale photos were conducted in 1993 and 1994 by NMML. Not all surveys had equal effort and opportunity to observe whales. Many were not completed to the terminal point of the survey at Sekiu Point in the Strait of Juan de Fuca or Sea Lion Rock on the Pacific coast of Washington due to weather, fog, mechanical failures, or conflicting objectives. All surveys with entered data were included in our analyses and are presented in Table 1. In total, 189 unique gray whales were identified from the CRC photo-identification catalogue of PCFG whales from surveys conducted in the Makah U&A from 1993 to 2009 in the months of June through November.

Gray Whale Counts

We analyzed the number of whales observed per survey hour by NMML and the Makah Tribe from 2000-2009 to assess monthly and annual use of the Makah U&A survey area. Gray whale use of the Makah U&A survey area during June to November was variable by both month and year (Table 2). Gray whale use had strong yearly variation in whales observed per hour of effort (ANOVA, p = 0.00387); for example, there was a ten-fold difference in whales per unit effort for 2000 as compared to 2008 (Figure 2). Whale use of the survey area was greater from 2004-2009 than for 1996-2000. More years of data need to be collected, but it does appear that gray whale use of the survey area is cyclical (Figure 2). A clearer pattern of use of the survey area was apparent when we assessed whales per hour of survey effort by month. The number of whales observed per hour of effort is low in June and July, peaks in September and plateaus in late fall (Figure 3). Pair-wise comparisons found that September has significantly more whales per hour of observation than June or July (T-test, p=0.004 and p = 0.003 respectively), while pair-wise comparisons of other months were not significant. The observed increase in whales per hour of effort following July coincides with a shift in distribution of whales from predominately in the Pacific Ocean to predominately in the Strait of Juan de Fuca. The high observed average number of whales per survey hour in the month of November is driven by 2008 when a large number of whales utilized the Strait of Juan de Fuca (Table 2).

There are caveats to interpreting data on the number of whales per hour of survey effort. First, the range of surveys was not consistent by year. Gray whales congregate near the harbor of Neah Bay. If only one half hour of survey effort is conducted it may increase the estimated whales per hour as compared to a survey that travels to Sea Lion Rock and crosses many sandy beaches where gray whales are rarely observed. Survey effort is also influenced by weather which could bias the results. Weather patterns in the fall often bring rough seas on the ocean versus the calmer ocean conditions observed in the entrance of the Strait of Juan de Fuca. The Strait of Juan de Fuca is much easier to survey and this shift in research effort may partially explain the large jump in observed whales per hour in the fall compared to the summer. The last caveat is that survey effort from 1996-1999 was taken from summary tables in Gosho *et al.* (2001) and it is possible that effort was summed for both travel on surveys away and returning to Neah Bay rather than just on travel away from Neah Bay as was used for data from 2000-2009. If this is correct, then whales per hour of effort would be doubled for 1996-1999 and whales per hour for those years would be more similar to observations in later years (Figure 2).

Spatial distribution of gray whale sightings in the Makah U&A survey area was only assessed from data collected on Makah Tribe or combined NMML-Makah surveys (2004-2009). Spatial distribution patterns of observed gray whales are variable by season and year (Figure 4 and 5). Variability is likely due to seasonal and annual availability of forage (Feyrer, 2006). For instance, there is a marked shift in distribution from summer to fall months during which whales appear to shift from using coastal ocean areas to areas in the Strait of Juan de Fuca (Figure 4). Larger aggregations of whales were seen in 2006 and 2008 than in other survey years (Figure 5). Some of the observed variability is due to survey effort. For example, prior to 2007, Makah Tribe researchers rarely went east of Kydaka Point (48°17.45'N, 124°21.82'W) or south of Sand Point (48°07.38'N, 124°44.19'W) whereas after 2007 it was standard for Makah survey effort to extend east to Sekiu Point (48°16.58'N, 124°18.15'W) and south to Sea Lion Rock (47°59.58'N, 124°43.45'W).

Most gray whale sightings occurred in waters between 8 and 15 meters of depth in areas that are characterized by rocky substrate and kelp forests composed of *Macrocystis sp*. or *Nereocystis sp*. (Berry *et al.* 2005). This depth range coincides with the depth range of mysid shrimp (Nelson *et al.* 2009). Mysid shrimp have been reported to be the primary food source for whales near Vancouver Island (Dunham and Duffus, 2002; Olsen, 2006) and it is likely mysid shrimp are also the primary prey species in the Makah U&A. In 2009, gray whales were observed foraging in 30-35 meters of water at the southern extent of the survey area near Carroll Island and Sea Lion Rock; it is not known what these whales were foraging on as these depths are deeper than mysid shrimp are likely to be found.

Uniquely identified gray whales

Fifty-two percent of whales observed between 1 June and 30 November in the Makah U&A from 1993-2009 were only observed in one year (Figure 6, Table 3). In comparison, Calambokidis *et al.* (2010) found that 80% of whales observed between 1 June and 30 November have been seen in subsequent years within the larger and encompassing range of the PCFG. Comparing the 1993 to 2007 data from the Makah U&A survey area to the CRC catalogue of PCFG whales seen through 2008 yields a more similar result of 82% of whales seen were seen in multiple years within the PCFG.

Assessing site fidelity in the Makah U&A is challenging. On average, whales were only observed in 2.2 of the 14 dedicated survey years. When whales only seen in one year were excluded from the analysis the average number of years observed increased to 3.5 of the 14 years with dedicated survey effort. Gray whales seen in more than one year also have an average period of 2.2 years in which they are not seen between subsequent years sighted. Some whales are not seen in the Makah U&A survey area over long periods of time before being sighted again. For example, CRC 94 had a 14 year gap between subsequent resights and two other whales had a nine-year gap.

The majority of whales (78.9%) photographed in more than one year were seen in consecutive years within the Makah U&A survey area. The longest observed consecutive tenure of a whale in the Makah U&A was seven straight years (CRC 92, Table 3);

interestingly this whale also had a consecutive period of four years in which it was not observed. In total, this whale was observed nine years in the survey area.

The number of days between the first sighting of a whale in the Makah U&A and when it is last sighted during dedicated survey effort in a single year (hereafter called "minimum residency time") is likely a function of both survey effort and other factors (e.g., foraging success) which in turn influence whale site fidelity. Whales are rarely observed using the Makah U&A survey area throughout an entire feeding season; whales observed in the Makah U&A had an average minimum residency time of 23.5 days (range 1 to 151 days of a possible 183 total days) between 1 June and 30 November (Figure 7). Survey effort in the Makah U&A was very similar from 2000-2003 (Table 1) which suggests that the short observed average tenure of whales in 2002 (3.9 days) relative to other years was not driven by survey effort (Figure 7).

We examined whether a whale's minimum residency time within year Y influenced the probability it was seen in the year Y+1. We found that 39% of whales in the Makah U&A survey area between June and November in year Y were sighted in year Y+1 during the same time period. The percentage of whales seen in year Y+1 was positively correlated with whale residency time (Figure 8) in year Y. Sixty percent of whales with minimum residency time of 100 days were seen the next year. The fact that 40% of whales are not sighted in the Makah U&A in year Y+1 despite being observed over a 100-day span suggests that factors other than foraging success influences future year site selection. This may be due to gray whales over-utilizing their prey base and causing depletion of prey in year Y+1. With less available prey, the whales may not return to the same site or stay in the survey area long enough to be observed.

Calambokidis *et al.* (2010) paint a compelling picture of gray whales observed in the Makah U&A not demonstrating strong fidelity to the small survey area but rather to a larger regional area that extends from at least Oregon through Northern British Columbia. We found that gray whales sighted in the Makah U&A are seen for a short duration in terms of years observed and residency time. Whales sighted in the Makah U&A in five or more consecutive years (n=7) average 43.6 days of residency in the survey area (range 10.3 to 89.8 days of a possible 183 total days) during the period of consecutive sightings. This suggests that even whales that appear to have "strong fidelity" to the Makah U&A are also feeding in areas outside of the U&A.

We also examined whether the number of years a whale is sighted in the Makah U&A influences the number of months in which a whale is sighted. We found that 59.0% of whales sighted in just one year are seen multiple months within the Makah U&A survey area. Of whales sighted in multiple years, 48.5% are seen in just one month of each year they are observed (*e.g.,* always visiting in the month of June). Three whales were sighted in greater than six years in the Makah U&A survey area and were only observed in one month; interestingly all three were in different months. These results suggest individual gray whales may have spatial and temporal consistency in foraging among years and their use of the Makah U&A does not last for an entire feeding season but rather only for a short and defined time period. The number of whales sighted in only one month is greatest in June and lowest in August (Figure 9).

For the time period from 1996-2008, an average of 12.7 new whales were sighted in the Makah U&A survey area during each year; of these an average of 5.6 individuals (44%) were sighted in subsequent years. Calambokidis *et al.* (2010) found that in the area encompassing the Makah U&A and Southern Vancouver Island survey area an average of 22.7 new whales were seen each year; of these new whales, on average 10.1 whales (44%) were seen in subsequent years. The proportion of newly sighted whales that are seen in subsequent years is the same for both survey areas; the difference in total number of observed new whales and new returning individuals between the survey areas is likely driven by the larger sampling area of the Calambokidis *et al.* paper.

We performed a discovery curve analysis on the cumulative number of individual whales observed in the Makah U&A from 1993-2009 to estimate the population of whales utilizing the Makah survey area (Figure 10). We assumed that if the sightings of new whales were occurring from a finite population that we would see the number of new individuals per year decrease with each additional year of effort. Our assumption was incorrect as the cumulative number of individual whales observed increased linearly through time ($y=11.52x - 22968$; $R^2=0.9838$) which is not conducive for using a discovery curve to calculate abundance. Calambokidis *et al.* (2010) suggested that whales seen in just one year, but not in subsequent years, are not actually a part of the PCFG but are rather "stragglers" from the much larger group of whales which feed north of the PCFG survey area. A second discovery curve was attempted with whales observed in multiple years from 1993-2008. The best fit line to the data points was again linear ($y=5.7286x - 11417$; $R^2=0.9823$) which suggests either the population within the Makah survey area is not a closed population or we are on the beginning of the discovery curve for the Makah survey area.

General conclusions

Gray whale use of the Makah U&A survey area is variable within and between years. We currently do not know what drives this variability but it is reasonable to suggest it is linked to prey populations. Feyrer (2006) found that average mysid density is significantly correlated with the average number of whales in her survey area near Vancouver Island. It is possible that mysid density is also driving the observed variability in gray whale counts in the Makah U&A since most gray whale sightings occurred in optimal mysid habitat.

Site fidelity was assessed through examination of minimum residency time and annual capture histories. On average, individual whales utilizing the Makah U&A are observed for a small portion of the June-November feeding season. Most gray whales were only seen in one year; individuals sighted in multiple years averaged a 2.2 year period of time that they were not observed in the study area. A discovery curve analysis did not suggest that gray whales exclusively use the Makah U&A during the summer and fall feeding season. Together these results suggest that most gray whales sighted in the U&A survey area do not have strong fidelity to this area. This conclusion supports the conclusion of Calambokidis *et al.* (2010) that gray whales in the Makah U&A have fidelity to a region that extends from at least Oregon through Northern British Columbia.

ACKNOWLEDGEMENTS

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TABLES AND FIGURES

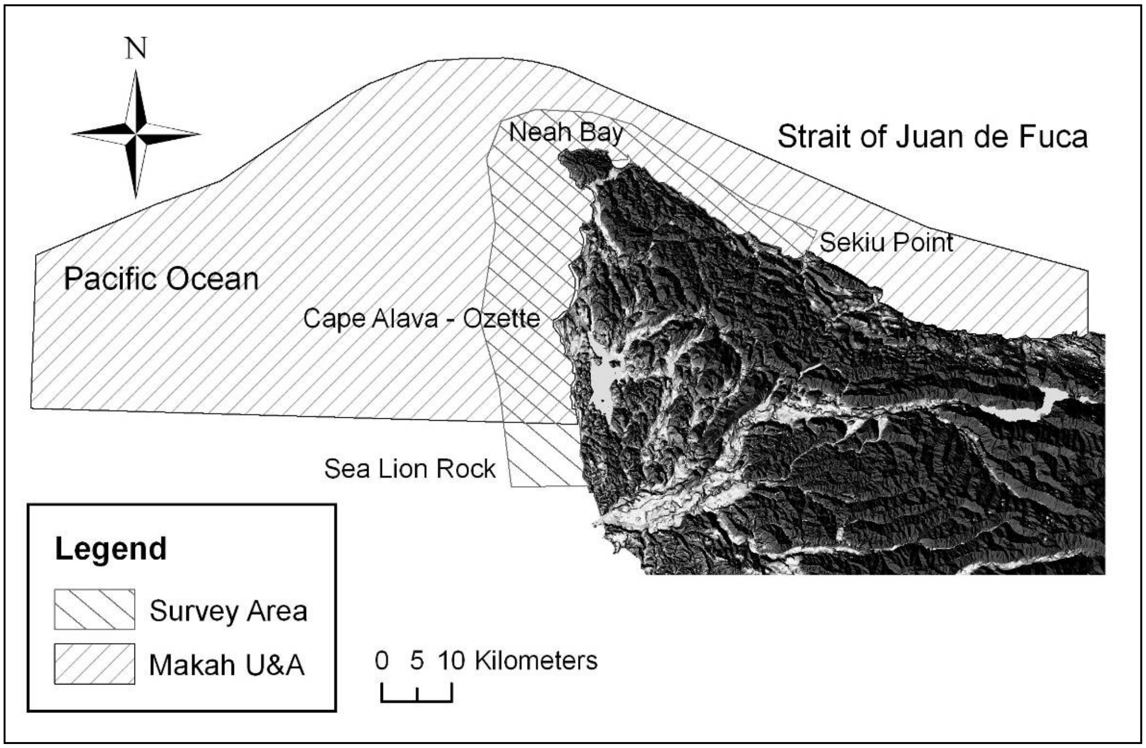


Figure 1: Map of the Makah usual and accustomed fishing grounds and standard survey area of NMML and the Makah Tribe.

Table 1: Number of gray whale surveys conducted in the Strait of Juan de Fuca and along the Northern Washington coast by NMML, Makah, and combined NMML-Makah research teams from 1996 through 2009.

	Straits of Juan de Fuca				Northern Washington Coast			
Year	NMML	NMML-Makah	Makah	Total	NMML	NMML-Makah	Makah	Total
1996	39			39	24			24
1997	56			56	26			26
1998	75			75	41			41
1999	33			33	19			19
2000	28			28	13			13
2001	29			29	15			15
2002	23			23	8			8
2003	28			28	16			16
2004	0	6		6	0	1		1
2005	13	3	7	23	9	2	3	14
2006	12	3	17	32	7	1	7	15
2007	5	6	13	24	3	4	4	11
2008	5	9	21	35	3	5	2	10
2009	6	7	19	32	3	3	5	11

Table 2: Whales observed per hour of effort during surveys of the Makah U&A survey area.

Year	Jun	Jul	Aug	Sept	Oct	Nov	Yearly Average
1996	0.31	0.14	0.82	3.35	0.00	0.00	0.77
1997	0.92	0.78	1.55	0.95	0.20	0.00	0.73
1998	0.03	0.59	0.28	0.59	1.26	0.72	0.58
1999	0.11	0.05	0.30	0.79	0.72	0.57	0.42
2000	0.09	0.20	0.00	0.40	0.86	0.15	0.28
2001	0.83	0.56	1.90	1.83	0.40	1.17	1.11
2002	0.15	0.00	0.40	0.73	0.59	0.00	0.31
2003	0.88	0.93	1.08	1.53	0.98	0.22	0.94
2004			0.40	1.42	2.85	4.03	2.17
2005	0.30	1.03	0.97	2.10	0.77		1.03
2006	0.73	0.58	1.95	2.89	2.15		1.66
2007	0.39	1.73	1.06	1.16	0.79	2.10	1.21
2008	0.62	0.78	2.32	2.33	4.79	5.96	2.80
2009	2.52	1.11	3.34	1.80	1.63	0.60	1.83
Monthly Average	0.61	0.65	1.17	1.56	1.28	1.29	1.09

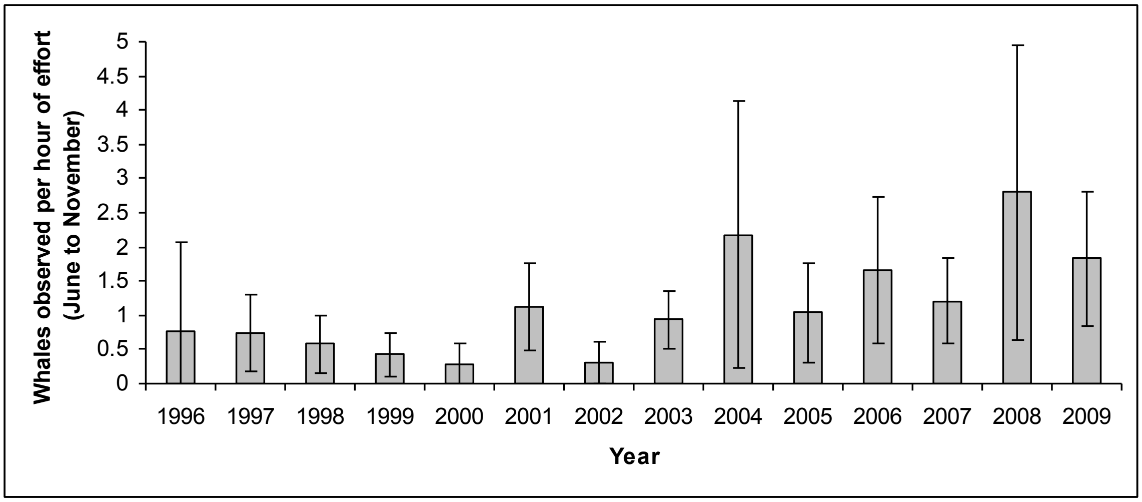


Figure 2: Whales observed per hour of survey effort within the Makah U&A survey area from 1 June to 30 November by year. Error bars are 95% confidence intervals.

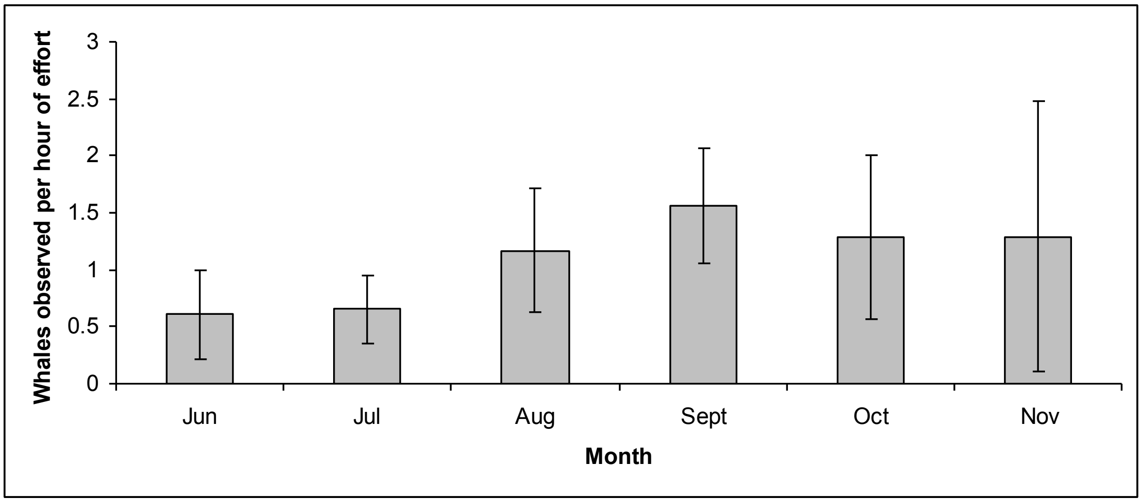
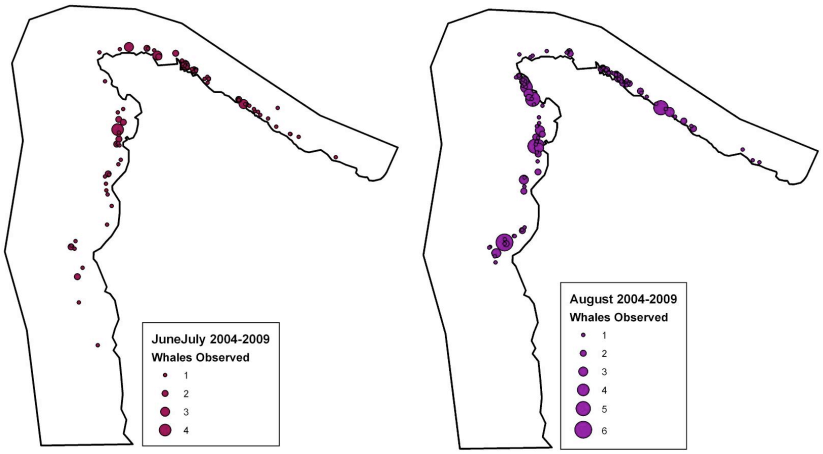
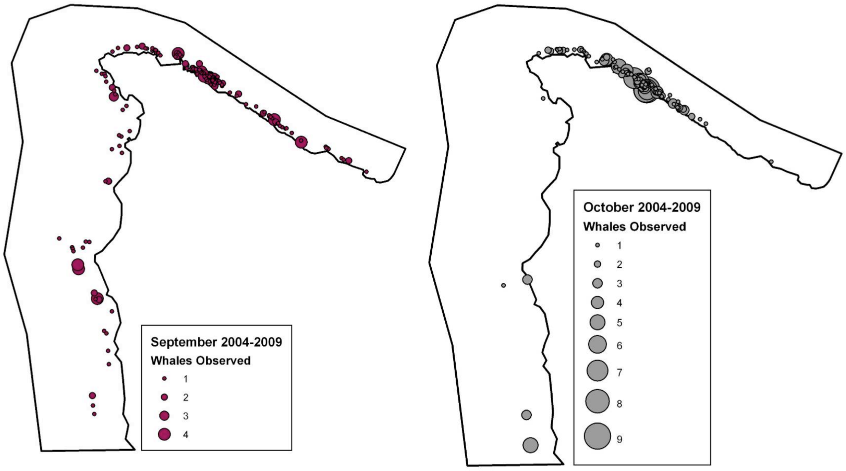


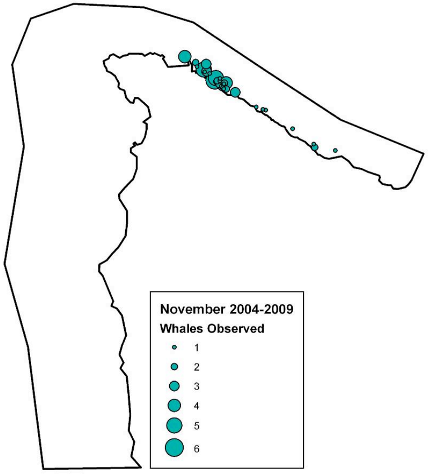
Figure 3: Whales observed per hour of survey effort within the Makah U&A between 1996 and 2009 by month. Error bars are 95% confidence intervals.



a. June and July 2005-2009 (n= 29) b. August 2004-2009 (n=26)

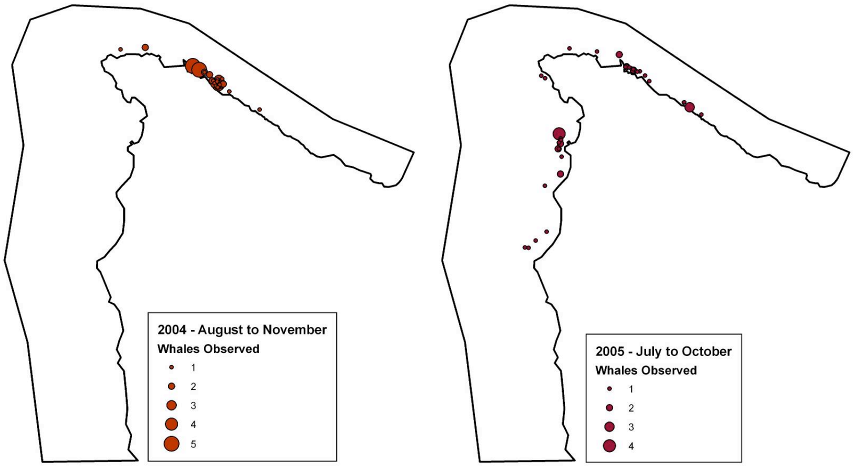


c. September 2004-2009 (n=28) d. October 2004-2009 (n=22)

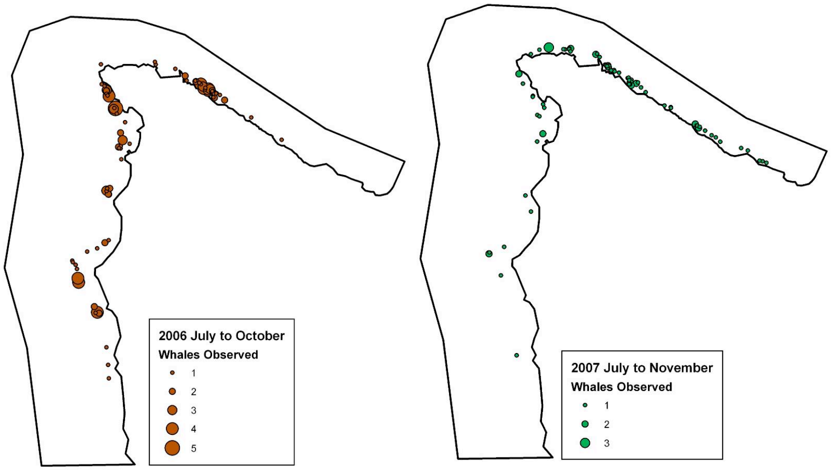


e. November 2004, 2007-2009 (n= 6)

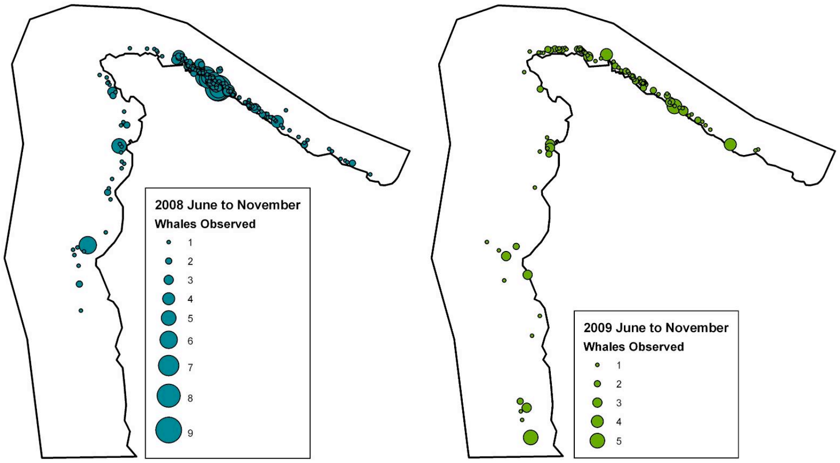
Figure 4: Whales observed per sighting during surveys by Makah and joint NMML-Makah surveys by month as indicated in each subtitle. Each subtitle includes the number of surveys included in the distribution analysis.



a. 2004 August to November (n=7)   b. 2005 July to October (n=15)



c. 2006 July to October (n=28)   d. 2007 July to November (n=27)



e. 2008 June to November (n=37)   f. 2009 June to November (n=34)

Figure 5: Whales observed per sighting during surveys by Makah and joint NMML-Makah surveys by year as indicated in each subtitle. Each subtitle includes the number of surveys included in the distribution analysis.

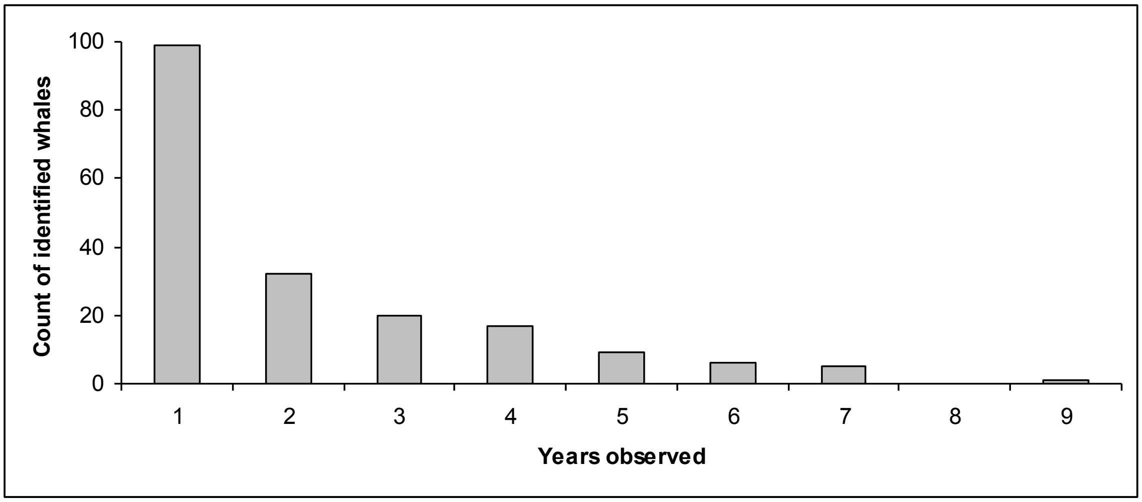


Figure 6: The number of whales identified from photographs taken during surveys in the Makah U&A research area during the months of June through November by the number of years the whale was observed over the 14 years of dedicated research surveys.

Table 3: Sighting history of gray whales identified from photographs on surveys of Makah U&A from June to November between 1993 and 2009. Sighting history includes: first and last year observed in the Makah U&A; years observed in Makah U&A; longest consecutive tenure in the Makah U&A; longest absence from being observed in the Makah U&A; and the year the whale was first observed at a survey site within the PCFG.

CRC ID	Year First Observed	Last Year Observed	Years Observed	Longest Absence	Longest Tenure	First Year Observed in PCFG
6	2009	2009	1	0	1	1986
14	2001	2001	1	0	1	1989
15	1997	1998	2	0	2	1984
30	1998	1998	1	0	1	1983
37	1998	1998	1	0	1	1988
41	2006	2009	2	2	1	1990
42	1993	2008	4	8	2	1984
43	1994	2003	4	4	2	1984
67	1997	2006	5	4	3	1992
68	1994	1997	3	0	3	1992
76	2001	2005	3	1	1	1993
79	1999	1999	1	0	1	1993
80	1994	2005	4	5	2	1993
81	1997	2006	4	6	3	1993
83	1996	2000	4	1	3	1993
84	2006	2009	4	0	4	1990
85	1998	1998	1	0	1	1984

CRC ID	Year First Observed	Last Year Observed	Years Observed	Longest Absence	Longest Tenure	First Year Observed in PCFG
87	1996	2008	3	9	1	1993
88	1996	1996	1	0	1	1990
89	2005	2009	3	2	2	1993
91	1998	1998	1	0	1	1993
92	1997	2009	9	4	7	1993
93	1998	2002	2	3	1	1984
94	1993	2009	3	14	2	1993
96	1993	1993	1	0	1	1993
101	1998	2008	3	7	1	1984
105	2006	2007	2	0	2	1994
107	1994	2008	7	4	3	1994
120	2001	2001	1	0	1	2001
127	1997	2001	2	3	1	1986
130	2001	2009	3	6	2	1998
135	2008	2008	1	0	1	1998
136	2008	2008	1	0	1	1998
140	1998	1998	1	0	1	1998
141	1997	2007	4	5	1	1990
145	1996	2006	2	9	1	1990
166	1996	2008	5	6	3	1995
169	2001	2008	4	3	2	1995
171	1994	1994	1	0	1	1994
174	1996	1997	2	0	2	1995
175	1996	2007	6	6	3	1995
177	1997	1999	2	1	1	1995
178	1996	2009	6	7	3	1995
180	1997	1997	1	0	1	1995
185	1996	2009	6	5	2	1996
186	2004	2004	1	0	1	1994
187	1996	1998	3	0	3	1996
191	2003	2003	1	0	1	1996
192	1997	2009	5	7	2	1996
196	2006	2009	3	1	2	1996
204	2000	2009	3	4	1	1996
205	1997	2009	7	4	3	1996
209	1997	1998	2	0	2	1996
210	1996	1996	1	0	1	1996
212	1996	1997	2	0	2	1995
215	2003	2003	1	0	1	1996
216	1997	2005	3	5	1	1997

CRC ID	Year First Observed	Last Year Observed	Years Observed	Longest Absence	Longest Tenure	First Year Observed in PCFG
217	1997	1997	1	0	1	1997
218	1997	1997	1	0	1	1997
219	1997	2009	5	6	2	1997
220	1997	1997	1	0	1	1997
226	2001	2006	2	4	1	1998
228	1998	1998	1	0	1	1998
231	2006	2006	1	0	1	1998
239	1998	1998	1	0	1	1998
242	1998	2008	7	4	4	1998
244	2005	2009	5	0	5	1998
249	1998	1998	1	0	1	1998
250	1998	1998	1	0	1	1998
251	1998	1998	1	0	1	1998
252	1998	1998	1	0	1	1998
253	1998	1998	1	0	1	1998
255	1998	1998	1	0	1	1998
265	2004	2004	1	0	1	1998
272	1998	1998	1	0	1	1998
291	2003	2006	2	2	1	1998
295	2006	2006	1	0	1	1991
296	2000	2008	7	2	4	1998
297	2003	2003	1	0	1	1998
301	2005	2005	1	0	1	1998
302	2006	2008	2	1	1	1998
303	2006	2006	1	0	1	1998
304	1998	1998	1	0	1	1998
308	2006	2008	2	1	1	1998
317	2008	2009	2	0	2	1998
319	2000	2008	4	4	2	1998
328	2008	2008	1	0	1	1998
355	1999	1999	1	0	1	1999
372	2000	2009	3	5	1	1999
392	2003	2003	1	0	1	1999
396	2000	2009	7	2	4	1999
507	2001	2001	1	0	1	2000
508	2000	2000	1	0	1	2000
510	2000	2008	4	5	3	2000
515	2000	2001	2	0	2	2000
516	2000	2000	1	0	1	2000
525	2008	2008	1	0	1	2000

CRC ID	Year First Observed	Last Year Observed	Years Observed	Longest Absence	Longest Tenure	First Year Observed in PCFG
532	2000	2008	5	3	2	2000
542	2000	2000	1	0	1	2000
551	2009	2009	1	0	1	2000
554	2006	2009	3	1	2	2000
561	2006	2006	1	0	1	2000
567	2003	2003	1	0	1	2001
576	2001	2001	1	0	1	2001
583	2008	2009	2	0	2	2001
592	2001	2001	1	0	1	2001
595	2001	2001	1	0	1	2001
596	2001	2001	1	0	1	2001
602	2001	2001	1	0	1	2001
603	2001	2001	1	0	1	2001
604	2001	2001	1	0	1	2001
605	2001	2004	4	0	4	2001
607	2001	2002	2	0	2	2001
608	2001	2001	1	0	1	2001
610	2001	2001	1	0	1	2001
641	2003	2003	1	0	1	2001
659	2009	2009	1	0	1	2002
669	2009	2009	1	0	1	2002
682	2004	2009	4	1	2	2002
683	2004	2005	2	0	1	2002
687	2006	2006	1	0	1	2002
688	2006	2008	2	1	1	2002
696	2002	2009	6	1	5	2002
698	2006	2006	1	0	1	2002
701	2006	2007	2	0	2	2002
712	2009	2009	1	0	1	2002
714	2006	2009	3	1	2	2002
718	2009	2009	1	0	1	2001
719	2008	2008	1	0	1	2002
720	2003	2008	4	1	2	2002
759	2008	2009	2	0	2	2002
782	2003	2003	1	0	1	2003
785	2003	2005	3	0	3	2003
786	2006	2006	1	0	1	2003
787	2004	2006	3	0	3	2003
788	2003	2005	2	1	1	2003
789	2006	2009	3	1	2	2003

CRC ID	Year First Observed	Last Year Observed	Years Observed	Longest Absence	Longest Tenure	First Year Observed in PCFG
797	2008	2008	1	0	1	2003
800	2005	2005	1	0	1	2003
813	2004	2009	5	1	3	2004
818	2006	2006	1	0	1	2004
819	2004	2009	6	0	6	2004
823	2004	2009	6	0	6	2004
824	2004	2009	4	2	2	2004
826	2006	2009	4	0	4	2004
840	2009	2009	1	0	1	2005
842	2004	2008	5	0	5	2004
843	2004	2006	2	1	2	2004
847	2005	2005	1	0	1	2005
850	2004	2006	2	1	2	2004
851	2007	2009	3	0	3	2005
854	2005	2005	1	0	1	2005
858	2005	2005	1	0	1	2005
860	2003	2006	3	1	2	2003
864	2005	2005	1	0	1	2005
866	2005	2008	3	1	2	2005
872	2005	2006	2	0	2	2005
877	2007	2009	2	1	2	2005
878	2005	2009	5	0	5	2005
880	2006	2006	1	0	1	2005
881	2004	2004	1	0	1	2004
882	2006	2009	4	0	4	2005
884	2004	2004	1	0	1	2004
932	2006	2009	4	0	4	2006
987	2009	2009	1	0	1	2007
990	2008	2009	2	0	2	2007
991	2009	2009	1	0	1	2007
1047	2008	2008	1	0	1	2008
1050	2008	2008	1	0	1	2008
1051	2008	2009	2	0	2	2008
1052	2008	2009	2	0	2	2008
1053	2008	2008	1	0	1	2008
1054	2008	2008	1	0	1	2008
1055	2008	2008	1	0	1	2008
1056	2008	2009	2	0	2	2008
1057	2008	2008	1	0	1	2008
1059	2008	2009	2	0	2	2008

CRC ID	Year First Observed	Last Year Observed	Years Observed	Longest Absence	Longest Tenure	First Year Observed in PCFG
1061	2008	2008	1	0	1	2008
1062	2008	2008	1	0	1	2008
1063	2008	2008	1	0	1	2008
1064	2008	2008	1	0	1	2008
1065	2008	2008	1	0	1	2008
1067	2009	2009	1	0	1	2008
1105	2009	2009	1	0	1	2009
1123	2009	2009	1	0	1	2009
1125	2009	2009	1	0	1	2009
1194	2009	2009	1	0	1	2009
1195	2009	2009	1	0	1	2009
1196	2009	2009	1	0	1	2009

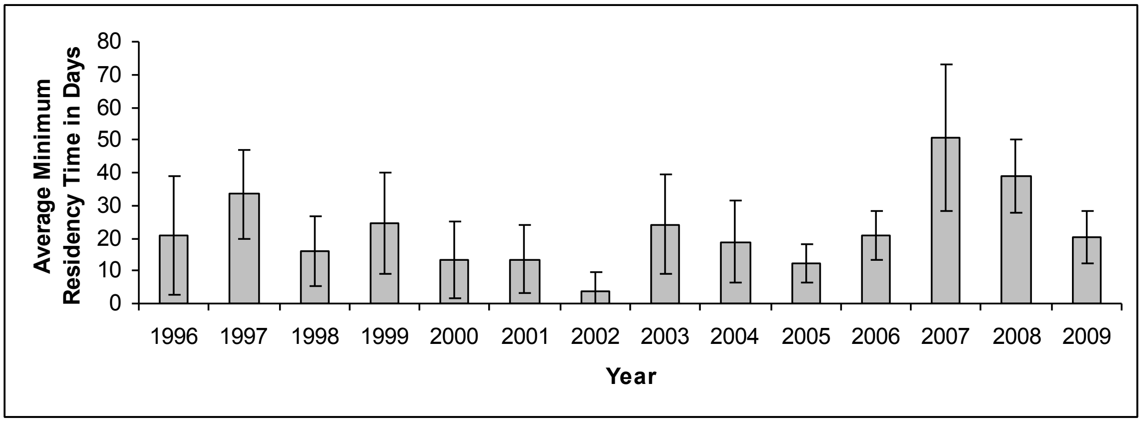


Figure 7: Average number of days between the first and last sighting within a dedicated year of survey effort of individual gray whales in the Makah U&A. Error bars are two times the standard error.

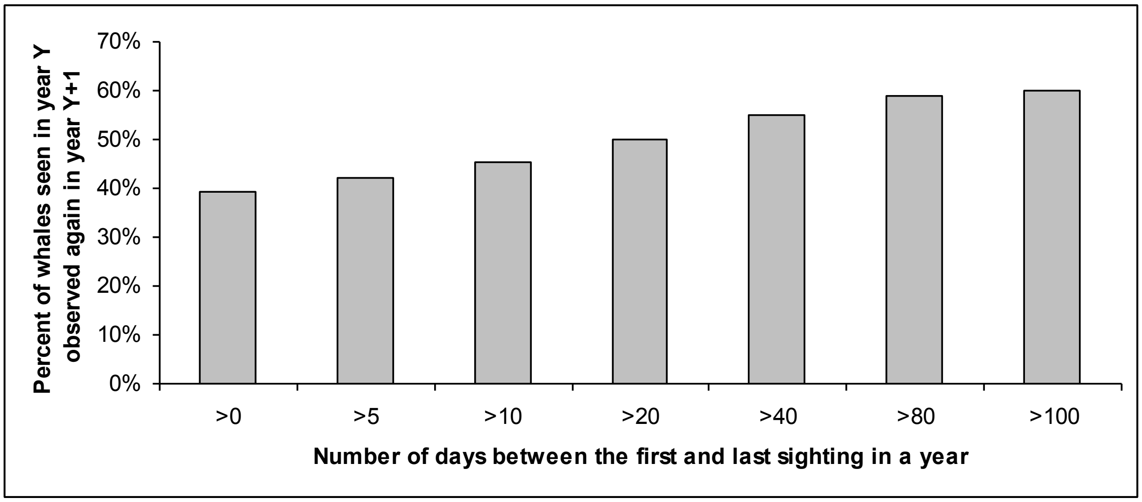


Figure 8: The percent of whales observed in year Y that are again observed in year Y+1 as compared to a whale's residency time in year Y (the number of days between the first and last sighting of the year).

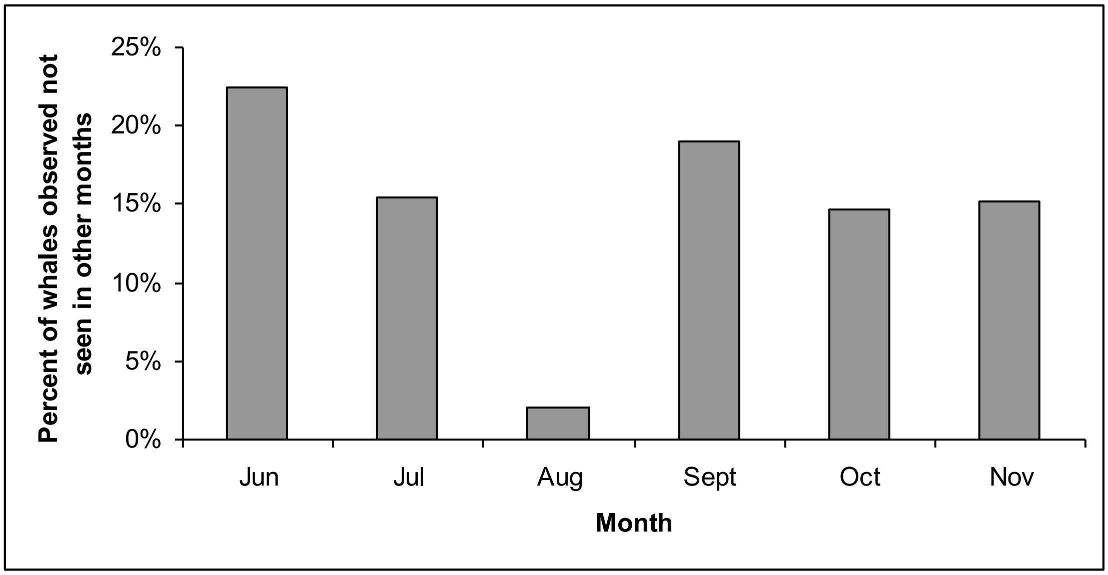


Figure 9: Percent of whales identified in the Makah U&A survey area from 1993-2009 during each month that were only observed in that month.

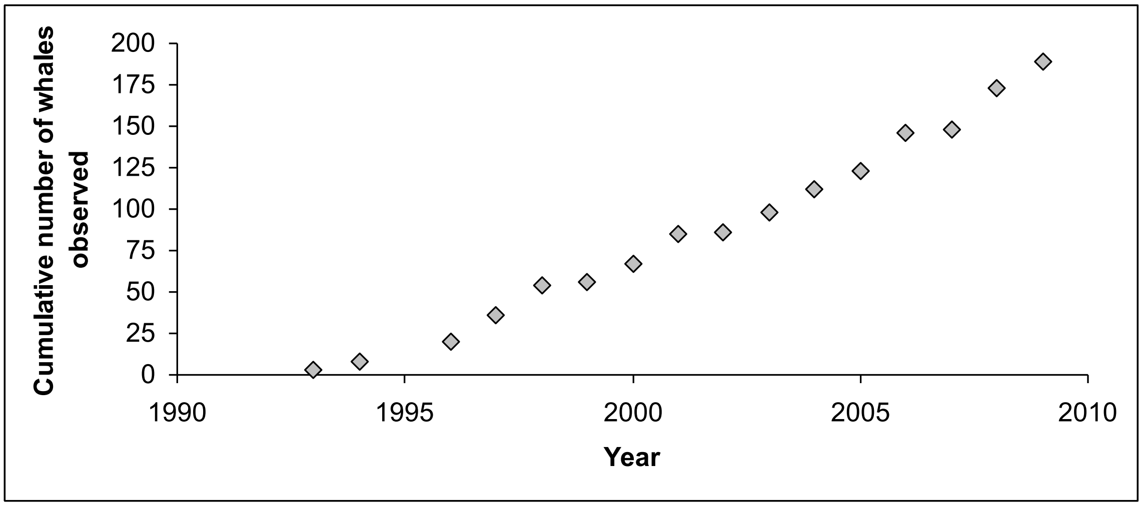


Figure 10: Cumulative number of gray whales seen by year during NMML and Makah surveys of the Makah U&A.

Summary of collaborative photographic identification of gray whales from California to Alaska for 2007

Final Report for Purchase Order AB133F-05-SE-5570. *April 2009*

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A collaborative effort involving multiple research groups to examine the occurrence and abundance of gray whales primarily in Summer and Fall from California to SE Alaska began in 1998 with the support of the National Marine Mammal Laboratory (NMML). Previous reports have summarized the results of this work through 2006 (Calambokidis et al. 2002, 2004, Calambokidis 2008). The purpose of this report is to summarize results of the matching of identification photographs for the 2007 field season and compare these results with those reported previously. This collaborative research effort has focused on the gray whales that feed through the summer and fall in the Pacific Northwest, a group that has been referred to as “seasonal residents” or the Pacific Coast Feeding Aggregation (PCFA). While the collaborative effort reported here began in 1998, there had been indications of the existence of such a group much earlier; photographic identification tracking of individuals began in the 1970s off Vancouver Island (Darling 1984).

Identification photographs of gray whales were taken by different research groups working from California to southeastern Alaska in 2007 (Table 1). Ten different groups contributed significant numbers of identification photographs of gray whales during the period. Some of these were done with support from NMML, but effort was also conducted outside or beyond the level of effort that was contracted.

Table 1. Summary of photo-IDs of gray whales by year and contributor through 2007.

Research Group	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	Total
Brian Gisborne	373	343	779	586	435	875	326	429	527	117	4,790
Coast. Ecos. Res. Found.	101	150	251	466	295	180	781	11	42	11	2,288
Cascadia Research	170	234	118	79	135	112	183	33	62	102	1228
Nat Marine Mammal Lab	132	194	135	128	88	76		133	92	39	1,017
Univ. Vict.	351	159	128		121					1	760
Humboldt State Univ.	21	89	60	75	71						316
Makah Tribe							44	60	142	79	325
Wendy Szaniszlo								127	44	48	219
Volker Deecke	39	42	28	11		7			50		177
Jim Darling	50			35	14						99
Carrie Newell									13	73	86
Other	4	12	1	1	0	7	0	1	30	49	105
Total	1,241	1,223	1,500	1,381	1,159	1,257	1,334	794	1,002	519	11,410
Unique IDs	156	248	178	198	254	178	198	206	180	157	891
Unique >1 June NCA-SEAK	135	157	139	175	206	161	182	139	131	123	501

Effort was distributed over a broad area and time period overall (Table 2). Some effort was undertaken early in the season in several areas, especially the Puget Sound and Grays Harbor areas of Washington (by Cascadia Research) and along the S and W sides of Vancouver Island (by Brian Gisborne, Volker Deecke, and Wendy Szaniszlo). These early-season efforts were important for looking at the identity of some of the animals that break off from the migration early in the season to feed in specific areas. These identifications were not included in the overall mark-recapture estimates or other elements of the analysis of PCFA animals that have generally only included animals seen after 1 June to avoid overlap with the migration.

Table 2. Summary of month and region for identifications made by all contributors in 2007.

	Month												
Region	**1**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**Total**	**Unique**
SE AK					1	3						4	3
N Brit Col.							10	1				11	5
W Vanc. Is.		40	2		8	9	15	18				92	41
S Vanc. Is.		12	1	3	7	25	24	4				76	44
N Puget Sound		7	21	1								29	6
Puget Sound				2								2	1
Str Juan de Fuca					2	12	28	26	5	7	11	91	18
N Wash.						6	15	2				23	12
Grays Harbor area	2		1		16			27				46	41
N Oregon				3	4	40	30	9	20			106	39
S Oregon						8		19				27	23
N California								2				2	1
C California			1	9								10	5
Total	2	59	26	18	38	103	122	108	25	7	11	519	
Unique	2	36	9	9	31	53	41	64	14	7	8		157

A total of 519 identifications were made (157 unique individuals) in 2007. Of these identifications, 414 were made after 1 June 2007 representing 123 unique individuals. Of the 157 individuals identified, 42 (27%) were new to the Cascadia catalog and 115 (73%) were already known from past years. A higher proportion of these new whales were from the identifications made either before 1 June or in areas outside the core region (Oregon to British Columbia) where PCFA whales are known to occur. For the 34 whales identified only prior to 1 June, only 15 (44%) were known from past years (most of these from the N Puget Sound Region) and for the 123 whales seen at least once after 1 June, 100 (81%) had been identified previously.

Even though effort in most regions was similar to past years, there were shifts in the number of sightings by region reflecting changes in gray whale distribution in 2007. The numbers of identifications at all sites from N Washington north through British Columbia were dramatically lower than in other recent years. This was most dramatic off southern Vancouver Island where the daily effort by Brian Gisborne covering one of the areas of highest gray whale density has generally contributed close to 50% of the identifications from all contributors. Only 76 identifications of 44 individuals were made in this region in 2007 that contrasts with 2006 when

472 identifications (close to 50% of all the identifications that year) were made of 70 individuals. Both the number of individuals identified and the number of times each individual was seen were down despite similar effort showing that fewer animals used this area in 2007 and those that did spent less time there. Similarly, the number of identifications made in the Cape Caution area of northern British Columbia (mostly by CERF) also dropped from 23 individuals identified in 2006 to just 5 in 2007.

In contrast to the lower numbers of gray whales seen at study areas to the north, more whales were identified at some of the southern study areas in 2007 compared to previous years (where there was consistent effort). Both off of Grays Harbor in southern Washington and in Oregon, higher numbers of whales were identified than in most past years. One of the most dramatic changes was the 41 individuals identified in just a couple of days of effort offshore of Grays Harbor in 2007 and this is discussed in more detail in a later section. Of the 86 whales identified off Grays Harbor and Oregon in 2007, 46 or 53% of them had been identified in previous years off southern Vancouver Island.

Whales identified in 2007 matched to those seen in past years going back to at least 1998 when broader scale effort began. Between 29% and 58% of the whales identified each year since 1998 were also seen in 2007 (Table 3). This proportion as highest for 2005 and 2006 where 50% and 58% of the whales identified matched to 2007. The proportion was slightly lower for 1998 to 2004 (29% to 43%) but was fairly steady within that period.

Table 3. Number of gray whales identified from N California to SE Alaska (excluding Puget Sound area) after 1 June by year and the proportion that matched whales identified in 2007.

Year	**Unique IDs**	**Match to 2007**	**% match**
1998	135	46	34%
1999	157	46	29%
2000	139	52	37%
2001	175	56	32%
2002	206	75	36%
2003	161	70	43%
2004	182	71	39%
2005	139	69	50%
2006	131	76	58%
2007	123	123	100%

For the 10 years of fairly consistent effort at least for the core area of Oregon to northern British Columbia, a total of 428 whales have been identified after 1 June. Almost half of these (198 or 46%) were whales seen only one year and most of these (107) were seen only one time in that year. There was a clear relationship between the number of times per year a whale was seen and how many years it was seen (Figure 1). While only 19% of the identified whales were seen seven or more of the 10 years from 1998 to 2007, these whales accounted for 65% of the sightings of gray whales, both reflecting the high number of times they were seen each year and the large number of years they were seen.

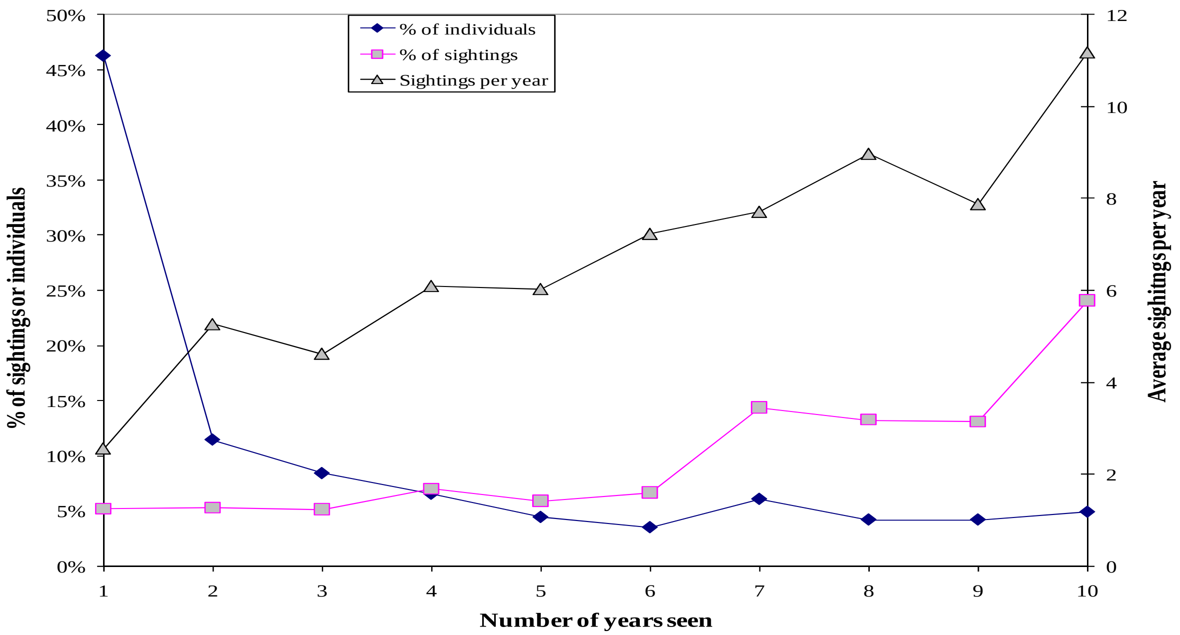

Figure 1. Relationship between number of years different whales were seen in the core region of Oregon to Northern British Columbia after 1 June for 1998 to 2007 and how many times per year they were seen and what percent of the individuals and sightings these whales represented.

A total of 171 gray whales have been identified in the regions that include the Makah Usual and Accustomed areas (N Washington and Strait of Juan de Fuca) after 1 June in any year (Table 4). The proportion of whales identified in other regions that match to this area decrease with distance from the Makah U&A (Table 4). The exception to this is that whales identified in Puget Sound generally did not match to this region. Other than Puget Sound, 40% or more of the whales identified from Oregon to northern Vancouver Island had been seen at least once in the Makah U&A. The proportion matching the Makah U&A dropped to intermediate rates (20 to 32%) for N California, N British Columbia, and SE Alaska, and to 1% or less for Kodiak and central and southern California.

Table 4. Number of gray whales identified after 1 June by region for all years and proportion matching the whales seen in the N Washington and Strait of Juan de Fuca (Makah U&A).

Region	**IDs**	**Match NWA/SJF**	**% match**
Kodiak	107	1	1%
SE AK	21	5	24%
N Brit Col.	114	37	32%
W Vanc. Is.	212	86	41%
S Vanc. Is.	250	104	42%
Puget Sound	33	3	9%
N Wash./Str. Juan de Fuca	171	171	100%
Grays Harbor area	50	20	40%
N Oregon	90	46	51%
S Oregon	72	32	44%
N California	128	25	20%
C and S California	13	0	0%
Total	675		

Sightings of gray whales in northern Puget Sound continued to reveal that this area is used as a springtime feeding area for a small regularly occurring group of gray whales (Table 5). Only six unique whales were identified from the 29 times good identification photographs were obtained in 2007 and all of these whales had been seen in past years. These whales were primarily identified from late March through May. All six of these whales had been identified in the region going back to at least 2000.

Table5. Sighting histories of gray whales identified in northern Puget Sound. Includes all individuals that have been sighted in this region since 2001. Numbers indicate times seen. Values for 2008 shown as X indicates animal has been sighted at least once in 2008.

ID	1990	1991	1992	1993	1994	1995	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008
21	1	16	5	2		7	6	4	5			1	13	1	9	3	X
22	1	1	2	1		5	7	4	3			4		2	14		X
44		14	9	3		3		1	1	1		1	16	2		5	X
49		6	4	2	2	2	5	1	1	5	2	2	11	2	5	5	X
53		12		2	2	2		1	2		2	5	9	2	9		
56		2					1		5	2		1	6	2	7	2	X
356								1		1		1	1		1		X
383								2		1		1	7	1	7	6	X
531									2					2	3	8	X
723													19	3	5		

Identification of whale killed in September 2007

As a part of the matching of the 2007 whales we specifically attempted to determine the identity of the gray whale killed in the Strait of Juan de Fuca on 8 September 2007 by a group of Makah whalers operating without the permission of the Makah Tribe or NMFS. We made initial attempts to identify this whale in the aftermath of this hunt but were unable to find a match of this whale because none of the photographs taken on 8 September showed the dorsal part of the side that we use for our photo-ID (a biologist only arrived on the scene only well after the whale had been mortally wounded preventing it from surfacing normally). These photographs did show markings on the front of the animal and we searched for some of these distinctive markings on the front of the whale while matching other collections from 2007. As a part of this effort we were able to find a match to photographs taken near Neah Bay by NMML in 2007 that helped link it to a good identification photograph. These results have also been reported in a statement from the Makah Tribe (http://www.makah.com/images/Whale_ID_PressRelease_5.6.09.pdf).

The whale that was killed was CRC-175 (Figures 2 and 3) which had a long sighting history with 143 sighting records in our database from a number of research groups between 1995 and 2007. The locations of the previous sightings extended from northern California to central Vancouver Island (Figure 4). The earliest sightings in our records were by Calambokidis on 22 and 23 July 1995 less than a mile south of Cape Flattery. The latest identification made prior to when it was killed on 8 September 2007 was on 30 August 2007, east of Neah Bay during a NMML survey. The whale had been seen frequently in the past in the Neah Bay area with sightings in at least 7 years in the Makah U&A. Most sightings were in June to October but there were four identifications made in mid and late May off southern Vancouver Island in 1993, 2000, and 2003. It had also been identified by many other groups including; Cascadia Research, NMML, UVIC (WL035 and WL060), Jim Darling, Wendy Szaniszlo, Makah Tribe, Volker Deecke (UK98-11), Brian Gisborne, and Carrie Newell (*Orion, Ruler,* and *Saucer*).

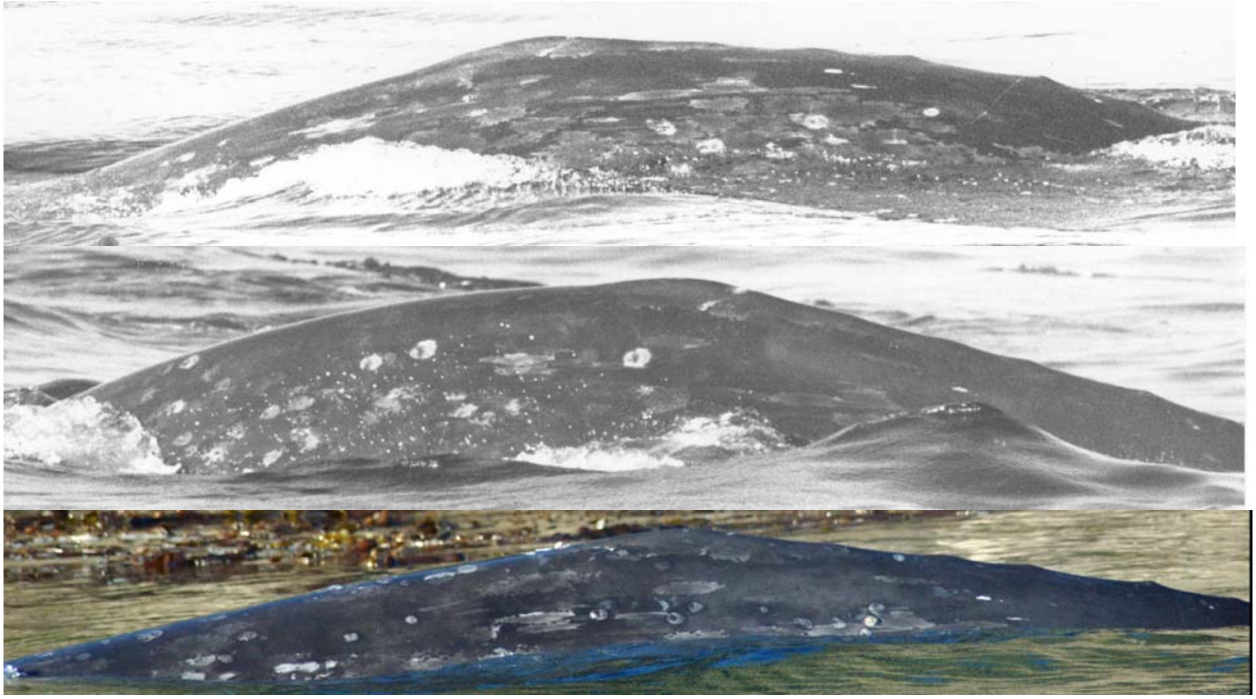

Figure 2. Left side views of CRC-175, the whale that was killed in Fall 2007 near Neah Bay. Top photo by Merrill Gosho, middle by Jim Darling, and bottom by Nate Pamplin. The variability in the lighting alters the distinctiveness of some of the marks.

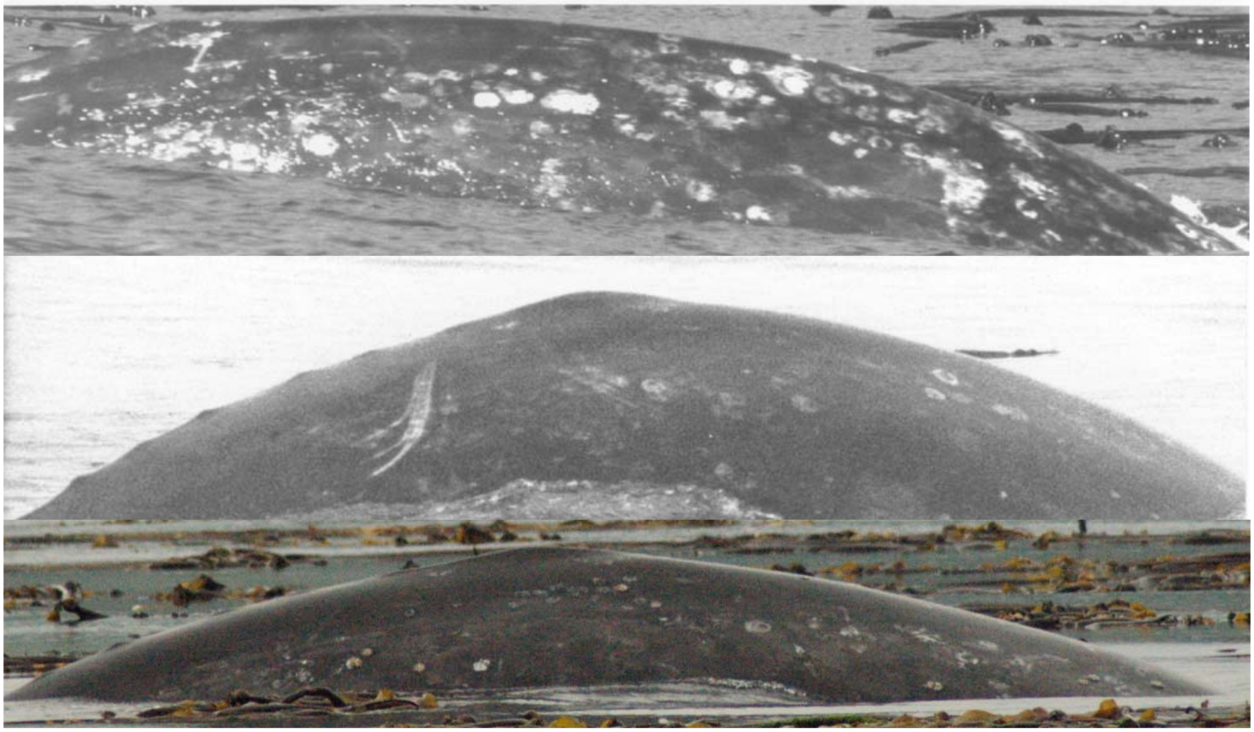

Figure 3. Photos of the right side of whale CRC-175. Top photo by Christina Tombach, middle by Merrill Gosho, and bottom by Nate Pamplin. These are a more difficult match than typical.

The timing and location that this whale was taken made it by definition part of the PCFA group. The sighting history also demonstrates that it was a well-known whale seen over many years. A whale that is killed and landed as planned by the Makah would provide a more reliable opportunity for obtaining identification photographs. Despite the challenges faced in 2007 with the difficulty of obtaining good identification photographs, the ability to identify this whale also demonstrates that this can be an effective way to identify future whales that may be hunted in the spring to determine if they are PCFA whales.

Figure 4. Locations CRC-175 was sighted off northern Washington and British Columbia prior to being killed in September 2007. Additional sightings off northern California and Oregon are not shown.

Surveys off Grays Harbor

As a part of a separate project examining both visual and acoustic detections of marine mammals off the central Washington coast in collaboration with Scripps Institution of Oceanography for the US Navy, we obtained sightings and photographic identifications of gray whales that are summarized below (see also Oleson et al. 2007, In prep). There were seasonal differences in the distribution and habitat utilization of gray whales corresponding to three time periods matching stages in their life history (Figure 5):

1) Sightings in December and January (corresponding to the southbound migration of gray whales from their primary feeding ground in Alaska to their breeding grounds in Mexico when whales were primarily in deep water far offshore (average of 29 km offshore and 126 m water depth).
2) Sightings for February to April (northbound migration past Washington as the main population heads back to Alaskan waters) tended to be close to shore mostly on a north-south distribution averaging about 10 km offshore.
3) Sightings in May to October (when primarily gray whales from the PCFA are present) were clustered in two areas, in and around the entrance to Grays Harbor and also 20-25 km offshore in depths of about 60 m.

Figure 5. Sighting location of gray whales by season (circles - winter, triangles - spring, and squares - summer and fall . Lines show survey tracks for approximately monthly surveys conducted from 2004 into 2008. Shaded area shows location of concentration of feeding gray whales seen from June to September 2007.

The offshore sightings of gray whales during the summer represented a surprising finding given the typical pattern of gray whales feeding in the Pacific Northwest, which tend to feed close to shore in shallow waters. These offshore sightings were all made between 8 June and 1 September of just 2007 and while they were grouped into just 6 sightings, they totaled 42 whales since each sighting represented a concentration of up to 14 whales in one area.

Identifications from the concentration of gray whales in 2007 found feeding almost 10 nmi offshore in the summer and fall. The identifications revealed that this unusual offshore feeding concentration consisted almost exclusively of animals known as “seasonal residents” in other parts of the Pacific Northwest. All but one of the 28 individuals had been identified in other feeding areas in the Pacific Northwest.

Mark-recapture abundance estimates

Data for 2007 was used to update estimates of abundance using Petersen mark-recapture estimates with adjacent years as samples (Table 6, Figure 6). As in past years, only identifications from after 1 June and excluding the Puget Sound area were used in the abundance estimates. Estimates of abundance based on 2006 and 2007 were 212 and 203 depending on the regional cut-offs used (Table 6). This estimate is just slightly higher than the estimates from 2005-2006 though still at the low end of the range of values obtained from these estimates based on adjacent-year samples (Figure 6). Rather than reflecting any real change in abundance these fluctuations are more likely the result of small shifts in distribution and effort affecting how these animals are sampled.

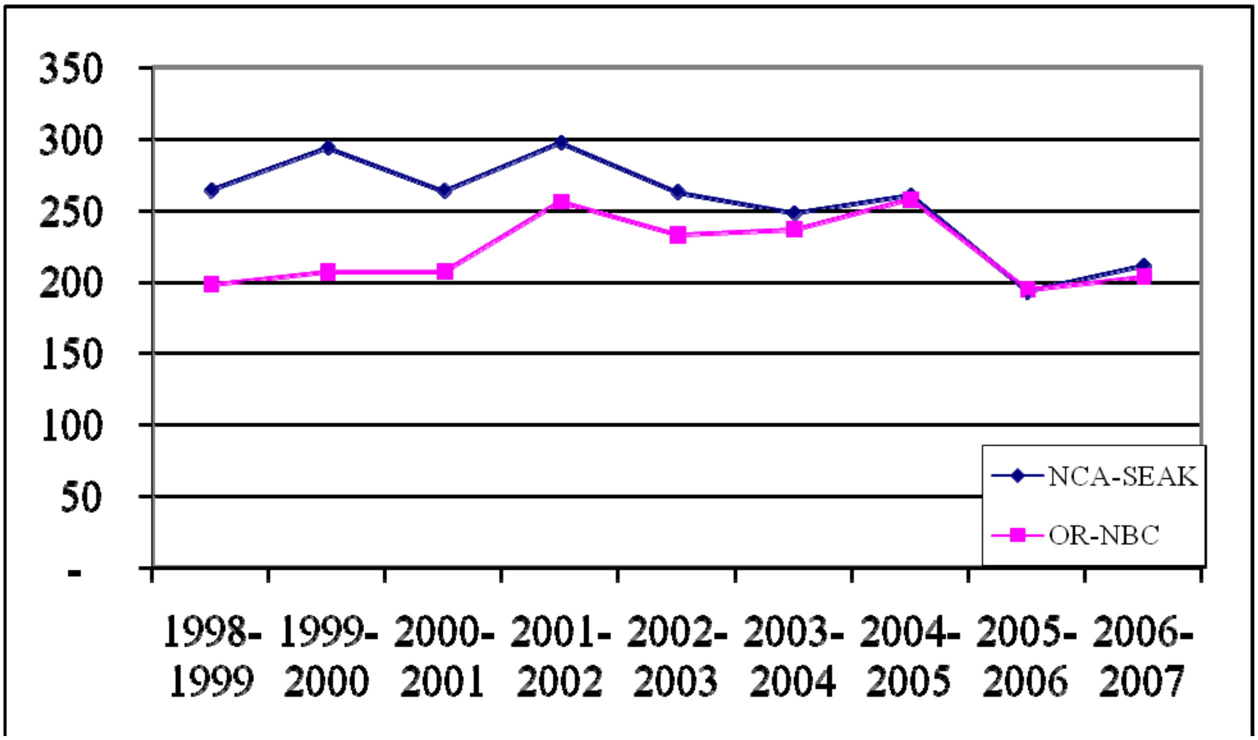

Figure 6. Plot of Petersen mark-recapture estimates of abundance based on photo-IDs of gray whales identified after 1 June and excluding (Puget Sound).

Table 6. Petersen mark-recapture estimates of abundance based on photo-IDs of gray whales identified after 1 June. Estimates below are shown for two different core areas (a larger Northern California to SE Alaska and a smaller core area of Oregon to British Columbia (both exclude peripheral areas including Puget Sound, Kodiak, and central or southern California).

	Unique Ids				
Sample periods	**n1**	**n2**	**Recapt.**	**Estimate**	**CV**
NCA-SEAK					
1998-1999	135	157	80	**264**	0.05
1999-2000	157	139	74	**294**	0.06
2000-2001	139	175	92	**264**	0.04
2001-2002	175	206	121	**298**	0.03
2002-2003	206	161	126	**263**	0.03
2003-2004	161	182	118	**248**	0.03
2004-2005	182	139	97	**260**	0.04
2005-2006	139	131	94	**194**	0.03
2006-2007	131	123	76	**212**	0.05
OR-NBC					
1998-1999	116	120	70	**198**	0.05
1999-2000	120	114	66	**207**	0.05
2000-2001	114	151	83	**207**	0.04
2001-2002	151	180	106	**256**	0.03
2002-2003	180	154	119	**233**	0.03
2003-2004	154	180	117	**237**	0.03
2004-2005	180	139	97	**258**	0.04
2005-2006	139	129	92	**195**	0.03
2006-2007	129	120	76	**203**	0.04

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Acknowledgements

This analysis would not have been possible without the collaborating organizations contributing identification photographs listed in Table 1. Support for the photographic identification reported here, the comparison of gray whale photographs and preparation of this report came primarily from the National Marine Mammal Laboratory (coordinated by Jeff Laake). Permission to conduct some portions of this research was provided by the U.S. National Marine Fisheries Service and the Makah Tribal Nation.

We thank the operators of the boats that allowed us to gather data from their boats in northern Puget Sound. A number of people assisted in the field effort and in the printing and matching of photographs at Cascadia Research. Erin Falcone compiled the data from the different contributors. Cascadia field effort on gray whales was conducted by a number of volunteers and staff at Cascadia.

Appendix Table 1. Sighting histories of gray whales identified in 2007.

ID	count	1^{st} 2007	Last 2007	CA	NCA	SOR	NOR	GH+	NWA	SJF	PS	NPS	SVI	WVI	NBC	SEAK	1sr Yr
6	1	14-Sep-07	14-Sep-07			1											1986
21	3	31-Mar-07	21-Apr-07									3					1990
30	3	8-Jun-07	1-Sep-07					2					1				1983
32	2	24-Mar-07	24-Mar-07										1	1			1985
42	2	23-Jun-07	1-Sep-07					1					1				1984
44	5	6-Apr-07	4-May-07									5					1991
49	5	24-Mar-07	27-Apr-07									5					1991
56	2	24-Mar-07	31-Mar-07									2					1991
81	2	16-Jun-07	16-Jun-07											2			1993
84	7	21-May-07	11-Jul-07						2				5				1990
86	15	13-Aug-07	21-Sep-07										1	14			1977
87	1	14-Sep-07	14-Sep-07			1											1993
89	8	17-Jul-07	14-Sep-07			3	5										1993
91	2	11-Jul-07	14-Jul-07			1	1										1993
92	10	8-Jun-07	26-Sep-07					1	4	2			3				1993
94	5	8-Jul-07	5-Aug-07				1						3	1			1993
101	1	8-Jun-07	8-Jun-07					1									1984
105	3	22-Jun-07	4-Aug-07							2			1				1994
107	3	7-Aug-07	1-Sep-07				2	1									1994
123	1	1-Sep-07	1-Sep-07					1									1998
127	4	14-Jul-07	14-Sep-07			2	2										1986
130	2	14-Jul-07	18-Jul-07										2				1998
135	2	8-Jun-07	7-Dec-07					1		1							1998
138	12	18-Jun-07	21-Sep-07										1	6	5		1998
141	6	24-Mar-07	1-Sep-07					1	1				1	1		2	1990
143	18	24-Mar-07	21-Sep-07										1	17			1998
144	3	31-Mar-07	27-Jul-07										1	2			1998
154	1	8-Jun-07	8-Jun-07					1									1998
169	2	29-Jul-07	1-Sep-07					1					1				1995
175	10	15-Jul-07	8-Sep-07*				4		1	1			4				1995
178	12	19-Jun-07	7-Dec-07						2	7			1	2			1995
185	1	1-Sep-07	1-Sep-07					1									1996
186	3	8-Jun-07	27-Jul-07				2	1									1994

ID	count	1st 2007	Last 2007	CA	NCA	SOR	NOR	GH+	NWA	SJF	PS	NPS	SVI	WVI	NBC	SEAK	1sr Yr
192	2	8-Jun-07	1-Sep-07					2									1996
196	6	7-Jul-07	12-Sep-07						4				2				1996
204	4	17-Jul-07	5-Aug-07				4										1996
206	2	14-Sep-07	11-Oct-07			1	1										1996
215	3	26-Jul-07	14-Sep-07			1	2										1996
219	4	31-Mar-07	13-Oct-07				1	1					1	1			1997
227	2	10-Jul-07	11-Jul-07										2				1998
231	1	14-Sep-07	14-Sep-07			1											1998
242	2	15-Aug-07	30-Aug-07							2							1998
244	10	18-Jul-07	26-Sep-07						2	7				1			1998
254	3	24-Mar-07	14-Sep-07			1	1							1			1998
265	1	24-Mar-07	24-Mar-07										1				1998
280	2	8-Jun-07	26-Jun-07					2									1998
281	1	14-Sep-07	14-Sep-07			1											1991
289	1	1-Sep-07	1-Sep-07					1									1991
295	2	11-Jul-07	14-Jul-07			1	1										1991
296	3	14-Aug-07	25-Aug-07						2				1				1998
300	4	26-Jul-07	5-Aug-07				4										1998
302	6	8-Jun-07	1-Sep-07				1	3					1		1		1998
303	1	5-Aug-07	5-Aug-07				1										1998
308	6	11-Jul-07	12-Oct-07				5						1				1998
309	1	19-Jul-07	19-Jul-07										1				1998
311	1	1-Sep-07	1-Sep-07					1									1998
317	5	31-Mar-07	14-Sep-07			1	2							2			1998
328	1	24-Mar-07	24-Mar-07											1			1998
364	6	19-Aug-07	17-Oct-07				6										1999
372	1	1-Sep-07	1-Sep-07					1									1999
383	6	31-Mar-07	28-Apr-07									6					1999
392	3	19-Sep-07	13-Oct-07				3										1999
411	2	11-Oct-07	13-Oct-07				2										1999
510	1	1-Sep-07	1-Sep-07					1									2000
525	3	1-Sep-07	7-Dec-07					1		2							2000
531	9	24-Mar-07	26-Apr-07									8	1				2000
537	1	14-Jul-07	14-Jul-07			1											2000

ID	count	1st 2007	Last 2007	CA	NCA	SOR	NOR	GH+	NWA	SJF	PS	NPS	SVI	WVI	NBC	SEAK	1sr Yr
554	1	14-Jul-07	14-Jul-07			1											2000
561	1	1-Sep-07	1-Sep-07					1									2000
565	8	12-Aug-07	13-Oct-07				8										2000
581	1	30-Jun-07	30-Jun-07										1				2001
583	11	24-Mar-07	15-Sep-07										9	2			2001
584	2	3-Aug-07	22-Aug-07												2		2001
594	1	24-Mar-07	24-Mar-07											1			1999
611	1	14-Jul-07	14-Jul-07			1											2001
624	2	13-Sep-07	27-Sep-07		2												2001
635	2	11-Oct-07	11-Oct-07				2										2001
639	1	27-Jul-07	27-Jul-07				1										2001
642	1	31-May-07	31-May-07	1													2001
657	3	3-Apr-07	14-Sep-07			1	1	1									2002
668	1	19-Aug-07	19-Aug-07				1										2002
669	1	14-Sep-07	14-Sep-07			1											2002
682	2	3-Jul-07	1-Sep-07					1					1				2002
687	1	1-Sep-07	1-Sep-07					1									2002
688	2	1-Aug-07	8-Aug-07				1								1		2002
694	12	24-Mar-07	1-Sep-07										7	3	2		2000
698	1	1-Sep-07	1-Sep-07					1									2002
701	2	27-Jun-07	8-Jul-07				1		1								2002
703	1	13-Sep-07	13-Sep-07			1											2002
712	1	1-Sep-07	1-Sep-07					1									2002
718	1	1-Sep-07	1-Sep-07					1									2001
719	5	24-Mar-07	31-Mar-07										1	4			2002
720	6	17-Jul-07	1-Sep-07				5	1									2002
723	2	24-Mar-07	31-Mar-07											2			2002
759	2	7-Dec-07	7-Dec-07							2							2002
786	5	29-Jun-07	27-Oct-07				4						1				2003
787	9	23-May-07	14-Sep-07			1	7						1				2003
789	2	24-Mar-07	31-Mar-07										1	1			2003
797	12	27-Jun-07	13-Oct-07				12										2003
803	1	17-Jul-07	17-Jul-07				1										2003
813	1	11-Jul-07	11-Jul-07				1										2004

ID	count	1^{st} 2007	Last 2007	CA	NCA	SOR	NOR	GH+	NWA	SJF	PS	NPS	SVI	WVI	NBC	SEAK	1sr Yr
818	1	24-Mar-07	24-Mar-07										1				2004
819	19	19-Jun-07	1-Nov-07							19							2004
823	5	8-Jul-07	5-Aug-07				4		1								2004
826	6	28-Jul-07	7-Dec-07							6							2004
842	6	24-Mar-07	7-Dec-07							4			2				2004
851	5	14-Aug-07	21-Sep-07						2	3							2005
857	4	24-Mar-07	11-Aug-07										1	3			2005
860	2	29-Jul-07	29-Jul-07											2			2004
866	1	7-Dec-07	7-Dec-07							1							2005
877	5	24-Mar-07	27-Jul-07							2			1	2			2005
878	12	15-Aug-07	21-Dec-07							12							2005
882	11	1-Jul-07	1-Nov-07						1	8			2				2005
932	12	24-Mar-07	1-Nov-07							10				2			2006

*Date CRC-175 killed in hunt

FINAL REPORT

GRAY WHALE PHOTOGRAPHIC IDENTIFICATION IN 1998

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Research in 1998 was funded in part by the National Marine Mammal Laboratory, and we thank Merrill Gosho and Pat Gearin for orchestrating this support. We thank the skippers and staff of the whale watch boats in Westport, the *Victoria Express,* the *Deluxe,* and the *Lucky Piere*, which allowed us to collect data and obtain identification photographs from their boats. The Olympic Coast National Marine Sanctuary provided support for some humpback surveys, which yielded opportunities to survey for gray whales. Some support came from Cascadia's adoption program and we thank those participating in this program.

EXECTUTIVE SUMMARY

In 1998, Cascadia Research and the National Marine Mammal Laboratory conducted photographic identification surveys for gray whale found in the waters of Washington State and along the southern coastline of Vancouver Island. A larger regional effort was also conducted from California to Southeastern Alaska involving a number of other collaborators including researchers with Humpboldt State University, West Coast Whale Research Foundation, University of Victoria, University of British Columbia, Vancouver Aquarium, Department of Fisheries and Oceans, Coastal Ecosystem Research Foundation, and the operator of a coastal ferry service. This research updates previous research efforts, which have revealed that a large number of gray whales seen off Washington State and British Columbia exhibit localized site fidelity. The information provided by this research contributes to an ongoing study of abundance, movements, residence times, and return rate of gray whales that feed in the Washington State waters for extended periods. This report summarizes activities and preliminary results of gray whale research conducted in Washington State and southern Vancouver Island in 1998 by Cascadia and NMML. Results of the larger effort from California to Alaska will be summarized in a future report.

Between 2 March and 17 November 1998, Cascadia personnel conducted a total of 53 gray whale surveys in the waters of Washington State and off the southern coastline of Vancouver BC. The National Marine Mammal Laboratory (NMML) provided identification photographs from # surveys, conducted between 6 June and 18 November 1998. On 249 occasions, 74 different gray whales where successfully identified by Cascadia Research and NMML in 1998.

Fewer whales were present on the northern Washington and western Strait of Juan de Fuca than previous years and most of the identifications in this region were made late in the season (after 1 September). Of the 57 seen on the northern Washington coast and on the north and south side of the Strait of Juan de Fuca, 32 (56%) had been identified in past years, a lower proportion than previous years. Individual whales moved between S. Vancouver Island and the Strait of Juan de Fuca and Washington outer coast. At least six different whales were present (from 27 identifications) in northern Puget Sound; four of these were animals that have been seen regularly each spring in this area since the early 1990s. None of the four gray whales identified in southern Puget Sound had been seen previously, consistent with past findings that this area is not used by regular returning animals.

INTRODUCTION

In 1998, Cascadia Research and the National Marine Mammal Laboratory continued photographic identification surveys for gray whales, in Washington State and along the southern coast of Vancouver Island, BC. These surveys are part of an ongoing research effort to study the abundance, movements, residence times and return rates of gray whales that feed in Washington State waters in spring, summer, and fall (so-called "seasonal residents". Summer feeding aggregations of gray whales have been observed in a number areas along the coasts of California (Patten and Samaras 1977, Malonee 1991, Avery and Hawkinson 1992), Oregon (Sumich 1984), Washington (Flaherty 1983, Calambokidis *et al*. 1992, 1994, Wietkamp *et al*. 1992) and British Columbia (Darling 1984, Murison *et al.* 1984, Plews *et al.* 1985). Gray whales in these regions feed on a variety of prey including herring eggs/larvae, crab larvae, amphipods, mysids, and ghost shrimp, with locations of feeding often shifting from year and by season in response to shifting prey types (Darling *et al*. 1998, Nerini 1984).

Previous research has revealed that a significant number of the gray whales observed in Washington State exhibit localized site fidelity (Calambokidis *et al*. 1994, Calambokidis 1996, Calambokidis and Quan 1997, Calambokidis and Schlender 1998). The issue of "seasonal resident" whales has also gained significance due to the resumption of whaling for gray whales by the Makah. Currently abundance estimates, genetic make-up and recruitment mechanisms that may maintain this aggregation are unknown.

In addition to the field work reported here for 1998 a larger regional effort was also conducted from California to Southeastern Alaska involving a number of other collaborators including researchers with Humboldt State University, West Coast Whale Research Foundation, University of Victoria, University of British Columbia, Vancouver Aquarium, Department of Fisheries and Oceans, Coastal Ecosystem Research Foundation, and the operator of a coastal ferry service. Results of the larger effort from California to Alaska will be summarized in a future report.

This report summarizes activities and preliminary results of gray whale photo-ID research conducted by Cascadia Research and the National Marine Mammal Laboratory in Washington State and southern Vancouver Island in 1998.

METHODS

Between 2 March and 17 November 1998, Cascadia personnel conducted a total of 53 gray whale surveys in the waters of Washington State and off the southern coastline of Vancouver B.C. (Table 1) Surveys were conducted by: 1) placing observers on whale watch boats, the *Victoria Express*, the *Deluxe* and the *Lucky Piere* out of Westport, WA (between 21 March through 30 June 1998), 2) small boat surveys conducted in Puget Sound, the western and eastern portions of the Straight of Juan de Fuca, Washington outer coast and southern Vancouver Island, and 3) placing biologist aboard the National Marine Sanctuary vessel, the *Tatoosh*, in conjunction with humpback whale surveys being conducted in the Olympic Coast National Marine Sanctuary.

Biologist from the National Marine Mammal Laboratory (NMML) provided identification photographs from surveys they conducted between 6 June and 18 November 1998. The photographs from NMML represent surveys from the Washington outer coast, the western Straight of Juan de Fuca and southern Vancouver Island, BC.

Procedures during Cascadia vessel surveys were similar to those used previously (Calambokidis *et al.* 1994). Effort data was recorded every 30 min and when there was either a course change or a change in the environmental conditions. We recorded time position (latitude and longitude from GPS), and environmental conditions (sea state, visibility, precipitation, cloud cover, and swell height). When a gray whale was found, the time, position, number of animals, and behaviors were recorded. Whales were approached to 30-50 m and followed through several dive sequences until suitable identification photographs could be obtained. At the end of a sighting the time, location, and roll and frame numbers of photographs taken during each observation were also noted.

For photographic identification of gray whales, both left and right sides of the dorsal region around the dorsal hump were photographed. *Ilford* HP-5 negative film was shot using *Nikon* 35mm cameras with 300mm f4.5 lenses. We also photographed the ventral surface of the flukes for identification when possible. The latter method was not as reliable as the sides of the whale because they did not always raise their flukes out of the water. Markings used to distinguish whales included pigmentation of the skin, mottling, scarring, and barnacles, which varied among individuals. These markings have provided a reliable means of identifying gray whales over periods of close to 20 years.

We also utilized the relative spacing between the knuckles along the ridge of the back behind the dorsal hump. The size and spacing of these bumps varies among whales and does not change over the years we have tracked whales. Measurements were made using a scaled loop and compared to a database of values for all the whales in our catalog. A computer program (developed by Joe Evenson) provided a prioritized list of potential matches and then the match was verified or rejected based on the markings described above.

Comparison of whales to determine any matches were made in a series of steps. First, the negatives of gray whales were examined and the best shot of the right and left side of the whales (for each sighting) selected and printed (7 x 2.5 inch). To determine the number of whales seen during the season, the prints were then compared to one another to identify whales seen multiple days. Finally a comparison was made to our catalog of whales seen in past years. Whale photographs that were deemed of suitable quality but did not match our existing catalog (compared by two independent matchers) were assigned a new identification number and added to the catalog.

RESULTS AND DISCUSSION

On 249 occasions, 74 different gray whales where successfully identified by Cascadia Research and NMML in 1998 (Tables 2-3). Each whale was seen from 1 to 14 times with a mean of 3.4 (SD= 3.1). The most identifications and individuals seen was off southern Vancouver Island; there were 75 identifications of 32 animals (Table 3). The northern Washington coast and the western Strait of Juan de Fuca had the next highest number of individuals seen (21 and 14). There were a large number of identifications made in Grays Harbor (59) but these were of only seven individuals. The high number of resightings in this area is partly the result of the more intense effort from whale watching boats over a less than 2 month period in Grays Harbor.

Identifications off southern Vancouver Island were made between 1 July and 11 November, although the highest number were seen in July, when 23 different individuals were identified (Table 4). This compares to only 12 individuals identified in July on the Washington outer coast and on the Washington side of the Strait of Juan de Fuca, an area that was being more intensely surveyed. Large numbers of whales remained off southern Vancouver Island through September, although in lower numbers than July. Numbers of whales identified in Washington waters off the outer coast and in the western strait, dropped to 6 in August and then came back up to 10 individuals in both August and September (Table 4). There was an increased number of whales identified on the Washington side of the Strait of Juan de Fuca, including the eastern portion, in October and November with nine and seven individuals seen each month, respectively.

Identifications in northern Puget Sound were all made from March through May, coinciding with the period that we have seen animals in this region in past years (Table 4). Four of the six animals identified in this region were animals that have been seen regularly in this area going back to 1990 (Table 5). Our sightings of these animals in early March (two on the 12th and one on the 14th) are the earliest in the season we have positively identified these animals in any year, although sighting reports in this region typically begin in early March. We made no identifications after 20 May and sighting reports from this region also dropped off in May. As in past years none of these regular animals were seen in this or any other region later in the season.

Identification of gray whales in southern Puget Sound were made on six occasions and represented four individuals. One animals was identified several times in March and then not seen again and three other animals were identified from mid-October to mid-November. As in past years, none of these whales were individuals that had been identified in past year in any region (Table 5).

Individual gray whales were documented moving among three regions; the Strait of Juan de Fuca (both the eastern and western portion), the Washington outer coast, and the southern portion of Vancouver Island (Table 6). Most common were whales seen on both the Washington outer coast and southern Vancouver Island (eight whales). Three of these whales were documented making multiple trips between these regions.

The proportion of whales identified off northern Washington) that had been identified in previous years was lower in 1998 (63%) than had been seen in some previous years (Table 5). It appears that in addition to there being fewer whales present most of the season, more of the whales were animals that had not been common in this region in the past. The lower number of whales seen off the northern Washington coast and high numbers seen off southern Vancouver Island was likely related to prey; gray whales are know to shift areas they feed in response to shifts in prey types and densities (Darling *et al*. 1998). If prey was not as plentiful on the northern Washington coast this may have discouraged the animals that typically use this area from being there and make animals encountered in this area more likely to be whales moving between areas.

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Table 1. Photo-ID survey effort by Cascadia Research in Oregon and Washington waters in 1
Does not include photo-ID effort aboard whale watching boats.

Date	**Vessel**	**Time**		**Latitude**		**Gray whale**	
		Begin	**End**	**South**	**North**	**Sit**	**Num**
03/12/98	*Thom.* Launch	14:27:00	17:45:00	47 53.0	48 05.0	1	2
03/14/98	*Tully* Launch	10:29:00	14:20:00	48 07.9	48 13.1	1	1
03/18/98	N1	15:00:00	18:45:00	47 03.5	47 11.2	1	1
03/21/98	*Victoria Express*	11:06:00	13:30:00	Grays Harbor		3	6
03/21/98	*Tully* Launch	6:49:00	16:30:00	47 38.7	48 13.2	1	1
03/22/98	*Victoria Express*	14:05:00	16:53:00	Grays Harbor		5	10
03/22/98	*Tully* Launch	10:25:00	16:05:00	47 53.4	48 31.9	2	3
03/26/98	N1	16:00:00	17:42:00	47 03.4	47 05.3	1	1
03/27/98	N1	8:40:00	18:23:00	47 49.3	48 10.2	3	5
03/28/98	*Victoria Express*	11:02:00	16:45:00	Grays Harbor		11	21
03/29/98	*Victoria Express*	11:06:00	16:57:00	Grays Harbor		9	22
04/02/98	*Victoria Express*	11:03:00	13:33:00	Grays Harbor		4	6
04/04/98	*Victoria Express*	11:00:00	17:00:00	Grays Harbor		12	15
04/05/98	*Victoria Express*	14:10:00	17:01:00	Grays Harbor		4	4
04/07/98	HH	10:15:00	16:48:00	47 37.0	48 08.3		
04/09/98	*Victoria Express*	11:16:00	14:00:00	Grays Harbor		7	11
04/10/98	*Victoria Express*	11:00:00	13:30:00	Grays Harbor		2	3
04/11/98	*Victoria Express*	11:00:00	16:50:00	Grays Harbor		7	9
04/12/98	*Victoria Express*	14:01:00	16:50:00	Grays Harbor		6	11
04/12/98	HH	11:20:00	19:00:00	48 06.0	48 20.2		
04/15/98	HH	10:57:00	18:12:00	47 48.7	48 05.9	2	4
04/16/98	N1	11:10:00	19:45:00	47 51.4	48 25.4	3	7
04/16/98	Victoria Express	10:49:00	13:30:00	Grays Harbor		8	14
04/17/98	Victoria Express	11:00:00	13:35:00	Grays Harbor		3	3
04/18/98	Victoria Express	10:57:00	16:59:00	Grays Harbor		13	21
04/19/98	Victoria Express	10:58:00	17:00:00	Grays Harbor		9	14
04/19/98	N1	9:17:00	17:08:00	47 53.4	48 25.3	1	2
04/23/98	HH	8:47:00	12:20:00	47 53.7	48 00.0	1	1
04/24/98	*Victoria Express*	11:00:00	13:20:00	Grays Harbor		2	2
04/25/98	*Victoria Express*	11:04:00	16:55:00	Grays Harbor		3	5
04/26/98	*Victoria Express*	11:00:00	17:00:00	Grays Harbor		7	9
05/01/98	*Victoria Express*	11:04:00	13:30:00	Grays Harbor		4	7
05/02/98	*Victoria Express*	14:00:00	16:45:00	Grays Harbor		4	5
05/03/98	*Victoria Express*	11:00:00	13:30:00	Grays Harbor		2	2
05/08/98	HH	10:03:00	16:20:00	47 50.0	48 07.0		
05/11/98	*Dulexe*	11:40:00	13:30:00	Grays Harbor		2	2
05/20/98	HH	13:00:00	14:59:00	47 56.3	47 57.1	1	1
06/30/98	*Lucky Piere*			Grays Harbor			
07/14/98	DIS	6:57:00	15:38:00	48 19.6	48 26.9	1	3
07/21/98	Tatoosh	8:56:00	20:02:00	Olympic Marine Sanctuary			
07/22/98	Tatoosh	8:22:00	18:13:00	Olympic Marine Sanctuary			
08/25/98	N2	6:30:00	18:30:00	44 27.1	44 56.8	24	35
08/26/98	N2	7:40:00	19:20:00	46 54.3	48 23.4		
08/27/98	N2	7:05:00	20:48:00	48 14.2	48 42.2	8	14
09/29/98	N1	9:35:00	19:30:00	48 16.5	48 51.8	3	3
10/6/98	N1	8:00:00	19:08:00	41 41.7	41 55.0	2	7
10/10/98	N1	9:20:00	19:00:00	41 43.2	41 57.7	12	12
10/15/98	N1	14:30:00	16:19:00	47 06.1	47 08.0	1	1
10/21/98	HH	13:23:00	18:00:00	48 07.1	48 08.7	2	3
10/28/98	HH	12:25:00	16:00:00	48 07.0	48 07.5	1	1
11/11/98	HH	11:25:00	15:07:00	48 07.0	48 17.7	2	3
11/12/98	N1	16:00:00	16:50:00	47 06.1	47 08.3	1	1
11/17/98	DEB	14:16:00	15:42:00	47 01.1	47 01.5	2	2
Total		53 days				204	316

Table 2. Sightings of gray whales identified by Cascadia or NMML in Washington and S. Vancouver Island in 1998.

ID	Temp#	Collection	Date	Sight#	Region	Location comments
14		CRC	21-Mar-98	VE-6	GH	Inside
14		CRC	28-Mar-98	VE-9	GH	Inside
14		CRC	29-Mar-98	VE-9	GH	Inside
14		CRC	29-Mar-98	VE-1A	GH+	Entrance
14		CRC	10-Apr-98	VE-1	GH	Inside
14		CRC	12-Apr-98	VE-6	GH	Inside
14		CRC	12-Apr-98	VE-16	GH	Inside
14		CRC	16-Apr-98	VE-05	GH+	Entrance
14		CRC	18-Apr-98	VE-13	GH	Inside
14		CRC	18-Apr-98	VE-8	GH	Inside
15		NMML	01-Jul-98		SVI	Tsusiat Falls
15		NMML	16-Jul-98		NWA	Greenbank
15		CRC	27-Aug-98	N2-26	SVI	
21		CRC	22-Mar-98	T1-2	NPS	
21		CRC	27-Mar-98	N-8	NPS	
21		CRC	15-Apr-98	DS-6	NPS	
21		CRC	16-Apr-98	N-1	NPS	
21		CRC	16-Apr-98	N-10	NPS	
21		CRC	19-Apr-98	N-2	NPS	
22		CRC	14-Mar-98	T1-1	NPS	
22		CRC	22-Mar-98	T1-2	NPS	
22		CRC	27-Mar-98	N-8	NPS	
22		CRC	15-Apr-98	DS-6	NPS	
22		CRC	16-Apr-98	N-1	NPS	
22		CRC	16-Apr-98	N-10	NPS	
22		CRC	19-Apr-98	N-2	NPS	
30		NMML	25-Sep-98		WSJF	Jensen Creek
37		NMML	15-Sep-98		NWA	Fuca Pillar-Skagway
41		NMML	01-Jul-98		SVI	Tsusiat Falls
41		NMML	01-Sep-98		SVI	E. Pachena
41		CRC	21-Oct-98	W-1	ESJF	Green Pt.
41		CRC	11-Nov-98	W-3	ESJF	Green Pt.
42		NMML	14-Oct-98		WSJF	Sail Rock
42		NMML	15-Oct-98		WSJF	Seal/Sail Rock
43		NMML	24-Jul-98		NWA	Bodelteh
49		CRC	12-Mar-98	TL-1	NPS	
49		CRC	27-Mar-98	N-8	NPS	
49		CRC	15-Apr-98	DS-6	NPS	
49		CRC	16-Apr-98	N-1	NPS	
49		CRC	16-Apr-98	N-10	NPS	
56		CRC	12-Mar-98	TL-1	NPS	
62		CRC	04-Apr-98	VE-6	GH+	Outside
62		CRC	12-Apr-98	VE-16	GH	Inside
62		CRC	12-Apr-98	VE-2	GH	Inside
62		CRC	12-Apr-98	VE-1	GH	Inside
62		CRC	16-Apr-98	VE-7	GH+	Entrance
62		CRC	17-Apr-98	VE-5	GH+	Entrance
79		CRC	14-Jul-98	D-2	NWA	Makaw Bay
79		NMML	26-Aug-98		SVI	W. Tsusiat
79		CRC	27-Aug-98	N2-19	SVI	
80		NMML	01-Jul-98		SVI	Tsusiat Falls
80		CRC	14-Jul-98	D-2	NWA	Makaw Bay
80		NMML	25-Aug-98		SVI	.5 mi. W. Carmanah
80		CRC	27-Aug-98	N2-24	SVI	
80		CRC	27-Aug-98	N2-25	SVI	
80		NMML	28-Aug-98		SVI	Bonilla Pt.
80		NMML	04-Sep-98		SVI	W. of Carmanah
80		NMML	22-Sep-98		SVI	E. of Bonilla
81		NMML	15-Sep-98		NWA	Fuca Pillar-Skagway
83	T69	NMML	16-Aug-98		NWA	Guano Rock
84		NMML	01-Jul-98		SVI	Tsusiat Falls
84		NMML	01-Jul-98		SVI	Tsusiat Falls

Table 3. Summary of gray whales identified by Cascadia and NMML in Washington State and S. Vancouver Island in 1998.

	Times	Times seen by region							Seen by group		Dates seen	
ID	seen	SPS	NPS	GH	ESJF	WSJF	NWA	SVI	CRC	NMML	First	Last
14	10			10					10		21-Mar	18-Apr
15	3						1	2	1	2	1-Jul	27-Aug
21	6		6						6		22-Mar	19-Apr
22	7		7						7		14-Mar	19-Apr
30	1					1				1	25-Sep	25-Sep
37	1						1			1	15-Sep	15-Sep
41	4				2			2	2	2	1-Jul	11-Nov
42	2					2				2	14-Oct	15-Oct
43	1						1			1	24-Jul	24-Jul
49	5		5						5		12-Mar	16-Apr
56	1		1						1		12-Mar	12-Mar
62	6			6					6		4-Apr	17-Apr
79	3						1	2	2	1	14-Jul	27-Aug
80	8						1	7	3	5	1-Jul	22-Sep
81	1						1			1	15-Sep	15-Sep
83	1						1			1	16-Aug	16-Aug
84	2							2		2	1-Jul	1-Jul
85	3						2	1		3	1-Jul	30-Jul
91	2					1	1			2	9-Jul	31-Aug
92	4						1	3		4	1-Jul	22-Sep
93	2						1	1		2	21-Jul	24-Aug
101	4					1		3		4	1-Jul	25-Sep
107	1						1			1	6-Jun	6-Jun
123	1							1		1	3-Jul	3-Jul
130	1							1		1	3-Jul	3-Jul
135	1							1		1	1-Jul	1-Jul
138	1							1		1	22-Sep	22-Sep
140	1					1				1	17-Aug	17-Aug
141	1							1		1	1-Jul	1-Jul
150	2							2		2	1-Jul	22-Sep
166	3						3		1	2	14-Jul	1-Sep
175	3						3			3	22-Jul	16-Oct
186	2							2		2	1-Jul	1-Jul
187	11					1	10			11	24-Jul	18-Nov
190	2			2					2		5-Apr	19-Apr
192	10						7	3	1	9	1-Jul	21-Oct
209	1						1			1	22-Jul	22-Jul
212	7							7	2	5	1-Jul	29-Sep
219	7							7	2	5	1-Jul	29-Sep
227	2							2		2	1-Jul	3-Jul
228	2					2				2	1-Nov	4-Nov
231	8							8	2	6	1-Jul	29-Sep
232	3							3	1	2	17-Jul	27-Aug
233	2							2		2	1-Jul	3-Jul
234	1							1		1	1-Jul	1-Jul
236	3							3	1	2	25-Aug	28-Aug
237	1							1	1		27-Aug	27-Aug
239	4					4				4	14-Oct	22-Oct
242	7					4	2	1		7	17-Jul	5-Nov
243	1							1		1	17-Jul	17-Jul
244	1							1		1	22-Sep	22-Sep
246	1							1		1	3-Jul	3-Jul
248	1							1		1	1-Jul	1-Jul
249	5				1	4			1	4	14-Oct	21-Oct
250	1					1				1	7-Nov	7-Nov
251	1						1			1	9-Jul	9-Jul
252	1					1				1	5-Nov	5-Nov
253	1					1				1	31-Oct	31-Oct
254	1							1		1	1-Sep	1-Sep
255	7					7				7	14-Oct	28-Oct
258	1	1							1		15-Oct	15-Oct
259	2	2							2		12-Nov	17-Nov
260	1	1							1		17-Nov	17-Nov
262	2	2							2		18-Mar	26-Mar
264	7		7						7		21-Mar	20-May
267	2				2				2		21-Oct	11-Nov
268	2				2				2		28-Oct	11-Nov
269	10			10					10		22-Mar	19-Apr
270	11			11					11		22-Mar	18-Apr
271	14			14					14		4-Apr	11-May
272	1						1			1	31-Aug	31-Aug
273	6			6					6		21-Mar	26-Apr
304	3						3			3	15-Sep	21-Oct
305	1		1						1		27-Mar	27-Mar
Total times	249	6	27	59	7	31	44	75	116	133		
Total IDs	74	4	6	7	4	14	21	32	32	54		

Table 4. Summary of dates and regions individual gray whales were identified by CRC and NMML in Washington and S. Vancouver Island in 1998.

	March									April															
ID	12	14	18	21	22	26	27	28	29	2	4	5	9	10	11	12	15	16	17	18	19	23	24	25	26
14				GH				GH	GH					GH		GH		GH		GH					
15																									
21					NPS		NPS										NPS	NPS			NPS				
22		NPS			NPS		NPS										NPS	NPS			NPS				
30																									
37																									
41																									
42																									
43																									
49	NPS						NPS										NPS	NPS							
56	NPS																								
62											GH					GH		GH	GH						
79																									
80																									
81																									
83																									
84																									
85																									
91																									
92																									
93																									
101																									
107																									
123																									
130																									
135																									
138																									
140																									
141																									
150																									
166																									
175																									
186																									
187																									
190												GH									GH				
192																									
209																									
212																									
219																									
227																									
228																									
231																									
232																									
233																									
234																									
236																									
237																									
239																									
242																									
243																									
244																									
246																									
248																									
249																									
250																									
251																									
252																									
253																									
254																									
255																									
258																									
259																									
260																									
262			SPS			SPS																			
264				NPS	NPS		NPS										NPS	NPS				NPS			
267																									
268																									
269					GH			GH		GH	GH							GH		GH	GH				
270					GH					GH	GH	GH	GH	GH	GH	GH				GH					
271											GH								GH	GH	GH		GH	GH	GH
272																									
273				GH											GH				GH		GH			GH	GH
304																									
305							NPS																		

	May				June	July											August								
ID	1	3	11	20	6	1	3	9	14	16	17	21	22	24	29	30	6	16	17	24	25	26	27	28	31
14																									
15						SVI				OC													SVI		
21																									
22																									
30																									
37																									
41						SVI																			
42																									
43														OC											
49																									
56																									
62																									
79									OC													SVI	SVI		
80						SVI			OC												SVI		SVI	SVI	
81																									
83																		OC							
84						SVI																			
85						SVI									OC	OC									
91								OC																	WSF
92						SVI	SVI									OC									
93												SVI								OC					
101						SVI	SVI														SVI				
107					OC																				
123							SVI																		
130							SVI																		
135						SVI																			
138																									
140																			WSF						
141						SVI																			
150						SVI																			
166									OC							OC									
175													OC												
186						SVI																			
187														OC		OC	OC	OC							WSF
190																									
192						SVI															SVI		SVI		
209													OC												
212						SVI															SVI		SVI	SVI	
219						SVI	SVI					SVI									SVI		SVI		
227						SVI	SVI																		
228																									
231						SVI	SVI					SVI									SVI		SVI		
232											SVI										SVI		SVI		
233						SVI	SVI																		
234						SVI																			
236																					SVI		SVI	SVI	
237																							SVI		
239																									
242											SVI														
243											SVI														
244																									
246							SVI																		
248						SVI																			
249																									
250																									
251								OC																	
252																									
253																									
254																									
255																									
258																									
259																									
260																									
262																									
264				NPS																					
267																									
268																									
269																									
270																									
271	GH	GH	GH																						
272																									OC
273																									
304																									
305																									

	September											October									November								Day
ID	1	4	5	6	15	16	19	21	22	25	29	14	15	16	17	18	21	22	28	31	1	4	5	7	11	12	17	18	see
14																													7
15																													3
21																													5
22																													6
30										WSF																			1
37					OC																								1
41	SVI																ESF								ESF				4
42												WSF	WSF																2
43																													1
49																													4
56																													1
62																													4
79																													3
80		SVI							SVI																				7
81					OC																								1
83																													1
84																													1
85																													3
91																													2
92									SVI																				4
93																													2
101										WSF																			4
107																													1
123																													1
130																													1
135																													1
138									SVI																				1
140																													1
141																													1
150									SVI																				2
166	OC																												3
175			OC											OC															3
186																													1
187			OC	OC			OC							OC			OC											OC	11
190																													2
192			OC	OC	OC	OC											OC												8
209																													1
212		SVI							SVI		SVI																		7
219		SVI									SVI																		7
227																													2
228																					WSF	WSF							2
231		SVI							SVI		SVI																		8
232																													3
233																													2
234																													1
236																													3
237																													1
239												WSF	WSF					WSF											3
242								OC								WSF	WSF			WSF			WSF						6
243																													1
244									SVI																				1
246																													1
248																													1
249												WSF	WSF			WSF	ESF												4
250																								WSF					1
251																													1
252																							WSF						1
253																				WSF									1
254	SVI																												1
255												WSF	WSF		WSF	WSF	WSF	WSF	WSF										7
258													SPS																1
259																										SPS	SPS		2
260																											SPS		1
262																													2
264																													7
267																	ESF								ESF				2
268																			ESF						ESF				2
269																													7
270																													9
271																													10
272																													1
273																													6
304					OC		OC										OC												3
305																													1

Table 5. Number of whales identified by region and prportion seen in previous years

			Seen prev. years	
Region	**Identifications**	**Unique IDs**	**#**	**%**
N Wa. (Straits and outer coast)	82	35	22	63%
N. Wa. incl BC side of straits	157	57	32	56%
Grays Harbor	59	7	3	43%
N. Puget Sound	27	6	4	67%
S. Puget Sound	6	4	0	0%

Table 6. Number of whales identified by NMML/CRC in study area in 1998 and within-season inter-regional movements.

		Region						
Region	**IDs**	**SPS**	**NPS**	**GH**	**ESJF**	**WSJF**	**NWA**	**SVI**
S Puget Sound	4							
N Puget Sound	6	0						
Grays Harbor	7	0	0					
E Strait of Juan de Fuca	4	0	0	0				
W Strait of Juan de Fuca	14	0	0	0	1			
N Washington outer coast	21	0	0	0	0	3		
S Vancouver Is.	32	0	0	0	1	2	8	

ID	Other-ID	Collec	Date	Year	Sight#	Region	Location
15	Estevan		3-Aug-84	1984	-	SVI	59 48 46.0 125 09.5
15	Estevan		21-Aug-84	1984	-	SVI	59 48 46.5 125 09.0
15			10-Aug-89	1989	MB-1	NWA	99 48 17.1 124 42.2
15			23-Aug-90	1990	-	SVI	59 48 22.0 123 51.0
15	JD9612		8-Oct-96	1996	JD-	WVI	59 49 10 125 57
15	JD9612		16-Oct-96	1996	JD-	WVI	59 49 10 125 57
15			9-Aug-97	1997	N2-4	SVI	59 48 42.1 124 59.9
15			6-Sep-97	1997	NML-2	SJF	49 48 18.4 124 25.2
15			20-Sep-97	1997	NML-2	SJF	49 48 19.6 124 27.9
15			28-Sep-97	1997	NML-2	SJF	49 48 22.8 124 35.4
15			29-Sep-97	1997	NML-1	SJF	49 48 22.3 124 34.6
15			29-Sep-97	1997	NML-2B	SJF	49 48 21.7 124 32.9
15			29-Sep-97	1997	NML-3	SJF	49 48 21.9 124 32.8
15			29-Sep-97	1997	NML-4	SJF	49 48 21.7 124 33.2
15			30-Sep-97	1997	NML-1	SJF	49 48 19.7 124 28.2
30			2-Sep-83	1983	-	SVI	59 49 00.5 123 00.2
30	102		23-Sep-90	1990	-	SVI	59 48 21.0 123 47.0
30			24-Jun-92	1992	-	CS	59 49 20.8 126 15.7
30	JD926		21-Jul-92	1992	JD-	WVI	59 49 23 126 30
30	JD926		18-Sep-92	1992	JD-	WVI	59 49 23 126 30
30	G010			1994	-	NBC	59 51 10 127 48
30	JD926G10	CERF	24-Aug-91	1995		NBC	500m S of Cape Caution, 800m offshore 51 8.6 127 48.1
30	JD926G10	CERF	27-Aug-91	1995		NBC	700m N of Wentworth Rk. 50 57.7 127 31.2
30	JD926		19-Sep-95	1995	JD-	WVI	59 49 23 126 30
30	JD926G10	CERF	1-Sep-92	1996		NBC	off Grinch Bay 51 8.3 127 43.8
37			1-Jul-88	1988	-	SVI	59 48 42.0 125 00.0
37	JD9210		21-Jul-92	1992	JD-	WVI	59 49 23 126 30
37			18-Sep-92	1992	-	CS	59 49 10.6 126 01.5
37	JD9210		18-Sep-92	1992	JD-	WVI	59 49 10 125 54
37			25-Oct-92	1992	-	CS	59 49 10.4 126 01.5
37	JD9210		25-Oct-92	1992	JD-	WVI	59 49 10 125 54
37			27-Jul-96	1996	NMM-1	SVI	59 48 21.8 124 26.0
41			23-Aug-90	1990	-	SVI	59 48 22.0 123 51.0
41			9-Sep-91	1991	-	SVI	59 48 25.5 123 16.0
41			27-Jun-92	1992	-	CS	59 49 10.6 126 11.0
41	JD924		27-Jun-92	1992	JD-	WVI	59 49 19 126 14
41			27-Jul-96	1996	NMM-1	SVI	59 48 21.8 124 26.0
41			16-Aug-96	1996	WDW-	SJF	49 48 07.3 123 16.7
42	792		10-Aug-84	1984	-	SVI	59 48 46.0 125 09.0
42	792		16-Aug-84	1984	-	SVI	59 48 46.0 125 10.0
42	792		21-Aug-84	1984	-	SVI	59 48 43.0 125 05.0
42	F		1-Jul-88	1988	-	SVI	59 48 43.0 125 02.0
42			23-Aug-90	1990	-	SVI	59 48 22.0 123 51.0
42			5-Jul-93	1993	-	SJF	49 48 22 124 31
42			14-Jul-93	1993	N18-1	SJF	49 48 23.6 124 39.1
42			15-Jul-93	1993	N18-1	SJF	49 48 23.3 124 38.0
42			15-Jul-93	1993	N18-26	SJF	49 48 23.2 124 38.0
42			1-Aug-93	1993	N18-14	SJF	49 48 23.2 124 37.9
42	JD9417		13-Jul-94	1994	JD-	WVI	59 49 19 126 14
42	JD9417		6-Aug-94	1994	JD-	WVI	59 49 17 126 15
42	JD9417G34	CERF	30-Aug-91	1995		NBC	N of Wilkie Pt. 51 8.3 127 43.6
42			24-Oct-95	1995	NOV-5	SJF	49 48 18.7 124 25.9
42	JD9417		13-Aug-96	1996	JD-	SVI	59 48 42 124 57
42	JD9417		9-Oct-96	1996	JD-	WVI	59 49 10 125 57
43	Friendly		16-Aug-84	1984	-	SVI	59 48 46.5 125 09.0
43	Friendly		21-Aug-84	1984	-	SVI	59 48 43.0 125 04.0
43			24-Aug-90	1990	-	SVI	59 48 39.0 124 48.0
43			28-Aug-92	1992	-	SVI	59 48 46.5 125 11.5
43			21-Jul-93	1993	N18-8	NWA	99 48 10.5 124 45.6
43			1-Aug-93	1993	N18-9	NWA	99 48 09.3 124 44.9
43			9-Jul-94	1994	NOV-6	NWA	99 48 10.4 124 44.5
43			4-Aug-94	1994	-	NWA	99 48 11 124 44
43			22-Jul-95	1995	NOV-11	NWA	99 48 21.1 124 42.4
43			23-Jul-95	1995	NOV-14	NWA	99 48 21.1 124 42.5
43	JD9510		9-Aug-95	1995	JD-	WVI	59
43	JD9510G36	CERF	10-Jul-92	1996		NBC	Middle of Burnett Bay, 40m offshore 51 7.5 127 40.8
43	JD9510G36	CERF	16-Jul-92	1996		NBC	Middle of St. JohnIs Bay 51 8.4 127 42.2
43	JD9510G36	CERF	17-Jul-92	1996		NBC	Middle of Burnett Bay, 50m offshore 51 7.5 127 40.8
43	JD9510G36	CERF	17-Jul-92	1996		NBC	W-end of St. JohnIs Bay off Brentwood Rks. 51 8.3 127 42.4
43	JD9510G36	CERF	20-Jul-92	1996		NBC	N-side of Burnaby Rks. 51 7.9 127 41.5
43	JD9510G36	CERF	20-Jul-92	1996		NBC	1km N of Raynor Pt. 400m offshore 51 9.1 127 45.9
43	JD9510G36	CERF	21-Jul-92	1996		NBC	About 1/2 way across Burnett Bay 51 7.3 127 41.3

ID	Other-ID	Collec	Date	Year	Sight#	Region	Location
43	JD9510G36	CERF	29-Jul-92	1996		NBC	3/4nm N of Neck Ness 51 13.1 127 47.9
43	JD9510G36	CERF	5-Aug-92	1996		NBC	in Bay S of Neck Ness 51 11.6 127 47.3
43	JD9510G36	CERF	15-Aug-92	1996		NBC	N.A.
43	JD9510G36	CERF	20-Aug-92	1996		NBC	just S of Neck Ness 51 11.7 127 47.7
43	JD9510G36	CERF	21-Aug-92	1996		NBC	near 2m Reef in S-Hoop Bay 51 12.4 127 47.6
43	JD9510G36	CERF	27-Aug-92	1996		NBC	off Indian Cove in kelp bed inside RK. #2.5 51 11.6 127 47.2
43	JD9510G36	CERF	28-Aug-92	1996		NBC	N-side of Sylvester Bay near 46 Rk. 51 9.4 127 45.5
43	JD9510G36	CERF	29-Aug-92	1996		NBC	Lougheed Bay 51 8.3 127 42.8
43	JD9510G36	CERF	1-Sep-92	1996		NBC	S-side of Fab 4 51 12.3 127 47.1
43			9-Aug-97	1997	N2-5	SVI	59 48 42.4 125 00.4
43			2-Sep-97	1997	NML-5	NWA	99 48 21.8 124 33.5
79			14-Jul-93	1993	N18-2	SJF	49 48 23.5 124 40.2
79			14-Jul-93	1993	N18-19	SJF	49 48 23.6 124 38.8
79			15-Jul-93	1993	N18-25	SJF	49 48 23.6 124 39.7
79			21-Jul-93	1993	N18-3	NWA	99 48 22.7 124 44.1
79	JDG5	CERF	27-Jul-90	1994		NBC	between Knight I. and the Tinsons (W opening to Tinson Pass) 50 59.7 127 32.1
79	JDG5	CERF	31-Jul-90	1994		NBC	W of Foxtrott Pt. 51 4.7 127 38.7
79	JDG5	CERF	14-Aug-90	1994		NBC	Middle of Burnett Bay, 1/4nm off sandy beach 51 7.3 127 41.2
79	JDG5	CERF	12-Jul-91	1995		NBC	off Nina Pt. 51 2.9 127 35.3
79	JDG5	CERF	20-Jul-91	1995		NBC	Allison Reefs 51 2 127 31.8
79	JDG5	CERF	22-Jul-91	1995		NBC	on Slater Rks. 51 1.7 127 32.7
79	JDG5	CERF	24-Jul-91	1995		NBC	SW-end Elizabeth Rks. 51 1 127 32.9
79	JDG5	CERF	5-Aug-91	1995		NBC	100m E of Elizabeth Rks. 51 .6 127 33
79	JDG5	CERF	23-Aug-91	1995		NBC	off E-rock 51 2.3 127 33.7
79	JDG5	CERF	25-Aug-91	1995		NBC	off E-Rk. 51 2.3 127 33.8
79	JDG5	CERF	26-Aug-91	1995		NBC	N-Bay 51 2.6 127 34
79	JDG5	CERF	27-Aug-91	1995		NBC	on 2 o'clock Rk. 51 1.6 127 33.7
79	JDG5	CERF	28-Aug-91	1995		NBC	off S-side Elizabeth Rks. 51 .7 127 32.8
79	JDG5	CERF	29-Aug-91	1995		NBC	in kelp bed 100m SE of E-Rk. 51 2.2 127 33.3
79	JDG5	CERF	30-Jun-92	1996		NBC	Ketchikan N 51 .6 127 32.2
79	JDG5	CERF	1-Jul-92	1996		NBC	N-side Seahorse 51 2.7 127 34.1
79	JDG5	CERF	2-Jul-92	1996		NBC	N.A.
79	JDG5	CERF	3-Jul-92	1996		NBC	Tip of Bramham Pt. 75m offshore 51 3.4 127 36.3
79	JDG5	CERF	5-Jul-92	1996		NBC	on Slater Rks. 51 1.6 127 33.3
79	JDG5	CERF	6-Jul-92	1996		NBC	Middle of Pass between Tinsons and Knight I. 50 59.8 127 32
79	JDG5	CERF	7-Jul-92	1996		NBC	E of No Justice Reef 51 2.7 127 33.8
79	JDG5	CERF	9-Jul-92	1996		NBC	300m NE of Bremner Pt. 51 6.7 127 40.3
79	JDG5	CERF	10-Jul-92	1996		NBC	Pisspott Reef 51 2.6 127 33.9
79	JDG5	CERF	14-Jul-92	1996		NBC	SW -side Elizabeth Rks. 51 1 127 32.5
79	JDG5	CERF	17-Jul-92	1996		NBC	in Bay between Loblaws Rks. and SobeyIs Rks. 51 4.7 127 37.3
79	JDG5	CERF	18-Jul-92	1996		NBC	W-side of Seahorse on S-side of kelp bed 51 2.7 127 34.3
79	JDG5	CERF	20-Jul-92	1996		NBC	off inside of Bramham Pt. (Miles Inlet) 51 3.5 127 35.9
79	JDG5	CERF	23-Jul-92	1996		NBC	20m off centre ElizaIs S-side 51 1.9 127 33.4
79	JDG5	CERF	27-Jul-92	1996		NBC	just N of Town Rk. 51 2.2 127 31.7
79	JDG5	CERF	28-Jul-92	1996		NBC	off Rks. S of Mayor 51 2.6 127 35.6
79	JDG5	CERF	31-Jul-92	1996		NBC	S-side middle Seahorse 51 2.6 127 34.3
79	JDG5	CERF	1-Aug-92	1996		NBC	S-end of #4 Reef 51 2.4 127 34.2
79	JDG5	CERF	3-Aug-92	1996		NBC	1 WL SW of Albert 51 2.6 127 33.4
79	JDG5	CERF	18-Aug-92	1996		NBC	Entrance to Southgate Pass 51 1 127 31.6
79	JDG5	CERF	31-Aug-92	1996		NBC	off 3 Sisters
80			14-Jul-93	1993	N18-5	NWA	99 48 15.0 124 42.7
80			15-Jul-93	1993	N18-21	NWA	99 48 11.0 124 44.4
80			21-Jul-93	1993	N18-4	NWA	99 48 15.2 124 42.7
80			25-Aug-94	1994	-	NWA	99 48 23 124 44
80			25-Aug-94	1994	-	NWA	99 48 21.5 124 43
80			29-Aug-94	1994	-	NWA	99 48 13.5 124 43
80			23-Jun-95	1995	-	SJF	49 48 23.5 124 40
80	JD967		8-Aug-96	1996	JD-	WVI	59 49 10 125 57
80			16-Aug-96	1996	NMM-2	NWA	99 48 17.6 124 41.5
80			23-Aug-96	1996	NMM-3	NWA	99 48 17.9 124 42.0
80			27-Aug-96	1996	NMM-1	NWA	99 48 18.9 124 42.0
80			27-Aug-96	1996	NMM-2	NWA	99 48 18.9 124 42.0
80			18-Sep-96	1996	NMM-1	NWA	99 48 17.7 124 41.5
80			18-Sep-96	1996	NMM-3	NWA	99 48 17.6 124 41.5
80			26-Sep-96	1996	NMM-1	SJF	49 48 21.1 124 34.8
80			6-Oct-96	1996	N2-8	NWA	99 48 11.2 124 44.1
81			14-Jul-93	1993	N18-7	NWA	99 48 10.8 124 44.4
81			21-Jul-93	1993	N18-5	NWA	99 48 13.0 124 42.0
81			1-Aug-93	1993	N18-10	NWA	99 48 09.4 124 44.6
81			19-Aug-95	1995	NOV-5B	SJF	49 48 21.5 124 31.9
81			19-Aug-95	1995	NOV-16	SJF	49 48 23.5 124 38.2
81			23-Sep-97	1997	NML-1	SJF	49 48 23.4 124 42.4

ID	Other-ID	Collec	Date	Year	Sight#	Region	Location
83			14-Jul-93	1993	N18-8	NWA	99 48 10.3 124 45.2
83			14-Jul-93	1993	N18-14	NWA	99 48 09.3 124 44.8
83			15-Jul-93	1993	N18-18	NWA	99 48 09.3 124 44.8
83			15-Jul-93	1993	N18-19	NWA	99 48 10.2 124 45.3
83	JD944		18-May-94	1994	JD-	WVI	59 49 10 125 57
83	JD944		7-Jun-94	1994	JD-	WVI	59
83	JD944		22-Jun-94	1994	JD-	WVI	59 49 10 125 57
83	JD944		2-Jul-96	1996	JD-	WVI	59 49 10 125 57
83			23-Jul-96	1996	NMM-1	NWA	99 48 26.2 124 42.8
83			12-Jul-97	1997	NML-2	NWA	99 48 10.0 124 45.2
84	Fig 4.left		1-Aug-90	1990	-	SVI	59 48 43.5 125 03.0
84			14-Jul-93	1993	N18-11	NWA	99 48 09.2 124 44.7
84			14-Jul-93	1993	N18-12	NWA	99 48 09.2 124 44.7
84			14-Jul-93	1993	N18-16	NWA	99 48 07.7 124 43.8
84			21-Jul-93	1993	N18-11	NWA	99 48 11.0 124 44.7
85	kelp/Mystr		15-Aug-84	1984	-	SVI	59 48 46.0 125 09.5
85	Kelp/Mystr		16-Aug-84	1984	-	SVI	59 48 42.5 125 02.0
85			14-Jul-93	1993	N18-10	NWA	99 48 09.3 124 44.6
85			14-Jul-93	1993	N18-12	NWA	99 48 09.2 124 44.7
85			14-Jul-93	1993	N18-13	NWA	99 48 09.4 124 44.4
85			15-Jul-93	1993	N18-17	NWA	99 48 09.4 124 44.3
85			21-Jul-93	1993	N18-14	NWA	99 48 09.2 124 44.6
85			1-Aug-93	1993	N18-6	NWA	99 48 09.3 124 44.6
85			1-Aug-93	1993	N18-8	NWA	99 48 09.3 124 44.6
91			1-Aug-93	1993	N18-5	NWA	99 48 09.2 124 44.1
91			1-Aug-93	1993	N18-11	NWA	99 48 10.3 124 45.2
92			1-Aug-93	1993	N18-12	NWA	99 48 10.3 124 45.2
92			27-Jul-96	1996	NMM-3	SVI	59 48 39.0 124 50.2
92			6-Oct-96	1996	N2-1	SVI	59 48 44.7 125 08.9
92			6-Oct-96	1996	N2-3	SVI	59 48 46.1 125 08.1
92			9-Aug-97	1997	N2-2	SVI	59 48 38.8 124 48.9
92			2-Sep-97	1997	NML-4A	NWA	99 48 10.2 124 45.5
93	Bob		8-Aug-84	1984	-	SVI	59 48 08.0 125 23.5
93	Bob		17-Aug-84	1984	-	SVI	59 48 09.0 125 25.0
93			1-Aug-93	1993	N18-7	NWA	99 48 09.1 124 44.1
93	JD965		17-Jul-96	1996	JD-	WVI	59 49 10 125 57
93	JD965		13-Aug-96	1996	JD-	SVI	59 48 42 124 57
93			23-Sep-97	1997	NML-2	SVI	59 48 42.2 125 00.5
101	Smoking Wh		8-Aug-84	1984	-	SVI	59 48 53.0 125 23.5
101	Smoking Wh		8-Aug-84	1984	-	SVI	59 48 45.5 125 10.0
101	Smoking Wh		10-Aug-84	1984	-	SVI	59 48 45.4 125 10.1
101	Smoking Wh		15-Aug-84	1984	-	SVI	59 48 45.6 125 10.0
101	Smoking Wh		17-Aug-84	1984	-	SVI	59 48 54.0 125 27.5
101	Smoking Wh		17-Aug-84	1984	-	SVI	59 48 54.0 125 26.0
101	Smoking Wh		20-Aug-84	1984	-	SVI	59 48 51.5 125 27.0
101	Whale A		15-Jul-88	1988	-	SVI	59 48 40.0 124 51.0
101			28-Aug-92	1992	-	SVI	59 48 46.5 125 12.5
101	927,9217		11-Sep-92	1992	-	WVI	59 49 15.0 126 07.0
101	JD927		11-Sep-92	1992	JD-	WVI	59
101	927,9217		25-Oct-92	1992	-	WVI	59 49 15.6 126 09.0
101	JD927		25-Oct-92	1992	JD-	WVI	59 49 10 125 57
101	JD927		22-Jun-94	1994	JD-	WVI	59 49 10 125 57
101	JD927		6-Aug-94	1994	JD-	WVI	59 49 17 126 15
101	JD927		6-Sep-95	1995	JD-	WVI	59 49 23 126 30
101	JD927		19-Sep-95	1995	JD-	WVI	59 49 23 126 30
101	JD927		5-Sep-96	1996	JD-	WVI	59 49 19 126 14
107			9-Jul-94	1994	NOV-6	NWA	99 48 10.4 124 44.5
107			4-Aug-94	1994	-	NWA	99 48 10 124 46
107			19-Aug-95	1995	NOV-4	SJF	49 48 21.4 124 32.0
107			11-Jul-97	1997	NML-1	SVI	59 48 39.5 124 20.1
107			22-Aug-97	1997	NML-1	SJF	49 48 19.0 124 40.7
123		Banf	15-Aug-84	1984		SVI	
130	JD9424G42	Gjisser	8-Aug-84	1988		SVI	Barkley Sound
130	JD9424G42	Gjisser	12-Aug-84	1988		SVI	Barkley Sound
130	JD9424G42	Gjisser	14-Aug-84	1988		SVI	Barkley Sound
130	JD9424G42	CERF	31-Jul-90	1994		NBC	kelp bed off Foxtrott Pt. (see map) 51 4.5 127 38.4
130	JD9424G42	J Darli	1-Nov-90	1994		WVI	Siwash Rks. 49 16 126 11
130	JD9424G42	CERF	21-Jul-92	1996		NBC	S-end of Cranstown Pt. 51 21.8 127 47.3
130	JD9424G42	CERF	22-Jul-92	1996		NBC	N.A.
130	JD9424G42	CERF	21-Aug-92	1996		NBC	in kelpbed off Bay Pt. (S) between + and *(37) 51 21 127 47.4
130	JD9424G42	CERF	27-Aug-92	1996		NBC	off E-side S-Ruby Rk. 51 18.3 127 49
130	JD9424G42	CERF	28-Aug-92	1996		NBC	N-side Ruby Rks. 51 18.4 127 49.2

ID	Other-ID	Collec	Date	Year	Sight#	Region	Location
130	JD9424G42	CERF	1-Sep-92	1996		NBC	off Ruby Rks. 51 18.2 127 49.3
130	JD9424G42	CERF	4-Sep-92	1996		NBC	N-end E-side False Egg I. (N of *, just S of rocks at NE-end) 51 19.4 127 48.2
135	JD928G28	Tober	29-Apr-53	1990		SVI	Barkley Sound
135	JD928G28	J Darli	17-Sep-88	1992		WVI	Ahous Bay 49 10 125 54
135	JD928G28	J Darli	27-Jul-89	1993		WVI	Estevan Pt. 49 23 126 30
135	JD928G28	J Darli	21-Apr-91	1995		WVI	Long Beach 49 22 125 43
135	JD928G28	CERF	24-Aug-91	1995		NBC	N-entrance to Eliza Bay 51 19 127 45.4
135	JD928G28	CERF	31-Aug-91	1995		NBC	Hoop Bay NE of Submarine Reef, in kelp beds on * Rks. 51 12.8 127 47.3
135	JD928G28	J Darli	12-Aug-92	1996		SVI	Pachena Pt. 48 43 125 06
135	JD928G28	J Darli	19-Aug-92	1996		WVI	Siwash Rks. 49 16 126 11
135	JD928G28	J Darli	4-Sep-92	1996		WVI	Siwash Rks. 49 16 126 11
138	JD7923G6	J Darli	22-Aug-75	1979		SVI	WCT
138	JD7923G6	J Darli	6-Sep-77	1981		WVI	Ahous Bay 49 10 125 54
138	JD7923G6	J Darli	17-Jul-86	1990		WVI	Ahous Bay 49 10 125 54
138	JD7923G6	CERF	22-Aug-90	1994		NBC	Burnett Bay near Hayes Rk. 51 6.7 127 41.7
138	JD7923G6	CERF	24-Aug-91	1995		NBC	just W of Islets at N-End of Burnett Bay 51 8 127 41.5
138	JD7923G6	CERF	31-Aug-91	1995		NBC	0.5nm S of Cape Caution light 51 2.4 127 34.1
138	JD7923G6	J Darli	18-Sep-91	1995		WVI	Estevan Pt. 49 23 126 30
138	JD7923G6	J Darli	29-Oct-91	1995		WVI	Ahous Bay 49 10 125 54
138	JD7923G6	CERF	8-Jul-92	1996		NBC	Sylvester Bay 51 9.5 127 45.2
138	JD7923G6	CERF	16-Jul-92	1996		NBC	Middle of St. JohnIs Bay 51 8.2 127 41.7
138	JD7923G6	CERF	17-Jul-92	1996		NBC	SE-end Sylvester Bay 51 8.9 127 44.6
138	JD7923G6	CERF	20-Jul-92	1996		NBC	between Neck Ness and Indian Cove 51 11.6 127 47.2
138	JD7923G6	CERF	21-Jul-92	1996		NBC	Just N of Raynor Pt. 51 8.7 127 44.6
138	JD7923G6	CERF	29-Jul-92	1996		NBC	3/4 t 1 nm S of Cape Caution on kelp bed 51 8.6 127 47.3
138	JD7923G6	CERF	5-Aug-92	1996		NBC	in Bay S of Neck Ness 51 11.7 127 47.4
138	JD7923G6	CERF	12-Aug-92	1996		NBC	200m S of Moody Pt. 51 7.9 127 41.7
138	JD7923G6	CERF	14-Aug-92	1996		NBC	off Wilkie Pt. 51 8.2 127 43.4
138	JD7923G6	CERF	14-Aug-92	1996		NBC	in St. JohnIs Bay 51 9.5 127 45
138	JD7923G6	CERF	15-Aug-92	1996		NBC	in Kask Bay (between Burnaby and St. JohnIs Bay) 51 8.3 127 42.3
138	JD7923G6	CERF	20-Aug-92	1996		NBC	300m S of Moody Pt. 51 7.9 127 42.3
138	JD7923G6	CERF	21-Aug-92	1996		NBC	100m S of Moody Pt. 51 8.3 127 42.4
138	JD7923G6	CERF	26-Aug-92	1996		NBC	300m off SW Caution 51 9.2 127 47
138	JD7923G6	CERF	27-Aug-92	1996		NBC	off Hoop 1.7 51 13.1 127 47.6
138	JD7923G6	CERF	1-Sep-92	1996		NBC	off Raynor Pt. 51 8.6 127 44.6
140	JD794	D		1979		WVI	
140	JD904	D		1990		WVI	
141			19-Jul-97	1997	N2-7	SVI	59 48 46.1 125 09.9
141			28-Aug-97	1997	NML-4	NWA	99 48 08.1 124 03.9
150	JD923	D		1992		WVI	
150	JD923	D		1993		WVI	
166			22-Jul-95	1995	NOV-3	SJF	49 48 21.6 124 32.6
166			22-Jul-95	1995	NOV-6	SJF	49 48 21.5 124 32.3
166			24-Jul-96	1996	NMM-1	SJF	49 48 15.9 124 20.0
166			24-Jul-96	1996	NMM-2	SJF	49 48 15.0 124 17.5
166			12-Jul-97	1997	NML-3	NWA	99 48 14.7 124 42.5
166			28-Aug-97	1997	NML-1	NWA	99 48 22.4 124 44.0
166			2-Sep-97	1997	NML-4A	NWA	99 48 10.2 124 45.5
166			6-Sep-97	1997	NML-1	SJF	49 48 21.7 124 33.2
166			6-Sep-97	1997	NML-2	SJF	49 48 18.4 124 25.2
175			22-Jul-95	1995	NOV-12	NWA	99 48 21.5 124 42.9
175			23-Jul-95	1995	NOV-15	NWA	99 48 22.3 124 43.9
175			13-Jun-96	1996	NMM-1	SJF	49 48 21.0 124 31.5
175			16-Aug-96	1996	NMM-1	NWA	99 48 17.6 124 41.5
175			27-Aug-96	1996	NMM-4	NWA	99 48 17.7 124 41.5
175			28-Aug-96	1996	NMM-1	NWA	99 48 17.6 124 41.5
175			26-Sep-96	1996	NMM-1	SJF	49 48 21.1 124 34.8
175			5-Oct-96	1996	N2-2	SJF	49 48 21.3 124 31.7
175			27-Jun-97	1997	DIS-1	SJF	49 48 21.3 124 32.7
175			27-Jun-97	1997	N2-1	SJF	49 48 22.5 124 35.3
175			27-Jun-97	1997	N2-3	SJF	49 48 21.9 124 33.6
175			27-Jun-97	1997	N2-5	SJF	49 48 21.4 124 32.7
175			28-Jun-97	1997	N2-1	SJF	49 48 21.6 124 33.1
175			28-Jun-97	1997	N2-8	SJF	49 48 21.5 124 32.8
175			1-Jul-97	1997	NML-1	SJF	49 48 21.7 124 32.7
175			1-Jul-97	1997	NML-3	SJF	49 48 20.3 124 29.5
175			3-Jul-97	1997	NML-2	SJF	49 48 21.7 124 32.7
175			29-Jul-97	1997	NML-4	SJF	49 48 23.5 124 42.5
175			1-Aug-97	1997	NML-1B	SJF	49 48 23.3 124 42.4
175			2-Aug-97	1997	NML-1	NWA	99 48 23.4 124 43.5
175			24-Aug-97	1997	NML-1	SJF	49 48 20.2 124 29.6
175			27-Aug-97	1997	NML-3	SJF	49 48 20.6 124 30.3

ID	Other-ID	Collec Date	Year	Sight#	Region	Location
175		6-Sep-97	1997	NML-1	SJF	49 48 21.7 124 33.2
175		6-Sep-97	1997	NML-2	SJF	49 48 18.4 124 25.2
186	JD9422	6-Aug-94	1994	JD-	WVI	59 49 17 126 15
186		27-Jul-96	1996	NMM-2	SVI	59 48 40.5 124 51.2
186	JD9422	13-Aug-96	1996	JD-	SVI	59 48 42 124 57
186		6-Oct-96	1996	N2-7	NWA	99 48 21.3 124 43.2
186		19-Jul-97	1997	N2-6	SVI	59 48 44.5 125 07.0
187		13-Jun-96	1996	NMM-1	SJF	49 48 21.0 124 31.5
187	188	5-Aug-96	1996	NMM-1	SJF	49 48 21.2 124 32.8
187	188	27-Aug-96	1996	NMM-3	NWA	99 48 18.9 124 42.0
187		12-Jul-97	1997	NML-1	NWA	99 48 09.1 124 44.7
187		19-Jul-97	1997	N2-3	SVI	59 48 41.4 124 56.3
187		1-Aug-97	1997	NML-1B	SJF	49 48 23.3 124 42.4
187		28-Aug-97	1997	NML-3	NWA	99 48 09.8 124 45.3
187		20-Sep-97	1997	NML-5	SJF	49 48 17.7 124 21.8
187		20-Sep-97	1997	NML-4	SJF	49 48 18.6 124 22.7
190		28-Jul-96	1996	NOV-1	GH	91 46 57.1 124 04.8
192		6-Oct-96	1996	N2-10	NWA	99 48 11.1 124 44.1
192		19-Jul-97	1997	N2-4	SVI	59 48 41.4 124 56.1
192		2-Sep-97	1997	NML-4B	NWA	99 48 09.2 124 45.4
209		6-Oct-96	1996	N2-4	SVI	59 48 44.9 125 08.8
209		20-Jun-97	1997	NML-3	SJF	49 48 23.4 124 37.8
209		3-Jul-97	1997	NML-1	SJF	49 48 23.7 124 38.1
209		3-Jul-97	1997	NML-3	SJF	49 48 23.6 124 41.0
209		6-Jul-97	1997	NML-1	SJF	49 48 23.7 124 40.0
209		10-Jul-97	1997	NML-1	SJF	49 48 23.2 124 42.4
209		18-Jul-97	1997	N2-6	SJF	49 48 23.5 124 41.6
209		18-Jul-97	1997	NML-1	SJF	49 48 23.4 124 37.6
209		18-Jul-97	1997	NML-2	SJF	49 48 23.6 124 39.4
209		1-Aug-97	1997	NML-1B	SJF	49 48 23.3 124 42.4
209		2-Aug-97	1997	NML-1	NWA	99 48 23.4 124 43.5
209		4-Aug-97	1997	NML-2	SJF	49 48 23.5 124 41.3
209		16-Aug-97	1997	NML-1	NWA	99 48 22.5 124 44.0
209		17-Aug-97	1997	NML-2	NWA	99 48 22.7 124 44.3
209		22-Aug-97	1997	NML-2	NWA	99 48 09.2 124 45.2
209		28-Aug-97	1997	NML-4	NWA	99 48 08.1 124 03.9
209		2-Sep-97	1997	NML-1	SJF	49 48 23.5 124 39.7
212		12-Sep-96	1996	NMM-1	NWA	99 48 21.0 124 43.0
212		18-Sep-96	1996	NMM-4	NWA	99 48 17.6 124 41.5
212		12-Jun-97	1997	NML-1	SJF	49 48 21.6 124 33.1
212		13-Jun-97	1997	NML-2	SJF	49 48 23.3 124 42.4
212		28-Jun-97	1997	N2-4	SJF	49 48 20.6 124 30.6
212		28-Jun-97	1997	N2-6	SJF	49 48 19.5 124 27.6
212		1-Jul-97	1997	NML-5	SJF	49 48 18.4 124 25.4
219		31-May-97	1997	NML-1	SJF	49 48 23.6 124 38.1
219		31-May-97	1997	NML-2	SJF	49 48 23.6 124 40.7
219		1-Jun-97	1997	NML-1	SJF	49 48 23.5 124 35.9
219		2-Jun-97	1997	NML-1	SJF	

85		NMML	01-Jul-98		SVI	Carmanah Pt.
85		NMML	29-Jul-98		NWA	Greenbank
85		NMML	30-Jul-98		NWA	Greenbank
91		NMML	09-Jul-98		NWA	Waatch Pt.
91		NMML	31-Aug-98		WSJF	Shipwreck
92		NMML	01-Jul-98		SVI	Carmanah Pt.
92		NMML	03-Jul-98		SVI	E. Nitinat
92		NMML	30-Jul-98		NWA	ESE of White Rock
92		NMML	22-Sep-98		SVI	E. of Bonilla
93		NMML	21-Jul-98		SVI	Waterfall-Pachena Pt.
93		NMML	24-Aug-98		NWA	Yellow Banks
101		NMML	01-Jul-98		SVI	Tsusiat Falls
101		NMML	03-Jul-98		SVI	E. Nitinat
101		NMML	25-Aug-98		SVI	.5 mi. W. Carmanah
101		NMML	25-Sep-98		WSJF	Jensen Creek
107		NMML	06-Jun-98		NWA	Waatch Pt.
123	T16	NMML	03-Jul-98		SVI	3.5 mi. SE Nitinat
130		NMML	03-Jul-98		SVI	3.5 mi. SE Nitinat
135		NMML	01-Jul-98		SVI	Tsusiat Falls
138	T21	NMML	22-Sep-98		SVI	
140		NMML	17-Aug-98		WSJF	Warmhouse
141		NMML	01-Jul-98		SVI	Tsusiat Falls
150	T27	NMML	01-Jul-98		SVI	Carmanah Pt.
150	T27	NMML	22-Sep-98		SVI	E. of Bonilla
166		CRC	14-Jul-98	D-2	NWA	Makaw Bay
166		NMML	30-Jul-98		NWA	Cannonball Bch.
166		NMML	01-Sep-98		NWA	E. Bodelteh
175		NMML	22-Jul-98		NWA	Skagway
175	T31	NMML	05-Sep-98		NWA	Portage Head-Shipwreck
175	T31	NMML	16-Oct-98		NWA	Portage Head
186		NMML	01-Jul-98		SVI	off Klanawa River
186		NMML	01-Jul-98		SVI	Tsusiat Falls
187	T15	NMML	24-Jul-98		NWA	Portage Head
187	T15	NMML	30-Jul-98		NWA	Mad Bear Reef-Makah Bay
187	T15	NMML	06-Aug-98		NWA	Greenbank
187	T15	NMML	16-Aug-98		NWA	Portage Head
187		NMML	31-Aug-98		WSJF	Shipwreck
187	T15	NMML	05-Sep-98		NWA	NW of Cooke Rock
187	T15	NMML	06-Sep-98		NWA	Portage Head
187	T15	NMML	19-Sep-98		NWA	Mad Bear Reef-Makah Bay
187	T15	NMML	16-Oct-98		NWA	Cooke Rock
187		NMML	21-Oct-98		NWA	Father and Son
187	T15	NMML	18-Nov-98		NWA	Bodelteh-Ozette Is.
190		CRC	05-Apr-98	VE-2	GH	Inside
190		CRC	19-Apr-98	VE-3	GH	Inside
192		NMML	01-Jul-98		SVI	Tsusiat Falls
192		NMML	25-Aug-98		SVI	W. Carmanah
192		CRC	27-Aug-98	N2-21	SVI	
192		NMML	05-Sep-98		NWA	NW of Cooke Rock
192		NMML	05-Sep-98		NWA	Father and Son
192		NMML	06-Sep-98		NWA	Cooke Rock
192		NMML	15-Sep-98		NWA	Cooke Rock
192		NMML	15-Sep-98		NWA	Father and Son
192		NMML	16-Sep-98		NWA	S. Father and Son
192		NMML	21-Oct-98		NWA	Bodelteh-Ozette Is.
209		NMML	22-Jul-98		NWA	Greenbank
212		NMML	01-Jul-98		SVI	Carmanah Pt.
212		NMML	25-Aug-98		SVI	.5 mi. W. Carmanah
212		CRC	27-Aug-98	N2-24	SVI	
212		NMML	28-Aug-98		SVI	Bonilla Pt.
212		NMML	04-Sep-98		SVI	NW of Carmanah
212		NMML	22-Sep-98		SVI	E. of Bonilla
212		CRC	29-Sep-98	N1-5	SVI	
219	T4	NMML	01-Jul-98		SVI	Tsusiat Falls
219	T4	NMML	03-Jul-98		SVI	3.5 mi. SE Nitinat

219	T4	NMML	21-Jul-98		SVI	Carmanah Pt.
219	T4	NMML	25-Aug-98		SVI	.5 mi. W. Carmanah
219	T4	CRC	27-Aug-98	N2-24	SVI	
219	T4	NMML	04-Sep-98		SVI	W. of Carmanah
219	T4	CRC	29-Sep-98	N1-4	SVI	
227	T2	NMML	01-Jul-98		SVI	Carmanah Pt.
227	T2	NMML	03-Jul-98		SVI	Nitinat
228	T5	NMML	01-Nov-98		WSJF	Jensen Creek
228	T5	NMML	04-Nov-98		WSJF	off Seal/Sail Rk. Area
231	T10	NMML	01-Jul-98		SVI	Carmanah Pt.
231	T10	NMML	03-Jul-98		SVI	W. of Carmanah Pt
231	T10	NMML	21-Jul-98		SVI	Carmanah Pt.
231	T10	NMML	25-Aug-98		SVI	Carmanah Pt.
231	T10	CRC	27-Aug-98	N2-22	SVI	
231	T10	NMML	04-Sep-98		SVI	Carmanah Pt.
231	T10	NMML	22-Sep-98		SVI	E. Nitinat
231	T10	CRC	29-Sep-98	N1-6	SVI	
232	T11	NMML	17-Jul-98		SVI	E. Carmanah
232	T11	NMML	25-Aug-98		SVI	E. Carmanah
232	T11	CRC	27-Aug-98	N2-24	SVI	
233	T12	NMML	01-Jul-98		SVI	Carmanah Pt.
233	T12	NMML	03-Jul-98		SVI	W. Carmanah
234	T14	NMML	01-Jul-98		SVI	off Klanawa River
236	T19	NMML	25-Aug-98		SVI	E. Carmanah
236	T19	CRC	27-Aug-98	N2-18	SVI	
236	T19	NMML	28-Aug-98		SVI	Bonilla Pt.
237	T26	CRC	27-Aug-98	N2-25	SVI	
239	T35	NMML	14-Oct-98		WSJF	Jensen Creek
239	T35	NMML	15-Oct-98		WSJF	Rasmussen Creek
239	T35	NMML	15-Oct-98		WSJF	Seal/Sail Rock
239	T35	NMML	22-Oct-98		WSJF	Snow Creek
242	T39	NMML	17-Jul-98		SVI	E. Carmanah
242	T39	NMML	21-Sep-98		NWA	Sand Pt.
242	T39	NMML	18-Oct-98		WSJF	Seal Rock
242	T39	NMML	21-Oct-98		NWA	Father and Son
242	T39	NMML	21-Oct-98		WSJF	Snow Creek
242	T39	NMML	31-Oct-98		WSJF	Sail River
242	T39	NMML	05-Nov-98		WSJF	off Sail River area
243	T41	NMML	17-Jul-98		SVI	E. Carmanah
244	T44	NMML	22-Sep-98		SVI	E. of Bonilla
246	T54	NMML	03-Jul-98		SVI	Campers Crk. Near Owen Pt.
248	T58	NMML	01-Jul-98		SVI	Tsusiat Falls
249	T65	NMML	14-Oct-98		WSJF	Rasmussen Creek
249	T65	NMML	15-Oct-98		WSJF	Seal Rock
249	T65	NMML	15-Oct-98		WSJF	Seal/Sail Rock
249	T65	NMML	18-Oct-98		WSJF	Seal Rock
249	T65	CRC	21-Oct-98	W-1	ESJF	Green Pt.
250	T67	NMML	07-Nov-98		WSJF	Sail Rock
251	T71	NMML	09-Jul-98		NWA	Guano Rock
252	T72	NMML	05-Nov-98		WSJF	Sail River
253	T73	NMML	31-Oct-98		WSJF	Sail River
254	T74	NMML	01-Sep-98		SVI	E. Pachena
255	T75	NMML	14-Oct-98		WSJF	Jensen Creek
255	T75	NMML	15-Oct-98		WSJF	Seal/Sail Rock
255	T75	NMML	17-Oct-98		WSJF	Chito Beach
255	T75	NMML	18-Oct-98		WSJF	Seal Rock
255	T75	NMML	21-Oct-98		WSJF	Snow Creek
255	T75	NMML	22-Oct-98		WSJF	E. Bullman Bch.
255	T75	NMML	28-Oct-98		WSJF	Rasmussen Creek
258	T82	CRC	15-Oct-98	N1-1	SPS	Nisquallly
259	T83	CRC	12-Nov-98	N1-1	SPS	Nisquallly
259	T83	CRC	17-Nov-98	DE-3	SPS	Nisquallly
260	T84	CRC	17-Nov-98	DE-4	SPS	Nisquallly
262	T87	CRC	18-Mar-98	N-1	SPS	
262	T87	CRC	26-Mar-98	N-1	SPS	

264	T89	CRC	21-Mar-98	T1-16	NPS	
264	T89	CRC	22-Mar-98	T1-3	NPS	
264	T89	CRC	27-Mar-98	N-3	NPS	
264	T89	CRC	15-Apr-98	DS-2	NPS	
264	T89	CRC	16-Apr-98	N-13	NPS	
264	T89	CRC	23-Apr-98	DS-4	NPS	
264	T89	CRC	20-May-98	DS-1	NPS	
267	T94	CRC	21-Oct-98	W-4	ESJF	Green Pt.
267	T94	CRC	11-Nov-98	W-6	ESJF	Green Pt.
268	T95	CRC	28-Oct-98	W-2	ESJF	Green Pt.
268	T95	CRC	11-Nov-98	W-3	ESJF	Green Pt.
269	T102	CRC	22-Mar-98	VE-3	GH	Inside
269	T102	CRC	28-Mar-98	VE-7	GH	Inside
269	T102	CRC	28-Mar-98	VE-5B	GH	Inside
269	T102	CRC	28-Mar-98	VE-8	GH	Inside
269	T102	CRC	02-Apr-98	VE-4	GH	Inside
269	T102	CRC	04-Apr-98	VE-9	GH	Inside
269	T102	CRC	16-Apr-98	VE-2	GH	Inside
269	T102	CRC	18-Apr-98	VE-15	GH	Inside
269	T102	CRC	19-Apr-98	VE-6	GH	Inside
269	T102	CRC	19-Apr-98	VE-4	GH+	Entrance
270	T106	CRC	22-Mar-98	VE-3	GH	Inside
270	T106	CRC	02-Apr-98	VE-2	GH+	Entrance
270	T106	CRC	04-Apr-98	VE-4	GH+	Entrance
270	T106	CRC	05-Apr-98	VE-3	GH	Inside
270	T106	CRC	05-Apr-98	VE-4	GH	Inside
270	T106	CRC	09-Apr-98	VE-1	GH	Inside
270	T106	CRC	10-Apr-98	VE-1	GH	Inside
270	T106	CRC	11-Apr-98	VE-3	GH	Inside
270	T106	CRC	12-Apr-98	VE-6	GH	Inside
270	T106	CRC	18-Apr-98	VE-12	GH	Inside
270	T106	CRC	18-Apr-98	VE-10	GH	Inside
271	T109	CRC	04-Apr-98	VE-2	GH	Inside
271	T109	CRC	17-Apr-98	VE-3	GH	Inside
271	T109	CRC	18-Apr-98	VE-16	GH	Inside
271	T109	CRC	19-Apr-98	VE-5	GH	Inside
271	T109	CRC	19-Apr-98	VE-7	GH	Inside
271	T109	CRC	19-Apr-98	VE-9	GH	Inside
271	T109	CRC	24-Apr-98	VE-1	GH	Inside
271	T109	CRC	25-Apr-98	VE-3	GH	Inside
271	T109	CRC	25-Apr-98	VE-4	GH	Inside
271	T109	CRC	26-Apr-98	VE-7	GH	Inside
271	T109	CRC	01-May-98	VE-1	GH	Inside
271	T109	CRC	03-May-98	VE-1	GH	Inside
271	T109	CRC	03-May-98	VE-2	GH	Inside
271	T109	CRC	11-May-98	DLX-1	GH	Inside
272	T110	NMML	31-Aug-98		NWA	Shi Shi
273	T111	CRC	21-Mar-98	VE-4	GH	Inside
273	T111	CRC	11-Apr-98	VE-2	GH	Inside
273	T111	CRC	17-Apr-98	VE-2	GH	Inside
273	T111	CRC	19-Apr-98	VE-9	GH	Inside
273	T111	CRC	25-Apr-98	VE-5	GH	Inside
273	T111	CRC	26-Apr-98	VE-1	GH	Inside
304	T201	NMML	15-Sep-98		NWA	Cooke Rock
304	T201	NMML	19-Sep-98		NWA	W. Cannonball Rock
304	T201	NMML	21-Oct-98		NWA	Bodelteh-Ozette Is.
305	T205	CRC	27-Mar-98	N-5	NPS	

Updated analysis of abundance and population structure of seasonal gray whales in the Pacific Northwest, 1996-2012

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Abstract

The existence of a small number of Eastern North Pacific gray whales that spend the spring, summer and fall feeding in coastal waters of the Pacific Northwest has been known for some time and localized short-term studies have examined aspects of the natural history of these animals. We report the results of a 17-year (1996-2012) collaborative study examining the abundance and the population structure of these animals conducted over a number of regions from Northern California to British Columbia using photographic identification. Some 16611 identifications representing 1303 unique gray whales were obtained during 1996-2012 from Southern California to Kodiak, Alaska. Gray whales seen from 1 June - 30 Nov (after the northward and before southward migrations) were more likely to be seen repeatedly and in multiple regions and years;therefore only whales seen during those data were included in the abundance estimates. Gray whales using the Pacific Northwest in summer and fall include two groups: 1) whales that return frequently and account for the majority of the sightings and 2) transients seen in only one year, generally for shorter periods and in more limited areas. A time series of abundance estimates of the non-transient whales for 1996-2012 was constructed. The most recent estimate for 2012 was 209 whales (se=15.4). The estimated abundance increased in the late 1990s and early 2000s during the period when the eastern North Pacific gray whale population was experiencing a high mortality event and this created an apparent influx of whales into the area. The earlier estimates for 1996-1997 are biased low because the survey coverage area was much smaller but those data were included to improve estimates later in the time series. The abundance estimates since the early 2000s has been relatively stable. The proportion of calves documented was generally low in the early portion of the time series and may have been biased downward by under-reporting and weaning of calves prior to entry in the study area or prior to much of the collaborative seasonal effort. In recent years, early season effort has increased and so has the number of calf observations. Observations of calves returning to the Pacific Northwest in subsequent years documents one possible mechanism for recruitment.

1 Introduction

Beginning in 1996, a collaborative effort among a number of research groups was initiated to conduct a range-wide photographic identification study of gray whales in the Pacific

Northwest (Calambokidis et al. 2000, 2002b). An initial publication of findings from 1998 demonstrated there was considerable movement of individual whales among sub-areas from northern California to southeastern Alaska (which we broadly refer to as the Pacific Northwest) and also provided initial estimates of the abundance of whales within that geographical area (Calambokidis et al. 2002a). The ability to look at movements and employ more sophisticated capture-recapture models, however, was restricted by the lack of multiple years of data with broad geographic coverage. A subsequent report by Calambokidis et al. (2004) characterized the group of whales feeding in these survey areas during the summer-fall period as a "Pacific Coast Feeding Aggregation" (PCFA). They proposed that a smaller area within the PCFA survey areas – from Oregon to Southern Vancouver Island (OR-SVI) – was the most appropriate area for abundance estimation for managing a Makah gray whale hunt (Calambokidis et al. 2004). Subsequently the IWC has adopted the term PCFG for Pacific Coast Feeding group so we will use PCFG in place of PCFA.

This report updates information through 2012 from a collaborative effort to collect photographic identifications of gray whales from California to Alaska has continued since 1996 and these data now cover 17 years (1996-2012) and span fifteen survey regions along the coast from Southern California to Kodiak, Alaska (Figure 1). We provide estimates of abundance for the summer-fall seasons (1 June to 30 November) during 1996–2012 for survey regions between Northern California and Northern British Columbia (NCA-NBC), the region chosen by the IWC to represent the PCFG. For the National Marine Fisheries Service development of an Environmental Impact Statement, we also provide estimates for the smaller regions between Oregon and Southern Vancouver Island (OR-SVI) and Makah Usual and Accustomed area (MUA) which includes the outer coastal area of the Olympic Peninsula (NWA) and the Strait of Juan de Fuca (SJF), even though this area is quite small relative to the observed movements of whales within the PCFG.

2 Methods

Gray whales were photographed during small boat surveys conducted from California to Alaska by collaborating researchers (Table 1) between 1996 and 2012. Gray whale identifications were divided into the following regions (Figure 1): 1) SCA: Southern California, 2) CCA: Central California, 3) NCA: Northern California, 4) SOR: Southern Oregon, 5) OR: central Oregon, 6) GH+: Gray's Harbor and the surrounding coastal waters, 7) NWA: Northern Washington coast, 8) SJF: Strait of Juan de Fuca, 9) NPS: Northern Puget Sound, 10) PS: which includes southern Puget Sound, Hood Canal (HC), Boundary Bay (BB) and San Juan Islands (SJ), 11) SVI: Southern Vancouver Island, 12) WVI: West Vancouver Island, 13) NBC: Northern Vancouver Island and coastal areas of British Columbia, 14) SEAK: Southeast Alaska, and 15) KAK: Kodiak, Alaska. With some exceptions, research groups work primarily in one or two regions. Details of identifications obtained by the different research groups are are summarized in Tables 1-2.

2.1 Photographic Identification Procedures

Procedures during surveys by different research groups varied somewhat but were similar to one another in identification procedures. When a gray whale was sighted, the time, position, number of animals, and behaviors were recorded. Whales were generally approached to within 40-100 m and followed through several dive sequences until suitable identification photographs and associated field notes could be obtained.

For photographic identification of gray whales, both left and right sides of the dorsal region around the dorsal hump were photographed when possible. Most identification photographs were obtained with were obtained with 35mm cameras prior to 2004 and primarily with digital SLR after 2004 with both camera types paired most often with a large 300mm lens. Researchers also photographed the ventral surface of the flukes for further identification when possible. The latter method was not as reliable since gray whales did not always raise their flukes out of the water. Markings used to distinguish whales included pigmentation of the skin, mottling, and scarring, which varied among individuals. These markings have provided a reliable means of identifying gray whales (Darling 1984). We also identified gray whales using the relative spacing between the knuckles along the ridge of the back behind the dorsal hump. The size and spacing of these bumps varies among whales and has not changed throughout the years these whales have been tracked, except with injury. Figure 2 shows typical photographs and features used in making gray whale identifications.

Comparisons of whale photographs were made in a series of steps. All photographs of gray whales were examined and the best photograph of the right and left sides of each whale (for each sighting) were selected and printed (7 x 2.5 inch). To determine the number of whales seen during the year, the prints were then compared to one another to identify whales seen multiple days. Finally a comparison was made to the CRC catalog of whales seen in past years. Whale photographs that were deemed of suitable quality but did not match our existing catalog (compared by two independent persons) were considered “unique” identifications and assigned a new identification number and added to the catalog.

2.2 Data Analysis

The abundance of gray whales was estimated with open population models for three nested spatial scales consisting of contiguous survey regions (Figure 1; Table 3) 1) NCA-NBC: the coastal survey regions from Northern California (NCA) through Northern Vancouver Island/British Columbia (NBC) which matches the IWC definition of the PCFG, 2) OR-SVI: survey regions from southern Oregon through Southern Vancouver Island (SVI) identified in the Makah waiver request, and 3) MUA - survey regions NWA and SJF. Inland waters in WA (other than SJF) and in BC are excluded from the abundance estimates because these are used primarily by transient whales in the northward spring migration.

Gray whales photographed and identified anytime during the period between 1 June and 30 November (hereafter referred to as the “sampling period”) within the defined region were considered to be “captured” or “recaptured”. For each unique gray whale photographed, a capture history was constructed using 17 years of data from 1996-2012. For example, the capture history 00010010010000000 could represent a gray whale photographed in 1999, 2002 and 2005 in the PCFG. The same gray whale may have had a capture history 00010010000000000 for a smaller spatial scale such as OR-SVI or may not have been seen at all (00000000000000000) and would not be used at the smaller spatial scale.

Multiple "detections" of a single whale within the sampling period were not treated differently than a single detection. A "1" in the capture history meant that it was detected on at least one day during the sampling period. However, multiple detections in the same year were used to construct an observed minimum tenure (MT) for each whale. MT was defined as the number of days between the earliest and latest date the whale was photographed with a minimum of one day for any whale seen.

We fitted open population models to the 17 yearly time series of capture history data for each spatial scale to estimate abundance and survival. Open models allow gains due to births/immigration and losses due to deaths/emigration. Using the RMark interface (Laake and Rexstad 2008) to program MARK (White and Burnham 1999), we fitted a range of models to the data using the POPAN model structure. The POPAN model structure (Schwarz and Arnason 1996) provides a robust parametrization of the Jolly-Seber (JS) model structure in terms of a super population size (N), probability of entry parameters (immigration), capture probability (p), and survival/permanent emigration (φ).

It is essential to consider the population structure and its dynamics to build adequate models. In particular, we know from previous analysis of a subset of these data (Calambokidis et al. 2004) that some whales were seen in only one year between 1 June and 30 November and were never seen again. Transient behavior is a well-known problem in capture-recapture models and it is often addressed using a robust design which involves coordinated multiple capture occasions within each year and typically assumes closure within the sampling period (June-November). Region-wide coordinated surveys may be possible but would be difficult with variation in weather conditions. Also, the closure assumption within the year would be suspect due to variable timing of whales arrivals and departures into the PCFG, so it would require nested open models. We know from prior analysis that whales newly seen in year (y) were less likely to return (i.e., seen at some year >y) than previously seen whales but also newly seen whales that stayed longer during their first year (i.e., longer MT) in the PCFG were more likely to return. Likewise, previously seen whales were more likely to be seen in the following year (y+1), if they had a longer MT in year y. Calambokidis et al. (2004) postulated that these observations were consistent with whale behavior that was determined by foraging success.

Transient behavior in which an animal is seen only once can be modeled by including a different "first year" survival (Pradel et al. 1997) for the newly seen animals. Survival in the time interval after being first seen is dominated by permanent emigration rather than true mortality. Survival in subsequent time intervals represents true survival under the assumption that animals do not permanently emigrate except in their first year. Pradel et al. (1997) were working with release-recapture data (Cormack-Jolly-Seber) where modeling this transient effect on survival is straightforward. For a Jolly-Seber type analysis where the first capture event is also modeled, the inclusion of a transient effect is less easily accommodated.

We divided the whales into cohorts based on the year in which they were first seen ("newly seen"). In the model, their first year survival could differ from subsequent annual survival as in Pradel et al. (1997). "Newly seen" is not a particularly useful concept for the first year of the study (1996), because all whales were being seen for the first time. The survey effort and coverage in 1996 and 1997 were not nearly as expansive as 1998 and later. We considered models that had three different first year survivals (1996&97, 1998, and >1998) and we also considered a model that allowed for a different first year survival for each year (cohort) to allow for different transient proportion in each year. The first year survival was also allowed to vary as a function of MT with a model in which the relationship was constant across years and varied for (1996&97, 1998, and >1998). We also considered models that allowed a different first-year survival for whales identified as calves under the presumption that their true survival might be lower but that their probability of returning to the PCFG might be higher. Discussion at the 2012 intersessional AWMP meeting led to consideration of an additional covariate which split whales into 2 groups for estimation of post-first-year survival. Whales seen initially as calves and any whale newly seen in 1998 or was in the CRC catalog because it had been seen prior to 1998 were put in one group and the remaining whales newly seen in 1999 or later were put in another group. The expectation was that the first group would have higher post-first-year survival because many of the newly seen whales that entered after the stranding event in 1999/2000 might eventually emigrate. When this covariate was included it made such a large improvement that any model without it would have no support. Therefore, it was included in all 10 models for survival (Table 4).

In Calambokidis et al. (2010) we estimated a cohort-specific super-population size for each cohort using the median MT covariate value for unseen whales but during the April 2011 AWMP meeting it became apparent that this may lead to bias in estimating abundance. Therefore, we used the method outlined in the 2011 AWMP report which is similar to the method used by Calambokidis et al. (2004) in that we assume that all whales in the PCFG for the first year are seen so the super-population size for each cohort is the number seen and thus there are no unknown covariate values. We fixed capture probability (p) and probability of entry (pent) to 1 for each cohort in their entry year. We are not interested in the number of transient whales so we used an estimator of abundance for non-transient whales (2011 AWMP report) which is a modification of the Jolly-Seber estimator which for any year can be expressed as:

$$\hat{N} = n/\hat{p} = (u + m)/\hat{p}$$

where $n = u + m$, n is the number seen in a year being composed of new animals (u=unmarked) and previously seen animals (m=marked), and $\hat{p}$ is the capture probability estimate. For the PCFG we are assuming that any new whale is sighted ($p = 1$) and we are only interested in estimating the abundance of whales that will remain part of the PCFG which is the portion of the new whales that do not permanently emigrate from the PCFG. We can modify the estimator for year j as follows:

$$\hat{N}_j = u_j\hat{\phi}_j + m_j/\hat{p}_j$$

where ϕ_j is the first year survival rate of "new" whales. When ϕ and p contain whale specific covariates like minimum tenure (MT) the estimator becomes:

$$\hat{N}_j = \sum_{i=1}^{u_j} \hat{\phi}_{ij} + \sum_{i=1}^{m_j} 1/\hat{p}_{ij}.$$

To obtain an abundance estimate for 2012, we assumed that the parameter for first year survival intercept in that year was the same as in 2011. A variance-covariance matrix for the abundance estimates was constructed using the variance estimator in Borchers et al. (1998) for a Horvitz-Thompson type estimator with an adaptation for the first component of the abundance estimator for prediction of number of new whales that do not permanently emigrate. For the estimated capture probabilities (p) not fixed to 1, we fitted 3 models that varied by time (year) and/or varied by MT in the previous year (Table 4).

We used Test 2 and Test 3 results from the Cormack-Jolly-Seber structure (Lebreton et al. 1992) as a general goodness of fit for the global model and as a measure of possible over-dispersion creating the lack of fit. We fitted each combination of models for S (survival) and p (capture probability) and used AICc (Burnham and Anderson 2002) to select the most parsimonious model of the 30 fitted models. Model averaging was used for all models to compute estimates and unconditional standard errors and confidence intervals.

3 Results

The database contains 20187 records for whales photographed between 1996 to 2012 from California to Kodiak, Alaska; however 3576 are replicate identifications of whales on the same day. We define a sighting as one or more photographs of a whale on a day. The number of sightings varied annually from 131 and 1648 with a total of 16611 sightings of 1303 unique gray whales (Table 1). The average number of sightings/whale was 12.7 (range: 1- 280). Identifications were made throughout the year but with most effort from June to September. Number of sightings were most numerous in NCA, SVI, WVI, and NBC and (Table 2). The number of uniquely identified whales was greatest in NCA, NWA, SVI and WVI (Table 2).

3.1 Seasonal Sighting Patterns

Whales have been photographed in every month of the year (Table 5) but with very few during December-February when most of the whales are in or migrating to Mexico and survey effort is reduced. Previous analysis of these data have always used 1 June - 30 November as the sampling period to describe the whales in the PCFG because whales seen prior to 1 June and after 30 November are more likely to be whales that are migrating through the region. The southbound migration starts in December and the separation between May and June is clearly supported by the data. For example, of the 1303 unique whales sighted from California to Kodiak, Alaska, 494 whales were only seen between 1 Dec - 31 May and 88.5% of those were only sighted once (one day). Of the 809 whales sighted between 1 June -30 November at some time, 37.1% were only sighted once (one day). If sightings in Alaska are excluded, then only 30.7% of the 698 were seen only once (one day).

The break between May and June is apparent in various measures such as proportion of whales sighted more than once, sighted in more than one region, and sighted in more than one year (Figure 3). However, the break is more apparent if we separate out SJF, NPS and SVI from the other survey regions (Figure 4). The difference across months is not as strong for inland waters of Washington and British Columbia (NPS, SJF) because these are whales that have diverted from the migration and are either more likely to remain after 1 June or demonstrate high year-to-year fidelity during spring such as with NPS. Also, even though Southern Vancouver Island (SVI) is in the main migration corridor and not an inland water, the pattern across months is also weaker because the sampling has been focused on the spring herring spawn in Barkley Sound (effectively an inland waterway) and has purposefully undersampled passing migrant whales (Brian Gisborne, pers. comm.). The break between May and June is much more apparent for NWA and the other areas in the migration corridor which is consistent with the northbound migration of gray whales proceeding past Washington through May. Resighting rates of whales seen after 1 June remained high through November.

The proposed Makah gray whale hunt in the MUA area (NWA and SJF) may occur in NWA after 30 November and prior to 1 June. A hunt conducted in spring (March-May) potentially could take whales from the PCFG although those chances are less in NWA than in SJF. There have been 181 whale sightings (a unique whale-day) in NWA prior to 1 June of which 40.33% (73) were of whales that were seen in the PCFG after 1 June at sometime. If we restrict the comparison to whales seen in at least 2 years in the PCFG, then the percentage is only reduced to 36.46% (66). If we restrict the area, only 37.02% (67) were of whales that were seen in OR-SVI after 1 June at some time, and 33.15% (60) were of whales that were seen in MUA after 1 June at some time (Figure 5). In comparison, 54 whale sightings were in SJF prior to 1 June of which 70% (39) were of whales that were seen in the PCFG after 1 June at sometime, emphasizing the importance of restricting a hunt to coastal waters of the MUA (i.e., the NWA) to limit the take of whales from the PCFG.

Capture (sighting) histories of whales seen at least once in the PCFG from 1 June - 30 November are provided in Appendix Table 1 which show sightings of whales in 1 Mar -31 May only, 1 June - 30 Nov only and in both time periods within a year.

3.2 Regional Sighting Patterns

There is considerable variation in the annual regional distribution of numbers of whales photographed during the sampling period (Table 6) which is in part due to variation in effort. Although not a true measure of effort, the number of days whales were seen (Table 7) does reflect the amount of effort as well as abundance of whales. In particular, in comparison to other regions, the large number of sightings in SVI partly reflects large numbers of sampling days by Brian Gisborne who has routinely sampled SVI from summer through fall on almost a daily basis. On the other hand, the decline in sightings in SVI during 2007 was not due to reduced effort but to the distribution of whales with many of the whales having moved to waters off Oregon and Washington (Calambokidis et al. 2009b). Similarly, there were 40 survey days in SJF in 2010 but only 4 whales were seen on 4 different days (Table 6, Table 7) so this drop relative to other years was not due to lack of effort.

Whales were sighted across various survey regions and the interchange of whales (Table 8) between survey regions during 1 June - 30 November depends on proximity of the regions (Calambokidis et al. 2004). During 1 June-30 November for 1996 to 2012, 656 unique whales were seen in the PCFG range and 66.8% (438 of the 656 whales seen in the PCFG range) were seen within the smaller OR-SVI region and approximately 34.6% (227 of the 656 whales seen in the PCFG range) were seen within the smaller MUA area; however, there is variation in interchange between areas in the PCFG and the MUA. Of the whales sighted in regions from NCA to NBC, from 35.5% to 58.8% of the whales were seen at some point within MUA (Figure 6). If we exclude transients (whales seen in only one year), the interchange rates with MUA are much higher but the pattern is similar (Figure 7) with a range of 41.3% to 78.9%. Appendix Table 2 provides capture histories using data from 1 June - 30 Nov of whales seen in the MUA at least once. For each year, the table shows whether the whale was sighted in PCFG but not in the MUA during that year, only seen in MUA that year, and seen in both MUA and another PCFG area in that year.

Whales seen in the PCFG exhibited a wide range of movement across and within years. The 118 whales seen in 9 or more years provide a useful example. None of those whales was seen exclusively in a single region, and 68.6% were seen in at least 4 of the 9 survey regions from 1996 to 2012. However, whales did regularly visit the same regions across years with 91.5% were seen in at least one of the regions during six or more of the years they were seen and 67.8% were seen in a region two-thirds or more of the years they were seen. SVI was the region with the maximum number of years seen for 56 of the 118 whales, which in part reflects the larger amount of survey effort in SVI (Calambokidis et al. 2004a, Calambokidis et al. 2013). Thus, some whales regularly visit particular regions more often than others, but they are seen across the other regions as well.

Some of the whales not seen in the PCFG in a year were seen in Kodiak and Southeast Alaska (Table 9). Of the 25 whales identified in Southeast Alaska and the 122 whales identified in Kodiak, Alaska, 14 (56%) and 20 (16.4%), respectively have been seen farther south in the PCFG. For example, whale 130 was only seen in Southeast Alaska in 1999, but had been seen in every other year in the PCFG. Likewise, whale 232 was only seen in Kodiak in 2002, but was seen along Vancouver Island in 2000, 2001, and 2003 but then wasn't seen again until 2011 and may have been somewhere in Alaska waters. Whale 152 was photo-identified in Kodiak in 2002, 2005 and 2010, but was seen in the PCFG as early as 1995 in the Cape Caution, British Columbia, area, and in 1992 in the Clayoquot Sound, British Columbia, survey area but has not been seen in the PCFG after 1 June since 1999, when it was seen along the west coast of Vancouver Island for most of the summer/fall. Another example is Whale 68, which was seen in northern Washington during 1996 and 1997 and then was seen in Southeast Alaska in 1998 and 1999 but not subsequently. While these are only a few examples of whale movements, they illustrate the extensive inter-year movement of whales, which partially explains the gaps in the observations for some whales and the disappearance of others from the PCFG. Whales not seen in a particular year represent a combination of whales that may have spent little time in the PCFG (perhaps primarily staying in some of these neighboring feeding areas) and whales that may have used been missed in the PCFG (coverage of the PCFG is not complete and is concentrated in particular areas and along the coastal zone).

If we look at latitudes of sightings of individual whales across the 17 years using whales that have been sighted on at least 6 different days (Figure 8), we see that sightings of some whales are highly clustered; whereas, sightings of other whales are highly dispersed across several regions. We defined each whales primary range by the 75% inner quantile which is the middle of the range that includes 75% of the locations. The length of the 75% inner quantile in nautical miles exceeded 60 nautical miles (or 1 degree of latitude) for 47.6% of the whales (Figure 9) and it was more than 180 nautical miles for more than 26.5% of the whales. Thus, it makes little sense to compute an estimate of abundance for any region that spans less than a degree of latitude.

3.3 Annual Sighting Patterns

The average number of whales identified in any one year was 146, 95, and 33 for the PCFG, OR-SVI, and MUA, respectively (Table 10). However, those numbers do not represent the total numbers of whales that use each of these areas because not all whales using a region in a year are seen, not all whales return to the same region each year, and not all of the whales return to the PCFG region each year. The annual average number of newly seen whales (excluding 1996-1998 when the photo-id effort expanded to cover all survey regions) was 35.4, 23.8, and 12.1 for PCFG, OR-SVI, and MUA, respectively. The annual average number of newly seen whales that were "recruited" (seen in a subsequent year), excluding 1996-1998 and 2012, was 14.3, 11.8, and 6.1 for PCFG, OR-SVI, MUA respectively. Thus, there were a substantial number of new whales seen each year and 42.1, 50.5, and 53 percent of those were seen again in a subsequent year in the 3 regions respectively. The number of newly seen whales and the number newly seen and recruited (i.e., seen in at least one more year after the initial year it was seen) (Table 11) are displayed as discovery curves in Figures 10 and 11.

Of the whales that were seen during June-November 1996-2012 in the PCFG (NCA to NBC) about half were only seen in one year and the whales that were seen in more years were sighted more often each year and therefore represented a large proportion of the sightings (Figure 12). Of the 603 identified whales first seen before 2012 between 1 June and 30 November in the PCFG range (NCA-NBC), 49% were seen in only one year and only represent about 5% of the sightings (Figure 12). Many of the newly seen whales did not return in subsequent years. Some whales were seen in every year with 7.3% that were seen in every year after their initial identification, including 5 whales first seen in 1996 that were seen in all of 17 subsequent years. The remaining 44% were seen more than once but not in every year.

Likewise, examination of MT in the first sighting year demonstrates that whales who stay longer in their first year were more likely to be seen in a following year (Figure 13). Whales "first" seen in the first few years of the study (1996-1998) includes some whales that were truly new to the PCFG in those years but many were only "new" because it was the first year of the study or as the surveyed regions expanded over time. This is evident (Figure 13) in the much higher proportions for 1996-1998 than for the other years. These relationships will be important in the capture-recapture models for abundance estimation because whales that do not return after their first year (a large percentage in this analysis) would appeared to have not survived because they have permanently emigrated (with a small fraction that died).

3.4 Mothers and calves

In 2011 and 2012, early season effort both prior to 1 June and in the first half of June, identified 18 mothers with calves that had not been seen in any other year and therefore were not known PCFG whales. The vast majority (16, 89%), were seen on only a single day and the only other two were seen on 2 or 3 days. Four of these 18 (including the two seen more than one day) were seen in early June and would qualify as PCFG whales based on the 1 June definition but were likely just late migrating mothers from the overall gray whale population. In 2012 with more intensive effort early in the season and greater attention to mothers with calves, 11 known PCFG mothers with calves were identified, higher than any previous year. This represented 44% of the previously identified PCFG mothers that were seen that year, also representing the highest proportion documented and close to a reasonable reproductive rate for this species.

Through 2012, 45 different PCFG gray whales were seen as definite or probable mothers with 60 calves (Table 12). Despite the many years of study, only 11 whales were seen with calves in multiple years (2 to 4) with only three whales that were sighted with calves in three or more years. One individual (ID#81) was observed with a calf in 2001, 2003, and 2009 and another ID #232 was seen with a calf in 2001, 2003, and 2011. The whale (ID#67) with the most calves included one seen in 1995, 2002, 2004 and 2011. Overall, 3 of the 61 observed calves (Table 12) occurred prior to 1998, leaving 58, about 3.9 per year during our primary study period 1998-2012 . These represent a minimum estimate of the births occurring because: 1) collaborators did not always note the presence or absence of calves, 2) as described below, calves weaned from their mothers, making them unidentifiable as calves, as early as June and July. Both these factors would tend to result in underestimates of the presence of calves. With greater attention to mother and calves in 2012, the number of calves identified of PCFG moms was 12.

The number of mothers seen with calves varied dramatically by year from 0 to 12. In addition to the record numbers of calves seen in 2012 (partly due to a change in effort and focus) there was also a four-year period (2001-2004) which accounted for 27 of the 60 sightings of known mothers with calves indicating there is some real inter-year variation in numbers of calves. During this 4-year period an average of 6.75 calves were seen while an average of 2.7 calves per year was seen in the other 11 years between 1998-2012 . Among the known or suspected mothers seen in 1998 or before, of the years they were seen during 1998-2012, the average proportion they were seen with a calf was 14.8% although it was 21.1% and 27.3% during the peak years of 2001 and 2002, which would be closer to what would be expected if females were getting pregnant almost every other year. In the most recent years of data, the percentages for those females were also higher at 22.2% in 2010, 21.4% in 2011 and 42.9% in 2012. While these years with higher number of calves were likely higher birth years, it is also possible that longer weaning times those years may have contributed to a higher proportion of new calves still with their mothers being documented. Also, recently there has been an increased effort in identification of calves and more sighting effort in the spring.

In 31 cases, a calf was seen associated with its mother early in the season and then the mother or the calf was resighted later in the season separately, suggesting weaning or calf death had occurred. In at least 14 cases separation had occurred prior to a July sighting.

In two cases either the mother or calf was seen separated in June, however, in neither case was the calf resighted in the future year (although the mother was) suggesting these calves may not have survived. If you use the last time mom and calf were sighted together as the separation date, most of the separation dates were in July (32), but 11 were before July and 14 were in August through October. These findings are consistent with weaning most commonly occurring in July.

Of the 45 definite or probable mothers, 32 had been seen four or more years in the study area (13 had been seen only 1, 2, or 3 years). Even those animals with long sighting histories were seen with calves in only a small proportion of the years. However, often the initial sighting of these animals was in late August or later, past the period when weaning may have occurred (Table 12).

While a high proportion of calves were seen in 2012, we also looked at some of the whales first seen in 2012 (after 1 June) that had not been seen as calves associated with mothers to see if they were potentially weaned calves. There were 10 cases where animals first seen in 2012 were resighted five or more times (indicating they were regularly using the area). In four of these case there were comments made in the field that this animal appeared to be a calf or was small and in two additional cases (6 total), the animal appeared to be a younger animal based on photos showing it near another animal. Of first sighting of these 6 animals were in May (1), June (3), and July (2) so spanning the period where weaning occurs. We cannot tell if these might have been calves of PCFG or non-PCFG animals.

Sightings of mothers with calves or known PCFG mothers were in somewhat atypical locations and may suggest some differences in occurrence based on reproductive condition. Four of the mothers identified with calves in 2012 had been seen off Kodiak, AK in 2005 and three of these had not been sighted since they were sighted as mothers in 2012 and the fourth only seen one year in that gap. One mother (ID#281) was regularly sighted in the PCFG area every year from 1999 to 2007. In only one of those years was she with a calf (2002) and in 2008 she was seen on 19 April off Santa Barbara, S California apparently in the migration with a small calf but neither of them were seen that year in any of our effort farther north from Northern California to SE Alaska. Another case not included in our summary because the calf was never seen in the our study area and also there was uncertainty of who was the mother, was an apparent calf (ID 962) sighted off San Miguel Island on 27 July 2006 but which was accompanied by two adults (ID 359 and 718) both of whom were seen in most years from 2002 to 2008 in the Pacific Northwest (N California to SE Alaska), but not in 2006. Both the mothers and calves from these two sightings were not seen in the Pacific Northwest in their birth year (despite the mothers being seen most other years) and were only opportunistically sighted outside the region, suggesting there may be additional calves born to animals that use the Pacific Northwest that perhaps do not come into sampled areas (either within or outside the Pacific Northwest) in their birth year. This would negatively bias estimates of the number of calves born to these animals.

We examined the sighting histories of the identified calves to determine if they tended to be seen in future years. Animals that were not seen in future years could reflect either mortality in the first year of life or animals that did not continue to feed in the Pacific Northwest in future years. Of the 40 calves identified prior to 2011, 60% were resighted in a subsequent year. Using only the 29 calves seen through 2004 (to allow a longer follow up period to resight animals, 19 (65.5%) have been resighted in a later year. In comparison, for non-calves the proportion resighted for those newly seen up through 2004 was lower at 54.9% (230 of 419). Thus, calves appear to be more likely to return to the PCFG than non-calves. The remainder not seen in a following year could be the result of: 1) the calf dying, 2) the calf not returning to the area or not yet resighted during its return, 3) the calf not being recognized by photo-ID since calves can undergo changes in markings rapidly especially if not seen for several years. Given all these factors the resighting rate of calves does suggest a high proportion of surviving calves appear to become part of the feeding aggregation that uses the Pacific Northwest.

3.5 Migratory movements of PCFG whales

A combination of satellite tag and photo-ID data have provided insights into the migratory movements of PCFG whales. Three location-only LIMPET (see Andrews et al. 2008 and Schorr et al. 2009 for details) on gray whales near La Push, WA on 31 May 2012. These tags were deployed as part of a larger study jointly supported by the US Navy and NOAA (though a grant to WDFW)(see Schorr et al. 2013 for details). Tags transmitted for 3–7 days (Table 14, Figure 14) with maximum rate of movement between consecutive points set at 10 kilometers/hour (km/hr) for gray whales. These gray whales were of particular interest because the timing of deployments were still within the migration period but there was a concentration of whales in this area north of La Push that appeared to be feeding. While the duration of the transmissions was fairly short (possibly due to contact with the bottom during feeding), they did confirm these whales were not migrating and almost exclusively stayed in a very localized area consistent with feeding. One whale did shift slightly north to the area off Cape Alava, another known gray whale feeding area, before transmissions ended. All the tagged whales remained very close to shore throughout the transmission period, and in a median water depth of 29 meters (m) (Table 14) which is consistent with the generally shallow feeding depth for gray whales.

Two of the whales that were tagged were known by photo-ID: 1) CRC-813, a known PCFG whale with more than 57 confirmed sightings going back to 2004, and seen every year since in the Pacific Northwest primarily off the northern Washington coast, the Strait of Juan de Fuca and southern Vancouver Island; and 2) CRC-1176 a known individual seen previously in 2009 in spring off south and west Vancouver Island, in January 2011 off northern California and June 2012 off Northern Washington.

Two previous studies have collected data on satellite tagged PCFG whales (Ford et al. 2013, Mate et al. 2010) and both of these combined with photo-ID sighting histories have provided some interesting insights into movements of PCFG whales. Ford et al. (2013) reported on the results of 5 gray whales tagged with LIMPET tags (similar to what we used) in March 2009, 2010, and 2011 during the northward migration off SW Vancouver Island. Durations of these transmissions ranged from 8-16 days and unlike our case these animals consistently continued north migrating up the coast as far as SE Alaska before transmissions ended. Somewhat surprisingly, photo-ID revealed that three of these five were known PCFG whales (CRC 307, 178, and 135 for tags 1, 2, and 3 respectively):

- ID 307 (Tag 1) was only previously known from sightings in June and July 1998 off Vancouver Island. Transmissions from this tag lasted 13 days during which the whale traveled 1,354 km and ended up north of SE Alaska (58.14 N).

- ID 178 (Tag 2) was not identified later in 2010 (the year it was tagged) but had been seen close to 100 times in the PCFG area both in previous years going back to at least 1995 as well as in 2011, the year following when it was tagged. While this tag transmitted the longest of any of the five deployed (16 days), this whale covered the shortest distance (893 km) and ended up only just barely into SE Alaska by the end of transmissions
- ID 135 (tag 3) which was tracked moving north for 8 days after tagging documented as far north as Sitka. Photo-ID documented this animal feeding from June to mid-September later the same year (2010) off S Vancouver Island and this animal was also seen in that same area in 2011 and 2012.
- ID 1380 (tag 4) and ID 1381 (tag 5) have only been identified by photo-ID on the tagging date (20 and 22 March 2011).

Mate et al. (2010) reported on the deployment and movements of 18 PCFG gray whales tagged off N California and S Oregon from September to December 2009. All 18 of these were previously identified PCFG whales and most have resighted in subsequent years although there is one known to have died and three others that have not been seen for 2 or more years (Table 15). There were some interesting relationships between the satellite tag data and photo-ID results:

- Tag 5200827 (ID 659) which was documented to migrate from south to the breeding grounds but spent 9 days of San Miguel Island, S California on route south and stopped there briefly on return, had also been documented feeding off San Miguel Island on 27 July 2006, a year it was not seen at all in the normal PCFG regions suggesting it may have spent the entire summer south of our normal coverage area.
- Tag 5205938 (ID 32) was documented by Mate et al. (2010) to migrate north in spring 2010 to Icy Bay, Alaska after having been tagged off N California in December 2009 and migrating down to Baja. While this whale had been photo-identified almost 50 times in the years prior to having been tagged, most of these are from two years (1999 and 2002) and it was not seen in most other years. Almost all sightings of this animals were from north of Vancouver Island, the northern end of the area regularly sampled by photo-ID. These together suggest this is an animal that has maintained a somewhat regular use of feeding areas north of the normally sampled PCFG area.

In several additional recent cases PCFG whales have been documented during their migration north while on transit in S California. Cascadia receives identification photographs from whale watch operators in the southern California Bight during each spring during the northbound migration. Starting in 2013, identification photographs of gray whales were quickly reviewed by one of matchers familiar with PCFG whales and if the whale was recognized as a potential PCFG whale it was compared to our catalog. While this process is underway initial efforts yielded several surprising matches. On 16 Feb 2013, three PCFG whales were identified in a group of what appeared to be 4 gray whales that were seen off

Santa Barbara by naturalists aboard the whale watch boat Condor Express. There were three sightings of this same apparent group at 10:50, 14:15, and 15:20. In two of those sightings four animals were reported in the sightings and 4 animals were identified with three of them being known PCFG whales (ID 303, 561, and 878) with a 4th unknown whale (in one sighting only two whales were reported and they were 878 and the same unknown whale). These animals were consistently moving west at a consistent speed of about 3 knots. These were the only sightings that day during the two different whale watch trips. It is highly improbable in the overall migration for three PCFG whales to be migrating together in a group of four whales and suggests either some social association or close synchrony in timing of PCFG whales in the migration. Two other PCFG whales (254 and 227) were also identified during the migration north on 21 and 24 February but were not associated with each other. This effort to identify PCFG whales on the migration will continue and should better identify some of the timing and associations of these animals.

3.6 Open Population Capture-Recapture Models

If the yearly cohorts were pooled, Test2+Test3 statistics indicated a significant lack of fit for the PCFG and subsets (Table 16) primarily resulting from Test 3. This was expected due to the different "survival" rates of previously seen whales (true survival) and newly seen whales of which many never returned (i.e., permanently emigrated) (Table 17) . By separating the cohorts, survival for each cohort was time-varying and thus each cohort has a separate first year survival. The goodness of fit test (Test 2) demonstrated a lack of fit for NCA-NBC and OR-SVI (Table 16). For those regions, we estimated an over-dispersion values of $\widehat{c}$=2.25 and $\widehat{c}$=1.4 respectively to adjust AICc and estimated standard errors.

For MUA and NCA-NBC, the best fitted model (Table 18) was model 2 for p with capture probability varying across years and higher when MT was greater in the previous year. For OR-SVI, the simpler model 3 with no year variation in capture probabilty was the best model and in turn it selected a more complex survival model. For φ the best model was model 3 or 4 for MUA, model 6 for OR-SVI and model 4 for NCA-NBC. Both models 4 and 6 included a separate first year survival which depends on MT. There was not much support for the calf covariate for higher first-year "survival" probably because the sample size of calves was small relative to non-calves and because much of the effect would have been absorbed by MT. In models 3 and 4, there are 3 intercepts for first year survival (1996&97, 1998, >1998) and in model 6 the intercept differs for each year. These results were consistent with Calambokidis et al. (2004) who demonstrated strong support for the effect of MT on first year survival (Figure 15) and capture probability (Figure 17) in the following year. These results differ some from Calambokidis et al. (2010) who used an annual median-centered MT. Use of MT with median centering was necessary to construct open model abundance estimates in the manner described in Calambokidis et al. (2010). However, that was not necessary for JS1 and the use of MT without median-centering resulted in lower AICc values.

There was large year to year variation in capture probability. The values for NCA-NBC ranged from 0.42 to 0.98 depending on the year and value of MT (Figure 17). The lowest values were from 2007 which reflects the temporary emigration of whales from MUA and SVI to waters offshore of Oregon in that year. In contrast, for MUA capture probabilities were much lower ranging from 0.09 to 0.86 depending on the year and value of MT (Figure 18). The lower overall capture probability and weaker relationship between capture probability and MT reflect the transitory behavior of whales in such a small area. The lower estimates of of capture probability in 1999-2004 for MUA was due to decreased effort by NMML which spread their survey effort across MUA to WVI during 1999-2002, lost a vessel in 2002 and had no funding in 2004 (Figure 18).

First year survival estimates were dominated by permanent emigration. For NCA-NBC, the estimates varied from 0.32 to 0.82 for non-calf whales with MT=1 in their first year and from 0.75 to 0.93 for MT>80 in their first year (Figure 15). Calf survival is by definition a first year survival rate and potentially includes permanent emigration from the PCFG. Depending on the value of MT, calf survival estimates ranged from about 0.35 to 0.90 (Figure 16). The average calf survival estimate was 0.54 (se = 0.047). There was little support for a different first year calf survival (ϕ models 7-10 in Table 18) possibly because true calf survival with a potentially lower permanent emigration rate happened to be close to first-year survival of non-calves with a higher permanent emigration rate. Unfortunately there is no way to separate these with the existing data.

Survival subsequent to the first year was assumed to be constant but was less for non-calf whales that were newly seen in 1999 or later. Post-first-year suvival for calves and whales present in 1998 or earlier presumably represents true survival assuming there was little permanent emigration after the first year. Those estimates were 0.969 (se=0.0075) and 0.963 (se=0.0079) for OR-SVI and NCA-NBC respectively. The post-first-year survival estimates for whales that entered in 1999 or later and not identified as a calf were 0.906 (se=0.0159) and 0.905 (se=0.0177) for OR-SVI and NCA-NBC respectively.

3.7 Abundance and Recruitment

For NCA-NBC, OR-SVI and MUA annual estimates of abundance were constructed with model averaged values for JS1 (Table 19-20). Estimates for NCA-NBC in Figure 19 are only shown for 1998-2012 with the open models $p = 1$ for 1996 so it will certainly be an underestimate and the survey coverage in 1996 and 1997 was not as extensive as the later years.

The value of N_{min} for 2012 is 197 for NCA-NBC (Table 19). To gain a sense for how these values might be relevant to estimating a possible level of removal (e.g., due to harvest) we computed the MMPA's Potential Biological Removal (PBR) (typically reserved for stock-level assessments). Using the PBR formula, with an Rmax of 6.2% and a recovery factor of 0.5 (Caretta et al. 2013), the PBR for NCA-NBC (PCFG) would be 3.1.

New whales that are not identified as calves have appeared annually and many of these new (non-calf) whales have subsequently returned and been re-sighted (Table 17). In NCA-NBC from 1999-2011, an average of 31.1 (range: 8.0, 69.0) new whales not identified as a calf were seen each year. Of these new non-calf whales, on average 12.5 (range: 1.0, 28.0) whales returned and were seen in subsequent years. It is unknown what proportion of the non-calves used the PCFG as a calf but were not seen in that year. Currently recruitment appears to be offset by losses (either mortality or permanent emigration) as the abundance estimates have been fairly stable since 2002.

4 Discussion

The population structure of gray whales using the Pacific Northwest in summer and fall is complicated and involves two elements. One group of whales return frequently and account for the majority of the sightings in the Pacific Northwest during summer and fall. This group is certainly not homogeneous and even within this group, there is some degree of preference for certain subareas. Despite widespread movement and interchange among areas, some of these gray whales are more likely to be seen returning to the same areas they were seen before. The second group of whales are transients that are seen in only one year, tend to be seen for shorter periods that year, and in more limited areas.

The existence of these two groups in the study area and their dynamics complicate estimating abundance. While the JS1 estimator may not be optimal, it provides a practical way of handling transients in this open population. Excluding 1996-1997, the JS1 sequence of abundance estimates provides the most reliable assessment of trend for the non-transient abundance and the best estimate of current abundance in 2012.

Despite extensive interchange among subregions in our study area, whales do not move randomly among areas. Abundance estimates were lower when using more limited geographic ranges but these more limited areas do not reflect closed populations. While the use of geographically stratified models can be useful in cases where populations have geographic strata they use (see for example Hilborn 1990), this would be difficult in our case because of the frequent sightings of animals in multiple regions within the same season and these models typically only allow an animal to be sighted in one strata per period. This could be dealt with by assigning animals to only a single region per season but this would be forcing the data into a somewhat inaccurate construct.

Several studies have considered the question of gray whale population structure. There is widespread agreement that at least two populations of gray whales in the North Pacific exist, a western North Pacific population (also called the Korean population) and an eastern North Pacific (ENP) population (sometimes called the California population) (Swartz et al. 2006; Angliss and Outlaw 2008; Rugh et al. 1999). The population structure of the gray whales feeding in the Pacific Northwest has remained in question and only a few studies have examined this. Steeves et al. (2001) did not find mtDNA differences in a preliminary comparison of gray whales from the summer off Vancouver Island and those from the larger ENP population. Ramakrishnan et al. (2001) did not find evidence that the Pacific Northwest whales represented a maternal genetic isolate, although even very low levels of recruitment from the larger overall population would prevent genetic drift. More recently, Frasier et al. (2011) generated mtDNA sequences from a larger sample of gray whales from Vancouver Island than tested by Steeves et al. (2001). They found significant differences in the haplotype frequencies between that sample and mtDNA sequence data reported for ENP gray whales, most of which were animals that stranded along the migratory route. The Frasier et al. (2011) samples were from a relatively small area; however, Lang et al. (2011) evaluated biopsy samples from California to southern Vancouver Island in the PCFG and ENP samples from whales sampled north of the Aleutians and also found significant mtDNA halpotype frequency differences. These two studies provide the strongest evidence to date that the Pacific Northwest whales might be sufficiently isolated to allow maternally inherited mtDNA to differ from the overall ENP population.

Population structure in other large whales has been the subject of recent inquiry and has revealed diverse results for different species. Clapham et al. (2008) examined 11 subpopulations of whales subjected to whaling that were extirpated possibly due to the loss of the cultural memory of that habitat and concluded subpopulations often exist on a smaller spatial scale than had been recognized. Studies of other baleen whales, particularly humpback whales, have shown evidence of maternally directed site fidelity to specific feeding grounds based on photographic identification studies (Calambokidis et al. 1996, 2001, 2008). This high degree of fidelity to specific feeding areas is often discernible genetically. In the North Pacific strong mtDNA differences were found among feeding areas even when there was evidence of low level of interchange from photo-ID (Baker et al. 2008). Similar findings were documented for humpback whales in the North Atlantic which feed in different areas but interbreed primarily on a single breeding ground (Palsboll et al. 1995) like ENP gray whales. In the North Pacific the differences for humpback whales were often dramatic. For example, humpback whales that feed off California have almost no overlap in mtDNA haplotypes with humpback whales feeding in Southeast Alaska (Baker et al. 1990, 1998, 2008). One difference between humpback and gray whales is the coastal migration route of gray whales which means gray whales going to arctic waters to feed would migrate right through the feeding areas to the south. Other species of large whales have not shown as strong site fidelity to specific feeding grounds. Blue whales have undergone an apparent shift in their feeding distribution in the North Pacific apparently due to shifting oceanographic conditions (Calambokidis et al. 2009a). Fin whales in the North Pacific have long migrations and while there do not appear to be multiple distinct feeding areas as was the case for humpback whales, there were some distinct and isolated apparently non-migratory populations (Mizroch et al. 2009; Berube et al. 2004).

Even though the population structure of gray whales off the Pacific Northwest remains unresolved, there is a consistent group of animals that use this area and we provide several estimates of their abundance. Different abundance methods and geographic scopes yield varied results but all suggest the annual abundance of animals using the Pacific Northwest for feeding through the summer is at most a couple hundred animals depending on the estimating method and how broadly the region is defined geographically.

The rapid increase in the abundance estimates at the start of this study is in part due to the smaller area of coverage during 1996 and 1997. We included those years to improve the estimate in 1998-1999 and the estimate for 1998 did increase by 7% from previous analysis. The increase from 1998-2000 occurred during a period the overall eastern North Pacific gray whale population was experiencing a high mortality event that included unusually high numbers of gray whales showing up in areas they were not common. The high rate of increase in the late 1990s and early 2000s should be verified with additional data such as compiling photographic identifications for this area from multiple sources to attempt to verify if the abundance of animals prior to the start of our study was as low as suggested by these trends. Even though the rate of increase may be too high, we believe the abundance did increase and now appears to be relatively stable since 2002.

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Table 1: Contributions of numbers of sightings (one or more photographs of a whale per day) by reseach group for 1996-2012 and resulting number of uniquely identified whales. Totals for whales are unique whales across all research groups.

	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	Whales
Brian Gisborne	0	4	342	304	633	504	363	786	288	393	407	100	483	297	556	541	521	399
Canada Fisheries/Oceans	0	0	0	0	0	0	0	0	0	0	0	0	0	1	14	9	0	23
Carrie Newell	0	0	0	0	0	0	0	0	0	0	12	71	0	18	2	0	135	68
CERF	13	260	101	124	203	346	271	125	761	11	33	11	38	4	7	40	26	134
CRC	54	36	126	179	91	60	89	85	136	31	61	92	68	58	50	56	82	449
Dawn Goley-HSU	0	0	21	74	56	60	63	0	0	0	0	0	42	19	50	229	228	288
Jan Straley-UASE	0	0	0	0	0	0	0	7	0	0	1	1	0	0	0	0	0	7
Jeff Jacobsen-HSU	0	0	0	0	0	0	0	0	0	0	0	1	0	5	127	323	121	216
Jim Darling	18	0	48	0	0	34	13	0	0	0	0	0	0	0	0	23	0	80
MAKAH	0	0	0	0	0	0	0	0	30	44	131	62	250	102	45	67	145	193
MAKAH-NMML	0	0	0	0	0	0	0	0	0	0	0	0	0	71	24	45	117	111
NMML	34	109	125	160	115	115	71	63	0	100	45	37	62	25	6	11	19	350
North Slope Borough	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Opportunistic	12	3	8	14	1	1	0	0	0	1	27	46	66	65	44	157	12	163
OSU	0	0	0	0	0	0	0	0	0	0	0	0	0	213	68	0	81	112
UAF	0	0	0	0	0	0	0	0	0	0	0	0	24	0	21	0	4	44
UVIC	0	0	308	125	128	0	113	0	0	0	0	1	0	16	0	32	21	154
Volker Deecke	0	0	39	40	26	3	0	0	0	0	12	0	0	0	0	0	0	74
Wendy Szaniszlo	0	0	0	0	0	0	0	0	0	87	49	59	117	4	23	96	136	123
Photo Totals	131	412	1118	1020	1253	1123	983	1066	1215	667	778	481	1150	898	1037	1629	1648	
Whale Totals	70	77	158	248	176	196	252	178	194	205	184	159	225	244	234	282	329	1303

Table 2: Regional distribution of numbers of sightings (one or more photographs of a whale per day) and resulting number of uniquely identified whales by reseach group for 1996-2012. Totals for whales are unique whales across all research groups. NPS is northern Puget Sound and PS includes southern Puget Sound, San Juan Islands, Hood Canal and Boundary Bay.

	CA	NCA	SOR	OR	GH+	NWA	SJF	PS	NPS	SVI	WVI	NBC	SEAK	KAK
Brian Gisborne	0	0	0	0	0	0	0	1	0	6372	147	2	0	0
Canada Fisheries/Oceans	0	0	0	0	0	0	0	0	0	19	5	0	0	0
Carrie Newell	0	0	0	238	0	0	0	0	0	0	0	0	0	0
CERF	0	0	0	0	0	0	0	0	0	0	48	2326	0	0
CRC	23	97	117	100	240	110	39	68	412	38	0	96	14	0
Dawn Goley-HSU	0	801	5	36	0	0	0	0	0	0	0	0	0	0
Jan Straley-UASE	0	0	0	0	0	0	0	0	0	0	0	0	9	0
Jeff Jacobsen-HSU	8	532	31	6	0	0	0	0	0	0	0	0	0	0
Jim Darling	0	0	0	0	0	0	0	0	0	9	127	0	0	0
MAKAH	0	0	0	19	0	374	483	0	0	0	0	0	0	0
MAKAH-NMML	0	0	0	0	0	202	54	0	0	0	1	0	0	0
NMML	0	10	50	0	0	277	278	0	18	181	146	10	0	127
North Slope Borough	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Opportunistic	38	2	4	39	0	0	22	34	89	205	3	12	7	0
OSU	0	292	3	67	0	0	0	0	0	0	0	0	0	0
UAF	0	0	0	0	0	0	0	0	0	0	0	0	0	49
UVIC	0	0	0	0	0	0	0	0	0	1	743	0	0	0
Volker Deecke	0	0	0	0	0	0	0	1	0	73	0	42	4	0
Wendy Szaniszlo	0	0	0	0	0	0	0	0	0	395	176	0	0	0
Photo Totals	69	1734	210	505	240	963	876	104	519	7293	1396	2488	34	176
Whale Totals	55	406	92	134	132	295	156	43	49	412	231	125	25	124

Table 3: Survey regions and region subsets used for abundance estimation. Numbers refer to locations on the map in Figure 1.

Survey Region	Region Description	NCA-NBC	OR-SVI	MUA
(1) SCA = Southern California				
(2) CCA = Central California				
(3) NCA = Northern California	Eureka to Oregon border; mostly from Patricks Pt. and Pt. St George	x		
(4) SOR = Southern Oregon		x	x	
(5) OR = Oregon Coast	Primarily central coast near Depoe Bay and Newport, OR	x	x	
(6) GH+ = Gray's Harbor	Waters inside Grays Harbor and coastal waters along the S Washington coast	x	x	
(7) NWA = Northern Washington	Northern outer coast waters with most effort from Cape Alava (Sea Lion Rock) to Cape Flattery	x	x	x
(8) SJF = Strait of Juan de Fuca	US waters east of Cape Flattery extending to Admiralty Inlet (entrance to Puget Sound) with most effort ending at Sekiu Point	x	x	x
(9) NPS = Northern Puget Sound	Inside waters and embayments from Edmonds to the Canadian border			
(10) PS = Puget Sound	Central and southern Puget Sound (S of Edmonds), including Hood Canal, Boundary Bay, and the San Juan Islands			
(11) SVI = Southern Vancouver Island	Canadian waters of the Strait of Juan de Fuca along Vancouver Island from Victoria to Barkley Sound, along West Coast Trail	x	x	
(12) WVI = West Vancouver Island		x		
(13) NBC = Northern British Columbia	British Columbia waters north of Vancouver Island, with principal effort around Cape Caution	x		
(14) SEAK = Southeast Alaska	Waters of southeastern Alaska with the only effort in the vicinity of Sitka			
(15) KAK = Kodiak, Alaska				

Table 4: Model specifications for survival (φ) and capture probability (p) parameters in POPAN models for gray whale photo-identification data. For survival models, β_0 is the baseline intercept for non-transient survival. Fy is 1 if it is year the whale was first seen and 0 otherwise. A subscript for Fy means that it applies only for that cohort except that Fy_{99}applies to cohorts 1999 and beyond and Fy_c represents each of the cohorts from 1996 to 2012. C is 1 if identified as a calf in its first year and 0 otherwise. R is 1 for calves or any whale seen in 1998 or was already in the catalog prior to 1998 and 0 otherwise. β_r is an adjustment to post-first-year survival. MT is minimum tenure value of a whale and β_M is the estimated slope parameter for φ or p. $\beta_{M,96-97}$ applies to 1996-97, $\beta_{M,98}$ to 1998 and $\beta_{M,99}$ applies to 1999-2011. $\beta_{Fy,96-97}$, $\beta_{Fy,98}$ and $\beta_{Fy,99}$ are the first-year survival intercept adjustments for 1996-97, 1998 and cohorts 1999-2011 respectively and $\beta_{Fy,c}$ represents 16 cohort-specific first year survival parameters for 1996-2011. β_{CF} is an adjustment for calf first year survival and β_{CM} is an adjustment for calves to the slope of MT for survival. For the capture probability models, β_t has 15 levels for t=1998,...2012 and β_0 represents the 1997 value. For 1996 p=1.

Model	Parameter Logit Formula	Number of parameters
φ		
1	$\beta_0 + \beta_{Fy} Fy + \beta_r R(1 - Fy)$	3
2	$\beta_0 + \beta_{Fy} Fy + \beta_M MT\,Fy + \beta_r R(1 - Fy)$	4
3	$\beta_0 + \beta_{Fy,96-97} Fy_{96-97} + \beta_{Fy,98} Fy_{98} + \beta_{Fy,99} Fy_{99} + \beta R(1 - Fy)$	5
4	$\beta_0 + \beta_{Fy,96-97} Fy_{96-97} + \beta_{Fy,98} Fy_{98} + \beta_{Fy,99} Fy_{99} + \beta_M MT\,Fy + \beta_r R(1 - Fy)$	6
5	$\beta_0 + (\beta_{Fy,96-97} + \beta_{M,96-97} MT) Fy_{96-97} + (\beta_{Fy,98} + \beta_{M,98} MT) Fy_{98} + (\beta_{Fy,99} + \beta_{M,99} MT) Fy_{99} + \beta_r R(1 - Fy)$	8
6	$\beta_0 + \beta_{Fy,c} Fy_c + \beta_M MT\,Fy + \beta_r R(1 - Fy)$	18
7	$\beta_0 + \beta_{Fy,c} Fy_c + \beta_M MT\,Fy + \beta_{CF} C\,F_y + \beta_r R(1 - Fy)$	19
8	$\beta_0 + \beta_{Fy,c} Fy_c + \beta_M MT\,Fy + \beta_{CF} C\,F_y + \beta_{CM} C\,MT + \beta_r R(1 - Fy)$	20
9	$\beta_0 + (\beta_{Fy,96-97} + \beta_{M,96-97} MT) Fy_{96-97} + (\beta_{Fy,98} + \beta_{M,98} MT) Fy_{98} + (\beta_{Fy,99} + \beta_{M,99} MT) Fy_{99} + \beta_{CF} C\,F_y + \beta_r R(1 - Fy)$	9
10	$\beta_0 + (\beta_{Fy,96-97} + \beta_{M,96-97} MT) Fy_{96-97} + (\beta_{Fy,98} + \beta_{M,98} MT) Fy_{98} + (\beta_{Fy,99} + \beta_{M,99} MT) Fy_{99} + \beta_{CF} C\,F_y + \beta_{CM} C\,MT + \beta_r R(1 - Fy)$	10
p		
1	$\beta_0 + \beta_t$	15
2	$\beta_0 + \beta_t + \beta_M MT$	16
3	$\beta_0 + \beta_M MT$	2

Table 5: Regional distribution of numbers of whales seen by month for 1996-2012.

	1	2	3	4	5	6	7	8	9	10	11	12
CA	0	2	5	8	5	2	6	7	13	1	0	9
NCA	118	18	1	43	42	103	131	57	42	90	93	84
SOR	0	3	0	2	3	1	24	28	55	32	0	0
OR	0	0	0	0	13	16	46	62	65	54	2	0
GH+	5	2	17	56	29	17	3	0	27	1	0	0
NWA	4	5	10	50	103	54	68	85	81	60	7	1
SJF	0	0	3	11	23	32	39	45	67	83	61	11
PS-HC-BB-SJ	0	1	6	21	8	10	5	2	1	1	3	1
NPS	1	2	17	28	30	11	1	0	0	0	0	0
SVI	5	6	72	87	101	195	224	172	140	56	14	6
WVI	0	1	9	5	2	50	148	146	97	19	0	0
NBC	1	0	0	0	2	26	84	108	83	0	0	1
SEAK	0	0	0	0	0	17	4	1	3	0	5	0
KAK	0	0	0	0	2	19	23	52	44	0	0	0

Table 6: Regional distribution of numbers of whales seen during June-November for 1996-2012.

	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012
CA	0	0	0	1	0	5	0	0	4	0	3	0	0	3	7	1	7
NCA	0	0	15	38	27	32	37	15	3	0	0	1	47	64	62	82	95
SOR	0	0	0	0	0	2	46	24	13	1	0	23	15	2	15	10	11
OR	0	0	17	31	8	15	0	0	16	4	9	38	6	38	18	7	42
GH+	1	0	0	1	1	1	0	0	1	0	0	38	0	2	0	0	0
NWA	13	15	22	7	9	31	7	19	0	19	44	12	35	30	22	36	62
SJF	9	22	18	4	5	2	1	9	21	17	21	14	54	37	4	11	11
PS-HC-BB-SJ	0	0	3	8	4	0	0	0	0	1	0	0	0	4	0	0	1
NPS	0	0	0	0	10	0	0	0	0	0	0	0	0	1	2	0	0
SVI	13	17	60	45	52	101	66	90	86	91	69	37	78	75	62	62	73
WVI	8	0	57	66	53	29	85	9	0	52	40	13	23	23	9	53	28
NBC	13	33	23	26	23	40	43	51	90	12	21	5	21	3	4	2	15
SEAK	0	0	5	6	0	1	0	6	0	1	2	3	0	5	0	0	0
KAK	0	0	0	0	0	0	42	4	0	48	0	0	23	0	17	0	2

Table 7: Number of days in which whales were seen for each region and year from 1996-2012 from 1 June - 30 November.

	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012
CA	0	0	0	1	0	2	0	0	2	0	1	0	0	2	4	1	2
NCA	0	0	7	8	20	13	20	2	2	0	0	2	9	19	21	31	28
SOR	0	0	0	0	0	1	4	1	1	1	0	3	1	1	7	6	3
OR	0	0	6	9	5	7	0	0	1	1	7	38	1	21	4	11	67
GH+	1	0	0	1	1	1	0	0	1	0	0	3	0	1	0	0	0
NWA	9	12	22	10	7	11	3	9	0	12	13	6	8	7	14	23	20
SJF	9	42	16	9	9	4	2	15	5	13	18	26	36	30	4	12	17
PS-HC-BB-SJ	0	0	3	11	4	0	0	0	0	2	0	0	0	4	0	0	1
NPS	0	0	0	0	1	0	0	0	0	0	0	0	0	2	3	0	0
SVI	9	10	91	87	82	55	68	66	48	73	59	39	82	71	80	106	75
WVI	10	0	54	46	28	7	10	3	0	6	14	27	31	5	1	22	7
NBC	7	53	39	50	53	43	34	29	53	11	16	9	13	2	8	1	3
SEAK	0	0	2	3	0	1	0	3	0	1	2	2	0	2	0	0	0
KAK	0	0	0	0	0	0	4	2	0	7	0	0	5	0	2	0	1

Table 8: Interchange of whales across regions for all years (1996-2012) for June-November. The diagonal is the number of unique whales seen in that region over the 17 year time span. Many of those whales were only seen once. Here PS includes NPS and CA represents SCA and CCA.

	CA	NCA	SOR	OR	GH+	NWA	SJF	PS	SVI	WVI	NBC	SEAK	KAK
CA	27												
NCA	8	259											
SOR	4	55	84										
OR	4	77	58	131									
GH+	1	18	9	20	43								
NWA	5	64	45	72	26	168							
SJF	3	31	18	35	16	79	138						
PS	0	0	0	0	0	1	1	31					
SVI	9	74	43	76	30	122	93	1	287				
WVI	3	57	35	64	26	94	73	1	160	220			
NBC	2	17	10	30	14	34	31	2	77	76	121		
SEAK	0	2	1	3	2	4	7	0	9	10	12	25	
KAK	1	7	1	4	0	1	0	1	11	8	8	1	122

Table 9: Sighting histories of whales seen in the PCFG during 1 June - 30 November in at least one year and also in Southeast Alaska (SEAK) or Kodiak (KAK) in one year. 1: whale sighted in PCFG but not SEAK or KAK that year, 2: only seen in SEAK or KAK that year, and 3: seen in both PCFG and in SEAK and KAK in that year.

	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012
68	1	1	2	2													
126		1	1			1			1	2			1				1
130		1	1	2	1	1	1	1	1	1	1	1	1	1	1	1	1
140		1	1	3	1	1	1	1	1		1		1	1	1	1	1
141		1	1	1		1	1	1	1	1	1	3	1	1			1
152		1		1			2			2					2		
229		1	1	1	1	1	1	1	1	1	2						
323		1	1				1	1	1	2	1		2				
328		1	1	1	1	1	1	1	1	1	1		1	3		1	1
899		1							1	2							
227			1	2	1	1	1	1	1	1	1	1		1		1	1
232			1		1	1	2	1								1	
261			2				1		1							1	
316			1					2		2							
628				2	1	1	1	1	1				1				
538					1	1	1		1	2							
555					1		1	1			1		2	1	1	1	1
566					1		2		1	2					1		
601					1	1		1	1	1	1						2
612					1	1	1	3	1	1	2						1
581						1		1	1	2	1	1					2
604						1		1		2					2	1	
639						1	2					1		1			
684							1	2				1					
687							1				1	1	1	3	1		
691							1	3	1	2			1				
760							1	1	1	3							1
800								3	1	1							
815									1				2				
836									1	3							
900									1					2			1
834										2				1			
893										2							1
918										2							1

Table 10: Number of unique whales seen by year for MUA, OR-SVI, and PCFG (NCA-NBC) during 1996-2012.

Region	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	Average
MUA	19	27	37	11	14	32	8	22	21	33	58	20	75	57	26	41	67	33
OR-SVI	30	36	86	71	67	128	103	110	114	109	98	114	123	118	92	91	127	95
PCFG	45	69	132	152	137	173	204	157	178	138	128	120	174	154	144	164	208	146

Table 11: Discovery of new unique whales over years 1996-2012 for PCFG,OR-SVI and MUA. Recruited only means that the whale was seen in at least one more year after the initial year it was seen. The number 'recruited' will be less than the abundance estimate because some whales die and others may permanently emigrate and do not return.

Region	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012
PCFG	45	90	161	230	281	343	396	416	447	468	476	496	546	569	584	603	656
ORSVI	30	50	105	128	152	208	247	273	302	321	332	354	376	393	401	410	438
MUA	19	34	57	58	69	88	89	100	112	123	146	148	177	190	194	205	227
PCFG-recruited	40	76	123	136	164	190	220	235	249	260	261	268	286	292	304	309	
ORSVI-recruited	26	39	76	85	100	122	150	170	184	195	198	205	216	220	227	230	
MUA-recruited	17	28	34	34	42	49	50	56	65	70	87	89	105	107	109	113	

Table 12: History of mothers seen with calves during study. Each year a whale was seen, the first conrmed sighting date is shown for that year. Years where a calf was documented are shown with an asterisk. Total years seen includes 16 sightings of whales during 1984, 1988, 1990-1993 that are not shown but no calves were seen in those few cases. For one of the calves a mother was not identified.

ID	Calves	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	Years seen
43	2	07-09*	07-22	07-15	08-09	07-11	07-16	06-19	07-18*	07-12	06-24	07-04									15
65	1		05-03																	06-23*	3
67	4		07-19*	07-02	07-06		08-10			08-07*		06-04*	08-03	05-04					06-23*	07-07	11
80	2	08-25	06-23	08-08		06-08	06-27	07-03	05-07	05-22*	04-27	06-25	06-18*								12
81	3		08-19		09-23	06-14	06-21	07-29	06-20*	06-24	07-28*	07-23	07-03	07-04	06-16		07-16*		02-10		15
91	1			07-02	07-28	06-23		07-22	08-15	07-05*	06-17		06-23		07-11	06-18			08-21		12
92	2			07-27	08-09	05-04	06-30	07-29	07-09	08-04	07-27	07-11	06-27*	06-18	06-08	05-22	04-04	06-05*	03-23	03-31	18
93	1			07-17	09-23	06-14	06-22	08-12	06-21	07-16	08-02	06-30*		07-04		06-18	06-08		06-17	07-18	16
94	1	08-04				06-27	07-06	07-24	07-07	07-15	07-23	08-05	07-13	03-18	07-08*	07-08	06-02	03-31	06-22	07-21	17
101	1	06-22	09-06	09-05		06-11	07-08	07-29	06-08	07-09	08-09	06-15*	08-01	06-07	06-08	06-28	04-24	06-15	05-18	06-20	21
105	1	07-09*				06-17	06-09	07-20	06-22	07-03	08-02	07-23	07-24	07-28	06-22						11
120	1								06-13*	06-11		06-02						07-06			4
126	1	07-25			07-27	07-08			07-12			08-31	08-31			08-27				06-25*	8
143	1			03-21	09-13	06-27	04-20	05-01	07-06	07-29*	08-17		09-05	03-12	03-24	06-22	08-14	03-10	09-10	03-31	16
144	2		08-25			07-11	08-13	09-06	07-06	07-05*	03-30	06-19	05-26	07-04	03-30	05-25	04-04	03-26	05-01*	03-31	16
175	1		07-22	06-13	06-27	05-26	06-09	05-29	06-15	07-03	05-12*	06-30	07-21	07-04	07-15						13
193	1	06-22		10-06	04-12	07-02				07-05	07-27	06-02	07-20	06-28		06-07	06-08		02-24	06-28*	13
196	1			05-09				08-17		07-17	06-17		05-27	06-28	07-07	05-24	03-12	01-27	06-22	06-02*	12
216	1				06-27	08-23	07-30	06-29	06-15	07-15	07-26*	06-04	06-09								9
232	3					07-06		07-30	07-05*	08-15	06-09*								05-20*	04-06	7
237	1			06-28	06-30	07-23	07-25	07-04	07-05	07-01	04-29*	07-19									9
281	2						07-20	07-15	06-21	08-17*	09-05	07-19	08-13	07-07	09-14	04-19*	08-14				12
291	1					10-01	07-12	08-24	06-08*	08-04	06-25	07-24	07-21	07-05		10-20	09-02	08-06	01-05	06-24	14
312	2					06-12*			07-07									06-22*			3
321	1			06-26	07-09	06-25*															3
324	1		08-15		08-12	07-07	06-29	03-21		07-18	07-15	07-17	06-15			08-16		09-15	08-19	05-07*	13
330	1				07-28	07-23				07-17		09-15					04-30			06-22*	6
364	1						10-12	08-09		08-17			07-11		08-19		06-17	01-27	01-10	01-08*	9
372	1						06-26	05-09		08-04	07-15	06-25*	07-07	07-03	09-01		07-10	08-05	06-16	07-09	12
566	1							07-06		08-17		08-14	09-02					06-22*	02-10		6
581	2								06-05*		07-07	08-02	05-03*	07-04	06-30					06-19	7
596	1								06-26*	07-03											2
612	1							06-23	08-01*	07-01	06-05	07-01	07-18	11-05						06-27	8
668	1									09-06		09-22			08-19			05-09*		07-05	5
683	1									07-25*		10-27	06-18								3
684	1									07-04*	08-11				06-13						3
717	2									07-03*										07-02*	2
760	1									08-05	07-03	07-10	06-14							05-07*	5
815	1											06-19*				07-14					2
893	1												09-04							06-05*	2
918	1												09-02							06-28*	2
973	1														09-14*			08-06			2
993	1													05-01	08-03*			08-06	06-02		4
1111	1																	09-12	06-10*	06-27	3
1426	1																			06-28*	1
Calves	60	2	1	0	0	2	0	0	8	9	5	5	3	0	3	1	1	4	4	12	

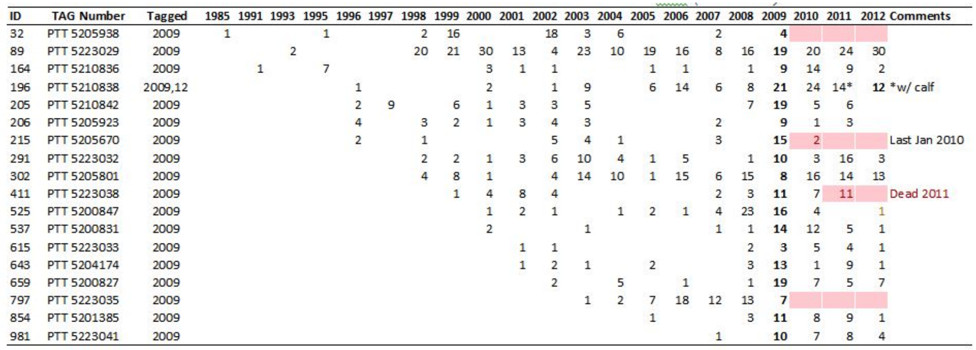
Table 13: Sighting histories of calves identified in the study area. First separate date represents sighting of either the calf or mother alone. An asterisk by the calf ID implies it is suspected to be a calf; others are all known to be calves.

CalfID	MomID	FirstDate	LastDate	CalfAloneDate	1994	1995	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	Years seen
104	105	9-Jul-94	9-Jul-94		1																		1
107	43	9-Jul-94	4-Aug-94		2	1	2	7		34	10	1	15	11	9	10	3	13	5	22	26	24	17
169*	67	19-Jul-95	23-Jul-95			4					3	5	10	5	3	6	2	5	4	1	2	9	13
246*		11-Aug-98	17-Aug-98					3															1
307	312	28-Jun-98	9-Jul-98					2															1
310	321	25-Jun-98	4-Jul-98	6-Jul-98				3	1														2
583	581	5-Jun-01	2-Jul-01	4-Oct-01							5	1	6		5	2	9	12	24	2	7	1	11
584	81	20-Jun-01	18-Jul-01	22-Jul-01							3	1		27	3	4	2						6
595	596	26-Jun-01	29-Jun-01								3												1
611	43	18-Jul-01	31-Jul-01	28-Oct-01							4						1		3	2	2	4	6
620	232	5-Jul-01	31-Jul-01								2												1
626	291	8-Jun-01	8-Jun-01	15-Jun-01							2												1
657	281	17-Aug-02	6-Sep-02									2	1				2	2	7	2	1	13	8
682	80	22-May-02	29-Jul-02	18-Aug-02								4	23	2	7	8	2	15	9	16	26	15	11
685	684	4-Jul-02	4-Aug-02									5											1
686	717	3-Jul-02	3-Jul-02									3											1
687	683	25-Jul-02	29-Jul-02									2				7	1	3	6	4			6
688	91	5-Jul-02	15-Jul-02	6-Sep-02								6	5	4	8	11	2	6		13	10	3	10
698*	67	7-Aug-02	6-Sep-02	14-Oct-02								4	8	1	11	8	1	11	3	1	65	12	11
714	144	5-Jul-02	4-Aug-02									1				6	1	16	7	1	18	27	8
720	143	29-Jul-02	3-Sep-02	30-Sep-02								1	10	7	6	5	6	19	6	14	6	15	11
786	232	9-Jun-03	3-Jul-03	15-Jul-03									11	6	1	16	5	12	3	24	53	17	10
797	81	28-Jul-03	28-Jul-03	30-Jul-03									1	2	7	18	12	11	3				7
798*	175	12-May-03	12-May-03	16-Jun-03																			0
860*	216	26-Jul-03	28-Jul-03	26-Aug-03									3	4	4	7	2	1	1	5	32	10	10
811	815	19-Jun-04	17-Jul-04											5									1
814	372	25-Jun-04	30-Jun-04											2									1
818	101	17-Jul-04	17-Jul-04	20-Aug-04										2	2	4							3
819	67	4-Jun-04	27-Aug-04	22-Sep-04										8	4	20	20	14	10	4	6	3	9
824	93	30-Jun-04	11-Jul-04	14-Aug-04										4	8			11	9	20	16	14	7
862*	581	3-May-05	3-May-05	21-Jul-05											3								1
863	92	27-Jun-05	24-Jul-05	4-Aug-05											10								1
882	80	18-Jun-05	19-Jun-05	4-Jul-05											3	10	13	13	16	2	11	17	8
976*	973	14-Sep-07	14-Sep-07														1						1
990	94	8-Jul-07	5-Aug-07														4	7	9				3
994	993	5-Aug-07	14-Aug-07														1						1
1066	281	19-Apr-08	19-Apr-08															2					1
1173	81	16-Jul-09	18-Jul-09																2				1
1212	668	9-May-10	9-May-10																				0
1234	566	22-Jun-10	1-Jul-10																	2		7	2
1237	312	22-Jun-10	1-Jul-10	6-Aug-10																4	3	2	3
1254	92	5-Jun-10	7-Jul-10	18-Jul-10																20	10	25	3
1303	144	26-May-11	4-Jul-11	28-Jun-11																	7	4	2
1305	1111	10-Jun-11	10-Jun-11	7-Dec-11																	1		1
1350	67	23-Jun-11	1-Sep-11	20-Sep-11																	14	7	2
1357	232	20-May-11	15-Jul-11	22-Jul-11																	8		1
1421	893	25-Jun-12	7-Jul-12																			4	1
1424	65	23-Jun-12	8-Jul-12																			8	1
1425	364	6-Jun-12	8-Aug-12																			8	1
1455	126	27-Jun-12	8-Aug-12																			5	1
1511	330	22-Jun-12	3-Jul-12	5-Nov-12																		2	1
1512	196	2-Jun-12	18-Jul-12	31-Jul-12																		13	1
1517	193	28-Jun-12	2-Jul-12	21-Jul-12																		2	1
1521	717	2-Jul-12	25-Jul-12	13-Sep-12																		15	1
1529	324	7-May-12	7-May-12																				0
1545	760	7-May-12	7-May-12	12-Jul-12																			0
1559	918	28-Jun-12	28-Jun-12	12-Sep-12																		9	1
1427	1426	28-Jun-12	7-Jul-12																			3	1

Table 14: Deployment and movement summary for LIMPET satellite tags on three gray whales near La Push on 31 May 2012. Cumulative minimum horizontal displacement is likely an under representation of the true distance covered by an individual, as it is calculated as a straight line between Argos locations and does not account for any vertical displacement (diving).

ER Tag ID	Trans. durat (Days)	No. locations which passed filter	Cumulative min. horizontal displacmt (km)	Median distance to deployment (km) (max)	Median depth (m) (Range)	Median distance to shore (km) (Range)
001	2.9	31	57	2 (5)	28 (9-32)	1.1 (0.2-3)
002	4.4	62	162	3 (10)	29 (1-34)	1.3 (0-6.3)
003	6.8	93	203	3 (22)	3 (22)	1.7 (0.1-7.3)

Table 15: Identification histories of PCFG gray whales that were tagged by OSU in fall 2009. Numbers underneath years indicate the number of times the whale was sighted that year. Red highlight indicates two whales not sighted in a subsequent year post-tagging, another whale that has not been seen since Jan 2010 and a 4th whale known to have die (in 2011).



ID	TAG Number	Tagged	1985	1991	1993	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	Comments
32	PTT 5205938	2009	1			1			2	16			18	3	6			2		**4**	🟥	🟥	🟥	
89	PTT 5223029	2009			2				20	21	30	13	4	23	10	19	16	8	16	**19**	20	24	30	
164	PTT 5210836	2009		1		7					3	1	1			1	1		1	**9**	14	9	2	
196	PTT 5210838	2009,12					1				2		1	9		6	14	6	8	**21**	24	14*	**12**	*w/ calf
205	PTT 5210842	2009					2	9		6	1	3	3	5					7	**19**	5	6		
206	PTT 5205923	2009					4		3	2	1	3	4	3				2		**9**	1	3		
215	PTT 5205670	2009					2		1				5	4	1			3		**15**	2	🟥	🟥	Last Jan 2010
291	PTT 5223032	2009							2	2	1	3	6	10	4	1	5		1	**10**	3	16	3	
302	PTT 5205801	2009							4	8	1		4	14	10	1	15	6	15	**8**	16	14	13	
411	PTT 5223038	2009								1	4	8	4					2	3	**11**	7	11	🟥	Dead 2011
525	PTT 5200847	2009									1	2	1		1	2	1	4	23	**16**	4		1	
537	PTT 5200831	2009									2			1				1	1	**14**	12	5	1	
615	PTT 5223033	2009										1	1						2	**3**	5	4	1	
643	PTT 5204174	2009										1	2	1		2			3	**13**	1	9	1	
659	PTT 5200827	2009											2		5		1		1	**19**	7	5	7	
797	PTT 5223035	2009												1	2	7	18	12	13	**7**	🟥	🟥	🟥	
854	PTT 5201385	2009														1			3	**11**	8	9	1	
981	PTT 5223041	2009																1		**10**	7	8	4	

Table 16: RELEASE goodness of fit results for each region using pooled and separate cohorts. When cohorts are separated as groups, Test 3 is always 0 because there are no sub-cohorts.

Region	Cohort	Test	χ^2	df	P
MUA	Pooled				
		Test 2	47.9483	24	0.0026
		Test 3	40.8	28	0.056
		Total	88.7483	52	0.0011
	Separate				
		Test 2	9.8441	55	1
OR-SVI	Pooled				
		Test 2	163.0315	38	0
		Test 3	282.9597	29	0
		Total	445.9912	67	0
	Separate				
		Test 2	139.681	100	0.0054
NCA-NBC	Pooled				
		Test 2	296.8194	38	0
		Test 3	544.2195	29	0
		Total	841.0389	67	0
	Separate				
		Test 2	215.955	96	0

Table 17: Number of whales seen each year, number that were new that year in that region, and number that were new and were seen in a subsequent year for whales seen between June-November 1996-2012 in each region. The year a whale was seen as new can vary across regions and if it differs will be later in the smaller region.

Region		1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012
MUA	Seen	19	27	37	11	14	32	8	22	21	33	58	20	75	57	26	41	67
	Non-calf: New	19	15	23	1	11	18	1	10	10	11	23	2	29	13	4	10	20
	Non-calf: New/Resighted	17	11	6	0	8	7	1	5	7	5	17	2	16	2	2	4	0
	Calf: New	0	0	0	0	0	1	0	1	2	0	0	0	0	0	0	1	2
	Calf: New/Resighted	0	0	0	0	0	0	0	1	2	0	0	0	0	0	0	0	0
OR-SVI	Seen	30	36	86	71	67	128	103	110	114	109	98	114	123	118	92	91	127
	Non-calf: New	30	20	54	23	24	50	32	23	24	16	11	20	21	16	7	6	21
	Non-calf: New/Resighted	26	13	37	9	15	19	23	17	11	10	3	6	11	4	6	2	0
	Calf: New	0	0	1	0	0	6	7	3	5	3	0	2	1	1	1	3	7
	Calf: New/Resighted	0	0	0	0	0	3	5	3	3	1	0	1	0	0	1	1	0
NCA-NBC	Seen	45	69	132	152	137	173	204	157	178	138	128	120	174	154	144	164	208
	Non-calf: New	45	45	68	69	51	56	44	17	26	18	8	17	49	22	12	15	43
	Non-calf: New/Resighted	40	36	46	13	28	23	23	12	11	10	1	6	18	6	9	3	0
	Calf: New	0	0	3	0	0	6	9	3	5	3	0	3	1	1	3	4	10
	Calf: New/Resighted	0	0	1	0	0	3	7	3	3	1	0	1	0	0	3	2	0

Table 18: Delta AICc and QAICc (for OR-NBC and NCA-NBC models) for 30 models fitted to each set of data.

		φ Model									
Region	p model	1	2	3	4	5	6	7	8	9	10
MUA	1	13.6	13.1	2.3	1.9	5.1	9.8	12.1	13.1	6.8	7.2
	2	11.2	11.6	0.0	0.5	3.9	8.7	11.0	12.1	5.9	5.8
	3	99.5	99.4	85.0	85.5	87.9	91.2	93.1	94.0	89.7	91.4
OR-SVI	1	165.3	145.5	160.1	138.8	142.0	140.1	142.2	144.0	144.0	145.8
	2	20.7	6.4	16.8	0.6	3.8	1.2	3.2	5.2	5.8	7.7
	3	20.9	6.4	16.4	0.0	3.2	0.2	2.2	4.1	5.2	7.0
NCA-NBC	1	153.8	129.2	130.9	104.3	107.8	110.1	112.2	114.0	109.3	111.2
	2	44.2	23.7	23.3	0.0	3.4	6.2	8.3	10.2	4.9	6.8
	3	50.0	29.7	29.6	6.4	9.7	12.1	14.1	15.9	11.2	13.0

Table 19: JS1 abundance estimates $(\widehat{N})$, standard errors and minimum population estimate $N_{min} = \widehat{N}e^{-0.842\sqrt{log(1+(se(\widehat{N})/\widehat{N})^2}}$ using data from 1996-2012 in OR-SVI and NCA-NBC regions.

Region	Year	$\widehat{N}$	$se(\widehat{N})$	N_{min}
OR-SVI	1996	25	2.8	23
	1997	42	6.3	37
	1998	86	10.6	78
	1999	83	9.8	75
	2000	89	12.3	79
	2001	139	16.7	125
	2002	135	15.7	122
	2003	164	14.4	152
	2004	159	17.0	145
	2005	169	15.4	157
	2006	154	15.4	142
	2007	165	14.5	153
	2008	181	20.6	164
	2009	161	13.3	150
	2010	148	17.5	134
	2011	143	14.8	131
	2012	165	16.6	152
NCA-NBC	1996	38	2.8	36
	1997	80	10.7	72
	1998	126	10.8	117
	1999	147	15.0	135
	2000	149	15.1	137
	2001	181	14.0	170
	2002	198	13.2	188
	2003	210	18.1	195
	2004	218	17.0	204
	2005	219	26.3	198
	2006	200	21.4	183
	2007	194	25.8	173
	2008	207	18.4	193
	2009	206	20.3	189
	2010	194	18.4	180
	2011	197	15.8	184
	2012	209	15.4	197

Table 20: JS1 abundance estimates $(\widehat{N})$, standard errors and minimum population estimate $N_{min} = \widehat{N}e^{-0.842\sqrt{log(1+(se(\widehat{N})/\widehat{N})^2}}$ using data from 1996-2012 in MUA region.

Year	$\widehat{N}$	$se(\widehat{N})$	N_{min}
1996	18	1.5	16
1997	32	4.6	28
1998	38	9.5	31
1999	37	14.1	27
2000	37	23.4	23
2001	52	12.9	42
2002	45	22.4	31
2003	52	16.6	40
2004	55	20.1	40
2005	60	12.4	50
2006	67	7.7	61
2007	67	18.9	53
2008	79	6.4	74
2009	82	10.7	74
2010	76	19.4	62
2011	74	13.6	63
2012	81	9.9	73

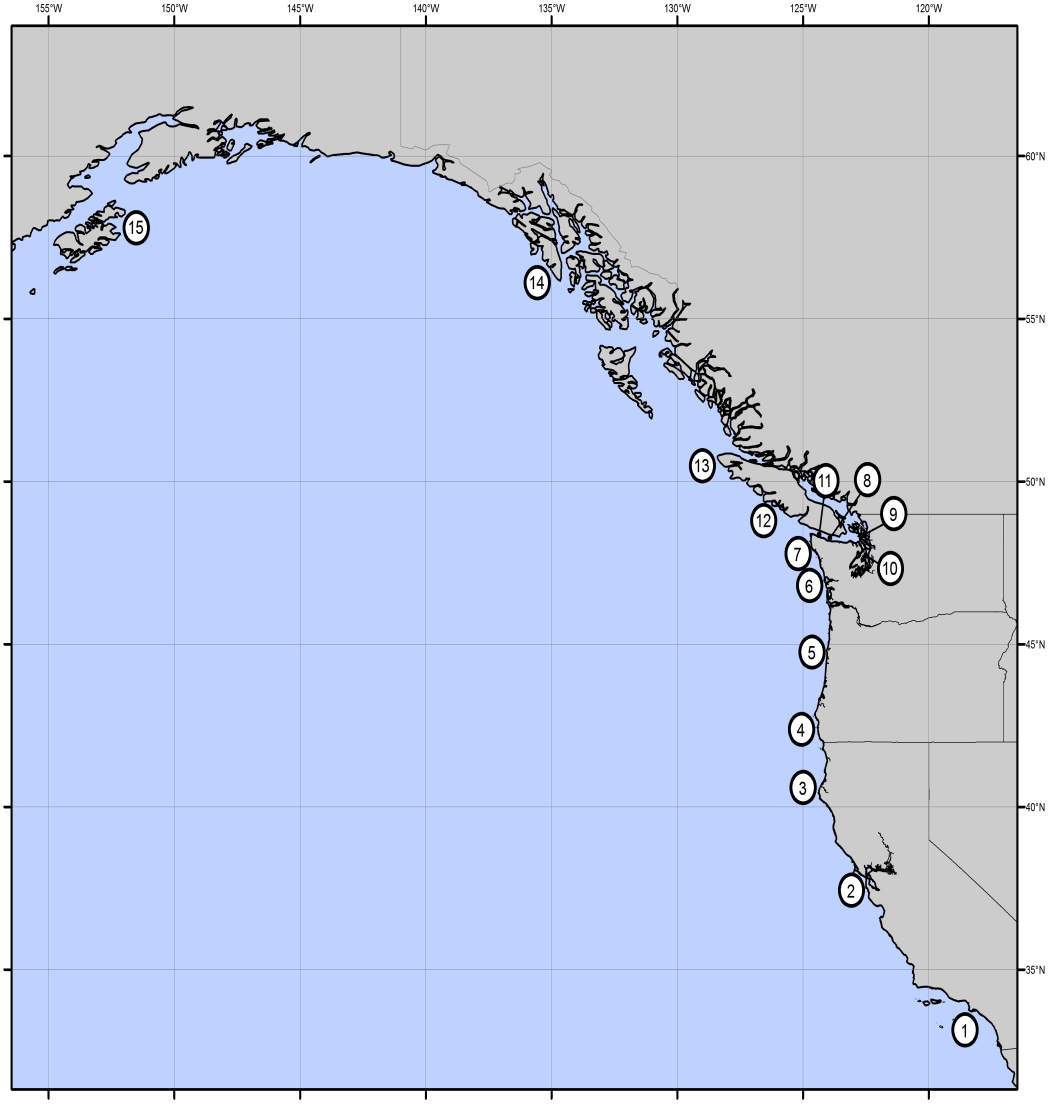


Figure 1: Locations for photo-identifications of gray whales. Numbers refer to values in Table 3.

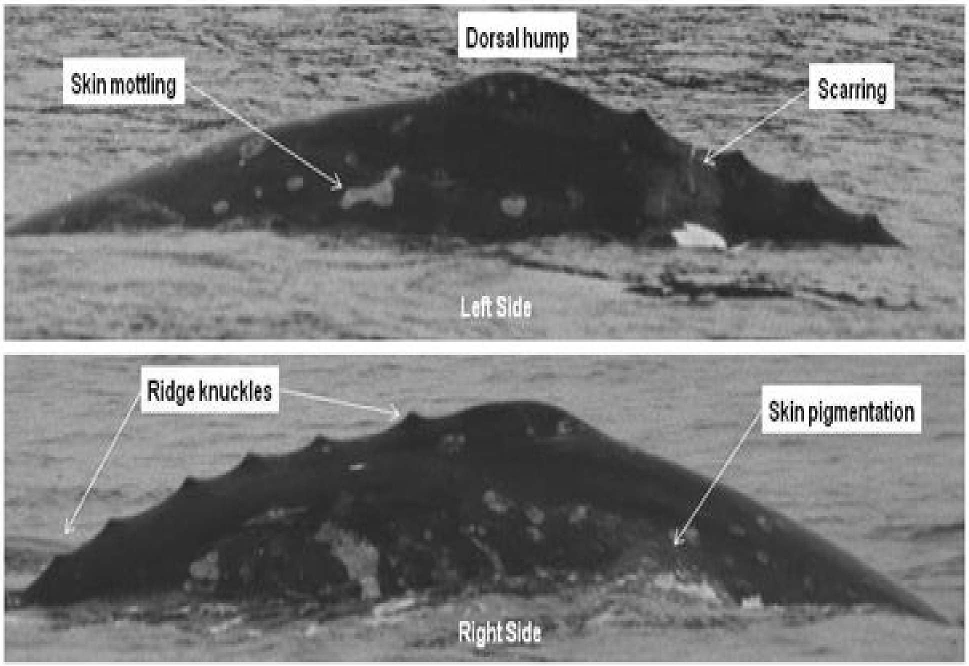


Figure 2: Characteristics used for gray whale photo-identification.

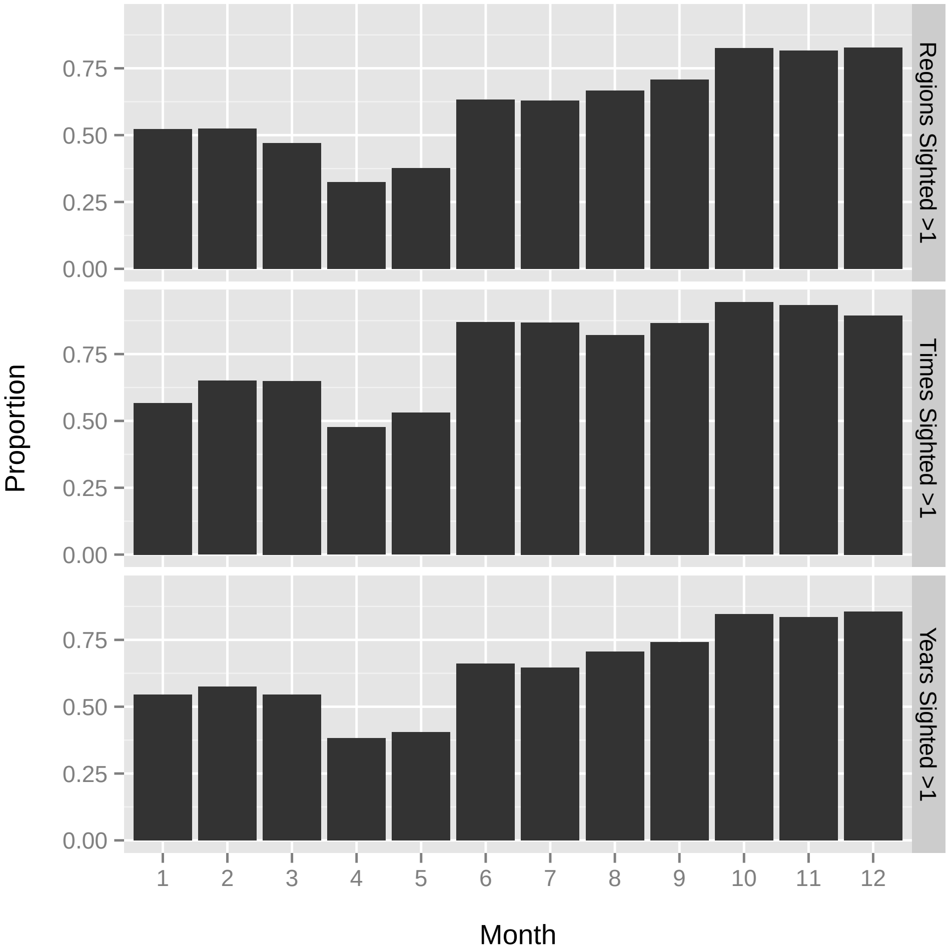


Figure 3: Monthly measures of proportion of whales that were seen in more than one region, seen on more than one day and seen in more than one year. The values include sightings from 1996-2012 in all regions from California to Alaska. Lower values imply whales were simply migrating through the area in a short time frame and were thus less likely to be seen at other times and in other regions. Values are not shown for months with fewer than 20 sightings. Whales seen more often are over-represented because they are used in each month they were seen. For example a whale seen in June, July and August will be in each summary. Thus, these values may be larger than values computed without splitting by month (e.g., overall proportion of whales seen in more than one year).

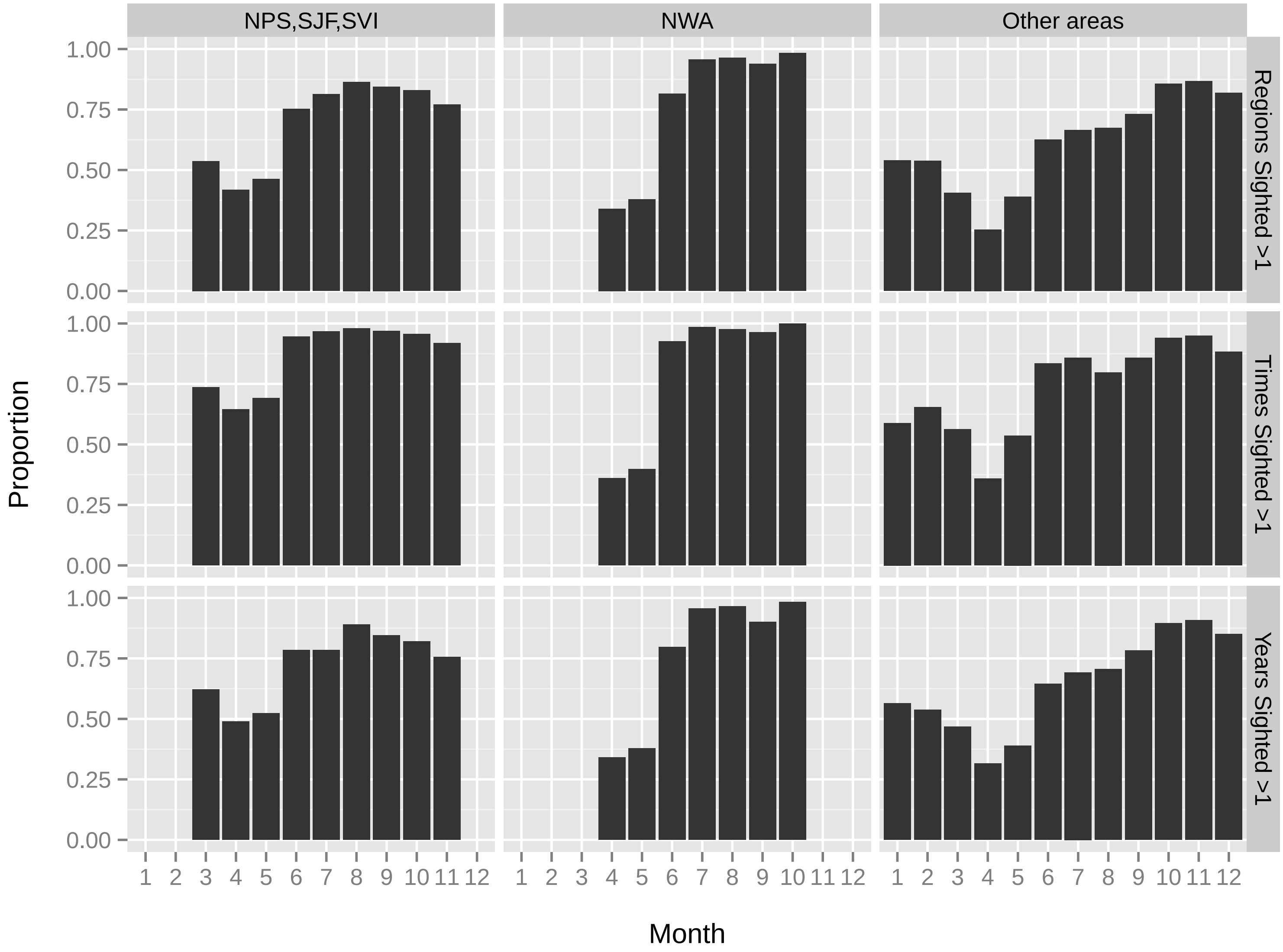


Figure 4: Region and monthly measures of proportion of whales that were seen in more than one region, seen on more than one day and seen in more than one year. The values include sightings from 1996-2012 in all regions from California to Alaska. Lower values imply whales were simply migrating through the area in a short time frame and were thus less likely to be seen at other times and in other regions. Values are not shown for months with fewer than 20 sightings. Whales seen more often are over-represented because they are used in each month they were seen. For example a whale seen in June, July and August will be in each summary. Thus, these values may be larger than values computed without splitting by month (e.g., overall proportion of whales seen in more than one year).

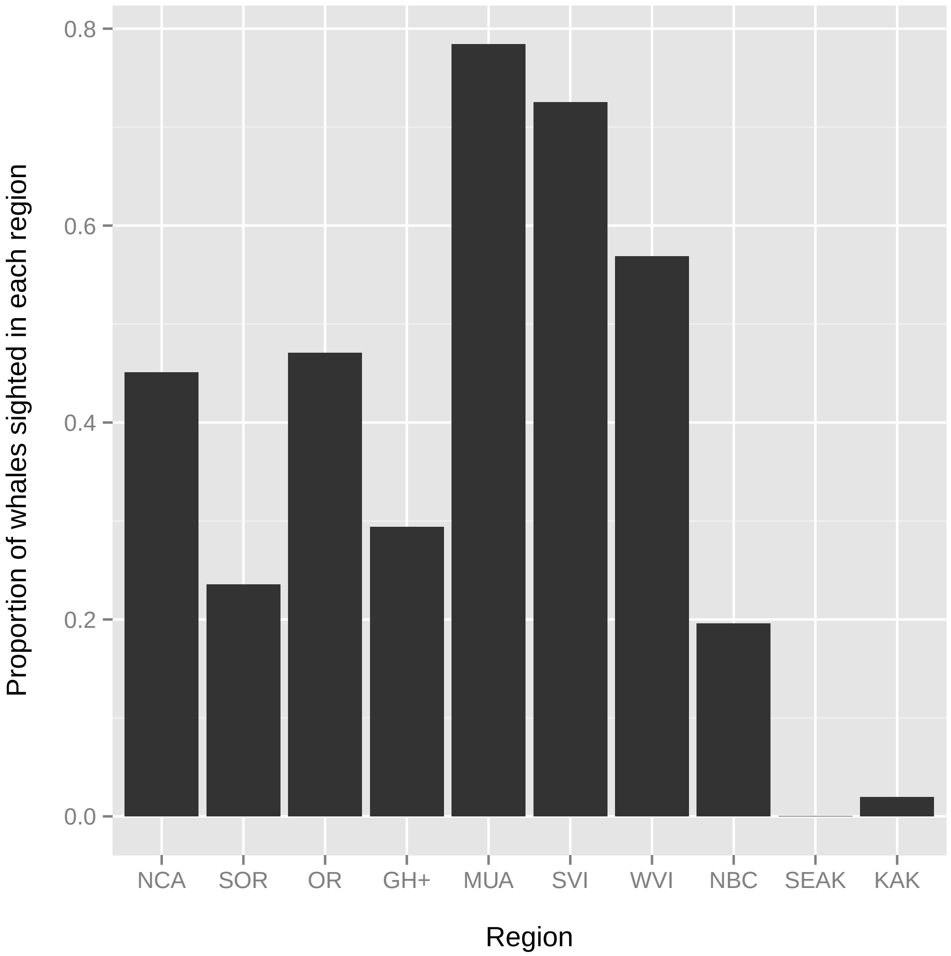


Figure 5: Proportion of the 51 unique whales seen in NWA during the spring and in the PCFG after 1 June that were seen in each PCFG sub-region after 1 June at least once from 1996-2012.

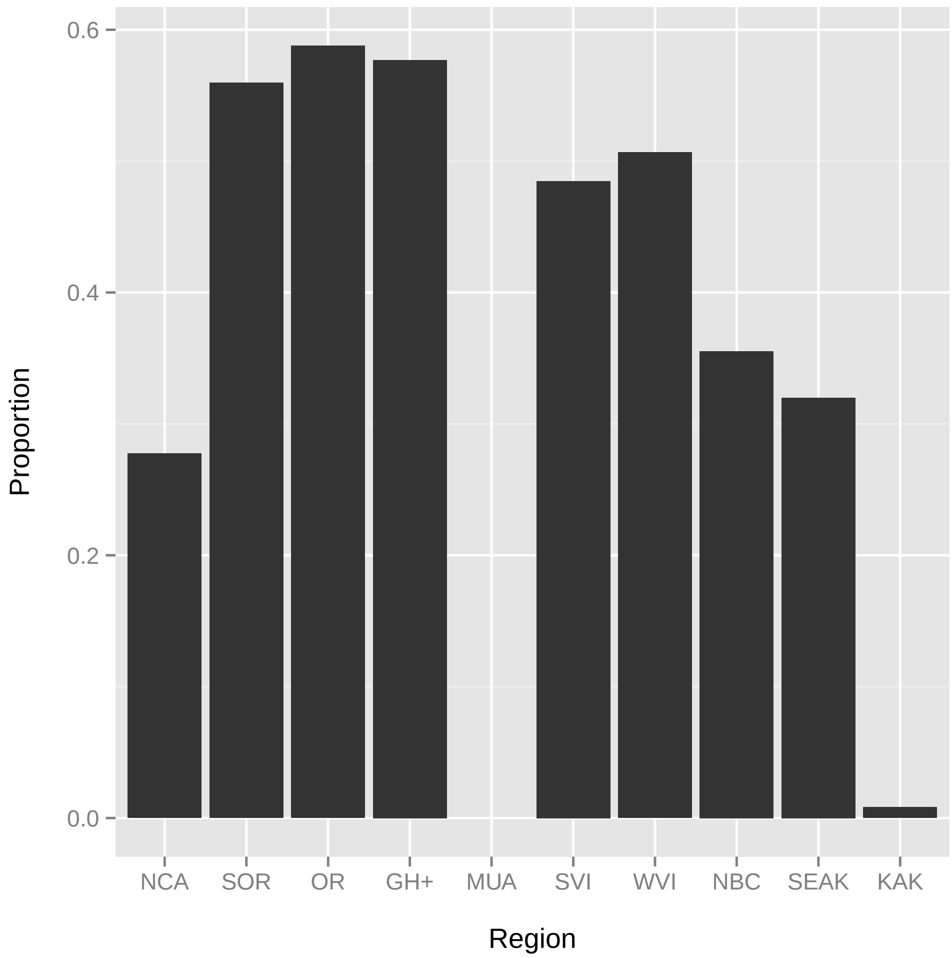


Figure 6: Proportion of whales in sub-regions from NCA to KAK that have been seen in the MUA using sightings after 1 June from 1996-2012.

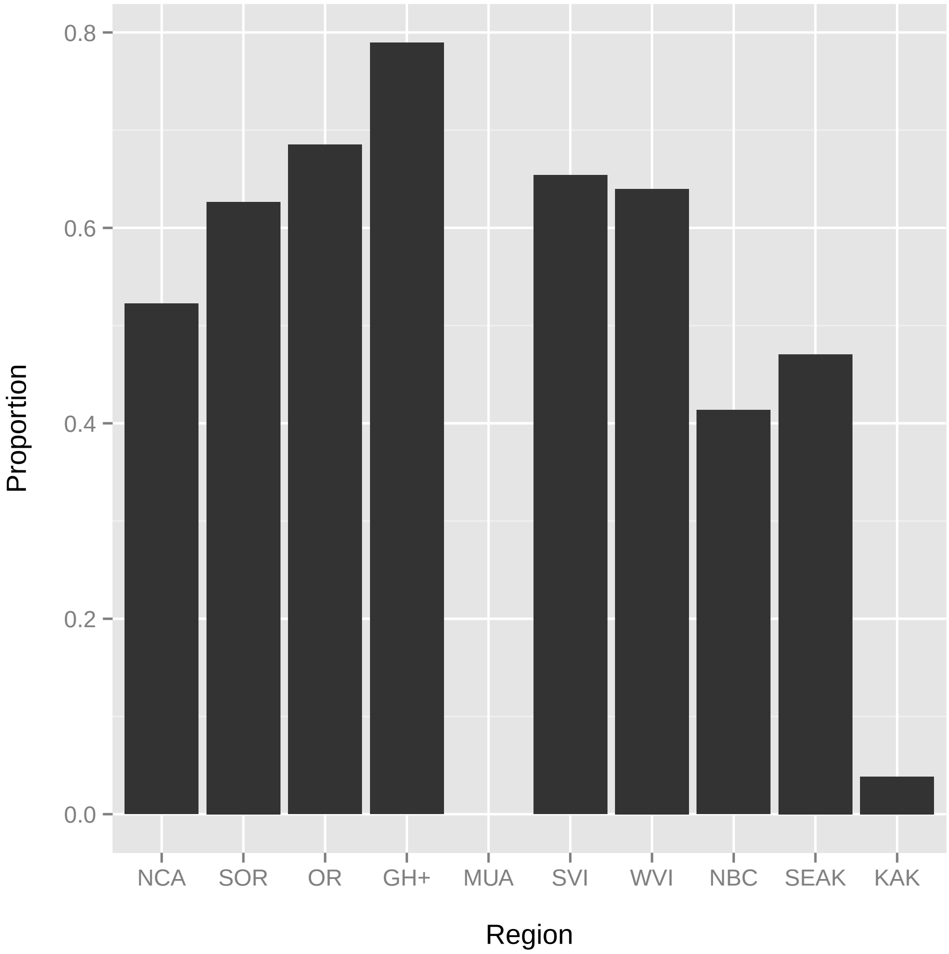


Figure 7: Proportion of whales seen in at least 2 years in sub-regions from NCA to KAK that have been seen in the MUA using sightings after 1 June from 1996-2012.

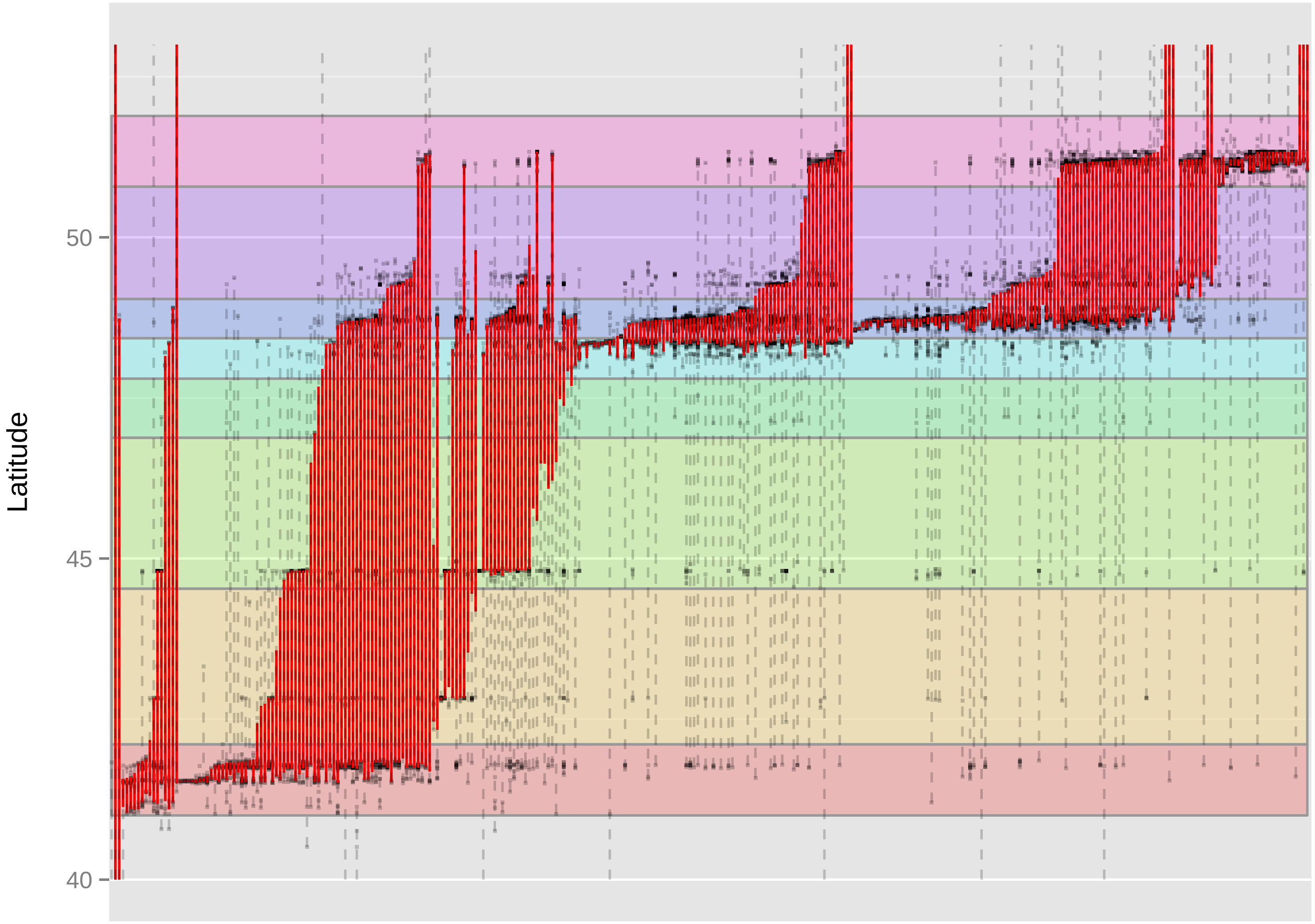


Figure 8: Distribution of latitudes of sightings (points) for whales with 6 or more sightings after 1 June from 1996-2012, the 75% inner quantile (solid thick line), and full range (light dashed line). Each position on the x axis represents an individual whale. Whales have been arranged on the plot by sorting first on the lower bound of the inner quantile (to a half-degree) and then the upper bound of the quantile. This has the effect of sorting from south to north and clusters whales with smaller quantile ranges followed by whales with larger ranges.

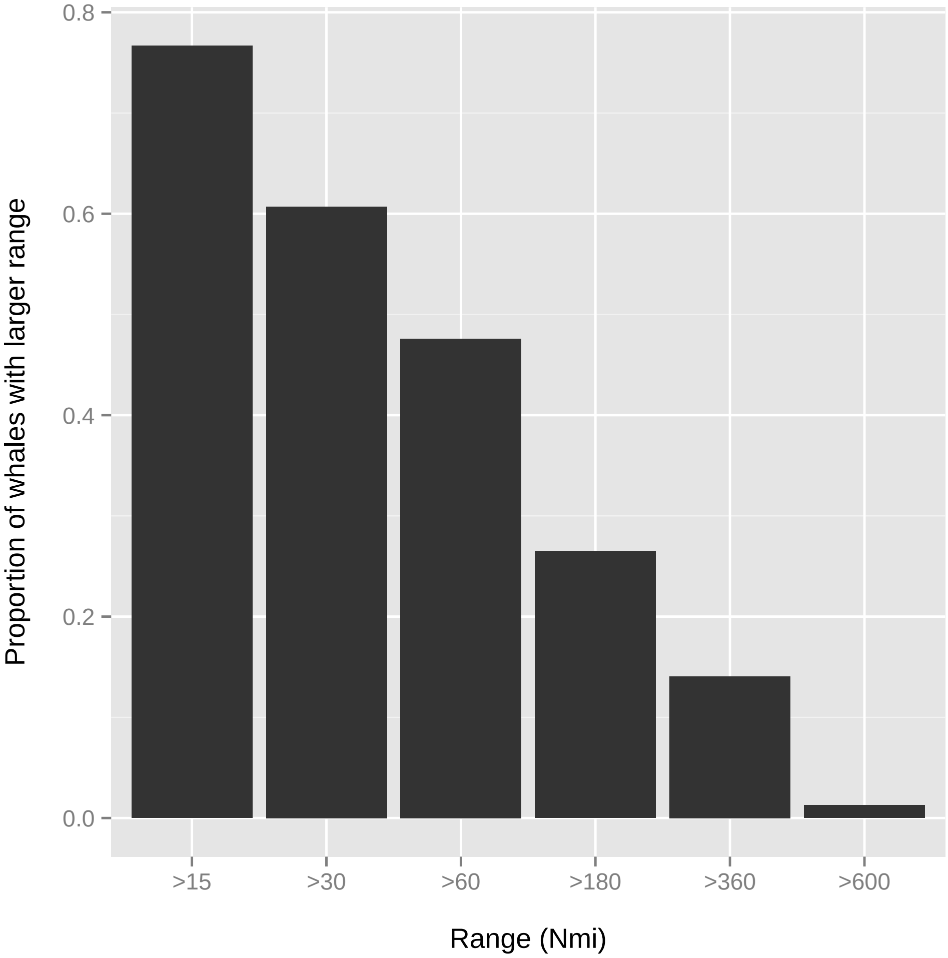


Figure 9: Distribution of ranges of 75% inner quantiles of latitudes expressed in nautical miles for whales sighted on 6 or more days during 1996-2012.

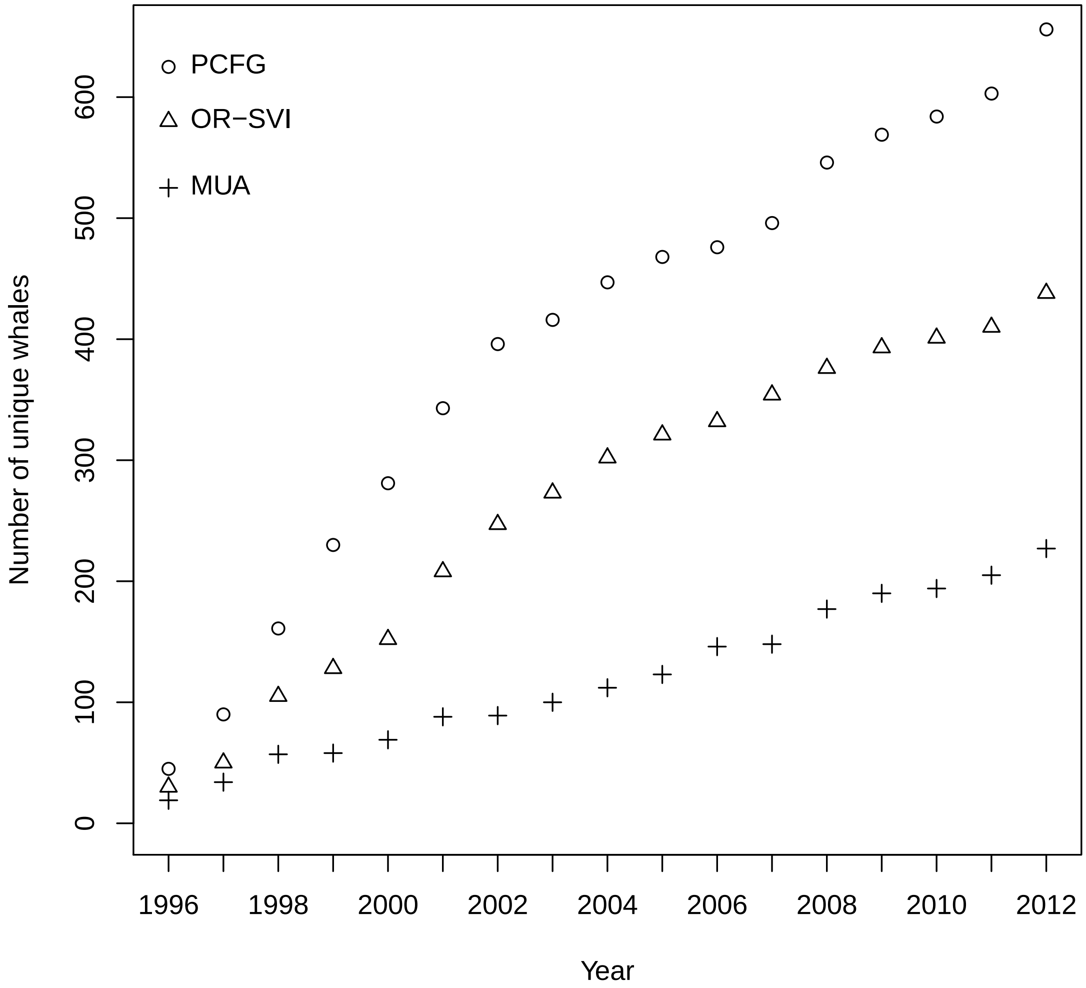


Figure 10: Discovery curves for unique whales seen in PCFG, OR-SVI and MUA for 1996-2012.

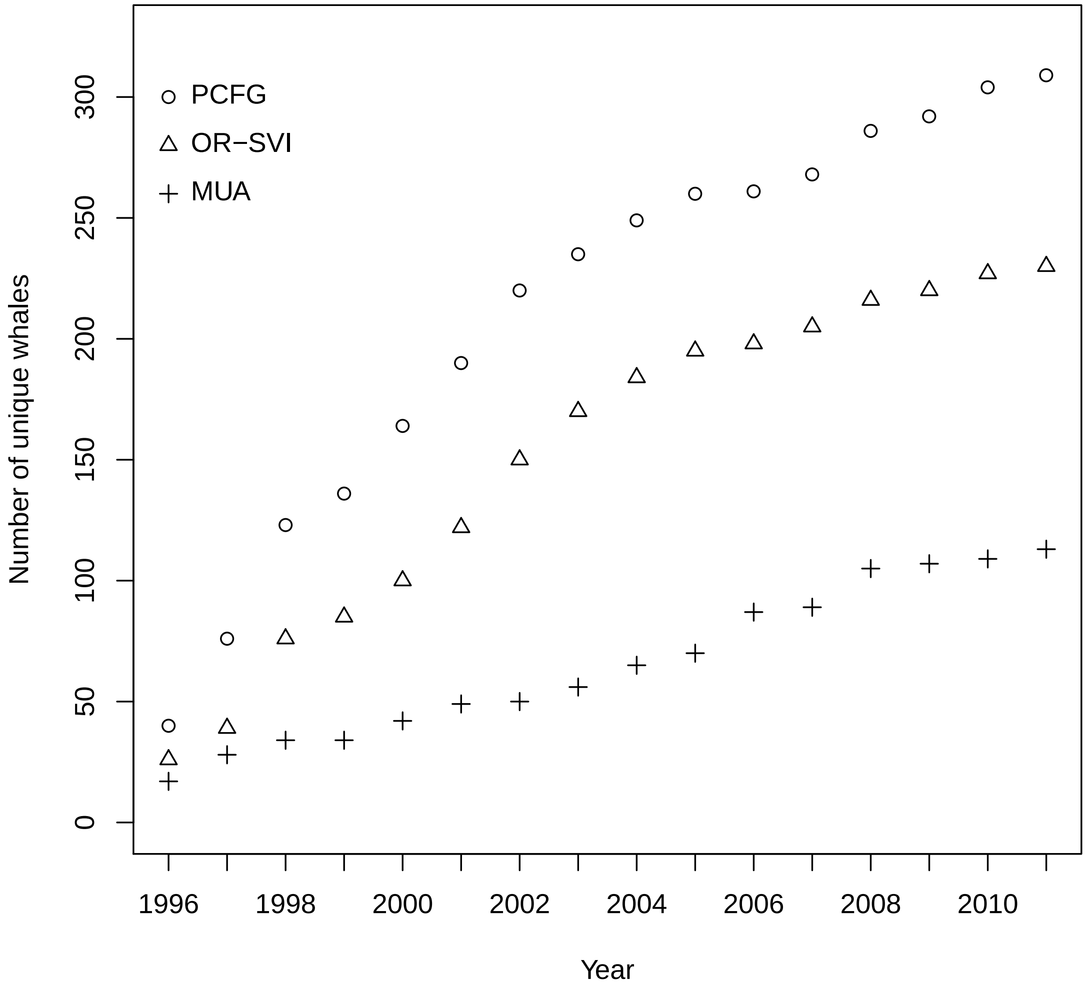


Figure 11: Discovery curves for unique recruited whales seen in PCFG, OR-SVI and MUA for 1996-2012.

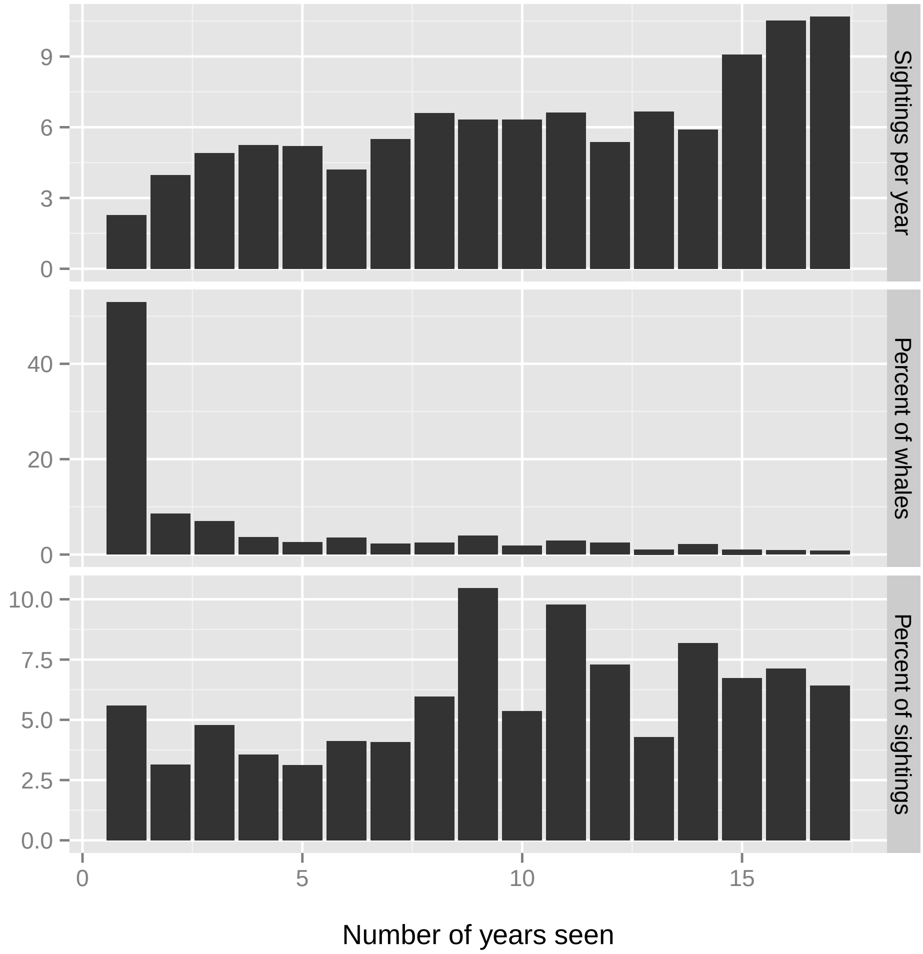


Figure 12: Average number of sightings per year and distribution of whales and numbers of sightings based on numbers of years a whale was seen in NCA-NBC between June-November during 1996-2012.

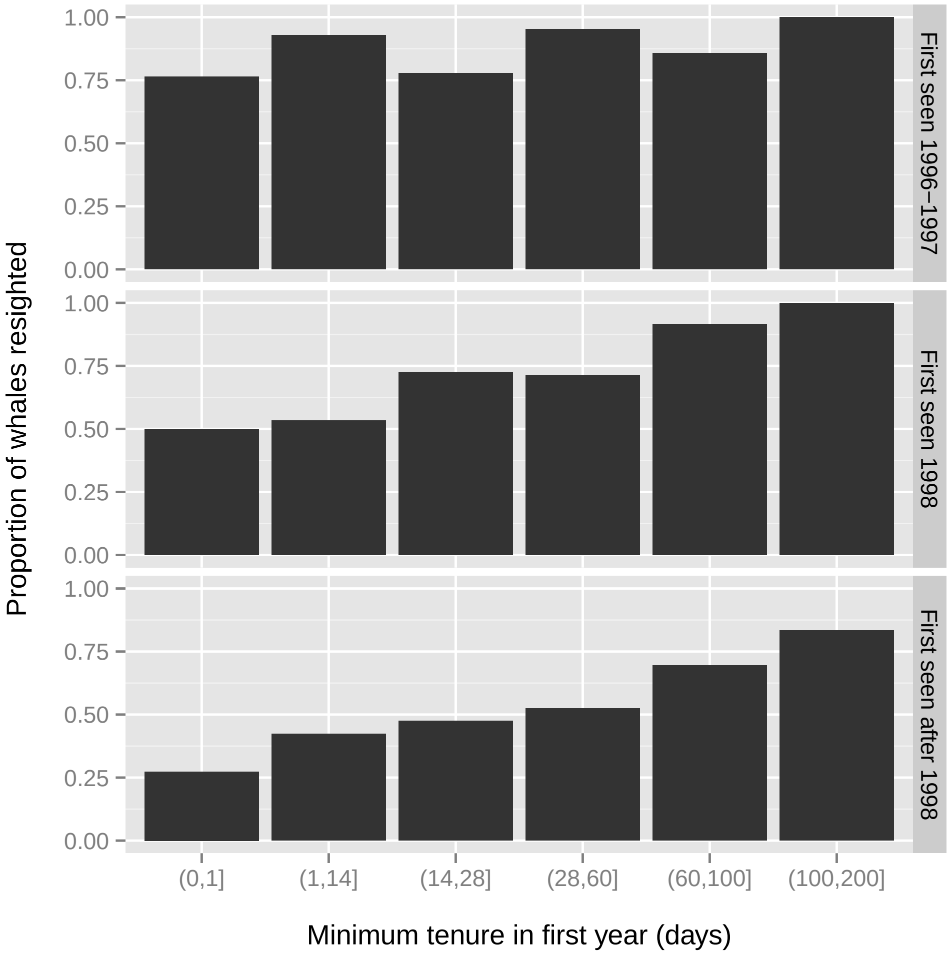


Figure 13: Influence of minimum tenure (MT) in the first year the whale was photographed on the probability it will be re-sighted in one or more following years for whales seen in NCA-NBC for June-November 1996-2012. The bar graphs are divided based on first year in 1996-1997, 1998 and after 1998. Re-sightings for 2012 are used but initial sightings for 2012 are excluded because there are no data beyond to evaluate re-sighting probability.

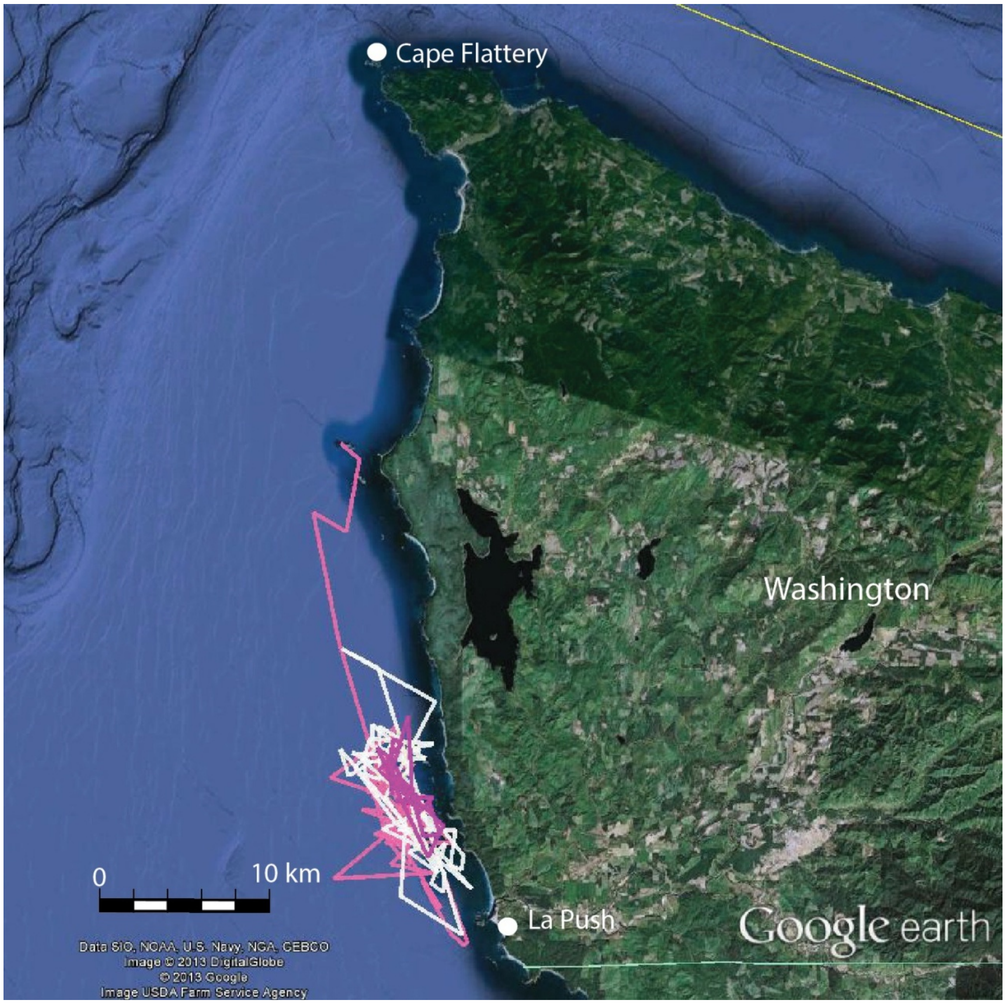


Figure 14: Map showing movements of three gray whales tagged 31 May 2012 near the northern tip of Washington.

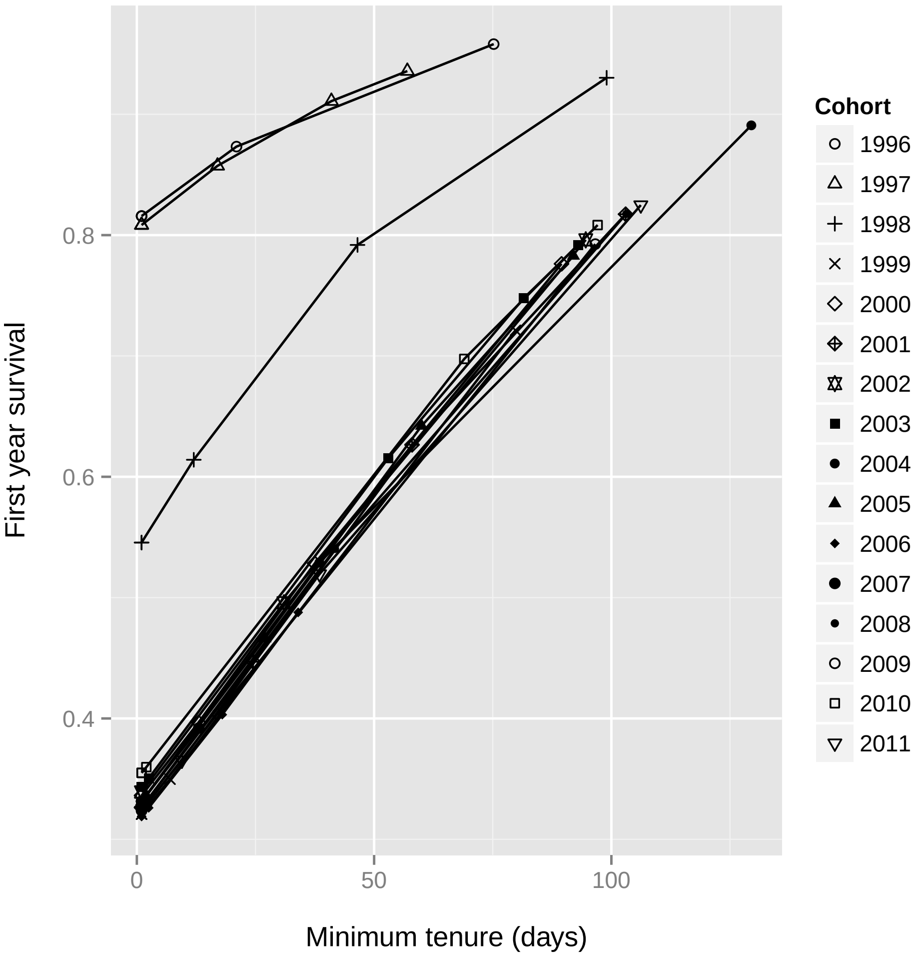


Figure 15: For NCA-NBC analysis of 1996-2012 data, model-averaged estimates of first year survival of non-calves for each cohort at 5%, 25%, 50%, 75%, and 95% quantiles of minimum tenure values for that cohort.

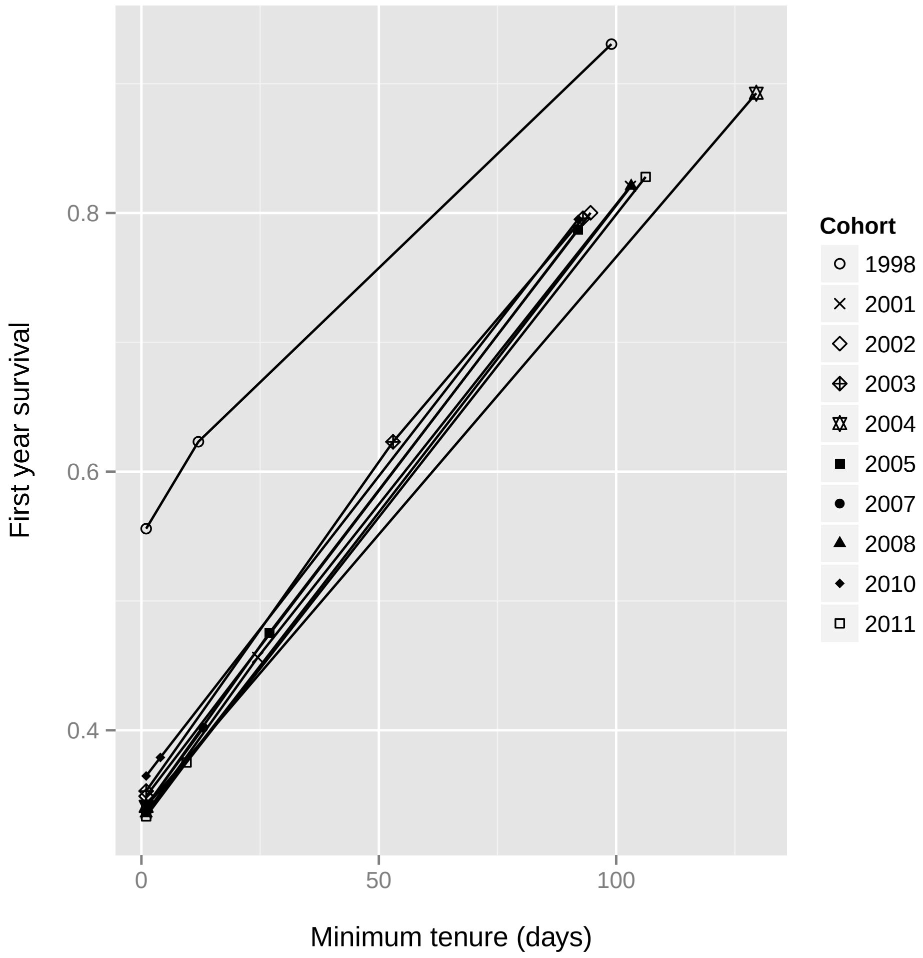


Figure 16: For NCA-NBC analysis of 1996-2012 data, model-averaged estimates of first year survival of calves for each cohort at 5%, 25%, 50%, 75%, and 95% quantiles of mini mum tenure values for that cohort.

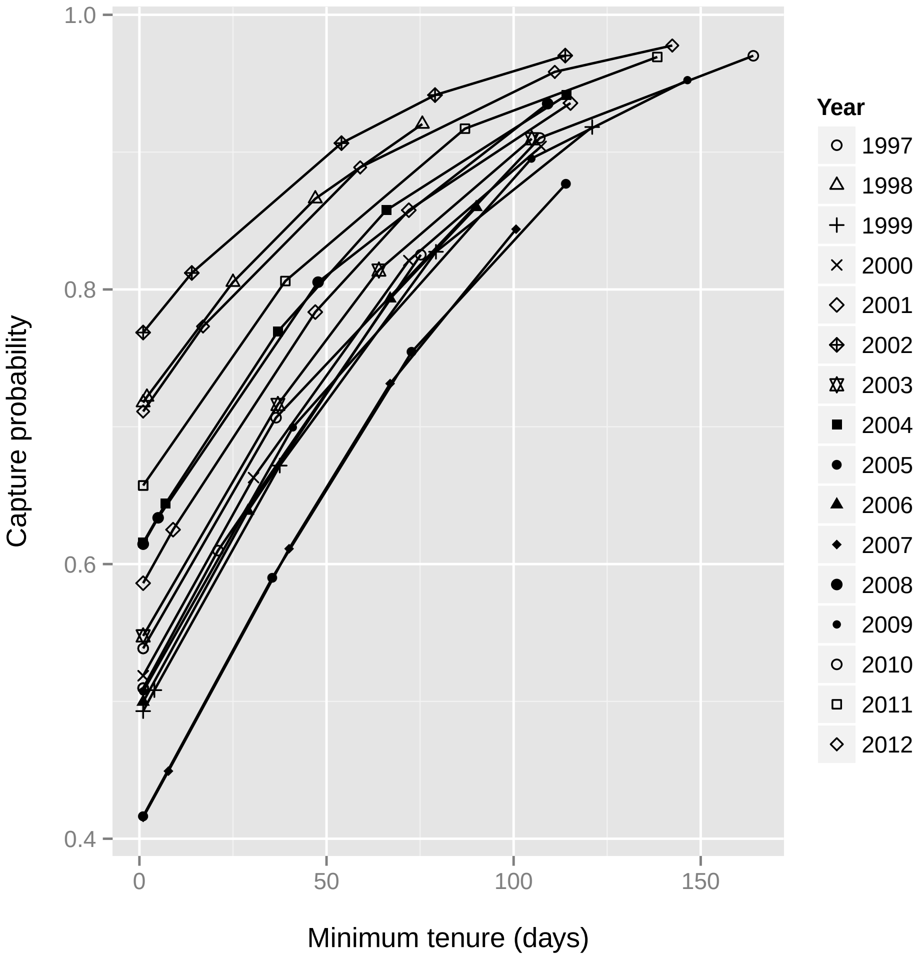


Figure 17: For NCA-NBC analysis of 1996-2012 data, model-averaged estimates of capture probability for each year at 5%, 25%, 50%, 75%, and 95% quantiles of minimum tenure values for whales in the previous year.

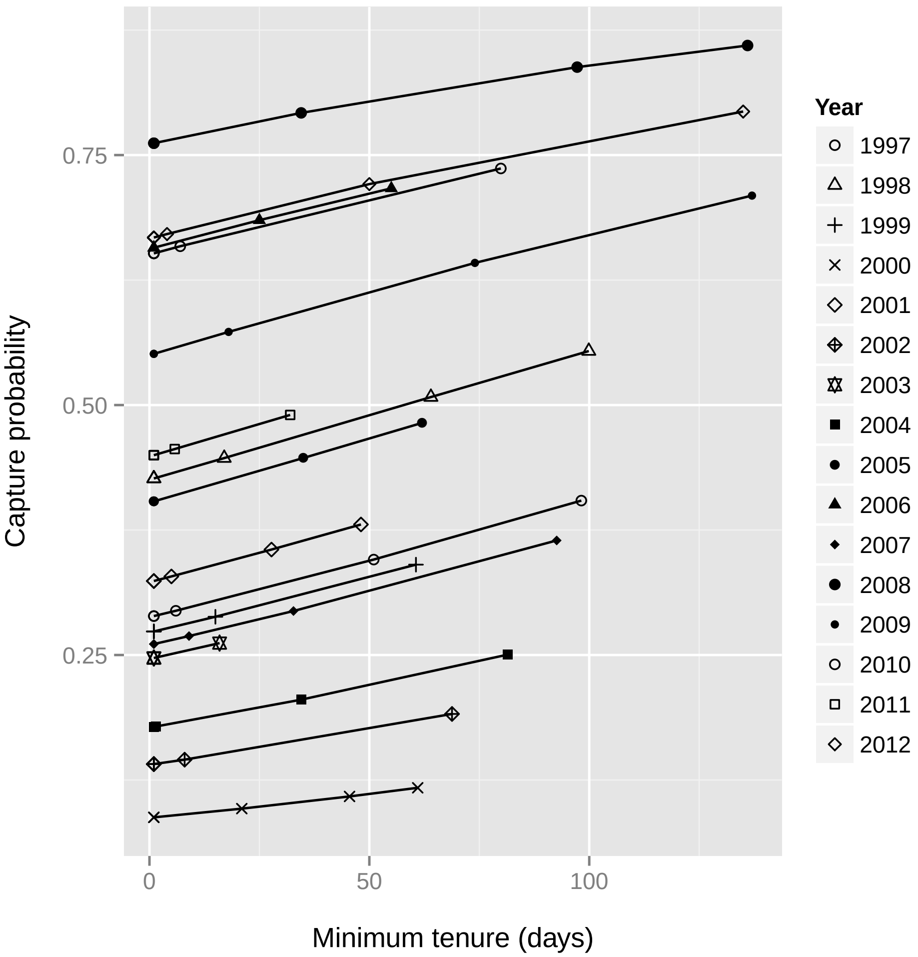


Figure 18: For MUA analysis of 1996-2012 data, model-averaged estimates of capture probability for each year at 5%, 25%, 50%, 75%, and 95% quantiles of minimum tenure values for whales in the previous year.

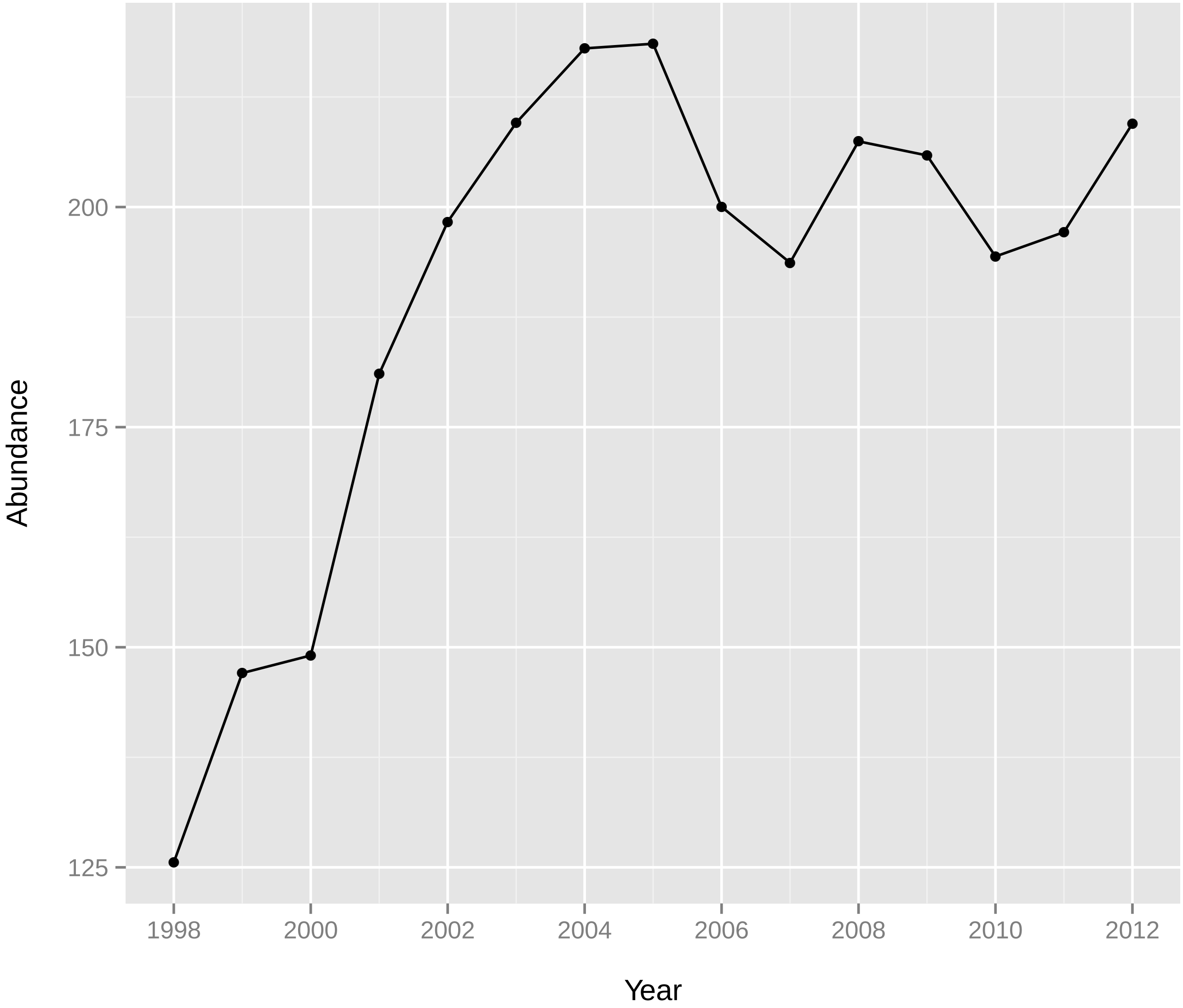


Figure 19: Annual abundance estimates for 1998-2012 in NCA-NBC using the open (Jolly-Seber; POPAN parametrization) population model approach JS1.

Appendix

Table 1 provides capture histories of whales seen in the PCFG at least once from 1 June - 30 November and displays by year, when they were seen only in spring (March-May), only from 1 June - 30 Nov and when they were seen in both time periods. Table 2 provides capture histories using data from 1 June - 30 Nov of whales seen in the MUA at least once. It shows when whales were seen only outside of the MUA but in the PCFG, only in the MUA and both inside the MUA and in the PCFG outside of the MUA

Table 1: Sighting histories of whales seen in the PCFG in at least one year. In year columns, a 1 means the whale was only sighted in the spring (March-May), 2 means it was only seen in June-Nov, and 3 means it was seen in both March-May and June-Nov. The region value is the nunber of years the whale was seen in that region.

1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	#years	NCA	SOR	OR	GH+	NWA	SJF	SVI	WVI	NBC	#areas
								2	2	2	2			2	2	2		2	2	2		2	2	2	2		2	2	17					1		3	12	8	4
								2	2	2	2	3			2														9				1				9		2
3																													1						1				1
2																													1						1				1
2					2	2							2	2	2	2	2	2	2		2	2	2							13					2	1	10	5	1	5
2						2			2	2	2	2		2	2	2	2	2	2	2	2	2	2	2	2				18	1			1		6	15	7	4	6
2						2		2	2	2	2	2	2	2	2	2	2	2	2	2									15		1	1		5	1	11	3	1	7
2									2					2	2														4			1		2		3	2		4
2									2			2	2	2	2	2	2	2	2	2		2		2	2		2	2	16	3		4		4		11	5	3	6
2				2				2		2	2	2		2	2	2	2	2	2	2	2	2	2	2	3	2	3	2	21				1	5	2	16	9	1	6
	2										2			2	2			2	2	2			1						8							2		6	2
		3																											1						1				1
		3																											1					1	1				2
		2																											1						1				1
		2													2		3	2		2		1	2	2	2	2	2	2	12	5	3	3	3	1	1				6
		2											2	2	2	2	2	2	2		2		2		2	3	3	2	14	6	2	3		1	1	4	1		7
			2																										1							1			1
				2				2				2		2	2	2	2	2	2	2	2	2		2		2	3	2	16					1	2	8	8	3	5
					2			3	3		2	1		1		3	2	2		2									10		1	1	6	2			1	1	6
					2																								1					1					1
					2																								1					1					1
					1			3							1														3				3						1
					1														2										2				1			1			2
						2																							1							1			1
						2																							1							1			1
						2		2		2	2	2		2	2	2	2	2	2	2	2	2	2	2		2	2	2	19				1		1	8	9	7	5
						2																							1							1			1
						2																							1							1			1
						2	2	2				2		2	2	2	2	2	2	2	2	2		2	2	3	3	2	18					1	3	14	5	6	5
						2			2	2		2																	4					2			2		2
						2			1		2		2	2	2		2	2	2	2	2	2	3	2	2	1		3	17			1	1	4		7	9	6	6
						2				2	2	2		2	2	2	2			2	2	3							11			1		2		4	9	2	5
							2				2					1	2	2			1	1		2	2	2	2	3	12	8			4						2
							2							2	2														3	3									1
							2							2		2	2	2											5	5									1
							2							2	2														3	3									1
							2								2	2	2	2	2	2	2	2	2	2	2				12	1	5	1				4	2	3	6
							2																						1	1									1
							2																						1	1									1
							2									2	2												3	3									1
							2										2	2							2	2	2	2	7	7		1							2
							2							2		2	2	2		2	2					3	2	2	10	7		2				2	1		4
							2																						1	1									1
							2							2		2	2	2					2		3	2	2		9	7			1	1			1		4
							2							2			2	2	2	2	2	2	2	2	2	2	2	2	14	8	6	2		1		4	1		6
								3																					1				1						1
								1			3																	2	3	1			2						2
								2							1														2				2						1
								2			2	2	2		2			2		2	2	3					2	2	11		1	2		5	7	3	1		6
								2	1	2		2	2																5					2	3				2
								2							2			2	2							2	2	2	7							2	1	5	3
									3	1	2					2	2	2		2				2	2		2	2	11	2		1	3			4	1		5
									2	2	2			2			2	2	2	2	2	1							10	2	3			5	1	6	2		6
									2	2	2	2		2	2	2	2	2	2	2	2								12					3	1	3	1	9	5
									2	2	2	2		2	2	2	3	3	3	2	2								12					7	3	8	3	2	5
									2		2		2	2	2	2	2	2	2	2	2	2	2		2				14					4	3	9	7	3	5
									2																				1					1					1
									2	3		2	2	2	2	2	2	2	2	2				2					12		2	1		5	1	1	6	5	7
									2		1		2	3	3	3	3	2	3	3	3	2	3	3	3	3	3	3	18		1	2		7	1	17	2		6
									2			3		2	2	2	2	2	2	2	2	2	2	2	2	3	2	2	17	5	1	2	1	5		12	5		7

Cont.

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1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	#years	NCA	SOR	OR	GH+	NWA	SJF	SVI	WVI	NBC	#areas
									2					2	3	3	3	2	2	2	2	2	2	3	2	2	2	2	16	5	4	6		7		13	4		6
									2																				1					1					1
									2			2	2	2		2	2	2	2		2		2	2			2		12		2	1		2	1	6	2	8	7
									2			2	2	3	2	2	2	2	2	2	2	2	2	3	3	2	3	3	18				1	10	5	16	3		5
									2	2				2	2	2	2	2	2	2	2	3	2	2	2	3	2	2	17	1	1	8		4	1	14	6		7
									2																				1					1					1
									2																				1					1					1
										2																			1					1					1
										2				2	2	2	2	2	2	2	2	2	2						11			1		1	2	7	3	5	6
										2																			1					1					1
										2	2		2	2	1	2	2	2	2	2	2	2	2	2	2	2	2	2	18			6	1	9	2	13			5
										2			2	2			2			2				2				2	7	2		1				1		5	4
										2	2		2	2		2	2	2	2	2	2	2	2	2	2	2	2	2	17		1			2	2	13	3	4	6
										2			2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	3	17							11	10	11	3
										2	2	1																	3				1	1	1				3
										2		2	2	2	2	2	2	2	2	2	2	3	2	3	2	2	2	3	18	1		5	1	1	1	16	9	1	8
										2		2	1	2				2	2	2	2	2		2	2		3	2	13				1			9	4	3	4
										2			2	2	2	2	2	2	2	2	2								10							4	2	7	3
										2			2			2			2	2		2							6							1		6	2
											2																		1						1				1
											3	1																	2				2						1
											3	1																	2				2						1
											2			2	2	2	2	2	2	2	2	2	2	2	2	3	2	2	16				1		1	13	10	5	5
											2	2		2	2	2	2	2	2		2	2		2	2	2	2	2	15	3				1		10	7		4
											2			2	2	2	2	2	3	2	3	2	3	3	3	1	3	3	16					1		12	9	5	4
											2		2		2												1		4							1	1	2	3
											2		2		2	2	2	2											6									6	1
											3																		1				1						1
											2	2	2	2	2	3	3	2	2	2	2	3		2	2	2			15	1		2	1	4	3	11	1	1	8
											2						2	2	2	2	2	3	2	2	2	2	2	2	13	2	1	2	2	5	1	5		2	8
											2																		1						1				1
											2																		1						1				1
											2																		1						1				1
											2	2	2	2															4					3	2	1	1		4
											2	2	2	3	2	3	2	2	3	2	2	2	2						13	1		1		5	5	9	7		6
											2		2	2	3														4					3	2	2	1		4
											2	3	2	2	3	2	2		2	2	2	2	2	2	2	1	2		16				1	4	7	1	9	2	6
											2		2																2						2				1
											2																		1						1				1
											2																		1						1				1
											2																		1						1				1
											2	2	2	3	2		3	2		2									8					1	2	5	2		4
											2		3	3	2	3	3	3	2	2	3	3	3	2	3	2	3	3	17			3	1	3	4	16			5
											2		2	2	2						2								5			1				1	1	5	4
											2		2	2	2		2	2	2	2	2	2		2	2	2		2	14							9	5	7	3
											2		2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	17					3	4	13	8	7	5
											2		2	2	2	2	2	2		2	2	2	2	2				2	13			1		1	2	3	6	7	6
											2		2	2				2	2	2		2							7								1	7	2
											2		2	2	2	3		2	2	2	2			2		2	2	1	13						1	1	1	12	4
											2		2	2	2														4									4	1
											2		2	2		2	2		2	2	2	2		2				2	11								2	10	2
											2		2	2	2	2	2	2	2	2	2	3	1	2	2	1	2	2	17						1	5	4	11	4
											2							2	2	2				2					5									5	1
											2		2					2	2	2		2						2	7									7	1
											2		2		2			2	2	2						1	2		8	1				1				6	3
											2									2									2									2	1
											2																		1							1			1
											2																		1							1			1
												2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	2	17	4			1			15	3	2	5
												1	2	2	3	3	2	2	2		2	3	3	2	2	1	2	3	16							15	9	2	3

Cont.

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1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	#years	NCA	SOR	OR	GH+	NWA	SJF	SVI	WVI	NBC	#areas
												2	2	2	2	3	3	2	3	2	2	2	2	3	2	3	3	3	17	1		1	1	7	3	14	7	1	8
												2	2	2	2	3	3	2	2	2				2		2			11					3	3	10	2		4
												2		1															2				2						1
												1			1			2	2	2	2	2							7				1	1	1	5	1	1	6
												2	2	3	3	3	3	3	3	2	2	2	2	2	3	3	3	3	17		1	3	1	7	3	15	2		7
												1				2		2	2		3	2	2	3	3	2	2	2	12	4	1	3	1	5		9	1		7
												1		2															2	1			1						2
												1	1	2	2	2	2	2	2		2	2	2	2	2	2	3	2	16	6	2	7	2	6		6	2		7
												3	2		2	2	2	2	2					2	2	2			10	1			1	7	4	3	2		6
												1		2	2	2	2	2	2				2		2	2	2	2	12	8	4	4	1						4
												1												2					2				1		1				2
												2	2	2															3					2	1	2			3
												2																	1					1					1
												1		2				2	2	2			2		2				7	2	3	3	1	1	1				6
												1		2		2	2	2	2	2	2	3	2		2	1	3	2	14							14	3	4	3
												2	2	2	2	2	2	2	3	2									9			1				2	2	9	4
												2		2	2	2	2	2			2		3		2	2	2	3	12	2	1	2		2		8	8		6
												2	2	2	2	2	2	2	2	2							2	2	11							1	1	11	3
												2	2	2	2	2	2	2		2		2							9							1	3	8	3
												2	2	2															3							1	1	3	3
												2					2	2	2	2				2					6									6	1
												2						2	2	2		3							5							1		5	2
												2																	1									1	1
												2																	1									1	1
												2																2	2								1	1	2
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													2	2	2	2	2	2	2	2	2								9					2	2	4	1	7	5
													2																1						1				1
													2																1						1				1
													2																1						1				1
													2	2															2							1		1	2
													2	2	2	2	3	2	2	2	2			2		2			11	1	1					10	2		4
													2	2			2	2	2	2	2	2					1		9							1		8	2
													2	2			2	2						2				2	6							3	1	5	3
													2	2				2		2					3			2	6	2		1	1					4	4
													2			2	2	2	2	2		2	2	2	2	2	2		12	6	3	1		3		2	1	2	7
													2					2	2	2									4									4	1
													2							2									2									2	1
													2																1									1	1
													2																1									1	1
													2																1							1			1
													2																1							1			1
													2																1							1			1
														2	2	2	2	2	2	2	2	2							9							1	7	4	3
														2	2														2							1	2		2
														2		2	2	2	2	2		3	2	3	3	3			11				1			9	5		3
														2	3	2	2	2			2	2				2			8	1	1			2		8	1		5
														2															1						1				1
														3	3			3	2	2	2	2	2	2	2	2	2	3	13	1	7	2		2		7			5
														2		2	2		2								3		5	1						4	3		3
														1										2					2							2			1
														2															1						1				1
														2	2	3	2	2		2	2	3	2	2	3				11					2	7	8	2	1	5
														2															1							1			1
														2															1							1	1		2
														2															1						1				1
														2															1						1				1
														2															1					1					1
														2															1						1				1
														2															1						1				1

Cont.

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														2															1						1				1
														2															1						1				1
														2															1						1				1
														2															1					1					1
														2		2									2		3	3	5	4				2			1		3
														2			2	2	2		2				2	3	3	2	9	7	1	1							3
														2															1	1									1
														2				2	2			2	2		2	2	2	2	9	5	1		1	1	1	2	2		7
														2															1	1									1
														2	2	2	2	2	2	2	2	2		2	2	2	2	2	14	10	2	4		1	1	3	1		7
														2															1	1									1
														2			2	2	2	2			2				2	3	8	3	3	4		1					4
														2															1	1									1
														2	2	2	2	2	2	2		2	2	2			3	2	12	3		2		7		5	1	1	6
														2	2		2	2	2		2	2		2	2		2	2	11	5	1	6		1					4
														2															1			1							1
														2	3	3			2			2	2	2	2				8	2		2		1		5	2		5
														2	2	2	2	2	2		2								7	2	1	3		1		3	2		6
														2	3	2		2	2	2	2	2	2	3	3	3	2	2	14	1		8	1	6	1	8	3	3	8
														2	2		2	2	2	2		2	2		2	2	2	2	12	1	1	6		1		4	3		6
														2															1					1					1
														2	2	2	2	2	2	2		2		2					9							2	6	4	3
														2											1				2								2		1
														2	2			3	2	2	2	2	2	2	2		3	2	12	2		1				4	5	4	5
														2	2														2	1							1		2
														2	2	2	2	2	2	2		2	2	2	3	3	2	3	14	5		4	1	3		1	8		6
														2			2									2			3	1						2	1		3
														2															1								1		1
														2	2	2	2	2	2	2	2	2	3	2	3		3	3	14		1	3		3	2	9	10		6
														2		2	2	2	2	2		2		2	2	2	2	2	12	4		2		4		3	4		5
														2	2	3	2	2	2	2	2								8							4	4	5	3
														2		2		2		2	2	2		2	2	2			9							4	3	7	3
														2				2	2	2		2		3	2	2		2	9					2	2	2		5	4
														2															1									1	1
														2															1						1				1
															2														1								1		1
															2														1						1				1
															2														1			1							1
															2														1	1									1
															2														1	1									1
															2														1	1									1
															2	2		2			2		2		2	2	2	2	9	4	2	7		1					4
															2	2	2	2	2					2	2	3	2	3	10	10	2								2
															2		2	2								2	2	3	6	2	1	3				1	3		5
															3	1	3	2		2						2	2	2	8	2	1	1	4			1			5
															2	3		2	2	2	2	2	2		2	2	2	2	12			1	1	5		10	2	1	6
															2														1			1							1
															2														1	1		1							2
															2														1	1									1
															2														1			1							1
															2														1	1									1
															2														1	1									1
															2														1	1									1
															2														1	1									1
															2				1										2							1	1		2
															2														1								1		1
															2														1								1		1
															2		2	2	2	2			2						6	1	2	1		1		2	1		6
															2														1								1		1
															2														1	1									1

Cont.

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															2														1			1							1
															2	2	2	2					2	2	2	3	3		9	8		3							2
															2														1	1									1
															2														1			1							1
															2														1								1		1
															2														1								1		1
															2														1	1									1
															2														1	1		1							2
															2														1	1									1
															2														1								1		1
															2														1								1		1
															2														1	1									1
															2														1	1									1
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															2														1	1									1
															2														1	1									1
															2														1	1									1
															2	2													2								2		1
															2														1			1							1
															1	2		2						2	2	3	2	2	8	6	1			1	1				4
															2														1	1									1
															2														1	1									1
															2														1	1									1
															2														1	1									1
															2														1	1									1
															2														1								1		1
															2														1	1									1
															2														1								1		1
															2														1								1		1
															2														1								1		1
															2														1	1		1							2
															2														1								1		1
															2	2	2												3							2	2		2
															2	2	2	2	2	2	2	2	1						9							4	1	8	3
															2														1							1			1
															3														1							1			1
															2														1									1	1
															2														1							1			1
															2														1								1		1
															2														1								1		1
															2														1								1		1
															2														1								1		1
																2	3	2	2	2		2		2	2	2	2	2	11				1	8	5	10	2	1	6
																2													1								1		1
																2													1								1		1
																2													1								1		1
																2													1								1		1
																2	2												2					1		2			2
																2													1			1			1				2
																2	2	2	2	2		2	2	2	2	2	2	2	12	4	2	1	1	6		8	2		7
																2													1							1	1		2
																2													1								1		1
																3	3	2											3					1	1	2	1		4
																2													1						1				1
																2													1								1		1
																2													1							1			1
																2	2	2		2	2	2	2	2	2	2		2	11	1		1	1	1	1	7	6	1	8
																2													1							1			1
																2													1								1		1
																2	2	2	2	2	2	2		2	2	2	2	2	12	4	1	3		7		7	1		6

Cont.

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																2			2				2	2	2	3	2	2	8	5	4	1		1					4
																2	2	2		2									4			1						3	2
																2		2											2					1			1		2
																2		2							2	3	2	2	6	4	3	2		1		1			5
																2		2		2	2								4	2						2			2
																2													1	1									1
																2		2	2			2			2	2	2	2	8	7	3	1				1			4
																2													1	1									1
																2													1	1									1
																2													1	1									1
																2													1	1									1
																2													1	1									1
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																2		2		2									3	2	1								2
																3													1	1									1
																2													1	1									1
																2		2					2		2	2	2	2	7	5	1	3							3
																2				2						2			3	2						1			2
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																2		2	2	2	2	1	3	2		1		2	10							8	2	7	3
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																2													1							1			1
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																	2		2	2	1	2	2						6						1	2	1	2	4
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																	2	2	2	2		1							5					4	2	2	1		4

Cont.

Table 1: Sighting histories of whales seen in the PCFG in at least one year. In year columns, a 1 means the whale was only sighted in the spring (March-May), 2 means it was only seen in June-Nov, and 3 means it was seen in both March-May and June-Nov. The region value is the nunber of years the whale was seen in that region.

1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	#years	NCA	SOR	OR	GH+	NWA	SJF	SVI	WVI	NBC	#areas
																	2												1							1	1		2
																	2	2											2	1				2					2
																	2												1					1					1
																	2												1						1				1
																	2						2		2	2	2	2	6	5	1	2				1	1		5
																	2	3	3										3							3	1		2
																	2												1							1			1
																	2	2						2	2	2	2	2	7	6						1			2
																	2												1	1						1			2
																	2												1							1			1
																	2												1	1									1
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																	2												1			1							1
																	2		2	2									3	1	2	1							3
																	2						2		2				3	2		1							2
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																	2	2	2										3	2				1		1			3
																	2	2											2	1	1								2
																	2	2	2		2			2	2	2	2	2	9	7		1		1		1	2		5
																	2												1	1									1
																	2												1									1	1
																	2	2	2	2				2				2	6							3		5	2
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																		2		2							2		3	1							1	1	3
																		2											1	1									1
																		2											1		1								1
																		2	2										2		1					1			2
																		2	2										2		2								1
																		2	2		1	1	3	2	2	2	2	3	10	4	6	2	3						4
																		2											1		1								1
																		2		2				2	2	2	3	2	7	3	6	1		1		2	1		6
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																		2											1		1								1
																		2											1	1									1
																		2		2			2			1		2	5	1	1	2		1					4
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																		2											1							1	1		2
																		3	2	2	2	3	3	2	3	3	3	2	11	1			1	5	4	10	4		6
																		2		2	2								3						2	2	2		3
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																		2											1							1			1
																		2	2	2	3	3		2	2	2	2	3	10	3		2		6	8	10			5
																		3			1						3		3						1	3			2
																		2	2	2	3	3	2	2	2	3	2	2	11	3	1	4	1	4		8			6
																		2	2	2	2								4	1						2	1		3
																		2											1	1									1
																		2		2		3	2		1				5	1		2	1	3		2			5
																		2											1	1									1

Cont.

Table 1: Sighting histories of whales seen in the PCFG in at least one year. In year columns, a 1 means the whale was only sighted in the spring (March-May), 2 means it was only seen in June-Nov, and 3 means it was seen in both March-May and June-Nov. The region value is the nunber of years the whale was seen in that region.

1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	#years	NCA	SOR	OR	GH+	NWA	SJF	SVI	WVI	NBC	#areas
																		2		2			2		2		2		5	4	1								2
																		2											1	1									1
																		2											1	1									1
																		2											1	1									1
																		2											1	1									1
																		2											1	1									1
																		2	2										2	1						1			2
																		2											1	1									1
																		2											1	1									1
																		2	2		2	2	2	2	3	2	2	2	10	2			1	1		3	6		5
																		2											1								1		1
																		2				2	2	2	2	3	2	3	8	2		2	1	4	1	2	5		7
																		2			1								2						1		1		2
																		2										2	2							1	1		2
																		2	2		2	2	1	2	3	3	3	3	10						1	9	7		3
																		2	2	2	2	2	2	2	3	2	2	3	11			1	1	5	3	9	4		6
																		2	2	2	2							3	5					1				5	2
																		2	2				2		2	3	2	3	7	4	2	2	1	1					5
																			2	2	2	2	2	2					6		1	2				2	2	1	5
																			3	2	3	2							2	5							5			1
																			2										1		1								1
																			2	2		2							3					1	2	1			3
																			3	2	3								3					1	3	2			3
																			2	2	3	2	3	2	2	3	3	2	10			2		2	1	10	1		5
																			3	2	2	2	3	2	1	2	3	2	10	2	1	1		3	4	5	1		7
																			2		2								2					2		1			2
																			3		2	3	1	2	3	3	3	3	9					5	1	9	3		4
																			2	2	2				2	2	2	3	7	4				2	2	5	1		5
																			2	2									2							2			1
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																			2										1							1			1
																			2	2									2							2			1
																			2	2	2	2	2	3	2				7			1		1	1	6	2		5
																			2	2	2								3			1			1	1		1	4
																			2										1									1	1
																			2	2			2						3			2						2	2
																			2	2	2	3	2	2	2	2	3	2	10			3		4	1	7	1		5
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																				2	2	3	1						4					1		4			2
																				2	3	2	2	2	2	2	3	2	9	1	1			3	6	6	2		6
																				2		1							2							2			1
																				2									1							1			1
																				2	2	2	2	2	2	2	2	3	9			1		8	1	3	1		5
																				2	2			2	3	2	3	3	7					2	5	7			3
																				2	2	2	2	2	3	2	2	2	9					3	5	7	2		4
																				2					2				2	2									1
																				2									1		1								1
																				2									1			1							1
																				2		2							2							1		1	2
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																				2	2								2							1		1	2
																				2	2	2	3	3	2	3	3	3	9					4	6	7	3		4
																				2		2		2					3						2		1		2

Cont.

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1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	#years	NCA	SOR	OR	GH+	NWA	SJF	SVI	WVI	NBC	#areas
																				2	2								2								1	1	2
																				2									1						1				1
																				2									1						1				1
																				2								2	2									2	1
																				2									1									1	1
																				2									1									1	1
																				2									1									1	1
																					2								1								1		1
																					2			2	2	2	2	3	6	4				2	1	3			4
																					2								1								1		1
																					2								1								1		1
																					2								1					1					1
																					2		2	2	2	2	2	2	7					1	4	1	3		4
																					2			2	2	3	3	2	6	5	3	2		1					4
																					2								1							1			1
																					2	2	3						3							1	3		2
																					2								1						1	1			2
																					2								1							1			1
																					3								1						1	1			2
																					2								1							1			1
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																					2	2	1	2		2	2	1	7					4	1	3	3		4
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																					2	2	3	3	2	1			6						2	4	1		3
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																					2	2							2						1	2			2
																					2	2	2	3	2	3	3	3	8					3	4	8	2		4
																					2	2							2							2			1
																						3	3	2	2		3		5					1	3	4	2		4
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																							2						1								1		1
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																								2	2	3	2	3	5	5				1					2
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Cont.

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1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	#years	NCA	SOR	OR	GH+	NWA	SJF	SVI	WVI	NBC	#areas
																								2					1								1		1
																								2			2	2	3					2	2	2	1		4
																								2					1									1	1
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																								2	2	1	3	3	5	3				1	4	2			4
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																								2	3	2	2	3	5						4	4			2
																								2					1						1				1
																								2	2	2			3						3				1
																								2					1						1				1
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																								2					1						1				1
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																								2					1						1				1
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																									2				1						1				1
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																									2				1							1	1		2
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Cont.

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																									2				1				1						1
																									1			3	2					1		1	1		3
																									2				1					1					1
																									2				1						1				1
																									2				1						1				1
																									2	2	2	3	4			2		1	1	2			4
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																											2		1	1									1
																											1	3	2					1		1			2
																											2	2	2					2	1	1			3
																											2		1	1									1
																											2	1	2	1				1					2
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																												2	1	1									1

Cont.

Table 1: Sighting histories of whales seen in the PCFG in at least one year. In year columns, a 1 means the whale was only sighted in the spring (March-May), 2 means it was only seen in June-Nov, and 3 means it was seen in both March-May and June-Nov. The region value is the nunber of years the whale was seen in that region.

1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	#years	NCA	SOR	OR	GH+	NWA	SJF	SVI	WVI	NBC	#areas
																												2	1	1		1							2
																												2	1	1									1
																												2	1	1									1
																												2	1	1									1
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																												2	1					1					1
																												3	1					1					1
																												2	1					1					1
																												2	1					1					1
																												2	1	1				1					2

Table 2: Sighting histories of whales seen in the MUA during 1 June - 30 November in at least one year. 1: whale sighted in PCFG but not in the MUA during that year, 2: only seen in MUA that year, and 3: seen in both MUA and another PCFG area.

1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012
1	3	3	1	1	1	1		1	1	1						
1		3	1	1	1	1	1	1	1	1	1	1		1	1	1
1		3	1	1	1	1	1	1	1	1		2		3	1	1
3		3	1	1	1	1	1	1	1	2		1	2	1	1	1
1		3	3	1	1	1	1	1	1	1	1	3	3			
1	3	3	1	1	1	1	3	1								
2	2		3			1		3	2	2					2	3
2	2															
1		3	3	1	1	1	1	1	1							
3		3	3	1	1	1	1	1	3							
3	2	3	1	3	3	1	1	1				1				
2		1	1	1	1	1	1	1	1	3	1	3	1	1	1	3
2																
1	1	3		1	1	1	1		1		1	1			1	
1	3	3	1	1	1	1	3	3	3	3	3	3	3	1	1	3
1	1	3	1	1	1	3	1	1		1		1	1		1	3
1		3	1	1	1	1	1	1	1	3	1	3	1	1	1	3
1		1	1	1	1	1	1		1	1		3	1	1	1	1
3		1	1	1	1			1	1	3						
2	2	3	1	1	3	1	1	1	1	1		3	1	1		
2	3	2														
2	2	3	1	1	1	1	1	1	3	3	3					
2	2	1	1	1	1		1	1	3	1	3	2	2		3	
3	2	1	3	1	1	1	1	1	3	3	1	3	3	1	3	3
3	1	1	1	1	1	1	1	3	1	1	1	1	1	1	1	1
2	3	3	1	1	1	1	1	1				1		1		
2	3	3	1	1	1	1	1	1	1	3	1	3	3	1	3	1
2	2		2	2	2	1	3					3	3	1		
1	2	3														
2																
2	2	1	1		1	1		1								
1		1	1	1	1	1			1		1		1	1	3	3
	2	3	3	1	3	1	1	1	1	3	1		1			
	1	1	1	1	1	1	1	1	1	3	3	3	3	1	3	3
	3	3		1	3	2	3	1	1	1	1	3	1	3	1	3
	2	1	1	1	3	1	1		1		1		1	1	1	1
	1	1		1	3	1	1	1	1	1	1	3	3	1	1	1
	1	3	1	1	1	1	1	1		1		1	1	1	1	1
	3	1	3		1	1	1	1	3	1	3	1	1			1
	2	1	3													
	2															
	2	1	1	1	1	1	2	1	3							
	2															
	2															
	2	1	1	1	1	1	1	3	1	3	1	3	3	1	1	3
	2															
	1	1	1	1	1	1	1	1	3	3	3	3	3	1	1	3
	1	1	1	1	1	1		1	1	3	1	3				1
	1	1	1	1	1	1	1	1	1	1		3	1		1	1
	1			1	1	1	1	1		2	1	3	3	1	1	
		1			3	1	3	1	3							
		3	1													
		1	1	1	1	1	1	1	3	1	1	3	3	3	3	3
		1	1	1	1	1	1	1	1	1	1	3	3	1	1	1
		1	1	1	1	1	1	1	1	3	3					
		1	1	1	1	1	1	1	1	1	1	3	1	1	1	1
		1	1	3	1	1	1		3	1	1	1	3	3	3	3
		1				1	2	1			1		1			
		1	1	1	3	1			1	3				1		
		2														
		1	1			1	1	1	1	3	1	1	1	1	1	3
		2														
		3	3	3	3	1		1	1	3	2	3	1			
		2														
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		2														
		2														
		2														
		2														
		1				1	1			1	1		1	1	3	1
		1	1	1	1	1	3	1	1	2		1	1	1	1	1
		1			1	1	1	1	1	2	1	1	1	1	1	1
		1	1	2	2	3	3	1		3	3	2			1	1
		1	1		1	1	2		1	1		1	1		1	1
		1	1	1	1	1	1		3							
		1	1	1		1	1	1	1	3	1	3	1	3	3	3
		1	1		1	1	1	1		2	1		1	1	1	1
		2														
		1	1	1	1	1	1	1		1	1	1	1	1	3	3
		1	1	1	1	1	1	1	1	1	1	3	3		1	3
		1		3	3	1	1	1		3		3	1	1	1	1
		1				1	1	1		1		3	2	2		1
		2														

Cont.

Table 2: Sighting histories of whales seen in the MUA during 1 June - 30 November in at least one year. 1: whale sighted in PCFG but not in the MUA during that year, 2: only seen in MUA that year, and 3: seen in both MUA and another PCFG area.

1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012
			1		1	1		1			1	1	3	1	1	1
			2													
			1	1		1			1		1		3	1	1	1
			1	3		1	1	1	1	3	1		3	3	1	3
			1		1	1	3	1			1					
				1	3	1		1								
				1		1	1		1	3	3	1	3	3	1	3
				3	3	3	3	1		3		3	3	3	3	3
				1		1						1	1	1	3	1
				1	3											
				3												
				2	2	3	1	1		1	1	3	1	3	1	3
				3	3	1										
				2												
				1	1	1		1	1	1	1	3	1	3		1
				3	2	1	1	1	2	3		3	1	1	3	3
				1			1				1	1	1	1	3	1
				2		1										
				1		1							1	3	1	1
				1	1	1	1	1	1	3	1	1	1	1	3	3
				1	1	1	1	1	1							3
					3	1		1						1		
					2	1	1	1	3	2	1	3	1	1	1	3
					3	1	3									
					3											
					1	1	1		1	1	1	3	3	1	1	1
					3											
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					3	1										
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					2											
					2		1								1	
					3	3	2	2								
					2	3										
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					1	1	3									
					1	1	1		1			1	1	1	1	3
					1	1	1	1	1		1	1	2	1	1	1
						1	3	1	1	1						
						1		1				1	1	1	1	3
						1		1			1					2
						1	1	2	1	3	1	3	3	1	3	1
						1		2	3							
						1				2	1	1	1	1		
						1	1	1	1	3	1	3		1	3	1
						3	3	3	3	2		3	3	3	3	3
						1	1	1	1	3	1	3	1	1	3	1
						1		1		3	3					
						1	1		1	1	1	1	3	1	1	1
						1				3	1	3	3	1	3	3
						1	1		1	1		3	1	1	1	1
						1	3	3	1	3	1	3	3	3	3	3
							2	1		2						
							3	3	2							
							1	1	1	3	1	3	1	1	1	3
							1	3	2	2	1	3		1	3	1
							3		2							
							1		1	3		3	3	3	1	3
							1	1	1				1	3	3	3
							1	1	1	1	1	3	1			
							1	1	3							
							2	3	1	2	1	1	1	3	1	3
								2								
								3	3	3	1	3	3	1	3	3
								1	1	3						
								3	2	3	2	3	3	1	1	1
								3	2	2	3	2	2	3	3	3
								3	3			3	3	3	3	3
								1	1	3	2	3	3	3	3	3
								2	3	3	3	3	1	3	1	3
								2		2		1				
								2								
								2								
									1			1	3	1	3	3
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									1		2	2	2	1	3	1
									2			1	1	1	1	1
									3							
									3							
									2	3		2		2	1	
									3	2		1				
									1	1	2	1	2			
									3	3	2	3	3	1	3	
									1	3						
									1	3	3	3	3	1	1	3
										3	2	3	3		1	

Cont.

Table 2: Sighting histories of whales seen in the MUA during 1 June - 30 November in at least one year. 1: whale sighted in PCFG but not in the MUA during that year, 2: only seen in MUA that year, and 3: seen in both MUA and another PCFG area.

1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012
										2						
											1	1				2
											1		2			
											1	2	3			
											1	1	3			
											1			1	2	
												2				
												1	1	1	3	1
												3			3	3
												2			2	
												3	3		2	1
												3	2			
												2				2
												2	3	1	3	3
												2				
												2	2	2		
												2				
												2	3	1		
												2				
												3		1	1	
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												2				
												2	3	1	1	
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												1	2	2	1	3
												2	3	1		
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																2
																2
																2
																3

TOWARD A FISHERIES ECOSYSTEM PLAN FOR THE NORTHERN CALIFORNIA CURRENT

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> We have witnessed changes in the landscape around us with the advent of technology evolved from the axe and the plow. We should expect equally profound ecological changes from modern, large-scale uses of the hook and the net. (EPAP 1999)

ABSTRACT

Recently the congressionally established Ecosystem Principles Advisory Panel issued a report on how best to amend single-species management. A major recommendation was that fisheries management councils develop a fisheries ecosystem plan (FEP) for every ecosystem under their jurisdiction. This document would be an umbrella document containing detailed information on the structure and function of the ecosystem under consideration. The U.S. portion of the northern California Current ecosystem (NCCE) may be an appropriate test case to develop some of the key elements of a draft FEP. Fishing pressure in the NCCE has been intense for decades, and the possibility of consequent large-scale ecosystem changes is large. Although fisheries science in this region has considerably advanced our understanding of the intricate linkages between fisheries production and large-scale oceanographic and atmospheric climate forcing, fisheries management efforts throughout the region may be insufficient for assessing the ecological impacts associated with fishing. We use Ecopath models to assess the state of the NCCE in the 1960s during a cool regime with low exploitation rates and high rates of zooplankton production, and also in the 1990s during a warm regime characterized by low productivity, declining stocks, and intense exploitation. We compile population parameters and diet data for 34 species/species assemblages for both time periods to generate a food web of basic trophic interactions. These models are in agreement with the general consensus that this system has been functioning at lower levels of productivity since the 1977 regime shift. More work is needed to understand the status of many NCCE populations, but stock assessments and fisheries data suggest that the observed fluctuations in many harvested populations may be rapid, highly variable, and increasingly undesirable.

INTRODUCTION

To date, most fishery management efforts in the United States continue to focus on regulatory mandates contained in management plans based on species-specific stock assessments. The Magnuson Fishery Conservation and Management Act, which provides the legal authority for marine fisheries management, mandates that fisheries scientists and managers "prevent overfishing while achieving, on a continuing basis, the optimum yield from each fishery" (16 U.S.C. 1851). Although there is legal authority for taking into account how fishing activities affect fish habitat, this authority has generally not been used by managers, and the Magnuson Act contains no explicit direction on how managers should actively consider the indirect consequences of fishing on trophic dynamics or structure.[1]

Recognizing the promise of an "ecosystem-based" approach to improving fisheries management, the U.S. Congress recently requested that the National Marine Fisheries Service (NMFS) convene a panel of experts, the Ecosystem Principles Advisory Panel (EPAP), to examine how best to build upon single-species management approaches. The EPAP's primary recommendation was that fishery management councils develop a fisheries ecosystem plan (FEP) for every ecosystem under their jurisdiction (EPAP 1999). An FEP is envisioned as an umbrella document containing detailed information on the structure and function of the ecosystem under consideration (e.g., a conceptual model of the food web and other ecosystem components, total removals from fishing, and assessments of the human elements of the ecosystem that most significantly affect fisheries). The FEPs would be intended to increase managers' and stakeholders' awareness of how their decisions affect the ecosystem. As such, FEPs would be the next major step in translating today's directed management efforts into more holistic approaches.

Our efforts have focused on using the U.S. portion of the northern California Current ecosystem (NCCE), which includes the heavily fished shelf and slope ecosys-

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[1] The extent to which the Magnuson Act explicitly mandates the consideration of ecosystem aspects could be arguable, as there is no mention of ecosystem considerations in the National Standards or in the FMP requirements. However, some authority is inferred in the definitions section of the act with regard to the word *optimum* with respect to yield from a fishery (Section 104-297 of 16 U.S.C. 1802), where it is suggested that optimum yield "means the amount of fish which will provide the greatest overall benefit to the Nation, particularly with respect to food production and recreational opportunities, and taking into account the protection of marine ecosystems."

tems between Cape Mendocino, California, and the northern tip of Vancouver Island, as a test case to develop what we believe to be some of the key elements of a draft FEP. Fisheries resources in the NCCE have been subjected to intensive fishing pressure for a protracted period. The abundance of coastal pelagic species such as sardine, anchovy, and herring has varied substantially over past decades, most likely in direct association with different modes of climate forcing. Precipitous declines in several stocks of Pacific rockfish (*Sebastes* spp.) and some roundfish have occurred over the last 20 years, and are evident in the corresponding declines of commercial landings (Ralston 1998). Similarly, many salmon fisheries of the NCCE, in particular ocean fisheries, have been in decline since the late 1970s. These declines are generally attributed to a combination of unfavorable ocean conditions (Hare et al. 1999), spawning and rearing habitat degradation and loss, and overfishing (NRC 1996). Juvenile salmon, a staple in the diet of many higher-trophic-level species, have been particularly affected by habitat loss and interdecadal variations in climate (Mantua et al. 1997; Hare et al. 1999); the recruitment of rockfish, the juveniles of which are also a staple in the diet of many larger predators in this system, has similarly been greatly reduced in recent decades (MacCall 2000).

The complex and fragmented design of interacting human and institutional elements hinders the transition to more holistic management efforts in this ecosystem. Under an ecosystem-based approach, management actions would be designed and monitored through an adaptive management approach (Ludwig et al. 1993), and management institutions should be designed so that resource ecology and institutional ecology overlap in a complementary manner. All of these issues of governance are particularly true in the NCCE, where numerous state, federal, and tribal institutions often seem to have different responsibilities with regard to the management of fishery resources. Of particular concern is the challenge of incorporating a longer time and broader spatial and biological view into this management arena. Thus the northern California Current may provide an opportunity to explore efforts for surmounting the impediments to sustainable and rational management of living marine resources.

WHY ECOSYSTEM-BASED MANAGEMENT?

In many fisheries it has become increasingly obvious that the ecological consequences of fishing are substantially greater and more complex than the biomass reductions of target species. These consequences may include but are not limited to mortality of nontarget species, alteration of benthic habitats and bottom topography, changes in age and size structure of fished (both target and nontarget) populations, changes in sex ratios of targeted populations, and changes in the genetic structure of fished populations (Botsford et al. 1997; NRC 1999).

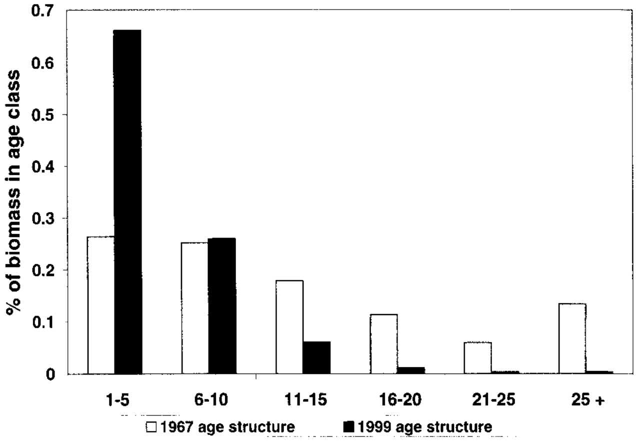

Figure 1. Changes in the age structure of the northern canary rockfish population (based on stock assessment data). Graph shows the percentage of population biomass in five-year groupings of age classes between 1967 and 1999, illustrating the shift in population biomass to younger, smaller individuals. During this same period the total population has been fished down to approximately 10% of its unfished population biomass.

As one simple example, figure 1, based on the stock assessment by Crone et al. (1999), shows how the age structure of the canary rockfish population has changed over the last three decades. This figure shows an extreme case of the truncation of the age distribution of this long-lived species. Recruitment of canary rockfish has been extremely low over the last two decades, and the large proportion of young individuals does not reflect increased recruitment, but rather removals of a substantial fraction of older individuals.

In addition to population impacts, structural changes to trophic webs have been described for numerous heavily fished ecosystems (Parsons 1993; Apollonio 1994; Fogarty and Murawski 1998; Pauly, Christensen et al. 1998). Furthermore, interannual and interdecadal climate shifts affect the productivity of marine populations, with dramatic effects on fisheries (Mantua et al. 1997; Anderson and Piatt 1999; Hare and Mantua 2000). The effects on marine ecosystems as a consequence of fishing activities, notably as direct effects of fishing gear on benthic habitats, are poorly understood in most systems, but have been shown to be substantial where evaluated (Auster et al. 1996; Engel and Kvitek 1998).

Figure 2 is a simplistic representation of how traditional approaches to fisheries management, which focus primarily on interactions between commercially important populations and fishing activities, could be broadened to include basic interactions between commercial and noncommercial species, the effects of fishing activities on habitat, and the large-scale impacts of climate forcing on ecosystem productivity and structure.

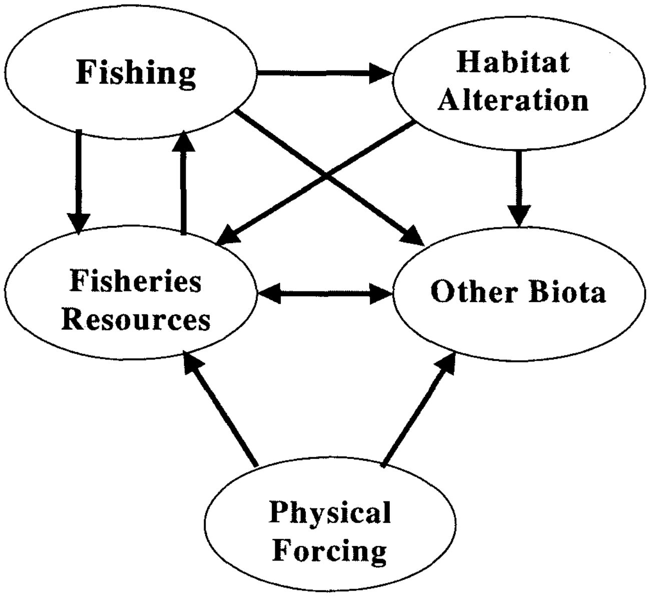

Figure 2. A conceptual outline for incorporating ecosystem considerations into fisheries management.

It is widely recognized that an ecosystem approach to fisheries management will have different meanings for different people. As with much environmental legislation, a mandated ecosystem-based approach will invite controversy about its implementation, regardless of the definitions put into the law. The discussion on what an ecosystem-based approach might mean to managers is broad and often tortuous, yet some mention of key views is worthwhile. For example, Grumbine (1994) suggests that managing for ecological integrity would mean that commodity extraction should be relegated to an ancillary goal. As the EPAP report (1999) points out, when fishing is examined from an ecosystem context the rationale for surplus production is unclear; before the advent of fisheries all production was recycled within ecosystems. Other stated consequences of fishing include inducing ecological changes among competitors, predators, and prey, and such changes could imply future levels of surplus production that approach zero for some populations well into the foreseeable future. This is in direct conflict with the assertion by some that the adoption of an ecosystem-based approach should lead to healthier and more dependable fisheries. For example, the NRC Council on Sustainable Fisheries Report (NRC 1999) suggests that the goals of an ecosystem-based approach are to "rebuild and sustain populations, species, biological communities and marine ecosystems at high levels of productivity and biological diversity, so as not to jeopardize a wide range of goods and services from marine ecosystems, while providing food, revenue and recreation for humans."

Like so many policy and management approaches, the purported objective in the NRC report is to maximize many variables at once, thereby implying that all of the objectives are mutually compatible. This approach, like that of traditional fisheries management, continues on the assumption that fisheries can safely remove surplus production without consequences to the ecosystem; as implied by the conclusion that although adaptation of such an approach will likely cause short-term economic losses and impacts to communities, the ultimate outcomes should not include decreased yield, since rebuilt populations should increase sustainable yield (NRC 1999).

These assumptions are difficult to justify given the current poor state of knowledge about the aforementioned ecological consequences of fishing on marine ecosystems, revelations that many long-lived species have considerably lower rates of production than previously thought and may take many decades to recover, and our inability to clearly define what might or might not constitute a "healthy" marine ecosystem. Moreover, there should be little reason to use higher potential yields as a selling point of ecosystem management, as the solution to a stock's inability to produce some level of sustainable yield would (and under the Sustainable Fisheries Act, legally should) ostensibly be reached through the adoption of quota reductions and stock rebuilding plans under a single-species approach. In the future, as policymakers and resource managers struggle to consider what ecosystem management is, perhaps it will be worthwhile to step back and consider what it is not.

One potential outcome of implementing an ecosystem-based approach could be reduced stability or predictability in future fishery yields. A reduction in predictability does not necessarily imply that most current yields are stable, but rather that the pursuit of stability for economic and allocation purposes may be in conflict with the notion of adaptive management of ecological resources. Holling and Meffe (1996) argue that the pursuit of stability is part of the explanation for why many resource management efforts have failed, because the objectives of many such efforts have been to reduce the natural bounds of variation in ecological systems in order to make them more predictable and more reliable for extractive needs. Holling and Meffe argue that the key to natural resource management, whether it be single-species or ecosystem management, is to retain critical types and ranges of natural variation in ecosystems, and to facilitate existing processes and variabilities rather than attempting to alter or control them.

Perhaps one example of such an approach can be observed in the recently approved fishery management plan for coastal pelagic species (PFMC 1998). The plan was based on the premise that the theoretical definition of maximum sustainable yield (MSY) as a constant level of catch should not be applied in fisheries for coastal pelagic species such as sardine, anchovy, and mackerel because of the high sensitivity of the productivity of these stocks to changes in environmental conditions. Instead, management is based on the application of a baseline "cutoff" population biomass, below which directed harvests are not allowed, and above which allowable landings are based on a fraction of the available biomass above the cutoff level. This approach allows for high harvest rates during favorable environmental conditions but forces fishing mortality to zero if the stock declines to a baseline biomass.

Apollonio (1994) suggests that in marine ecosystems, the ecological role of fishing is comparable to the role of apex predators. It follows that, analogous to the way biological feedback mechanisms underlie natural predator-prey relationships, appropriate feedback mechanisms between vessels and target species should exist to keep the system in balance. In order for fishing to be ecologically sustainable, Apollonio argues, the ecological impacts of fishing should be similar to the natural impacts of apex predators. This may imply that during unproductive years, decades, or even longer periods, the yield of many species, indeed of many ecosystems, may be unsustainable from the perspective of stock, species, or system productivity.

The Pacific Council's Coastal Pelagic Species FMP is one step toward the application of this principle, yet in practice these balancing mechanisms are scarce because of external subsidies, which have the effect of maintaining fisheries that might be otherwise unprofitable. Instead, fleet buildups continue far beyond what might be sustainable as stocks are fished down to (and often beyond) the estimated size that produces the maximum sustainable yield. The existence of strong incentives for vessels to switch rapidly from one fishery to another when catches decline, and the ability for effort to shift massively over short time periods would suggest that the feedbacks that might exist in a more typical predator/prey system are substantially diminished.

For the northern California Current, our initial work has focused on preliminary attempts to address three of the eight key minimum actions envisioned in the EPAP report as elements of demonstration fishery ecosystem plans. These include a characterization of biological dynamics of the ecosystem, development of a conceptual model of the food web, and the estimation of total removals and how those relate to standing biomass, production, and trophic structure. A summary of our early efforts to address these elements makes up the remainder of this paper.

The remaining five key elements of FEPs as envisioned by the EPAP panel are certainly no less crucial. They include descriptions of the habitat needs of different life-history stages for all plants and animals that represent the "significant food web" and how they are considered in conservation and management measures; an assessment of how uncertainty is characterized and what types of buffers are included in management actions; the development of indices of ecosystem health as targets for management; descriptions of long-term monitoring data and how they are used; and an assessment of the ecological, human, and institutional elements of the ecosystem that most significantly affect fisheries and are outside of Council/Department of Commerce authority (see Fluharty and Cyr, this volume, for greater detail). For all of these actions, the FEP process would provide an opportunity to refine, integrate, and further develop the substantial efforts that have already been made by government and academic workers.

THE NORTHERN CALIFORNIA CURRENT ECOSYSTEM

The continental margin of North America off the coasts of northern California, Oregon, Washington, and southern British Columbia is a productive coastal upwelling region that has long supported commercial harvest of a variety of marine resources. The entire California Current ecosystem (CCE) is an "open" system, meaning that it is a transition environment between subarctic and subtropical water masses and the freshwater systems that enter the ocean along its landward boundary (Hickey 1989).

This region is also an ecotone comprising a small number of endemic coastal species and a larger mixture of subarctic and subtropical species, many near the periphery of their distributional range (Bottom et al. 1993). The northern half of the CCE, the region of coastal ocean between Cape Mendocino, California, and the northern tip of Vancouver Island, B.C., is described as a zoogeographic transition between Californian and Aleutian biological provinces. We refer to this region as the northern California Current ecosystem, and presume that this system may be an appropriate ecological unit for regional management as the focus of this paper.

A growing body of research has shown that during the twentieth century, both El Niño-Southern Oscillation (ENSO) and Pacific Decadal Oscillation (PDO) processes had major impacts on the organization and dynamics of marine ecosystems of the NE Pacific Ocean and, as a result, on fisheries operating within those ecosystems (e.g., Wooster and Fluharty 1985; Francis et al. 1998; McGowan et al. 1998; Anderson and Piatt 1999). Because the effects of climate are so pervasive in the NCCE, as a first step to ecosystem reconstruction it is essential to understand past patterns of climate as they may have affected the NCCE. As an example of how past climate patterns have influenced the NCCE, we will briefly examine information about the presence of Pacific sardine in the region over the last two centuries.

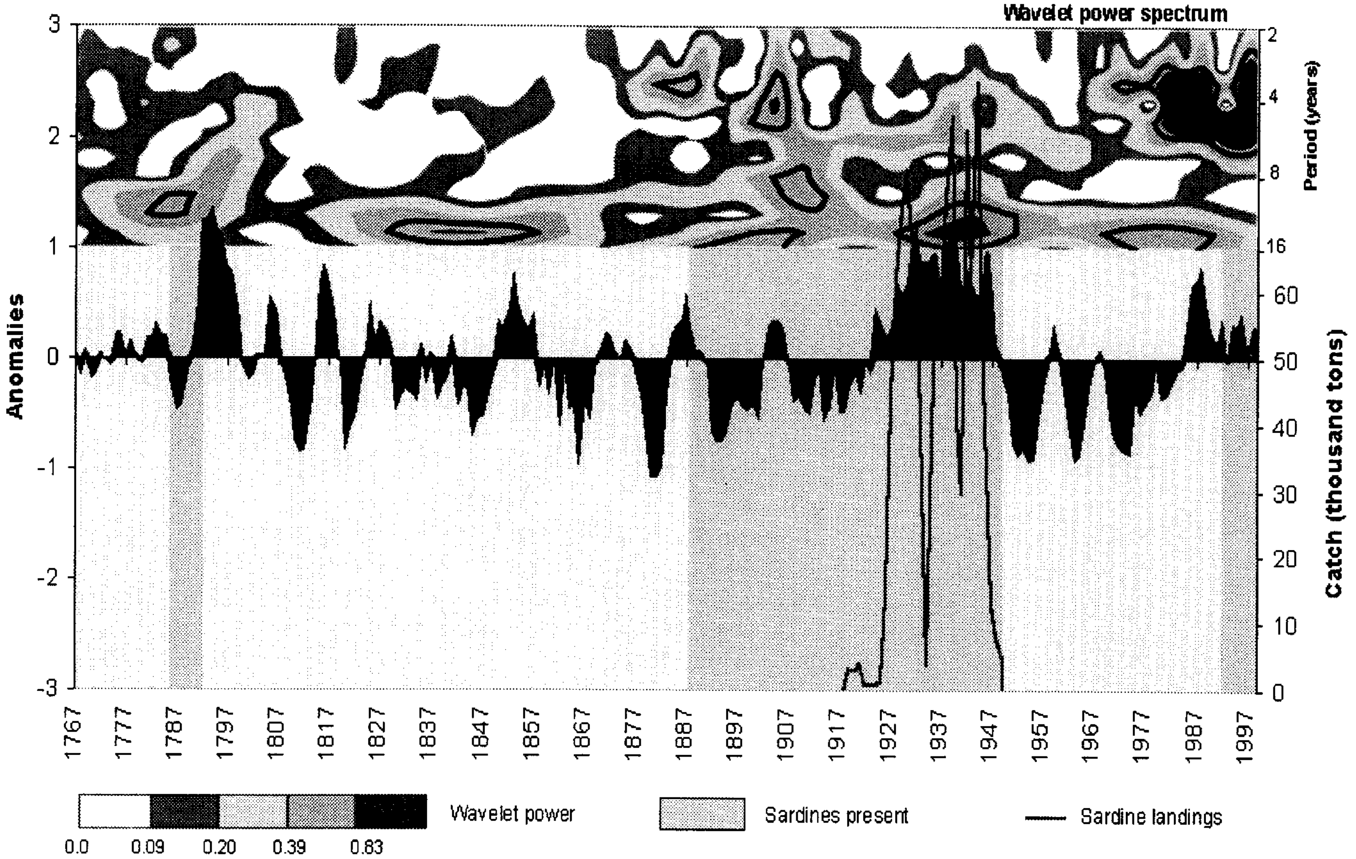

Figure 3. Pacific Northwest sardine occurrences charted against reconstructed winter PDO and ENSO wavelet power spectrum. (See footnote 1 for a summary of historical records of sardine presence/absence in the Pacific Northwest.)

Figure 3 is a composite that explores possible relationships between climatic influences and the presence and absence of sardines in the NCCE. Shaded areas indicate periods of sardine presence; solid lines indicate commercial landings in the Pacific Northwest. This information is plotted against a tree-ring reconstruction of the PDO time series (Dell'Arciprete et al. 1998) and a wavelet analysis of the ENSO cycle (top panel) as reconstructed by Mann et al. (1999). The wavelet analysis provides a graphic representation of the intensity, or magnitude, of climate variability at various frequencies (see Torrence and Compo 1998). Darker shades in the upper panel indicate more intense ENSO periods.

Figure 3 suggests that each range expansion of sardines documented since the latter part of the eighteenth century occurred during periods of increased North Pacific climatic activity.[2] The first period of increased activity occurred in the late 1700s, when sardines were

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[2] It appears that three major northward expansions in the range of sardines have occurred since the late 1700s. During the first two, sardines were abundant enough to support substantial fisheries that persisted for a number of years as far north as Puget Sound and Vancouver Island. Between 1786 and 1792 a number of accounts, including those of trained naturalists, described the native fisheries for sardines along the Pacific Northwest coast; John Meares (1791) described how "In the Spring, the herrings as well as the sardines frequent the coast in vast shoals.... The sardine resembles that of Portugal, and is very delicious: they are taken here by the people in prodigious quantities." By the beginning of the 19th century, however, sardines were no longer being noted in the journals of explorers, naturalists, or traders, despite more extensive exploration in the Pacific Northwest region following the Lewis and Clark expedition.

Apparently sardines did not return to the Pacific Northwest until the late 1880s. Extensive scientific investigations of fisheries resources—including those conducted by the Wilkes expedition in 1841 (Wilkes 1984), the Pacific railroad surveys of 1853–57 (Suckley 1860), and the investigations of the U.S. Fish Commission in 1880–81 (Goode 1884)—failed to locate sardines in Pacific Northwest waters. The U.S. Fish Commission reported in 1884 that sardines ranged from Chile to Cape Mendocino, California. By 1888–89, however, this range had expanded to encompass Puget Sound. Sardines were found in Puget Sound waters during "the warmer part of the season, and are taken with herring and other species for market" (Collins 1892). Landings of fresh sardines in 1888 were reported to be 60,000 lbs. By 1895 sardines were occurring in "large numbers" in Puget Sound (Jordan 1895), and in 1902 were described as "abundant" (Kershaw 1902). The first official records of sardines captured in Canadian waters did not appear until January 1900, when two specimens were collected in the Strait of Georgia near Nanaimo (Clemens and Wilby 1961). Concurrent with the development of the California sardine fishery in the 1920s, a lucrative fishery for sardines began in British Columbia in 1917–18 and lasted until 1948–49, when stocks once again disappeared (Schweigert 1988).

Sardines were again observed in the waters north of Cape Mendocino in the 1980s (Emmett and Brodeur 2000) and returned to the Pacific Northwest and British Columbia in 1992 (Hargreaves et al. 1994), though not in sufficient quantities to warrant a resumption of large-scale commercial fisheries. The return may also have been short-lived. In 1998 and 1999 there was a series of massive die-offs of sardines along northern sections of Vancouver Island. These mass deaths coincided with the 1998–99 La Niña that caused sharp declines in coastal ocean temperatures (Drouin 1999).

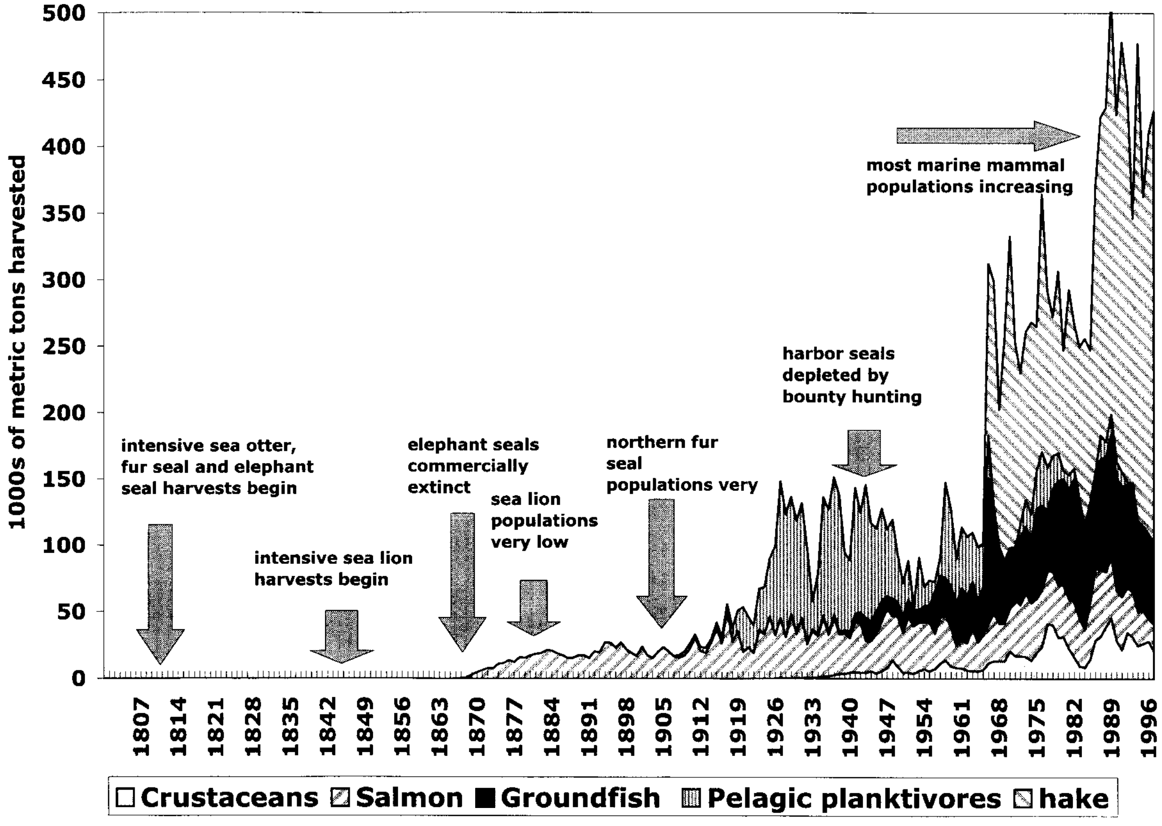

Figure 4. A summary of major removals by fisheries from the northern California Current ecosystem over the last two centuries.

apparently already in an expansion mode, the PDO was nearing a substantial peak, and ENSO activity may have been more intense and frequent than normal. It is unclear exactly when the sardines disappeared from Pacific Northwest waters during this period, but historical records suggest that they were no longer present by the early 1800s. Similarly, the expansion of the sardine population starting around 1880 coincided with increased power in both the ENSO signal and the magnitude of the PDO. Finally, the return of sardines to the British Columbia coast in the 1990s coincided with a general expansion of the coastal population, starting with the major climate shift of the late 1970s and the record El Niño activity of the 1980s and 1990s.

Sardines may epitomize the nature of change in key species in this system; their presence implies a different ecosystem state than during periods of their absence. This subsequently implies that key flows of energy and biomass in the system changed substantially prior to human intervention. Smith (1978) inferred changes of even greater magnitude in the abundance of Pacific hake in the California Current based on the scale record of Soutar and Isaacs (1974), which suggested that the abundance of hake (although these scales probably represent juvenile hake) at the turn of the twentieth century may have been as much as an order of magnitude greater than current levels. These observations illustrate that pronounced changes of boom and bust in the natural cycles of migratory coastal pelagic species such as sardines and hake imply massive changes in primary and secondary production within the NCCE. This in turn suggests that the ecosystem was structured very differently in previous centuries than it is now.

FISHERIES DEVELOPMENT IN THE NCCE

Fishing pressure in the NCCE has been intense for decades and has effected consequent large-scale changes in the relative abundance of many key populations. Knowledge of NCCE structure and dynamics comes primarily from stock assessments, fisheries and food habits data, and oceanographic records. These sources mostly cover recent decades, and indicate high levels of physical and biological variability on broad spatial and temporal scales.

Catch statistics provide perhaps the most complete record of population trends, and indicate that rapid and possibly undesirable changes are occurring in NCCE structure. Figure 4 presents a partial accounting of catch data and major biological removals over the last two centuries, illustrating both the magnitude of removals and the sequential nature of the development of the major fisheries in the region. This figure shows that although industrial-scale fishing pressure in the NCCE has been intense for only decades, various ecosystem components have been substantially exploited for at least two centuries.[3]

The first species to be the subject of major commercial exploitation were marine mammals. Fisheries for sea otters, fur seals, sea lions, and elephant seals grew to support enormous commercial harvests in the early and mid-1800s. Although few of these populations actively breed in the NCCE, all spend at least some of their time in Pacific Northwest coastal waters, and many are significant seasonal predators in the region. Estimates of actual take of most of these animals are difficult to derive: some estimates of otter and fur seal removals exist in fur trade records, but the number of elephant seals and sea lions taken for oil and meat can be only coarsely assessed.

Scammon (1874) suggested that hundreds of thousands of elephant seals must have been taken in the early part of the nineteenth century, and the species was commercially extinct by the 1870s. Specimen and museum collectors continued to take elephant seals even as the population was on the verge of extinction (Stewart et al. 1994).

Sea lions were originally taken for meat to supply the early hunters of sea otter along the California and Pacific Northwest coastline, and continued to be killed both as potential competitors for commercial fish as well as for their trimmings (the testes and penises of breeding bulls) following commercial depletion in the early twentieth century (Bonnot 1928).

Fishermen and bounty hunters along the U.S. and Canadian coastlines targeted harbor seals until the 1960s (Bonnot 1928; Newby[4]). Gray, humpback, sperm, and other whales were targeted for well over a century throughout the northeast Pacific. Such removals kept most pinniped and cetacean populations at low to moderate levels until the middle of the twentieth century, and only in the last several decades have populations of many marine mammals increased to substantial numbers.

Although many species of fish and shellfish throughout the NCCE have been harvested by native peoples for millennia, some at rates that may have approached later commercial levels (Yoshiyama et al. 1998), large-scale commercial harvests of fish in the region generally did not begin until many marine mammal populations had been substantially depleted. The salmon fisheries were among the first to develop: the first salmon cannery was opened in 1864 along the Sacramento River, but was soon moved to the much more productive Columbia River. By 1885, salmon catches in the Columbia alone topped 40 million pounds, and salmon fisheries had expanded to nearly every major watershed in the Pacific Northwest (Cobb 1930). Salmon fisheries continued to dominate the region, even as the soon-to-be legendary California sardine fishery was initiated in the early twentieth century.

Total coastwide sardine landings would reach over 700,000 metric tons (t) per year. Although the vast majority of sardine landings were made in the southern part of their range, up to 80,000 t a year were caught in the summer fisheries of the northern California Current between the 1920s and 1940s. When this fishery began to collapse in the 1940s, it did so from north to south, and it has long been suspected that changes in marine conditions played a role in this population decline (Ueber and MacCall 1992). In British Columbia, substantial herring fisheries had developed during the period of the sardine fishery, and grew rapidly following the sardines' departure from northern waters (Waddell and Ware 1995) while anchovy and mackerel populations underwent substantial (and perhaps sequential) fluctuations in the southern part of the sardines' former range (MacCall 1996). As the sardine population has increased over the last two decades, the fishery has also undergone a resurgence, with sardines once more being fished in commercial quantities between Baja California and British Columbia.

Pacific halibut was the first of the groundfish species to be targeted by commercial fisheries, although flatfish, lingcod, rockfish, and sablefish were all supporting substantial fisheries throughout the NCCE by 1900. Total landings of all groundfish grew gradually throughout the twentieth century, approaching 20,000 t per year in the early 1960s. During the mid-1960s the Soviet Union (and several other nations) began fishing for hake and rockfish in the coastal waters of Oregon, Washington, and British Columbia, and coastwide landings quickly reached several hundred thousand metric tons per year (primarily hake). As a result of the declarations of 200-mile fishing zones by both the United States and Canada in the late 1970s, these foreign fisheries were phased out as domestic fleets developed, and overall landings continued to grow as the fleets greatly exceeded the capacity needed to harvest the resource (PFMC 1993). Following the rapid development of domestic fisheries, it was found that many of these stocks were consider-

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[3] Data are incomplete, and from a variety of sources; salmon landings since 1911 were compiled by Hare et al. (1999), prior to 1911 are inferred from canned salmon production described by Cobb (1930). Pelagic planktivores (sardine, anchovy, herring, smelt, and shad) data were taken primarily from PFMC 1998, except for herring data taken from Waddell and Ware 1995 and very early landings from Sette and Fiedler 1928. Early groundfish and crustacean fishery data were also taken from Sette and Fiedler 1928, with later data from U.S. Bureau of Fisheries Statistical Digests. Groundfish and hake data between 1954 and 1980 were taken from Lynde 1986 and more recently from the Pacific Fishery Management Council (PFMC 1999) and Waddell and Ware 1995. Currently missing are Canadian data for groundfish landings prior to 1920 and all Canadian crustacean fisheries; errors are possible from other data sources, and not all estimates include unreported landings or estimates of discards, and thus should be considered minimum estimates of total mortality.

[4] Newby, T. C. Changes in the Washington state harbor seal population, 1942–1972. Unpubl. Rep.

ably less productive than originally thought. Subsequently, allowable landings of many groundfish species have been greatly curtailed in recent years, and recovery plans for depleted stocks are likely to limit effort for less-depleted stocks in the near future.

Crustacean fisheries also developed early in the Pacific Northwest, particularly fisheries for Dungeness crab and pandalid shrimp. For at least a century, landings of these populations appear to have fluctuated widely over relatively short periods of time. Evidence indicates that these fluctuations represent actual population swings, and recent research suggests that Dungeness crab dynamics respond to both internal population feedback, and large-scale environmental forcing (Higgins et al. 1997). It follows that such extreme population variability may be a response to a combination of anthropogenic influences (e.g., fishing, habitat degradation) and fluctuating oceanographic conditions.

Additionally, Hannah and Jones (1991) document an apparent change in the age structure of pink shrimp (*Pandalus jordanii*), which they believe is at least partially attributable to fishing. The pink shrimp is a sequential hermaphrodite in which age-1 shrimp are typically male and turn female as they reach age 2 (few, if any, of this species live beyond age 3). Hannah and Jones's work documented a shift in the age structure of landed shrimp to a substantially greater percentage of age-1 shrimp and fewer age-2 and -3 shrimp. These changes were accompanied by an increased percentage of shrimp maturing directly into females at age 1.

To summarize, it is clear that major shifts in the biomass, productivity, and life-history characteristics of key trophic components have occurred in response to both human activities and environmental variability. Figures 3 and 4 are intended to scale the importance of considering the long-term effects of both climate and human disturbance, in order to develop a sense of history for what little we might know about the nature of past population changes in this ecosystem. These population shifts include volatile increases and decreases (crustacean populations); predictable large-scale spatial migrations (pelagics such as hake and sardine as well as many seabird and marine mammal populations); periodic species range expansions and contractions (sardine); changes in age structure of harvested populations (groundfish and shrimp); and recent steady biomass declines (many groundfish and salmonids).

These dynamic species assemblages and interactions define the trophic structure of the northern California Current, a structure that has changed substantially over time and space. Furthermore, the large-scale physical and biological properties of the NCCE (e.g., temperature and flow patterns, primary and secondary production) also vary greatly over time and space with atmospheric forcing. Meine (1999) suggests that the "development of an historic sensibility ought to be considered fundamental to conservation biology"; we would argue that such a sensibility should be an integral part of fisheries biology and management as well, and is relevant in the context of both climatic and anthropogenic forcing mechanisms.

Although much more could be known about the trophic structure of the NCCE, it is clear that many species assemblages (and their ensuing interactions) are complicated and highly dynamic (Brodeur and Pearcy 1992). Thus, it may be that static fisheries models are not adequate for governing dynamic trophic systems, yet tangible objectives for ecosystem-level management initiatives remain ill-defined. If ecosystem-based approaches to fishery management are to be mandated by law or otherwise implemented, a major question will be how, if at all, managers might be able to ultimately incorporate insights and results of climate, trophic, dynamic, or other ecosystem models into management or policy objectives.

ECOLOGICAL MODELING OF THE NCCE

One opportunity for evaluating both the nature and the scale of such trophic interactions is to use ecological modeling. As a starting point, our efforts have focused on quantitatively defining NCCE trophic structure, using available information to explore the productivity of key populations in this region and evaluate how historical removals relate to standing biomass, production, and trophic structure. So far, we have centered on the initiation of an Ecopath modeling project designed to amass critical data on abundance, food habits, and other trophic factors. Future objectives include using dynamic simulations to incorporate modes of environmental forcing into dynamic simulations.

The intent of the discussion here is to explore the potential applications of one type of ecological model as a tool for describing the interacting effects of climate and trophic assemblages and deriving insights which could ultimately be useful for managers. With regard to the utility and application of multispecies or ecosystem models in particular, Hollowed et al. (2000) provide a comprehensive review of the most commonly used methods and their potential utility for measuring fishing impacts on marine ecosystems.

Ecopath was originally designed by Polovina (1984) and evolved into a software application, including a dynamic version called Ecosim, by workers at the University of British Columbia (Christensen and Pauly 1992; Walters et al. 1997). Essentially, Ecopath is a steady-state model that emphasizes natural rates of growth and consumption of marine populations. Given adequate data from fish bioenergetics models or diet composition studies, it provides a framework for summarizing information over

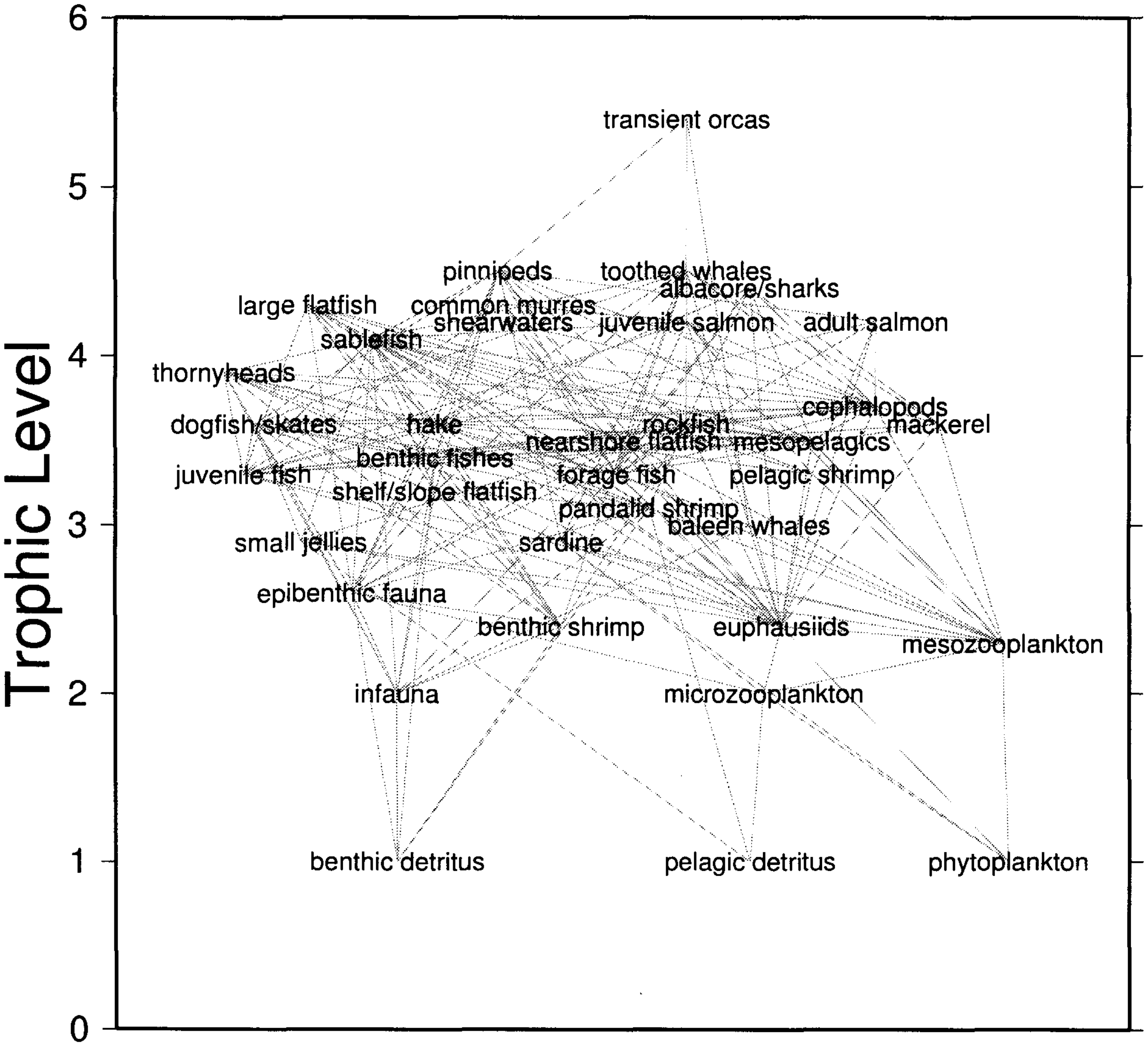

Figure 5. A model of the basic trophic components of the northern California Current food web. Despite massive aggregations of species and species assemblages, the picture illustrates the complexity of trophic interactions and the multitude of pathways for energy in this ecosystem.

trophic levels, emphasizing natural rates of growth and consumption of marine populations. This allows small-scale studies or models to be viewed in a common currency, in the context of the ecosystem as a whole. While the equilibrium assumptions of the Ecopath model do not allow for the determination of "true" biomasses or rates in a changing system, the modeler may use the software's bookkeeping to examine the basic trophic processes; for example, to learn whether a predator or fishery may be consuming more forage than is hypothesized to be available, and thus if its existence is putting pressure on other ecosystem components. The assumption is that over an appropriate period of time (say a decade or a regime) a mass-balance model can be generated to represent the basic trophic interactions between major ecosystem components.

Although the stochastic nature of most (if not all) populations and population parameters would suggest that a range of values would better explain seasonal and interannual changes, the static approach is useful from the standpoint of generating a "snapshot" of some mean state(s) of the ecosystem under different time periods or circumstances. The quick examination of many components of the system essentially extends the concept of maximum sustainable yield to multiple interacting species, suggesting a management framework for examining the consequences of altering species abundance and species assemblages.

It must be stated at the outset that these models rely heavily on "back-of-the-envelope" calculations—stable, oversimplified trophic webs—and thus cannot reliably model sudden ecosystem shifts to new states. Yet this generality and overstability may be their greatest recommendation. These models' potential may lie in developing metrics (e.g., the amount of primary production removed by fishing) relating measurable ecosystem quantities to levels of risk incurred by exploitation. At this time and despite great effort, measurable and meaningful metrics of ecosystem health, stability, and resilience have been elusive (Murawski 2000). Thus as a tool for developing management rules of thumb for avoiding ecological catastrophes, the comparison of simple, stable, pre- and postmanipulation equilibria or functional models with historic records of change in exploited ecosystems warrants further evaluation.

We have used preliminary Ecopath models to compare the state of the NCCE between the 1960s—a cool regime characterized by low exploitation rates and high rates of zooplankton production—and the 1990s—a warm regime characterized by low productivity, declining stocks, and intensively regulated fisheries following several decades of intensive exploitation. Population parameters and diet data for some 34 species or species assemblages were compiled or estimated for both time periods to generate a food web of basic trophic interactions (fig. 5).

The data used to estimate the parameters of this model come from a wide range of sources, including stock assessments, published literature, grey literature, and in many instances general review papers of basic population parameters. Model documentation and descriptions of data and data sources are available in Field and Francis.[5] The challenges in compiling adequate data to parameterize the model inevitably suggest suspect results; because of the paucity of information regarding the dominant planktonic and nektonic populations in this region, some gross estimation and generalization is unavoidable. Nevertheless, we believe such models are extremely useful both for visualizing the nature of the system being managed and beginning to understand how major changes in species abundance or productivity might reverberate up or down through the food web.

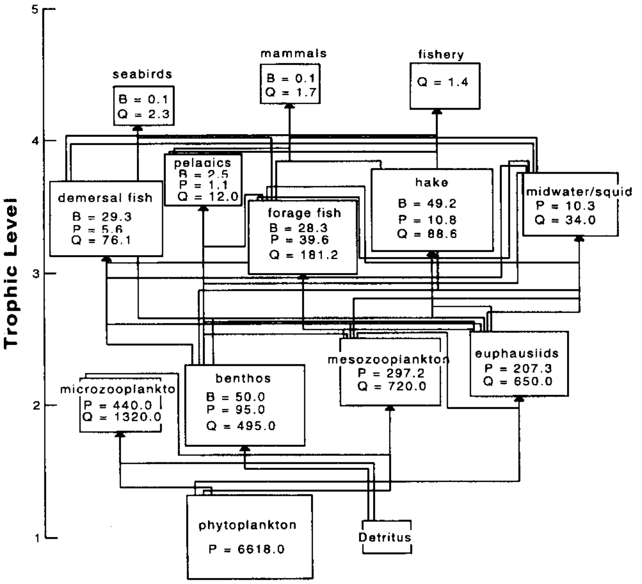

Figure 6. Simplified mass balance models of aggregated ecosystem components and major trophic flows in the northern California Current during the early 1960s. Units are wet weights of biomass (grams/square meter).

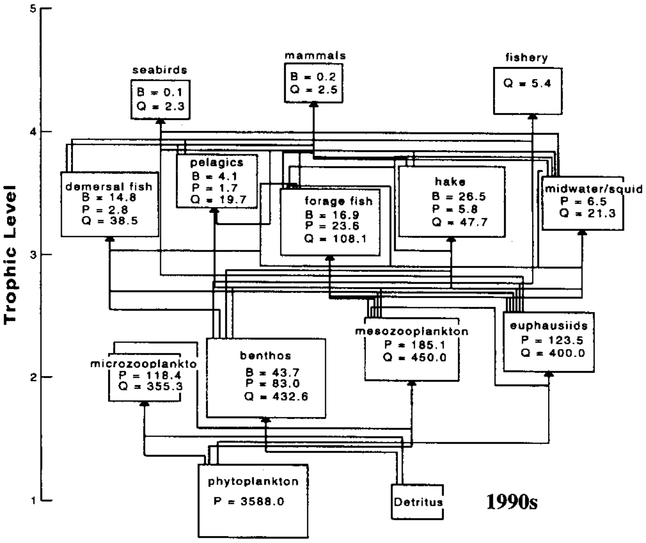

Figure 7. Simplified mass balance models of aggregated ecosystem components and major trophic flows in the northern California Current during the mid-1990s. Units are wet weights of biomass (grams/square meter).

Figures 6 and 7 show greatly simplified versions of trophic flow diagrams and energy pathways through the NCCE as modeled in the early 1960s and 1990s, and generated by aggregating the parameters for the 34 species and species assemblages shown in figure 5. The size of the boxes (if they were to be viewed in three dimensions) would be proportional to the log of estimates of average annual biomass (B) in the different assemblages. The average estimated production in the assemblages is given as P and consumption is given as Q. For lower trophic levels (in which annual production is the key parameter) these estimates are based on a top-down estimate of consumption requirements of upper-trophic-level predators, calibrated to the extent possible by existing assessments of planktonic and nektonic standing stocks and productivity for the two time periods in question. Although the parameters and estimates need further refinement, we believe that these figures represent a reasonable assessment of the key energy flows and trophic pathways through the system. At a minimum, these comparisons provide some measure of how the massive changes in the biomass of commercially important species have

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[5] Field, J. C., and R. C. Francis. MS. in prep. Static and dynamic models of the northern California Current ecosystem. Fisheries Research Institute Reports.

reduced the consumption requirements upon the lower trophic levels necessary to sustain those populations.

One interesting consequence of this change is that there does not appear to be any evidence for major shifts or increases in the abundance of other species or species assemblages to take advantage of what might be perceived as an increase in the availability of forage resulting from declines in the relative abundance of commercially important predators, as has been suggested in other systems such as the Georges Bank (Fogarty and Murawski 1998). Although data on the relative abundance of target and nontarget species are sparse, preliminary work to develop diversity indices of upper-trophic-level predators based on fisheries survey data for the early 1970s and the mid-1990s also suggests no major shift in the relative composition of groundfish assemblages in the INPFC Columbia area (S. Gaichas, pers. comm.), although Emmett and Brodeur (2000) have found substantial shifts in the relative abundance of pelagic predators.

The above situation may be in contrast with other heavily fished ecosystems, in which major shifts in species or community composition have followed major disturbances. Until recently, levels of secondary production throughout the 1990s have seemed far below long-term averages; the abundance of many key forage species has been greatly reduced (Emmett and Brodeur 2000); recruitment of rockfish and survival of salmon smolts have reached all-time lows (Hare et al. 1999); and the average weight-at-age for some species, such as hake and yellowtail rockfish, have been below the long-term means (Dorn et al. 1999; Tagart et al. 2000). Massive changes in the species composition and biomass of euphausiids, copepods, and other planktonic organisms have also been documented (McGowan et al. 1998; Mackas et al., in press). All of these factors suggest that this system has probably been functioning at lower levels of productivity over recent years, as associated with the aforementioned changes in climate forcing and physical conditions following the 1977 (and perhaps 1989) regime shift (Hare and Mantua 2000). As alluded to earlier, the evidence for a large-scale climate shift that has affected the distribution and abundance of key populations in the NCCE is widespread, and improving our knowledge of the mechanism and consequences of these shifts is the focus of major investigations by CalCOFI, GLOBEC, the JISAO Climate Impacts Group, and many other research entities.

The nature in which such a shift in productivity may be interacting with the concurrent and ongoing removal of a substantial fraction of the higher-trophic-level biomass in this ecosystem remains unclear. Our hope is that further insight into the nature and consequences of climate shifts, and into the interaction between such changes and ongoing effects associated with fisheries removals might be uncovered through both static and dynamic modeling of this and other ecosystems. Over recent years dynamic models have been used to consider the impacts of fishing on marine ecosystem dynamics (Kitchell et al. 1999; Trites et al. 1999; Olson et al.[6]), and we expect that such modeling efforts might have much to offer in terms of insights toward considering large-scale ecological interactions in fisheries management.

As suggested earlier, another application of such models could be in deriving metrics or indices, which might be useful in assessing ecological health or stability, or comparing the nature and magnitude of human-induced disturbance between ecosystems. Jarre-Teichmann and Pauly (1998) used an index of the flow from primary production to higher trophic levels imbedded in the Ecopath software to assess the relative effect of fishing removals as a percentage of the production necessary to support fisheries on coastal pelagic species in several coastal upwelling systems. Their findings suggested that major fisheries for coastal pelagics removed between 1% and 15% of the primary production in these systems during distinct time periods. Perhaps more significantly, the magnitude of exploitation was more dependent upon the target species than on the total landings between systems; in other words, removals of species with higher trophic levels had a correspondingly greater effect on the percentage of primary production required (PPR) to sustain them. In these models, estimates of PPR are made for each trophic pathway, and energy flows are raised to primary production equivalents by means of methodology suggested by Ulanowicz (1995) and described in more detail in Christensen et al. (2000). The statistic of primary production required to support fisheries removals is thus a measure of the total amount of new production removed from exploited populations, scaled to the appropriate trophic level.

An example of how this index might be useful for comparative purposes is presented as figure 8. This figure shows total removals (landings and some measure of discards) in metric tons per square kilometer from three ecosystems in different time periods plotted with the estimated percentage of relative production necessary to support these landings (as above, the primary production raised to the equivalent trophic levels of the catches).

In the Eastern Bering Sea (EBS) models (Trites et al. 1999) there were massive harvests of long-lived, slow-growing predators, primarily baleen whales, sperm whales, walrus, and seals, with a corresponding low volume of landings in terms of tonnage but representing nearly all of the production at those trophic levels in that system. What this showed was essentially the "mining

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[6] Olson, R. J., G. M. Watters, R. C. Francis, P. C. Fielder, J. J. Polovina, S. B. Reilly, K. Y. Aydin, and J. F. Kitchell. Climate forcing and ecosystem dynamics in the eastern tropical Pacific Ocean. MS. submitted to Ecol. App.

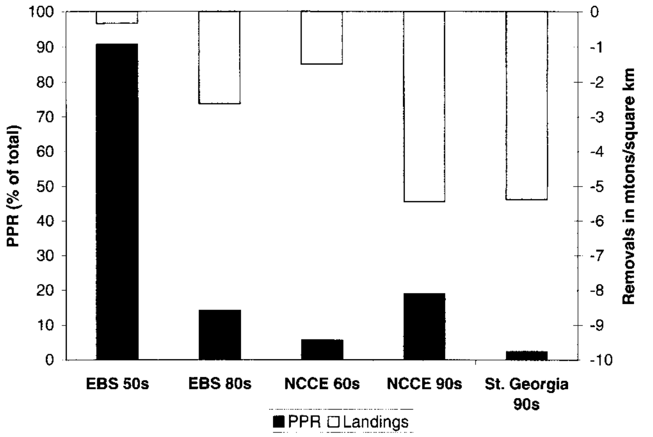

Figure 8. Fisheries removals (in metric tons/square kilometer) and percentage of primary production required (PPR) to sustain them, derived from five coastal ecosystem models. EBS = eastern Bering Sea; NCCE = northern California Current ecosystem; St. Georgia = Strait of Georgia.

out" of the biomass of higher trophic levels in the EBS during a period of intensive exploitation in the 1950s and 1960s. By contrast, in the 1980s the EBS supported the largest (by volume) fishery in the United States—the trawl fishery for walleye pollock—in addition to fisheries for Pacific cod, tanner crab, and many flatfish species. The removals (in t/km^2) increased substantially; however, due to the lower trophic levels of the target species, the percentage of system production that was removed annually declined considerably.

In the northern California Current, landings were relatively low in the 1960s, less than 1.5 t/km^2, and the corresponding percentage of primary production required to support those landings was on the order of 6%. By the 1990s, however, the total landings had increased substantially (see fig. 4; additionally, some groundfish landings had already peaked in the 1980s and dropped by the 1990s), to an average of nearly 6 t/km^2; this represented some 20% of the available production being removed by the fishery. By contrast, comparison with the (contemporary) Strait of Georgia model constructed by Pauly, Pitcher et al. (1998), removals were on the same magnitude between the NCCE and the Strait of Georgia in terms of tons per square kilometer, but because of the tremendous productivity and recycling of nutrients and energy in the Strait of Georgia, landings required a substantially greater percentage of the scaled production in the NCCE.

It is interesting to consider that the total removals per unit area, and the percentage of production accounted for in those removals, is greater in the NCCE than in the (contemporary) eastern Bering Sea. Whereas the latter is one of the most productive fishing grounds in U.S. waters, the immense area of this coastal shelf is what accounts for the tremendous volume of fisheries that it supports. While this construct of production required to support landings may seem vague, and is certainly fraught with major uncertainties about the real nature of the food web that supports these landings, we believe that this example illustrates the means by which simple ecological models may show the nature and magnitude of human-induced disturbances, and ultimately may provide a useful index or tool for scaling the extent and magnitude of human intervention in these complex ecosystems.

CONCLUSIONS

McEvoy (1996) suggested that successful fisheries management will require that managers and policymakers "cooperate with each stock's strategy for responding to the environment." Clearly, this environment is modulated by variability and change in climate as well as increasing measures of anthropogenic disturbance. We believe that the development and application of static and dynamic ecosystem models will ultimately reveal useful insights about how both climate and fishing affect NCCE structure and dynamics, and will provide valuable insight into system definition and behavior. Additionally, we hope to illuminate gaps in research or knowledge that create potential management limitations and increase uncertainty. Finally, we believe that the development of such models will lead to both static and dynamic visualizations that readily convey to managers and stakeholders the dynamics of this ecosystem and potential or probable effects of alternative management approaches. Ultimately, such efforts should lead to the development of more refined models to quantify the nature of ecological change in this system as a result of both climate effects and fishing, and will be useful as a framework for incorporating ecological considerations into fisheries management practices.

It is fair, however, to suggest that such insights are unlikely to lead to any meaningful short-term solutions to current crises in the management of northern California Current fisheries. The salmon crisis or the massive problems associated with effectively managing the groundfish fishery and the recovery of depleted populations can be addressed only by a massive change in the way in which large-scale system variability and human-induced impacts (both fishery and nonfishery related) are mitigated and managed in the future. The adoption of an "ecosystem-based approach" will result neither in obvious solutions to current crises nor in a substitute for more traditional means of assessing and managing fisheries. As McEvoy (1996) suggests, "If scientific fishery management could not predict or maintain the production of individual species, it seems a bit presumptuous to expect that we could now anticipate and direct the interacting components of an entire ecosystem."

Clearly, the adoption of a broader view of the interactions between fisheries (both their biological and human components) and marine ecosystems is necessary, and we must accept the dynamic and inherently unpredictable nature of entire systems and learn to operate within the bounds of uncertainty to ensure future sustainability. The nature of the coastal pelagics FMP is a step in such a direction, as is the movement toward using marine reserves to provide refugia for species as well as opportunities to assess how disturbed and undisturbed systems may differ in form and function. Equally necessary are basic reforms in the current approach to fisheries management away from traditional focused command-and-control practices. These changes are not mutually exclusive; both can and must occur if the resources and the communities which depend upon them are to persist in the future.

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Top-down modeling and bottom-up dynamics: Linking a fisheries-based ecosystem model with climate hypotheses in the Northern California Current

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Abstract

In this paper we present results from dynamic simulations of the Northern California Current ecosystem, based on historical estimates of fishing mortality, relative fishing effort, and climate forcing. Climate can affect ecosystem productivity and dynamics both from the bottom-up (through short- and long-term variability in primary and secondary production) as well as from the top-down (through variability in the abundance and spatial distribution of key predators). We have explored how the simplistic application of climate forcing through both bottom-up and top-down mechanisms improves the fit of the model dynamics to observed population trends and reported catches for exploited components of the ecosystem. We find that using climate as either a bottom-up or a top-down forcing mechanism results in substantial improvements in model performance, such that much of the variability observed in single species models and dynamics can be replicated in a multi-species approach. Using multiple climate variables (both bottom-up and top-down) simultaneously did not provide significant improvement over a model with only one forcing. In general, results suggest that there do not appear to be strong trophic interactions among many of the longer-lived, slower-growing rockfish, roundfish and flatfish in this ecosystem, although strong interactions were observed in shrimp, salmon and small flatfish populations where high turnover and predation rates have been coupled with substantial changes in many predator populations over the last 40 years.
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Keywords: California Current; Trophic interactions; Ecosystem model; Ecosystem management; Climate variability

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1. Introduction

In the California Current, many fish populations and the communities that depend upon them are in a state of crisis. Many long-lived, slow-growing groundfish have become severely depleted due to overharvesting, and

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obligatory rebuilding plans suggest that some stocks could take many decades to recover. The condition of several stocks is so poor that the Pacific Fisheries Management Council (PFMC) found it necessary in 2003 to close the majority of the continental shelf to most fishing, an action that has resulted in dramatic impacts to fishermen and fishing-dependent communities. Salmon crises, driven by a complex combination of natural and anthropogenic factors, have been ongoing in the Pacific Northwest for decades, although recent changes in ocean conditions have boosted production in some regions to record levels. Fisheries for highly variable coastal pelagic populations could be entering a new phase as well, as some stocks may have recently entered into a period of low productivity. Yet other fisheries, such as those for high turnover invertebrates such as Dungeness crab (*Cancer magister*) and pandalid shrimp (primarily the ocean shrimp, *Pandalus jordani*), have been highly variable over time, and in recent years have been thriving.

Historical management of these fisheries has generally been crisis-based rather than proactive. However there is a growing national and international recognition of the need to develop an ecosystem-based approach to fisheries management (EBFM) in response to the challenges and shortcomings of traditional resource management approaches in sustaining marine ecosystems (Botsford et al., 1997; EPAP, 1999; NRC, 1999; Pauly et al., 2002; Pikitch et al., 2004). The common threads of ecosystem-based management approaches involve taking a more holistic view of managing resources in the context of their environment. For marine fisheries, this implies greater consideration of the interactions between climatic and oceanographic processes, the connections and interactions between fished and unfished populations in the ecosystem, and the role of humans as both predators and competitors in such ecosystems. While efforts to develop an ecosystem focus in fisheries modeling and management are far from new, the desire to do so has increased as both stakeholder and public perceptions of fisheries have evolved from limitless frontiers to systems with limits and thresholds (Hanna, 1997; EPAP, 1999; NRC, 1999). Although the direct application of ecosystem modeling and management strategies in fisheries systems has historically been limited (Mangel et al., 2000; Goodman et al., 2002), the potential role of such approaches holds promise in the future of marine resource management. This paper uses a dynamic ecosystem model of the Northern California Current (NCC), a region of the larger California Current System (CCS), to improve our understanding of the relationships among physical, ecological and human (fisheries) processes in shaping the trajectories of commercially important populations of fish and shellfish. In particular, the model allows us to evaluate how conceptual and statistical relationships between climate and the commercially important biota in this ecosystem can be incorporated into a dynamic model and assessed against known or suspected trends in ecosystem behavior.

2. Data and methods

The California Current is essentially the eastern limb of the Central Pacific Gyre, and begins where the west wind drift splits into two broad coastal currents, the California Current to the south and the Alaska Current to the north, near the northern end of Vancouver Island. The location of the NCC relative to the large-scale circulation patterns and coastal domains of the northeast Pacific (Fig. 1, left-hand panel) is shown as adapted from Ware and McFarlane (1989), as is the general bathymetry of the area of the NCC modeled in this exercise (Fig. 1, right-hand panel). As there are really several major currents in the region, all of which vary in geographical location, intensity and direction with the seasons, this region is generally referred to as the California Current System (CCS, Hickey, 1979). In most cases, the shelf, slope and offshore regions of the California Current System have their greatest changes in physical and biological characteristics at major promontories along the west coast. These include Point Conception, Cape Mendocino, and Cape Blanco (US GLOBEC, 1994). The dynamics over the shelf are generally forced by regional wind fields, which tend to be equatorward in the spring and summer, and poleward in the winter. Spring and summer equatorward winds drive offshore Ekman transport of surface waters, which is balanced by the upwelling of deeper waters that tend to be cooler and nutrient rich. Although the scales of the wind fields tend to be large (100s of km), there are significant spatial differences over both alongshore and cross-shore directions, often related to the geographic barriers described earlier. The northern half of the CCS, the region of coastal ocean between Cape Mendocino and Vancouver Island, is often described as a zoogeographic transition between Californian and Aleutian biological provinces (Bottom et al., 1993). Although this entire area should rightly be referred to as the Northern California Current Ecosystem, the political boundary between the US and Canada (which runs

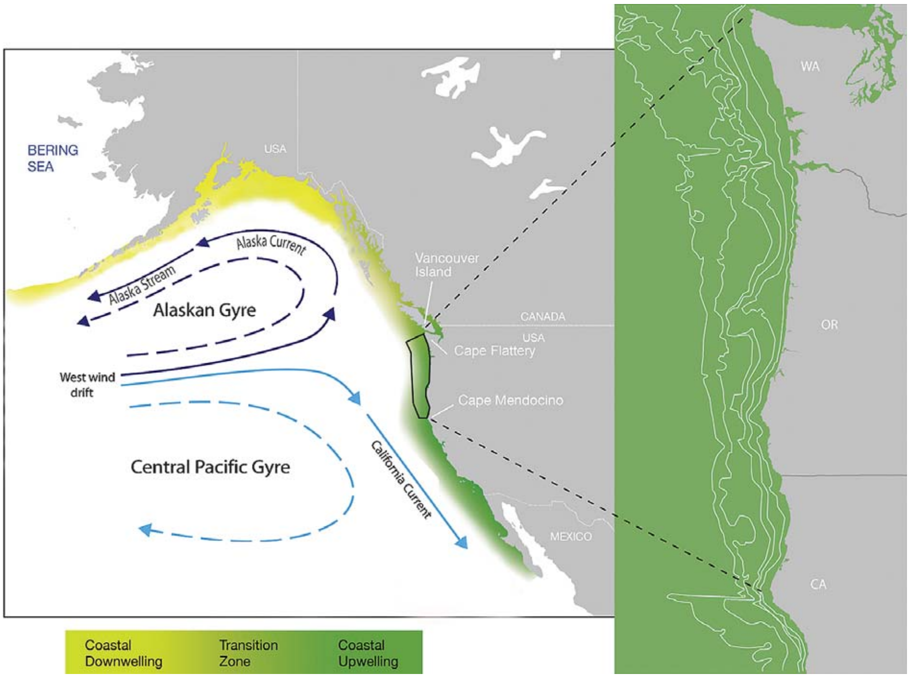

Fig. 1. Major current patterns and ocean domains of the Northeast Pacific and bathymetry (50, 100, 200, 500, 1000 and 2000 m contours) of the continental shelf and slope between Cape Mendocino and Cape Flattery.

southwest off of Cape Flattery, WA) has been used here as a northern boundary for the purposes of these modeling efforts, primarily due to data limitations.

The region modeled is the area between the nearshore and the continental slope to a depth of approximately 1280 m (typically 20–80 km offshore), as this represents the limits of available data from continental slope surveys and the approximate limits of most historical and contemporary fishing effort for trawl and fixed gear. Throughout this region, there are extreme gradients in physical conditions and biological communities between the highly energetic waters nearshore, and the cold, low oxygen waters of the continental slope. Although the true extent of the California Current itself is far seaward of these boundaries, and many important highly migratory species spend much of their lives outside this area, the shelf and shelf break waters represent most of the habitat for most resident groundfish species, and much of the range of Pacific hake (*Merluccius productus*), salmon (*Oncorhynchus* spp.), sardine (*Sardinops sagax*), mackerel (both *Trachurus symmetricus* and *Scomber japonicus*) and other migrants. This coastal margin also includes the regions of greatest biological production at lower trophic levels, and the greatest densities of migratory seabirds and marine mammals. Seabirds and marine mammals exemplify the problems associated with establishing boundaries around marine ecosystems, as some of the most ecologically important populations migrate from other ecosystems throughout the Pacific. For example, humpback whales (*Megaptera novaeangliae*) migrate north from the equatorial Pacific in summertime, northern fur seals (*Callorhinus ursinus*) migrate to the NCC from the Bering Sea during winter, and sooty shearwaters (*Puffinus griseus*) migrate to the NCC from the southern hemisphere.

The modeling framework employed in this paper is the Ecopath mass balance approach developed by Polovina (1984) and Christensen and Pauly (1992). Ecopath is currently available as part of a modeling package that includes a dynamic model, Ecosim (Walters et al., 2000), and a spatially-explicit dynamic model called Ecospace (Christensen and Walters, 2004a). Comparable software developed by one of the authors (K. Aydin) was also used for much of this work. The origins of the modeling approach can be traced back to Steele (1974), Laevastu and Favorite (1978), and deeper into the development of theory on thermodynamics, ecosystem structure and marine ecology (Margalef, 1963; Ryther, 1969; Odum, 1969). The resurgence in the popularity of these (and similar) modeling approaches is not necessarily explained in terms of an increased foundation of knowledge and data to parameterize such models, but rather to the present political interest in developing ecosystem-based fisheries management tools and insights. The approach used by Ecopath and Ecosim is but one of several potential modeling frameworks for investigating trophic interactions in large marine ecosystems. Most critical reviews of multispecies modeling approaches (such as multi-species biomass dynamics models, multi-species VPA, individual-based models, and others) agree that despite conceptual shortcomings and data limitations, ecosystem models have the potential to augment contemporary single-species models by confronting an array of interactions and dynamics that are more difficult to address with single-species models, such as competition, predation and environmental variability (Hollowed et al., 2000; Fulton et al., 2003; Plagányi and Butterworth, 2004). Such models have also been suggested as vehicles for qualitatively structuring ecosystem limitations for using quantitative information from single species stock assessments. Many criticisms of ecosystem modeling approaches are based less on the model structure, than on the misuse and misunderstanding of the model limitations, a characteristic shared with single-species models (Schnute and Richards, 2001). As Walters et al. (2005) suggest, no model can ever be expected to be a "complete" representation of a food web, particularly where size structured interactions and trophic ontogeny have the potential to lead to more complex ecological interactions than can be accounted for in simplistic models.

Ecopath is a steady-state model that emphasizes rates of production and consumption of marine populations. The model provides a template for integrating a wide range of biological and fisheries information from stock assessments, survey data, bioenergetics, food habits studies, and fishing mortality. The energetic accounting of the model also forces a critical evaluation of basic interspecific interactions, which in turn allows an evaluation of whether what is believed to be "known" about a system (from survey, stock assessment or other sources) "adds up" in a thermodynamic sense. The necessary assumption is that, over an appropriate period of time (typically one or several years), a mass-balance model can be generated to represent the basic trophic interactions between major ecosystem components. It is important to note that this need not constrain the model to equilibrium, but rather only to a thermodynamically consistent state. The equations are thermodynamically based, such that new production of any component is partitioned between consumption by predators, export from the system, yield to fisheries, and biomass accumulation or decline (the left hand side of Eq. (1), and consumption of prey by predators is partitioned into respiration, tissue production and egestion (the right hand side of Eq. (1). The main equation for the entire model is:

$$B_i\left(\frac{P}{B}\right)_i \mathrm{EE}_i + \mathrm{IM}_i + \mathrm{BA}_i = \sum_j \left(B_j \frac{Q}{B}\mathrm{DC}_{ij}\right)_j + \mathrm{EM}_i + C_i \tag{1}$$

where B is the standing biomass of a given group, i, and j represents all predators on i, P/B is the production to biomass ratio (typically in units of 1/year, and based on bioenergetic models, mortality rates or literature values), EE represents the ecotrophic efficiency of a component (essentially the fraction of new production that is passed up through the food web), IM and EM represent immigration and emigration used to account for model imbalances related to migration, BA is a biomass accumulation term used to reflect observed trends, Q/B is a consumption to biomass ratio (also in units of 1/year), DC is the proportional diet composition of predators j on prey i, and C is the catch by fisheries. Because the model is essentially a series of linear equations, matrix methods can be used to estimate one unknown for each component of the model. Typically the unknown to be "solved," or estimated, is the EE, or ecotrophic efficiency. However when biomass or P/B ratios are unavailable, this value can be specified at a predetermined level and the model can be balanced to estimate either the average biomass (B_i), the production to biomass ratio (P/B), or the consumption to biomass ratio (Q/B). Although the assumptions of constant transfer rates are unlikely to be met in reality (where the stochastic nature of population and biological rates would suggest that a range of values would be more appropriate), the static approach is useful from the standpoint of generating a "snapshot" of the mean state of the ecosystem during a particular time period or condition.

A mass balance model of the NCC representing the 1960s was developed by Field (2004), and detailed documentation of the derivation of model parameters and reviews of food habits studies are not included here for the sake of brevity. In general, stock assessments provide the most complete source of information on the abundance and productivity of roughly 15 commercially important stocks as far back as the 1960s. Stock assessments are reported in the Appendices to the Stock Assessment and Fishery Evaluation (SAFE) Reports published by the Pacific Fisheries Management Council (PFMC, 2002, 2003). Where stock assessments did not model population abundance as far back as the early 1960s, estimates of catches and the results of assessments were used to fit known biomass surplus production models (MacCall, 2002) to arrive at reasonable biomass estimates for the 1960s model. For most unassessed species and assemblages, survey results from triennial groundfish surveys conducted from 1977 through 2001 (e.g., Weinberg et al., 2002) and slope surveys done through much of the 1990s (e.g., Lauth, 1999) were used to develop abundance estimates (additional details of the survey history and potential shortcomings are summarized in Zimmerman et al., 2003). Catch and landings data are taken first from stock assessments (where available), from the Pacific Fisheries Information Network (PacFIN) database between 1981 and 2003, and from historical records compiled by Lynde (1986) between 1956 and 1980. Estimates of bycatch rates were obtained from stock assessments where available, or developed from the bycatch data collected during studies of shrimp and groundfish trawl fisheries in the mid-1980s (Pikitch et al., 1988).

Estimates of abundance and productivity for lower and higher trophic level model components (phytoplankton, zooplankton, benthic fauna, marine mammals, seabirds) were based on a compilation of survey estimates, literature values, or model estimates. Abundance and population rate data for top-level predators, particularly seabirds and marine mammals, were obtained primarily from NMFS Marine Mammal Stock Assessments (Carretta et al., 2002) and other sources (e.g., Briggs et al., 1992; Wahl et al., 1993). Estimates of abundance and productivity for lower trophic levels were based on literature values of standing stocks and population rates for populations within or near to the NCC where available (Robinson et al., 1993; Tanasichuk, 1998; Peterson and Schwing, 2003), but were more typically based on top-down balances. Food habits data from the NCC were available from a wide range of studies of groundfish and top-predator populations between 1960 and 2000; including over 30,000 stomach samples of groundfish, although many such studies were highly limited in space and time (Livingston, 1983; Brodeur and Pearcy, 1984; Buckley et al., 1999). Consumption-rate values for most commercially important species estimates were generated using weight-at-age data collected from the triennial surveys and a generalized version of the von Bertalanffy growth equation developed by Essington et al. (2001), and were typically based on literature estimates for lower and higher trophic levels (e.g., Hunt et al., 2000).

The final model includes 63 components; 21 of which are commercially significant species or stocks of fish or shellfish, 8 of which are aggregations (at the genus or family level) of commercially significant groups (e.g., salmon, skates), 11 of which are functional groups of top predators (seabirds and marine mammals), 4 of which are either producers (phytoplankton) or detritus (benthic, pelagic, fisheries offal), with the remaining 19 representing broad aggregates of zooplankton, benthic fauna, and non-commercial fishes. As such, the model emphasizes detail for mid-trophic level predators, in particular commercially important groundfish, for which considerably more data tend to be available. The model components and parameters for the 1960s model are provided (Table 1), as is the diet matrix developed for this model (Table 2). Additionally, we summarize the more significant taxa in the aggregated or functional groups in the model (Table 3) and provide full common and latin names for the species or stocks in the model (Table 4). We also present the steady-state model in a more graphical form (Fig. 2), consistent with the methods developed by Aydin et al. (2003).

The basic equations of the dynamic Ecosim model, and many of the associated assumptions and technical details, are developed in detail in Walters et al. (2000) and Christensen and Walters (2004a). Ecosim turns the energy flows of a given Ecopath model into dynamic, time-varying predictions by using coupled differential equations derived from the basic Ecopath equation (Eq. (1)), such that:

$$\frac{\mathrm{d}B_i}{\mathrm{d}t} = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (M0_i + F_i + e_i)B_i \tag{2}$$

where $\mathrm{d}B_i/\mathrm{d}t$ is the growth rate (in units of biomass) of the group i during the time interval $\mathrm{d}t$, g_i is the growth efficiency (defined as production, P, over consumption, Q), Q_{ji} represents predation by group i on group j, Q_{ij} represents predation on group i by group j, I_i is the proportional biomass immigration rate, $M0_i$ is the non-predation mortality, F_i is the fishing mortality rate, and e_i is the proportional emigration rate. More simply, the instantaneous change in biomass of a given group i is dependent upon the difference between the prey that i consumes (the Q_{ji}, multiplied by growth efficiency) and how much of that group is consumed by predators (the

Table 1
Parameter values for the 1960s NCC model

Group name	Trophic level	Biomass (t/km^2)	Production/ biomass	Consumption/ biomass	Ecotrophic efficiency	Production/ consumption	Total catches	Accumulation (t/km^2/year)
Phytoplankton	1.0	55.150	120.00	–	0.43	–	0.000	0.000
Infauna	2.0	35.700	2.50	12.00	0.89	0.21	0.000	0.000
Amphipods	2.0	4.380	3.50	22.00	0.80	0.16	0.000	0.000
Epibenthic	2.5	12.564	2.00	10.00	0.80	0.20	0.012	0.000
Micro-zooplankton	2.0	3.947	100.00	300.00	0.80	0.33	0.000	0.000
Copepods	2.2	16.609	14.00	70.00	0.80	0.20	0.034	0.000
Euphausiids	2.1	27.037	8.00	40.00	0.80	0.20	0.000	0.000
Carniv-zooplankton	3.1	7.731	2.00	10.00	0.80	0.20	0.158	0.000
Small jellies	2.3	1.342	9.00	30.00	0.80	0.30	0.000	0.000
Large jellies	3.2	1.168	3.00	12.00	0.80	0.25	0.000	0.000
Pandalid shrimp	2.8	1.518	2.00	10.00	0.80	0.20	0.000	0.000
Benthic shrimp	3.0	1.608	2.50	12.00	0.80	0.21	0.000	0.000
Dungeness crab	3.5	0.843	0.75	3.80	0.71	0.20	0.000	0.000
Tanner crab	3.0	0.975	0.30	1.50	0.80	0.20	0.000	0.000
Cephalopods	3.6	2.059	2.00	6.00	0.80	0.33	0.000	0.000
Forage fish	3.2	27.101	1.50	6.00	0.80	0.25	0.004	0.000
Mesopelagics	3.2	7.575	0.60	3.00	0.80	0.20	0.000	0.000
Benthic fish	3.3	4.110	0.50	2.50	0.80	0.20	0.100	0.000
Macrourids	3.7	0.468	0.20	1.00	0.38	0.20	0.000	0.000
Pacific sardine	2.8	0.663	0.50	5.00	0.80	0.10	0.000	0.000
Mackerel	3.5	0.286	0.35	6.00	0.71	0.06	0.001	0.000
Pacific salmon	4.1	0.367	0.93	5.82	0.83	0.16	0.014	0.000
Pacific hake	3.6	25.990	0.23	2.50	0.58	0.09	0.141	0.000
Skates	4.0	0.421	0.20	2.00	0.51	0.10	0.046	0.000
Dogfish	4.1	1.000	0.20	2.50	0.17	0.08	0.028	0.000
Sablefish	4.1	2.756	0.06	1.95	0.44	0.03	0.011	−0.008
Juvenile rockfish	3.3	0.704	1.50	6.00	0.80	0.25	0.029	0.000
Pacific Ocean perch	3.3	1.217	0.07	2.00	0.77	0.04	0.000	−0.010
Canary rockfish	3.2	0.757	0.10	1.60	0.43	0.06	0.045	−0.006
Widow rockfish	3.5	2.828	0.14	2.10	0.46	0.07	0.008	0.023
Yellowtail rockfish	3.6	1.966	0.11	1.60	0.65	0.07	0.027	0.000
Black rockfish	4.0	0.407	0.09	1.95	0.77	0.05	0.020	0.000
Shelf rockfish	3.7	1.179	0.10	1.90	0.64	0.05	0.006	0.000
Slope rockfish	3.3	0.864	0.06	1.45	0.86	0.04	0.025	0.000
Shortspine thornyhead	4.0	0.751	0.07	0.45	0.74	0.14	0.017	0.000
Longspine thornyhead	3.7	1.800	0.05	0.35	0.89	0.14	0.003	0.000
Juvenile thornyhead	3.4	0.714	0.50	2.50	0.80	0.20	0.009	0.000
Juvenile roundfish	3.2	0.247	1.50	5.13	0.80	0.29	0.000	0.000
Lingcod	4.3	0.522	0.24	2.20	0.13	0.11	0.012	−0.007
Juvenile flatfish	3.1	0.959	1.00	4.00	0.80	0.25	0.000	0.000
English sole	3.2	0.600	0.35	2.12	0.89	0.17	0.057	−0.019
Petrale sole	4.1	0.326	0.28	2.00	0.52	0.14	0.032	−0.015
Small flatfish	3.4	3.684	0.50	2.50	0.80	0.20	0.026	0.000
Rex sole	3.1	0.400	0.50	2.12	0.84	0.24	0.020	−0.005
Dover sole	3.1	3.861	0.08	1.10	0.42	0.07	0.093	−0.040
Arrowtooth flounder	4.3	0.321	0.34	2.12	0.47	0.16	0.027	0.000
Pacific halibut	4.3	0.089	0.34	2.12	0.51	0.16	0.003	−0.002
Northern albacore	4.3	0.014	0.36	7.30	0.64	0.05	0.000	0.000
Coastal sharks	4.4	0.050	0.18	2.80	0.47	0.06	0.000	0.000
Shearwaters	4.2	0.003	0.100	138.00	0.00	0.00	0.000	0.000
Common murres	4.2	0.009	0.100	129.00	0.27	0.00	0.000	0.000
Gulls	4.1	0.002	0.120	122.00	0.00	0.00	0.000	0.000
Orcas	5.0	0.001	0.020	11.15	0.00	0.00	0.000	0.000
Toothed whales	4.4	0.052	0.070	28.85	0.09	0.00	0.000	0.000
Sperm whales	4.7	0.037	0.020	6.61	0.55	0.00	0.000	0.000
Harbor seals	4.4	0.004	0.084	17.44	0.70	0.01	0.000	0.001

(*continued on next page*)

Table 1 (*continued*)

Group name	Trophic level	Biomass (t/km^2)	Production/ biomass	Consumption/ biomass	Ecotrophic efficiency	Production/ consumption	Total catches	Accumulation (t/km^2/year)
Sea lions	4.5	0.012	0.074	16.38	0.67	0.01	0.000	0.001
Fur seals	4.5	0.006	0.091	39.03	0.80	0.00	0.000	0.000
Grey whales	3.0	0.008	0.037	8.87	0.54	0.00	0.000	0.000
Baleen whales	3.6	0.075	0.037	7.58	0.95	0.01	0.000	0.003
Fishery offal	1.0	1.0	10.000	–	–	0.02	–	0.000
Pelagic detritus	1.0	1.0	10.000	–	–	0.09	–	0.000
Benthic detritus	1.0	1.0	10.000	–	–	1.09	–	1.000

See Table 3 for a description of the more significant taxa in the aggregated functional groups listed here, and Table 4 for the scientific names of the stocks or species listed here.

Q_{ij}), taking into account non-predation mortality ($M0$), fishing (F), immigration (I) and emigration (e). The differential equations are solved in Ecosim using either an Adams–Bashforth integration or a Runge–Kutta fourth-order routine (Walters et al., 2000). One of the more recent developments in Ecosim is the ability to handle ontogenetic shifts in life history characteristics with either "split-pool" juvenile and adult groups for model components, or multiple life history stanza models for species with more complex ontogeny (Christensen and Walters, 2004a). Although alternative versions of the NCC model were constructed with species-specific juvenile and adult pools, the lack of data on abundance, consumption, production and prey preferences made effective implementation of a split-pool or multi-stanza model unfeasible at the present time. Instead, juveniles of similar species have been pooled together, as rockfish, flatfish and roundfish juveniles, based on what predation could be reliably inferred from diet studies (where juveniles as prey are very rarely identified beyond genus or family level) and estimates from the literature and other models regarding plausible production and consumption rates.

The most important interactions in the dynamic model are the biomass flows between compartments, the consumption rates (Q_{ij}) themselves. These flows are calculated by the "foraging arena" concept (Walters and Juanes, 1993; Walters et al., 1997, 2000), which assumes a heterogeneous environment in which the biomass of a model component is partitioned into states vulnerable and invulnerable to predation. The transfer rate, v, between these two states in part determines whether control in the model is top-down (Lotka-Volterra), bottom-up, or intermediate. The non-vulnerable state is intended to represent mechanisms that prey use to avoid predation, such as daily vertical migrations or schooling; behaviors that can lead to strong competitive interactions between predators even when the biomass of prey is large. For example Bundy (2001) demonstrated a strong top-down effect of harp seals on cod when vulnerability parameters were set at either high (implying top-down control) or intermediate (default) values. When they were set to low (bottom-up) values, strong top-down effects did not occur. In this instance, high vulnerability is likely to be a reasonable assumption, particularly as marine mammals and other animals with high passive metabolism costs typically do not have the option of lowering consumption rates relative to prey availability. A low vulnerability implies weak top-down control on a prey biomass (closer to ratio-dependent predation rates), to the extent that control is bottom-up and production does not significantly increase with predator declines.[1]

Consumption is modeled in a manner that facilitates opportunities to manipulate consumption rates dynamically, such that the consumption rate of a prey i by a predator j (Q_{ij}) is determined by the equation:

$$Q_{ij} = \frac{a_{ij} v_{ij} B_i B_j T_i T_j S_{ij} M_{ij}/D_j}{v_{ij} + v_{ij} T_i M_{ij} + a_{ij} M_{ij} B_j S_{ij} T_j/D_j} \tag{3}$$

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[1] Walters et al. (2000) suggest that modeling in a low vulnerability scenario is comparable to the compensatory responses considered in contemporary single-species management. While this is true, the nature of compensation in Ecosim comes from increased per-capita consumption (at the expense of other species) rather than from the increasing growth rates (and conversion efficiencies) of relatively younger fish as older individuals are removed from the population in a typical catch-at-age stock assessment model (Aydin, 2004).

Table 2a
Diet matrix for the first 20 components of the NCC model

Prey/predator	Infauna	Amphipods	Epibenthic	Micro-zooplankton	Copepods	Euphausiids	Carniv-zooplankton	Small jellies	Large jellies	Pandalid shrimp	Benthic shrimp	Dungeness crab	Tanner crab	Cephalopods	Forage fish	Mesopelagics	Benthic fish	Macrourids	Pacific sardine	Mackerel
Phytoplankton		0.200		0.750	0.800	0.900	0.030	0.500											0.280	
Infauna			0.430							0.250	0.400	0.400	0.792				0.300	0.150		
Amphipods			0.020				0.020			0.020	0.040	0.025			0.010	0.030	0.180	0.050		0.010
Epibenthic										0.050	0.400	0.200	0.118	0.009			0.400	0.150		
Micro-zooplankton					0.200	0.050	0.030	0.250	0.030						0.100				0.020	
Copepods						0.050	0.500		0.300	0.100				0.150	0.450	0.320			0.400	0.050
Euphausiids							0.350		0.600	0.200				0.380	0.400	0.520			0.300	0.600
Carniv-zooplankton									0.020	0.030				0.150	0.025	0.040				0.070
Small jellies							0.050		0.050						0.010	0.045				
Large jellies							0.020									0.020				0.010
Pandalid shrimp														0.005			0.010	0.010		
Benthic shrimp												0.200		0.005			0.040	0.040		
Dungeness crab												0.005					0.005			
Tanner crab																	0.002			
Cephalopods												0.001		0.001	0.005	0.020	0.001	0.300		0.005
Forage fish												0.100		0.200			0.010			0.200
Mesopelagics														0.100		0.005		0.050		0.010
Benthic fish												0.010						0.050		0.004
Macrourids																				
Pacific sardine																				
Mackerel																				
Pacific salmon																				0.001
Pacific hake																		0.050		
Skates																				
Dogfish																				
Sablefish																				
Juvenile rockfish												0.001					0.003			0.005
Pacific Ocean perch																				
Canary rockfish																				
Widow rockfish																				
Yellowtail rockfish																				

(*continued on next page*)

Table 2a (*continued*)

Prey/predator	Infauna	Amphipods	Epibenthic	Micro-zooplankton	Copepods	Euphausiids	Carniv-zooplankton	Small jellies	Large jellies	Pandalid shrimp	Benthic shrimp	Dungeness crab	Tanner crab	Cephalopods	Forage fish	Mesopelagics	Benthic fish	Macrourids	Pacific sardine	Mackerel
Black rockfish																				
Shelf rockfish																				
Slope rockfish																				
Shortspine thornyhead																				
Longspine thornyhead																				
Juvenile thornyhead																				
Juvenile roundfish												0.002					0.002			0.005
Lingcod																				
Juvenile flatfish											0.010	0.010					0.020			0.020
English sole																				
Petrale sole																				
Small flatfish												0.020					0.010			0.010
Rex sole												0.001								
Dover sole																				
Arrowtooth flounder																				
Pacific halibut																				
Northern albacore																				
Coastal sharks																				
Shearwaters																				
Common murres																				
Gulls																				
Orcas																				
Toothed whales																				
Sperm whales																				
Harbor seals																				
Sea lions																				
Fur seals																				
Grey whales																				
Baleen whales																				
Fishery offal												0.020								
Pelagic detritus		0.100		0.250				0.250												
Benthic detritus	1.000	0.700	0.550							0.350	0.150	0.005	0.090				0.017	0.150		

See Table 3 for a description of the more significant taxa in the aggregated functional groups listed here, and Table 4 for the scientific names of the stocks or species listed here.

Table 2b
Diet matrix for the second 20 components of the NCC model

Prey/predator	Pacific salmon	Pacific hake	Skates	Dogfish	Sablefish	Juvenile rockfish	Pacific Ocean perch	Canary rockfish	Widow rockfish	Yellowtail rockfish	Black rockfish	Shelf rockfish	Slope rockfish	Shortspine thornyhead	Longspine thornyhead	Juvenile thornyhead	Juvenile roundfish	Lingcod	Juvenile flatfish	English sole
Phytoplankton																				
Infauna			0.020		0.020	0.009								0.050	0.160				0.575	0.340
Amphipods	0.001		0.020		0.001	0.006	0.005	0.001	0.035	0.002	0.002	0.005	0.010	0.050	0.030		0.011		0.210	0.250
Epibenthic		0.002	0.200	0.050	0.050	0.022	0.005			0.002	0.050	0.040	0.020	0.030	0.200			0.050	0.200	0.360
Micro-zooplankton																				
Copepods	0.001					0.390			0.002							0.200	0.818			0.040
Euphausiids	0.100	0.575		0.200	0.060	0.440	0.780	0.920	0.300	0.550	0.100	0.350	0.800			0.500	0.123			
Carniv-zooplankton	0.200	0.029			0.010	0.004	0.070	0.008	0.200	0.025	0.100	0.010	0.050	0.010		0.250	0.029			
Small jellies	0.002				0.040	0.001		0.001	0.320	0.050	0.080			0.005	0.010	0.050				
Large jellies	0.002			0.050	0.050				0.040	0.010	0.020		0.005							
Pandalid shrimp		0.020	0.020	0.001	0.015	0.030	0.030	0.030	0.001	0.020	0.001	0.120	0.030	0.050	0.010			0.010		
Benthic shrimp		0.007	0.200		0.002	0.075					0.042	0.010	0.010	0.150	0.250			0.010	0.015	0.005
Dungeness crab			0.050	0.020	0.001						0.001							0.050		0.005
Tanner crab			0.025		0.002	0.012								0.200	0.100					
Cephalopods	0.010	0.005	0.010	0.005	0.050		0.030		0.005	0.025	0.010	0.005	0.015	0.025	0.050			0.150		
Forage fish	0.612	0.324	0.050	0.200	0.250	0.004	0.010	0.020	0.015	0.200	0.500	0.250	0.040	0.020			0.019	0.105		
Mesopelagics	0.002	0.016			0.030	0.004	0.060	0.020	0.035	0.050		0.100	0.020	0.020	0.100					
Benthic fish	0.002	0.002	0.050	0.070	0.080	0.003	0.010			0.010	0.030	0.050		0.050	0.050			0.250		
Macrirounds					0.005									0.005						
Pacific sardine	0.010																			
Mackerel																				
Pacific salmon					0.006						0.020									
Pacific hake	0.002	0.014	0.050	0.200	0.128				0.020	0.010				0.120				0.100		
Skates					0.002															
Dogfish																				
Sablefish																				
Juvenile rockfish	0.025	0.002		0.010	0.020				0.020	0.030	0.020	0.015		0.050	0.015			0.024		
Pacific Ocean perch				0.001	0.003									0.001						
Canary rockfish				0.001	0.002							0.001						0.005		
Widow rockfish				0.001	0.010							0.005						0.010		

(*continued on next page*)

Table 2b (*continued*)

Prey/predator	Pacific salmon	Pacific hake	Skates	Dogfish	Sablefish	Juvenile rockfish	Pacific Ocean perch	Canary rockfish	Widow rockfish	Yellowtail rockfish	Black rockfish	Shelf rockfish	Slope rockfish	Shortspine thornyhead	Longspine thornyhead	Juvenile thornyhead	Juvenile roundfish	Lingcod	Juvenile flatfish	English sole
Yellowtail rockfish				0.001	0.010							0.003						0.010		
Black rockfish												0.001						0.010		
Shelf rockfish				0.001	0.003							0.001		0.002				0.010		
Slope rockfish				0.001	0.001									0.002						
shortspine thornyhead					0.005															
Longspine thornyhead					0.010									0.050						
Juvenile thornyhead					0.050									0.050						
Juvenile roundfish	0.010		0.020	0.010	0.025				0.002	0.002	0.004	0.004						0.004		
Lingcod				0.001	0.001															
Juvenile flatfish	0.010		0.050	0.020	0.003				0.002	0.002		0.005								
English sole			0.020	0.010	0.001						0.001	0.005						0.040		
Petrale sole			0.005	0.005														0.010		
Small flatfish	0.010	0.004	0.150	0.120	0.020				0.002	0.012	0.018	0.020		0.007	0.005			0.100		
Rex sole	0.001	0.001	0.030	0.010	0.002				0.001		0.001			0.001				0.020		
Dover sole			0.020	0.010	0.001									0.001				0.010		
Arrowtooth flounder			0.010	0.002										0.001						
Pacific halibut																				
Northern albacore																				
Coastal sharks																				
Shearwaters																				
Common murres																				
Gulls																				
Orcas																				
Toothed whales																				
Sperm whales																				
Harbor seals																				
Sea lions																				
Fur seals																				
Grey whales																				
Baleen whales																				
Fishery offal					0.030									0.050						
Pelagic detritus																				
Benthic detritus					0.001										0.020					

See Table 3 for a description of the more significant taxa in the aggregated functional groups listed here, and Table 4 for the scientific names of the stocks or species listed here.

Table 2c
Diet matrix for the last 19 components of the NCC model

Prey/predator	Petrale sole	Small flatfish	Rex sole	Dover sole	Arrowtooth flounder	Pacific halibut	Northern albacore	Coastal sharks	Shearwaters	Common murres	Gulls	Orcas	Toothed whales	Sperm whales	Harbor seals	Sea lions	Fur seals	Grey whales	Baleen whales
Phytoplankton																			
Infauna		0.150	0.550	0.850	0.001	0.006												0.025	
Amphipods	0.005	0.100	0.300	0.030	0.001													0.950	
Epibenthic	0.150	0.380	0.120	0.100		0.050					0.010				0.020	0.010		0.025	
Micro-zooplankton																			
Copepods		0.080								0.010									0.010
Euphausiids	0.005	0.100			0.040				0.030	0.010	0.010								0.500
Carniv-zooplankton		0.020			0.001		0.100		0.015		0.010								0.005
Small jellies			0.005																
Large jellies		0.010							0.005										
Pandalid shrimp	0.020	0.010		0.010	0.040	0.025													
Benthic shrimp	0.250	0.060	0.020	0.010	0.002	0.025													
Dungeness crab	0.005	0.005			0.002	0.025		0.005							0.025				
Tanner crab						0.001													
Cephalopods	0.005	0.005					0.250	0.010	0.100	0.030	0.170	0.100	0.200	0.650	0.050	0.200	0.300		0.035
Forage fish	0.100	0.050			0.300	0.150	0.300	0.350	0.750	0.817	0.579	0.110	0.350		0.350	0.259	0.260		0.350
Mesopelagics					0.004		0.200	0.025		0.010	0.020		0.070	0.050		0.020	0.024		
Benthic fish	0.190	0.010				0.050		0.025		0.002			0.010		0.050	0.020	0.011		
Macrourids														0.025					
Pacific sardine							0.050	0.050		0.001	0.001	0.005	0.050			0.010	0.010		0.090
Mackerel							0.080	0.025				0.005	0.030			0.021	0.021		0.010
Pacific salmon						0.050		0.050		0.010	0.010		0.020			0.050			
Pacific hake					0.500	0.450		0.250					0.150	0.050	0.100	0.220	0.148		
Skates								0.010				0.040	0.005	0.025		0.020			
Dogfish								0.010				0.040	0.005	0.025		0.020			
Sablefish						0.010						0.100	0.020	0.050		0.010	0.020		
Juvenile rockfish					0.002		0.010		0.085	0.094	0.082					0.015			
Pacific Ocean perch					0.001	0.010		0.005				0.002		0.020		0.005	0.010		
Canary rockfish					0.001	0.004		0.010				0.005	0.002	0.005	0.005	0.001	0.010		
Widow rockfish					0.001	0.004	0.005	0.010				0.010	0.023	0.015	0.005	0.020	0.036		

(*continued on next page*)

Table 2c (*continued*)

Prey/predator	Petrale sole	Small flatfish	Rex sole	Dover sole	Arrowtooth flounder	Pacific halibut	Northern albacore	Coastal sharks	Shearwaters	Common murres	Gulls	Orcas	Toothed whales	Sperm whales	Harbor seals	Sea lions	Fur seals	Grey whales	Baleen whales
Yellowtail rockfish					0.002	0.010	0.005	0.010				0.010	0.015	0.020	0.015	0.020	0.030		
Black rockfish								0.005				0.005	0.001		0.010	0.010			
Shelf rockfish					0.002	0.008		0.015			0.001	0.005	0.003	0.010	0.010	0.015	0.020		
Slope rockfish					0.001	0.002		0.005			0.001			0.020		0.005	0.020		
Shortspine thornyhead														0.010					
Longspine thornyhead																			
Juvenile thornyhead																			
Juvenile roundfish					0.002	0.010		0.005	0.015				0.010		0.005	0.005	0.010		
Lingcod								0.010							0.020	0.010			
Juvenile flatfish	0.010	0.010			0.010	0.010				0.008	0.005								
English sole	0.020				0.005	0.003		0.010					0.005		0.075	0.010			
Petrale sole					0.002	0.002		0.002							0.010	0.002			
Small flatfish	0.210		0.005		0.060	0.035		0.060		0.008	0.015		0.025		0.140	0.020			
Rex sole	0.025				0.010	0.010		0.010											
Dover sole	0.005				0.010	0.020		0.010					0.001			0.002			
Arrowtooth flounder						0.010		0.008				0.050	0.001		0.010				
Pacific halibut								0.010				0.050	0.001	0.025					
Northern albacore								0.005				0.005	0.001						
Coastal sharks												0.010	0.002						
Shearwaters																			
Common murres											0.001								
Gulls																			
Orcas																			
Toothed whales												0.140							
Sperm whales												0.018							
Harbor seals												0.003							
Sea lions												0.037							
Fur seals												0.060							
Grey whales												0.030							
Baleen whales												0.060							
Fishery offal											0.085								
Pelagic detritus																			
Benthic detritus		0.010				0.020													

See Table 3 for a description of the more significant taxa in the aggregated functional groups listed here, and Table 4 for the scientific names of the stocks or species listed here.

Table 3
Summary of the more significant species or taxa in aggregated functional groups

Phytoplankton	Functional group of all photosynthetic primary producers, diatoms generally dominate
Infauna	Functional group of polychaetes, bivalves, small crustaceans, and some echinoderms
Amphipods	Functional group of all gammarid, caprellid and hyperiid amphipods
Epibenthic	Functional group including many echinoderms (holothuroids, asteroids, ophiuroids), brachyurans, mysids, isopods, cumaceans, gastropods, and other organisms
Micro-zoop	Functional group of small heterotrophic zooplankton, primarily protozoans such as gymnodiniods, dinoflagellates, ciliates, and nanoflagellates
Copepods	All developmental stages of species in the subclass Copepoda
Euphausiids	All developmental stages of species in the order Euphaussiacea
Carniv-zoops	Functional group including pasiphaid, seregestid and other pelagic shrimps, chaetognaths, pelagic polychaetes, and the pelagic stages of many invertebrates, such as crab megalopae
Small jellies	Functional group of filter-feeding urochordate herbivores; salps, doliolids and larvaceans, as well as thecosome pteropods (such as *Limacina helecina*)
Large jellies	Functional group includes essentially all gelatinous carnivores, principally cnidarians (hydrozoans and scyphozoans), ctenophores and heteropods
Benthic shrimp	Functional group of benthic decapod shrimp (excluding *Pandalus jordani*) such as *Crangon*, *Eualus*, *Daridea*, and *Calocaris* species
Cephalopods	Functional group of cephalopods, such as *Loligo*, *Gonatus*, and *Octopus* species
Forage fish	Functional group of clupeids, osmerids and other taxa, including northern anchovy (*Engraulis mordax*), Pacific herring (*Clupea harengus pallasi*), eulachon (*Thaleichthys pacificus*), and whitebait smelt (*Allosmerus elongates*)
Mesopelagics	Functional group of mesopelagic taxa, such as California headlightfish (*Diaphus theta*), northern lampfish (*Stenobranchius leucopsarus*), and blue lanternfish (*Tarletonbeania crenularis*)
Benthic fish	Functional group, common families include eelpouts (Zoarcidae), snailfish (Cyclopteridae), poachors (Agonidae), and sculpins (Cottidae)
Macrourids	Functional group includes all grenadiers (family Macrouridae)
Mackerel	Includes jack mackerel (*Trachurus symetricus*) and Pacific mackerel (*Scomber japonicus*)
Salmon	Primarily Chinook and coho salmon (*Oncorhynchus tshawytscha* and *O. kisutch*)
Skates	Primarily *Raja* and *Bathyraja* species, such as big skate (*R. binoculata*), longnose skates (*R. rhina*) and black skate (*B. trachura*)
Dogfish	Primarily dogfish (*Squalus acanthias*), but includes cat sharks (*Apristurus* spp.)
Juvenile rockfish	All juvenile stages of *Sebastes* rockfish
Black rockfish	Primarily black rockfish (*Sebastes melanops*) but includes other common nearshore rockfish, such as blue (*S. mystinus*), China (*S. nebulosus*), and quillback (*S. maliger*)
Shelf rockfish	Based on PFMC designations, includes *Sebastes* species such as bocaccio (*S. paucispinis*), yelloweye (*S. ruberrimus*), chilipepper (*S. goodei*), and silvergrey (*S. brevispinus*)
Slope rockfish	Based on PFMC designations, includes *Sebastes* species such as aurora (*S. Aurora*), darkblotched (*S. crameri*), rougheye (*S. aleutianus*), sharpchin (*S. zacentrus*), and splitnose (*S. diploproa*)
Juvenile thornyheads	All juvenile stages of *Sebastolobus* species
Juvenile roundfish	All juvenile stages of sablefish, lingcod, and other commercially significant roundfish
Juvenile flatfish	All juvenile stages of Pleuronectiform fishes
Small flatfish	Functional group that includes most small flatfish, including sanddab (*Citharichthys* spp.), Slender sole (*Lyopsetta exilis*), butter sole (*Isopsetta isolepis*), and starry flounder (*Platichthys stellatus*)
Coastal sharks	Functional group includes soupfin (*Galeorhinus galeus*) and thresher sharks (*Alopias* spp.)
Shearwaters	Functional group primarily of *Puffinus griseus*, but including petrels (*Oceanodroma* spp.) and phalaropes (*Phalaropus* spp.)
Murres	Primarily common murre (*Uria aalge*), but including Cassin's auklets (*Ptychoramphus aleuticus*), Rhinoceros auklets (*Cerorhinca monocerata*), tufted puffins (*Fratercula cirrhata*) and other alcids
Gulls	Primarily *Larus* species, but including kittiwakes (*Rissa* spp.), northern fulmars (*Fulmarus glacialis*) and black-footed albatross (*Phoebastria nigripes*)
Toothed whales	Primarily harbor porpoise (*Phocoena phocoena*), Dall's porpoise (*Phocoenoides dalli*), and Pacific white-sided dolphin (*Lagenorhychus obliquidens*)
Sea lions	Primarily Steller sea lions (*Eumetopias jubatus*), but including California sea lions (*Zalophus californianus*) and northern elephant seals (*Mirounga angustirostris*)
Baleen whales	Primarily humpback whales (*Megaptera novaeangliae*), but including minke (*Balaenoptera acutorostrata*), fin (*B. physalus*), blue (*B. musculus*), and sei (*B. borealis*) whales

Table 4
Common and scientific names for specific species or stocks in the model

Common name	Scientific name
Pandalid shrimp	*Pandalus jordani*
Dungeness crab	*Cancer magister*
Tanner crab	*Chionoecetes tanneri*
Pacific sardine	*Sardinops sagax*
Pacific hake	*Merluccius productus*
Sablefish	*Anoplopoma fimbria*
Pacific Ocean Perch (POP)	*Sebastes alutus*
Canary rockfish	*Sebastes pinniger*
Widow rockfish	*Sebastes entomelas*
Yellowtail rockfish	*Sebastes flavidus*
Shortspine thornyhead (ssthorny)	*Sebastolobus alascanus*
Longspine thornyhead (lsthorny)	*Sebastolobus altivelis*
Lingcod	*Ophiodon elongates*
English sole	*Parophys vetulus*
Petrale sole	*Eopsetta jordani*
Rex sole	*Glyptocephalus zachirus*
Dover sole	*Microstomus pacificus*
Arrowtooth flounder	*Atheresthes stomias*
Pacific halibut	*Hippoglossus stenolepus*
Albacore	*Thunnus alalunga*
Orca	*Orcinus orca*
Sperm whale	*Physeter macrocephalus*
Harbor seal	*Phoca vitulina richardsi*
Fur seal	*Callorhinus ursinus*
Grey whale	*Eschrichtius robustus*

where a_{ij} is the search rate for prey i by predator j, v_{ij} is the transfer rate between the vulnerable (v_{ij}) and invulnerable prey behavior states,[2] B_i and B_j are the biomass of prey and predators, respectively, T_i and T_j represent the relative feeding time of prey and predators, respectively, S_{ij} is a user-defined seasonal or long-term forcing effect, M_{ij} is a parameter representing mediating forcing effects, and D_j represents the effects of handling time as a limit to consumption rate as a function of handling time. The values for search rates (a_{ij}) are inferred from a maximum consumption rate, $C^{\max}$. As with the vulnerability parameters, these parameters are difficult to estimate, measure or otherwise derive, although their influence on model dynamics is generally less than the influence of setting vulnerabilities. The general approach here has been to use default values unless otherwise noted.[3] Both S_{ij} and M_{ij} default to 1, but can be used to increase or decrease vulnerability with season, habitat change, climate or other factors.

Although this modeling framework was not originally developed to include biophysical processes, it is possible to drive productivity from the bottom-up with time series of either physical or biological data (Watters et al., 2003). Similarly, the ability to mediate the vulnerability of prey to predators dynamically is used to mimic some of the impacts of climate variability on the spatial distribution and production of some ecosystem components. For example, we can evaluate the extent to which forcing lower trophic level production with

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[2] The vulnerability rates chosen by the user range in a continuum between 0 and 1, with 0 representing "bottom-up" control, 1 representing "top-down" control, and 0.3 for mixed control. The values used in the computations are rescaled such that the computational v_{ij} is equal to $\exp(2*[\exp(v_{ij}) - 1])$ where v_{ij} is chosen by the user.

[3] The default value for $C^{\max}$ is 2, which translates into the expectation that if predator j numbers were very high, their maximum consumption rates of prey i would be twice the (Ecopath) default value. Thus, as with vulnerability, the estimated values for $C^{\max}$ can have an influence on model dynamics, with a high ratio of $C_{ij}^{\max}$ to C_{ij} implying strong top-down control and a low ratio implying bottom-up control. Similarly, the maximum relative P/B was set to 2, the maximum relative feeding time to 2, the feeding time adjustment rate 0.5, the predator effect on feeding time to 0, the density dependent catchability to 1, handling time $(Q/B_{\max})/(Q/B_0)$ to 1000, and the fraction of "other" mortality sensitive to changes in feeding time to 0. This is consistent with other approaches to these parameters (Bundy, 2001; Cox et al., 2002), although Olson and Watters (2003) vary the fraction of other mortality sensitive to feeding time by trophic level, setting it to 0 for large predators, 0.5 for medium-size fishes and 1 for forage components.

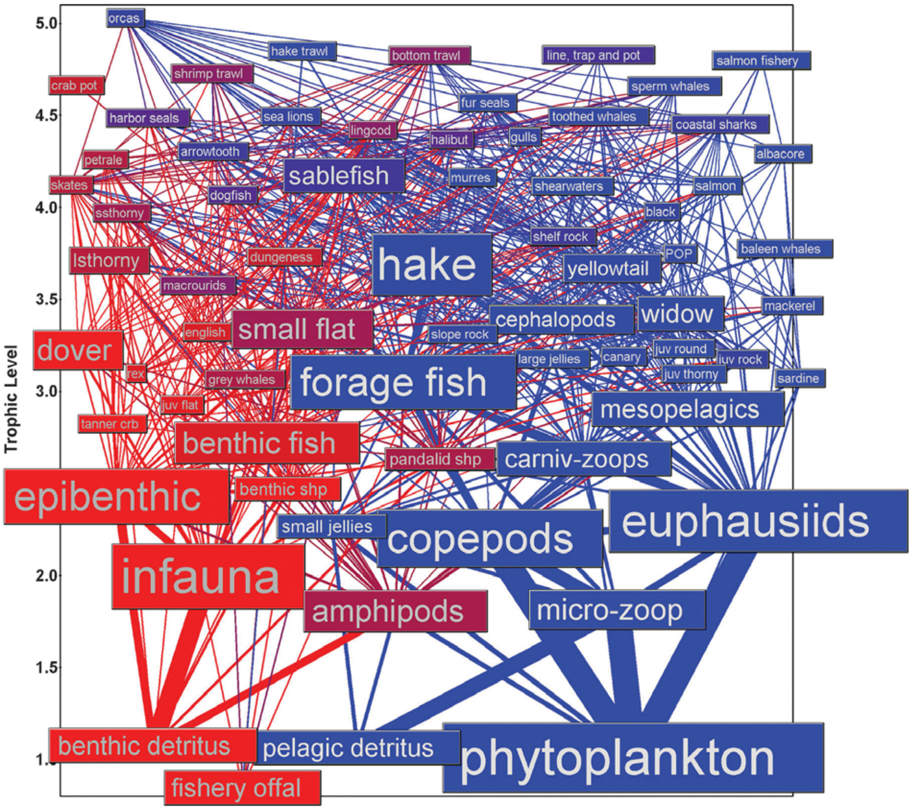

Fig. 2. The significant food web of the Northern California Current. Key taxa for functional groups are provided in Table 3. Common names and scientific names of species and stocks are given in Table 4. The estimated trophic level is along the *y* axis, the height of the boxes is scaled to the log of the standing biomass, the width of the bars represents biomass flux of prey to predators, and the colors represent the alternative energy pathways such that pelagic (primary production) energy pathways are shown in blue and the benthic (detrital loop) energy pathways are shaded in red.

physical indices improves the fit of model dynamics to the estimated or inferred trends from stock assessments and surveys relative to the fit obtained by running the model with no variability in bottom-up forcing. To attempt to validate the model performance, a series of simulations were run in which the 1960s model was projected to 2004. Fishing was represented by using fishing mortalities based on stock assessments and known catches (for hake and most groundfish), estimated changes in effort (for pandalid shrimp and Dungeness crab) and in one case a highly simplified assumption of constant fishing mortality (Pacific salmon) where attempting to estimate either fishing mortality or effort was impractical.

The model was run forward first under the assumption of a constant environment, then forced dynamically with several climate indices. A range of climate time series was tentatively explored as forcing functions, although only a subset are shown and discussed here. The indices discussed here include upwelling wind indices, indices of wind derived southward transport, the Pacific Decadal Oscillation (PDO) index, and an index of predicted Oregon coastal coho (*Oncorhynchus keta*) salmon survival (Logerwell et al., 2003). Upwelling wind indices were generated by the average of monthly offshore Ekman transport indices at 42, 45 and 48° N, as obtained from the Pacific Fisheries Environmental Laboratory (PFEL) Live Access Server (www.pfeg.noaa.gov). The southward transport and the PDO indices were chosen to represent the significance of large-scale environmental conditions on the abundance and dynamics of key predator stocks in the NCC; as discussed by Chelton et al. (1982). Transport estimates were averaged over a greater spatial area (36 to 51° N), with the expectation that this would better represent larger scale patterns of spatial distribution for migrant species. Similarly, the PDO is widely recognized to reflect patterns in SST variability, which in turn have been strongly linked to the production and distribution of salmon, hake, sardine and other species (Mantua et al., 1997;

Francis et al., 1998; Hare and Mantua, 2000; Swartzman and Hickey, 2003). Estimates of southward transport were obtained from PFEL, and the PDO was obtained from the JISAO Climate Impacts Group (www.cses.washington.edu/cig/). These indices are shown (Fig. 3) as either raw values (Logerwell index, PDO) or monthly standardized anomalies with monthly means removed and a 13 month running mean of average values (upwelling, transport).

The Oregon coastal coho marine survival index was developed by Logerwell et al. (2003) based on a conceptual model of the principal environmental processes thought to influence marine smolt-to-adult survival rates, as estimated by hatchery releases and adult returns in the coastal areas of the Pacific Northwest. The

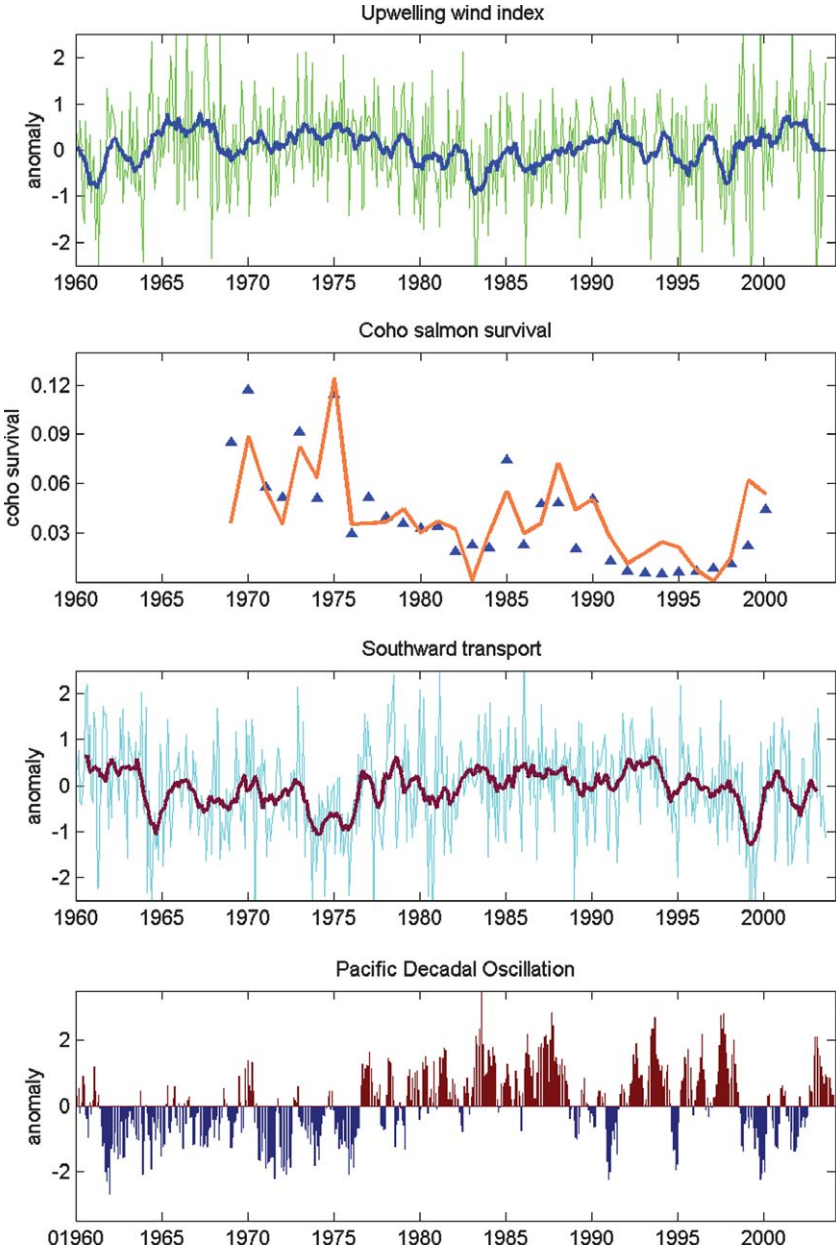

Fig. 3. Climate indices used to drive the dynamic model. From top to bottom, monthly anomalies of upwelling winds (from PFEG) with their 13-month running means, observed (points) and predicted (line) coho survival index from Logerwell et al. (2003), monthly anomalies of southward transport (from PFEG) with their 13-month running means, and the Pacific Decadal Oscillation (Mantua et al., 1997).

authors used a general additive model (GAM) to evaluate sequentially the non-linear relationships between ocean conditions and coho survival, including winter sea surface temperatures prior to migration (a "preconditioning" index), the date of the spring transition, relative sea level during the spring of smolt migration, and winter sea surface temperature the year after smolt migration. Their resulting model explains 75% of the variability in coho survival between 1969 and 2000, including both the monotonic declines in survival evident since the mid-1970s, and high interannual variability throughout the period of the study. The use of this index, hereafter referred to as the Logerwell index, is based on the assumption that the survival of coastal coho salmon is representative of system-wide variability in physical ocean conditions and lower trophic level productivity. In support of this argument is the observation by Peterson and Schwing (2003) of a strong relationship between coho survival and indices of the biomass of subarctic copepods off of the central Oregon coast.

All of the indices (with the exception of the Logerwell index, which is an annual index that begins in 1969) were converted to monthly standardized anomalies based on a climatology of 1950–1964, to set the baseline reasonably close to the mean of the starting period of the model runs. The climate indices were used here in two ways. The first, most straightforward way was as simple, "bottom-up" forcers of primary production over time. For the second way, indices were used as "top-down" forcing mechanisms that mediate the predatory impact (consumption), and consequently production pathways, of mid-trophic level consumers by altering the vulnerability of their prey to predation. The intent of this approach is to represent the effect of an increase in predator abundance (and thus predation) associated with changing spatial distributions of migrant species (hake, sardine and mackerel) during warm/low southward transport periods, as well as to reflect greater reproductive success of salmon, rockfish and other species during cool/high southward transport periods.[4] Although this is not strictly a "top-down" mechanism in the sense that it is driving changes in the very top of the food chain (marine mammals, seabirds, fisheries), it is driving massive changes in the dynamics of top piscivores and community behavior, by increasing the consumption (and consequently, the production) of select model components at the expense of others. A similar (although not identical) approach to forcing was used by Cury et al. (2000) as well as by Shannon et al. (2004) to simulate anchovy–sardine regime shifts in the southern Benguela (and other) ecosystems. In these instances, the vulnerability of the prey of small pelagic fishes (e.g., sardine and anchovy) was increased, while the vulnerability of these small pelagics to their respective predators was decreased, a mechanism they referred to as "middle-out" or wasp-waist forcing. As our mechanism varies from this in attempting to account for the ecosystem impacts of shifting distributions of higher trophic level predators, we will maintain the terminology of "top-down" climate forcing for the purposes of this paper.

This application of climate indices to drive the model is consistent with observations developed in the literature and observed in monitoring programs. For example, Dorn (1995), Ware and McFarlane (1995) and Swartzman and Hickey (2003) have all clearly demonstrated a positive relationship between sea surface temperature and the northerly extent of hake distribution, a characteristic shared by Pacific sardine and mackerel (Jacobson and MacCall, 1995; Emmett and Brodeur, 2000; McFarlane et al., 2002). Consequently, there is greater predation impact by hake and other coastal pelagics in such years, presumably to the detriment of other elements of the ecosystem. This impact can be represented by increasing the vulnerability of euphausiids, forage fish and other prey to predation by hake and other migrants during warm periods. By contrast, Mantua et al. (1997) showed that many west coast salmon populations are more productive during cooler conditions (negative phases of the PDO), and Hare and Mantua (2000) demonstrated that recruitment for many west coast groundfish stocks, particularly rockfish (*Sebastes*) species, responds similarly. Ralston (personal communication) has also demonstrated that rockfish reproductive success (as indexed by midwater trawl estimates of juvenile abundance) is extremely poor during periods of low transport in the California Current. Furthermore, Hare and Mantua (2000) as well as Hollowed et al. (2001) found that recruitment and productivity of many flatfish in the Gulf of Alaska seems to be greater during positive PDO conditions, and trends from assessments and surveys would suggest a similar relationship for NCC flatfish. Clark and Hare (2002) reported a strong relationship between Pacific halibut (*Hippoglossus stenolepus*) recruitment and the PDO throughout the range

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[4] This is done by creating a dummy biomass pool in the model that is driven deterministically by the climate time series. This biomass pool in turn is used to "mediate" the vulnerability of prey to select predators, such that the value M_i in Eq. (3) in any given time step is equal to the value of the input climate time series (scaled between 0 and 2, such that a value of 1 would have no effect).

of halibut in the northeast Pacific. Although the Oregon and Washington halibut stocks are not independently assessed, the trends in survey, catch, and catch per unit effort data for halibut in the NCC are consistent with trends for the assessed stocks over the past 50 years.

The results from the dynamic simulations were averaged to annual values and compared with the data (annual values from stock assessment results, survey information and catches) for 24 of the model components most significant in commercial fisheries by using a negative log likelihood estimator. Negative log likelihoods for each simulation were generated by estimating the likelihood for each time series with a lognormal probability density function for each observation, and taking the negative log of that value. These values are summed across all years for each group, and across all groups to get a total negative log likelihood for the simulation. These results were further evaluated using Akaike Information Criteria (Akaike, 1992), in which the best fitting model is determined to be that which has the lowest AIC. The AIC is estimated as

$$A_i = -2\log L(\theta) + 2K \tag{4}$$

in which L is the likelihood function maximized over the vector of estimated parameters (θ) and K is the number of parameters. In this case, the number of additional parameters was assumed to be equivalent to the number of years of climate indices included in the model (relative to the baseline case of 0 for no climate). Although the climate indices themselves are not free parameters, but rather fixed values based on a priori assumptions of their significance to ecosystem dynamics, this approach to measuring the relative improvement in model fit among models of differing complexity is appropriate.

3. Results

Select simulation results are presented as Figs. 4–7. In these figures, the first panels show the 24 model components (all commercially important groups) that were used to estimate fits, all but three being assessment or survey abundance estimates. As abundance estimates do not exist for pandalid shrimp, Dungeness crab, or salmon, reported catches were compared to predicted catches for these groups. Total negative log likelihoods for the key model runs are also reported (Table 5). These include a run with no climate forcing, runs with a single bottom-up index, runs with a single top-down index, and runs with both bottom-up and top-down indices. The results demonstrate that adding some of the climate indices as a forcing factor improves the fit modestly to substantially, an obvious exception being the addition of upwelling as a bottom-up forcer. The resulting likelihoods and AIC criteria for four select runs are also provided (Table 6), and discussed in greater detail throughout the remainder of this section. Finally, we show that these results hold up consistently with similar relative likelihood settings (Table 7), regardless of whether the baseline vulnerability parameters are set at low (“bottom-up”) or high (“top-down”) values. Although we limit the remaining discussion to the simulations made with the default (“mixed”) vulnerability, confirmation that the results do not change significantly under alternative settings is critical in evaluating model behavior.

The first run (Fig. 4) is a baseline simulation with only fishing mortality and relative effort as forcing factors. In this scenario, fishing mortality is presumed to be the major driver of population change, consistent with the single species assessment results for these stocks. This is particularly true for longer-lived rockfish (*Sebastes* and *Sebastolobus* sp.), roundfish (sablefish, *Anoplopoma fimbria* and lingcod, *Ophiodun elongatus*) and Dover sole (*Microstomus pacificus*). Interestingly, there are also suggestions that the observed increases in flatfish such as English sole (*Parophrys vetulus*), rex sole (*Glyptocephalus zachirus*), and other small flatfish are associated with decreasing predation on these species by higher trophic level piscivores. The fit of Pacific hake is not as good as many of the other assessed species, which is not surprising given that hake are coastwide migrants in which recruitment is largely a function of processes that occur outside the NCC. While the fits to pandalid shrimp and Dungeness crab landings are not remarkably poor in light of the nature of the forcing function (units of effort), they do lack some of the highly variable patterns exhibited by these stocks in actual landings (and presumed abundance). Furthermore, the near tripling of salmon landings (which reflect an index of biomass, based on a constant mortality rate) seems unrealistic; this may reflect both the simplistic assumptions made with regard to harvest rate, as well as the inability of the model to account for other salmon population impacts (hydropower, hatcheries) and the complexity of salmon life history patterns.

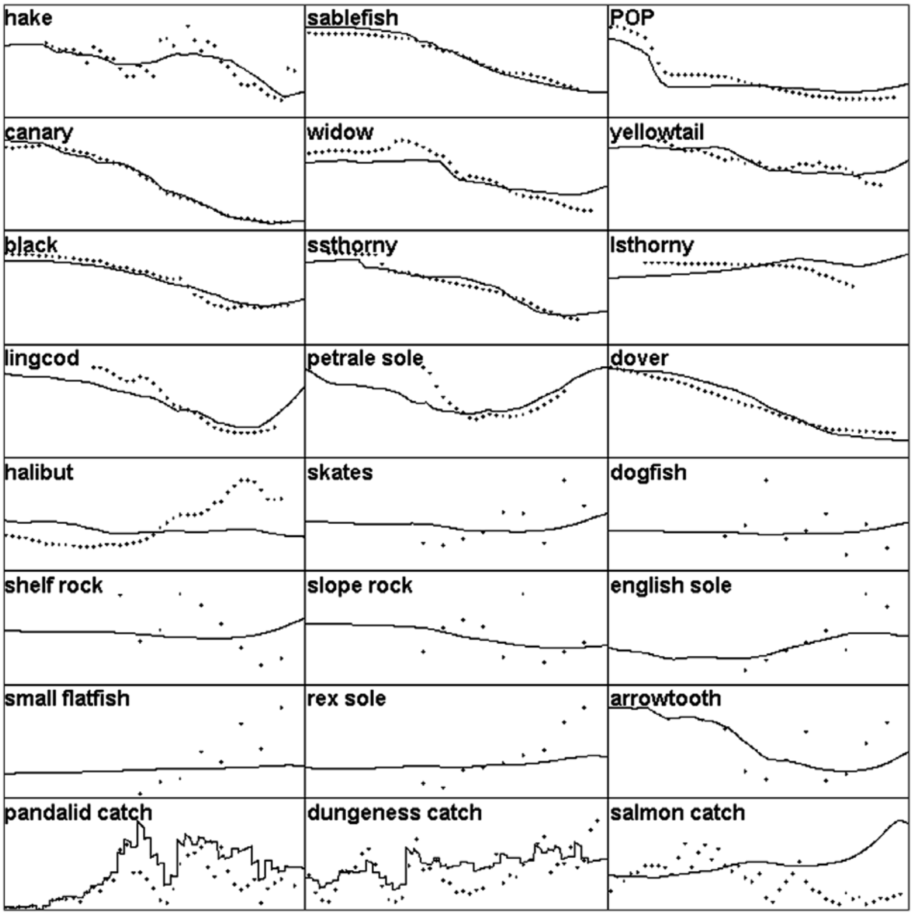

Fig. 4. Modeled population trajectories from 1960 to 2004 (solid lines) shown with stock assessment trends, survey indices, and landings (dotted lines) for commercially important species and functional groups, with no environmental forcing. Time (1960–2004) is along the *x* axis, relative or absolute biomass is along the *y* axis.

If we run the model with bottom-up forcing, the predicted time series run with the upwelling index has a poorer fit to the reference data (Table 5). Given that the wind-driven upwelling index excludes many factors relevant to productivity (such as ocean temperature, depth of the mixed layer, and nutrient concentrations), this result is not surprising. However, running the model with the Oregon coho survival index (Fig. 5) improves the fit substantially, and the AIC would suggest that this model is better supported by the data (Table 6). Much of the improvement in likelihood is observed in the more dynamic indices for shrimp, crab, salmon and lingcod. With top-down (but no bottom-up) forcing, southward transport improves the fit (Table 5), but the improvement is not sufficient relative to the AIC. Running the model with the PDO as a top-down forcing mechanism (Fig. 6) improves the likelihood substantially (to −389), and the resulting AIC suggests that this model is actually the most appropriate given the data. Running the model with the PDO as a bottom-up forcing mechanism (not shown) slightly decreases the fit relative to running the model with no climate forcing (to −320). Interestingly, when the model is run with both PDO and coho survival together as top-down and bottom-up respectively (Fig. 7), the overall negative log likelihood is improved (−374) relative to when the model is run with coho survival (bottom-up) alone, yet less than when the model is run with the PDO (top-down) alone. However the improvement is not adequate relative to the AIC, suggesting that the two-index model is a poorer fit than using either index independently.

With respect to other elements of the ecosystem, the top three rows of Fig. 8 show the behavior of a subset of 9 model components as “indicators” of how different trophic levels behaved throughout the simulation.

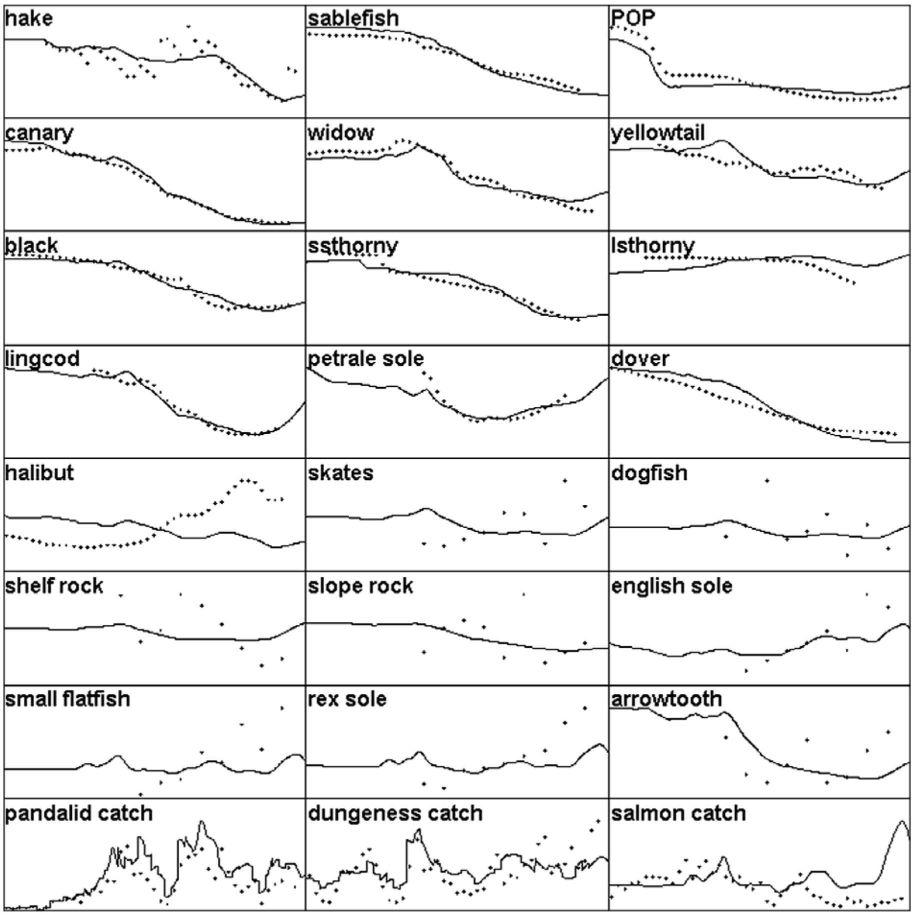

Fig. 5. Modeled population trajectories (as in Fig. 4) with "bottom-up" environmental forcing driven by the OPI coho survival predictive index. Time (1960–2004) is along the x axis, relative or absolute biomass is along the y axis.

This figure is shown for informative purposes only, to provide the reader with a sense of the scale of variability produced by the model for high turnover species (such as copepods, euphausiids and forage fish), as well as low turnover species (such as pinnipeds and baleen whales). Note that the high-turnover groups were not used in the fitting process, due to a lack of appropriate abundance data. Instead, select indices of relative abundance from a range of sources were shown for scale only. For example, model estimates of copepod biomass were shown with recent (1996–2003) relative biomass estimates by Peterson and Schwing (2003), and simulation estimates of euphausiid abundance were shown with the model estimates from the La Perouse Bank region over a similar time period by Robinson and Ware (1999). For forage fishes, abundance estimates (which are presumably uninformative) from the triennial groundfish trawl survey are shown for scale, for sardines the most recent coastwide stock assessment trend is shown for scale (Conser et al., 2002). For harbor seals (*Phoca vitulina richardsi*), counts reported in Carretta et al. (2002) are included for scale. For sea lions (including both *Zalophus californianus* and *Eumetopias jubatus*), pup counts from southern rookeries of California sea lions, where the population growth is considerably greater than that observed in the NCC, are shown for scale. Finally, point estimates of the number of California Current-wide humpback whales (*Megaptera novaeangliae*) from Carretta et al. (2002) are shown for scale for baleen whales. This illustrates the range of population behavior being produced by the model for both lower and higher trophic levels, as well as highlights that the model is able to allow known trends for top predators such as marine mammals to be incorporated into the model dynamics. Equally important is the point that the model is unable to replicate trends in coastal pelagic species such as sardine, where population changes of several orders of magnitude have

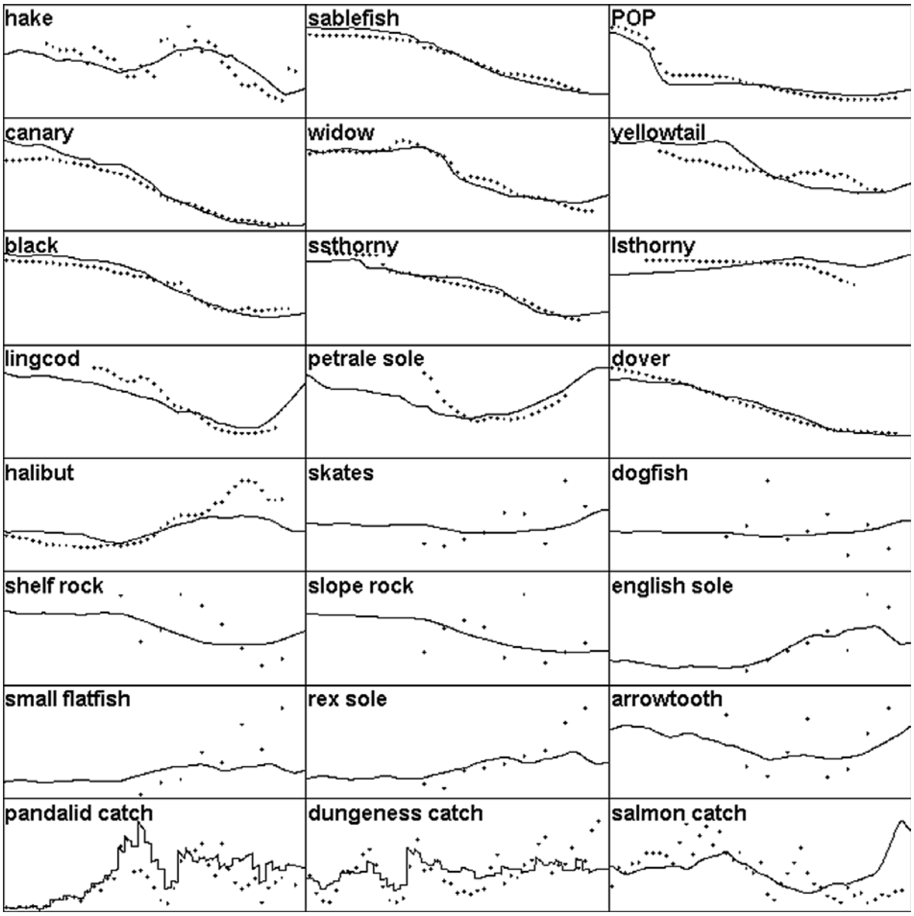

Fig. 6. Modeled population trajectories (as in Fig. 4) with "top-down" environmental forcing based on PDO mediation on the vulnerability of prey to key predators. Time (1960–2004) is along the *x* axis, relative or absolute biomass is along the *y* axis.

occurred over an extremely short time period. Note that neither the trends and "observations" shown at the top of Fig. 8, nor the observed and predicted catches from the bottom, were included in estimating likelihoods for evaluating improvement in model behavior. Instead, they are shown solely for informative purposes.

The bottom panels (Fig. 8) show observed and predicted catches for the 21 model components for which biomass estimates were used to estimate the model fit. Note that the "observed" catches here represent only reported landings for unassessed species (they include assessment estimates of discard mortality plus catches where available). Consequently, the often significant discrepancies between the observed and predicted landings in the unassessed groups (shelf and slope rockfish, small flatfish, rex sole, arrowtooth flounder, skates and dogfish) are partially explained by the catches of those species being forced by bycatch ratios relative to total landings by gear type. These bycatch ratios were estimated based on observed bycatch rates (relative to total catch) from the Pikitch et al. (1988) study, which were incorporated into the catch composition of the fishing fleets at the beginning of the simulation. For most species, it is clear that predicted catches are very similar to observed catches, which is not surprising given that simulations are run with fishing mortality rates based on the assessments themselves. For several, such as small flatfish, rex sole, skates and dogfish, "catches" are substantially higher than landings, reflecting the low retention and high discard rates observed for many of these groups. Interestingly, catches and reported landings for some of these groups, dogfish and skates in particular, do seem to converge in later years. This is a period in which limited fishing opportunities and developing markets for these species appear to have led to increased retention, and consequently an increase in reported landings.

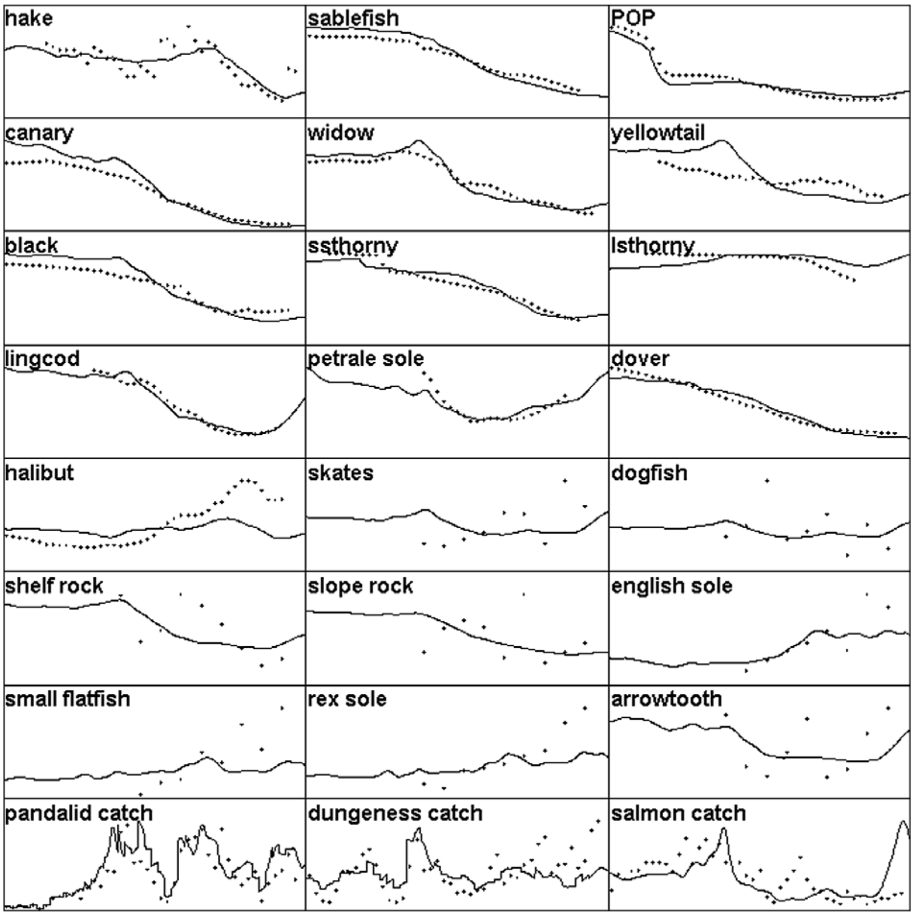

Fig. 7. Modeled population trajectories (as in Fig. 4) with a combination of "bottom-up" forcing from the OPI coho survival index and "top-down" forcing with PDO mediation on the vulnerability of prey to key predators. Time (1960–2004) is along the *x* axis, relative or absolute biomass is along the *y* axis.

Table 5
Total negative log likelihood estimates of simulations under alternative climate forcing scenarios

Bottom-up climate	Top-down climate		
	None	PDO	Transport
None	−329	−389	−337
Upwelling	−192	−210	−197
Coho index	−369	−374	−365

Table 6
Total negative log likelihoods, and the AIC for each of four key models when each year with a climate index is treated as a free parameter

	No climate	Logerwell index	PDO	Logerwell and PDO
Total negative log likelihood	−329	−369	−389	−374
Number of new parameters		33	45	78
Akaike Information Criteria	−658	−671	−688	−592

The final result relates to model estimates of the potential top-down consequences of changes in the abundance of marine mammals in the NCC. Over the last four decades, many populations of California Current pinnipeds, cetaceans, and even some seabirds have increased substantially, following nearly two centuries of

Table 7
Total negative log likelihoods for the four most significant runs under alternative vulnerability assumptions

		No climate	Logerwell index	PDO	Logerwell and PDO
$v = 0.1$	(bottom-up)	−166	−285	−301	−307
$v = 0.3$	(mixed)	−329	−369	−389	−374
$v = 0.5$	(top-down)	−313	−339	−397	−354

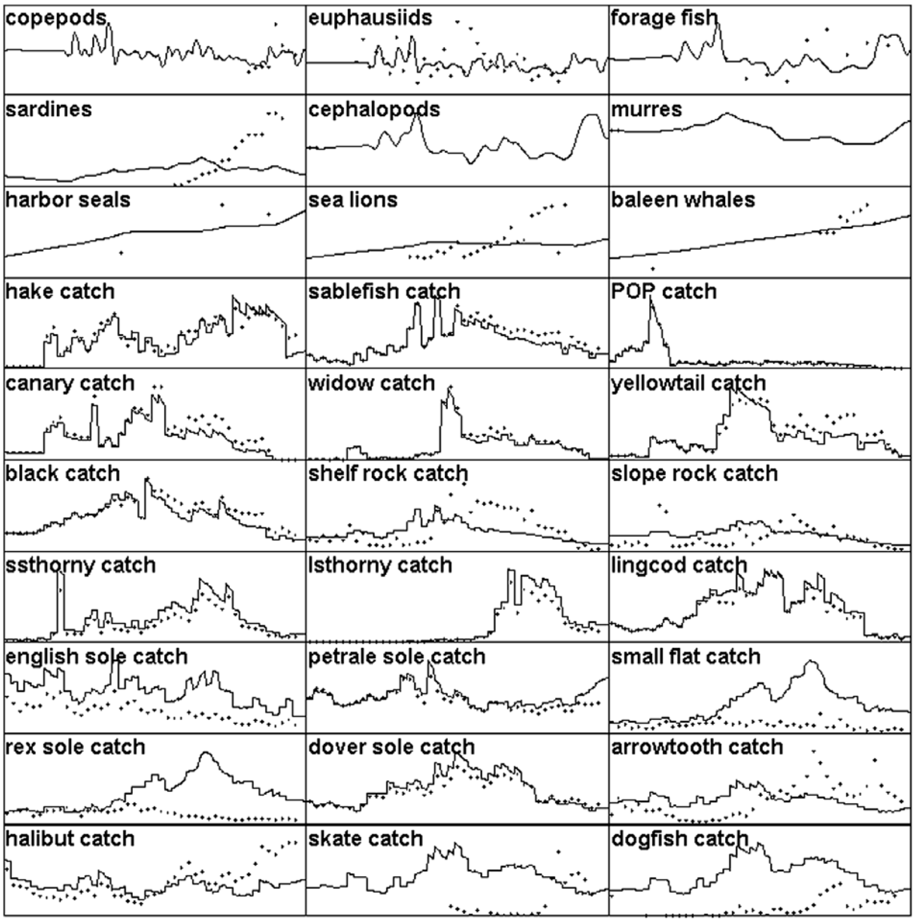

Fig. 8. Modeled population trajectories of lower and higher trophic level components (top nine panels) and catches of key species (bottom 21 panels) with a combination of "bottom-up" forcing from the OPI coho survival index and "top-down" forcing with PDO mediation on the vulnerability of prey to key predators. Time (1960–2004) is along the x axis, relative or absolute biomass is along the y axis.

often intensive hunting and culling (Scheffer and Slipp, 1944, 1948; Ainley and Lewis, 1974; Cass, 1985; Clapham et al., 1997). Food habits, based principally on studies from the 1960s, show that rockfish and other commercially important groundfish make up a modest, but significant, proportion of most pinniped diets (Fiscus and Baines, 1966; Perez and Bigg, 1986; NMFS, 1997). Although the relative impact of marine mammal predation on forage fish, cephalopods, and other lower trophic level groups seems to be fairly low in contrast to that of other predators, pinnipeds represent a greater fraction of mortality on commercially important stocks of roundfish, rockfish, flatfish, hake and sardine. For example, Fig. 9 shows the total (modeled) biomass of all stocks of *Sebastes* rockfish in the NCC over the last 42 years, along with model estimates of the total sources of mortality for these stocks. As fishing mortality increased dramatically in the 1980s, the model suggests declines in piscivore (principally sablefish, lingcod, and halibut) predation and increases in marine mammal

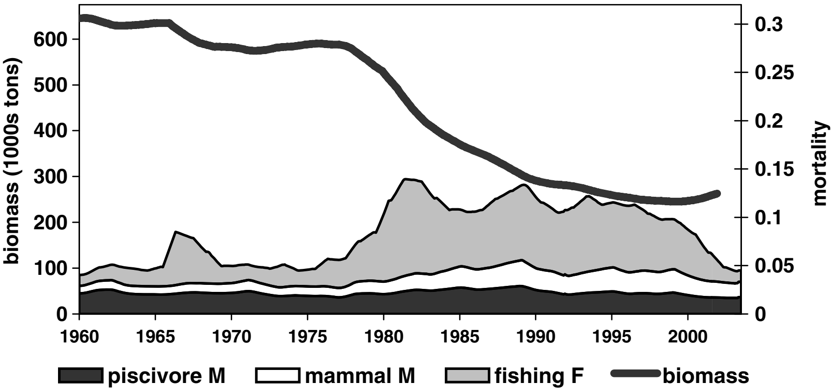

Fig. 9. Model estimated changes in natural mortality (predation) rates from marine mammals and piscivorous fish, relative to fishing mortality for all *Sebastes* spp.

(principally pinniped) predation. Yet rockfish stocks were declining over this period, and pinniped populations increasing, which implies that there was a significant decline in the relative consumption of rockfish (the fraction of rockfish in pinniped diets) over this period. With declines in many of these species, particularly rockfish, the model would suggest a shift in diet composition away from groundfish in favor of forage fish, flatfish, and cephalopods, as the total natural mortality to rockfish from pinnipeds would have increased if the diet composition had remained constant. This too is consistent with studies of California Sea Lions that suggest food habits tend to be temporally dynamic and related to the relative availability of prey (Lowry et al., 1991; Lowry and Carretta, 1999). Although the high sensitivity of marine mammal consumption estimates to Ecosim model parameters makes any such estimates highly questionable (Mackinson et al., 2003), in general the model suggests that the direct top-down impacts of marine mammal population growth on rockfish (and perhaps other commercially species) are likely to be negligible, at least in more northern waters where pinniped population growth is relatively moderate.

Finally, we consider a visual image of the results of the dynamic model. Fig. 10 shows the significant food web of the NCC (as in Fig. 2), with changes in biomass in 2002 relative to starting (1960) conditions represented by color. Red boxes indicate model elements that have declined relative to their starting values, green boxes indicate elements that have increased (flows between boxes are modeled the same way). The end year, 2002, was chosen to represent a year of high (above average) productivity, such that the forage groups at the base of the food web are relatively abundant. A number of commercially important species are green as well, including salmon, shrimp, sardine and many flatfish; observations consistent with recent record runs of salmon, catches of shrimp and crab, and production of forage fish. As discussed above, many marine mammals (harbor seals, sea lions, and baleen whales) have increased in abundance over this period as well. However much of the upper-middle level of the food web, in particular many groundfish, are slightly to very red, representing the observation that a very significant fraction of this low-turnover biomass has been removed by fishing. Clearly, many stocks in this ecosystem no longer fill the functional role that they used to, and although the potential consequences to ecosystem function and stability are difficult to estimate, their potential role in stabilizing ecosystem variability by virtue of their former high abundance and longevity has arguably been undermined (Apollonio, 1994).

4. Discussion

It is perhaps counterintuitive, that the "top-down" climate forcing scenario improves the model fit slightly more than the "bottom-up" scenarios. For the PDO in particular, it is difficult to imagine that the impacts are restricted to top-down influences on the distribution and abundance of predators, when there are clearly processes that are more "bottom-up" in nature associated with the PDO mode of variability. For example, Peterson and Schwing (2003) show that changes in both zooplankton community composition and biomass appear to be linked to changes in the PDO, indicating that the PDO has a major influence on secondary

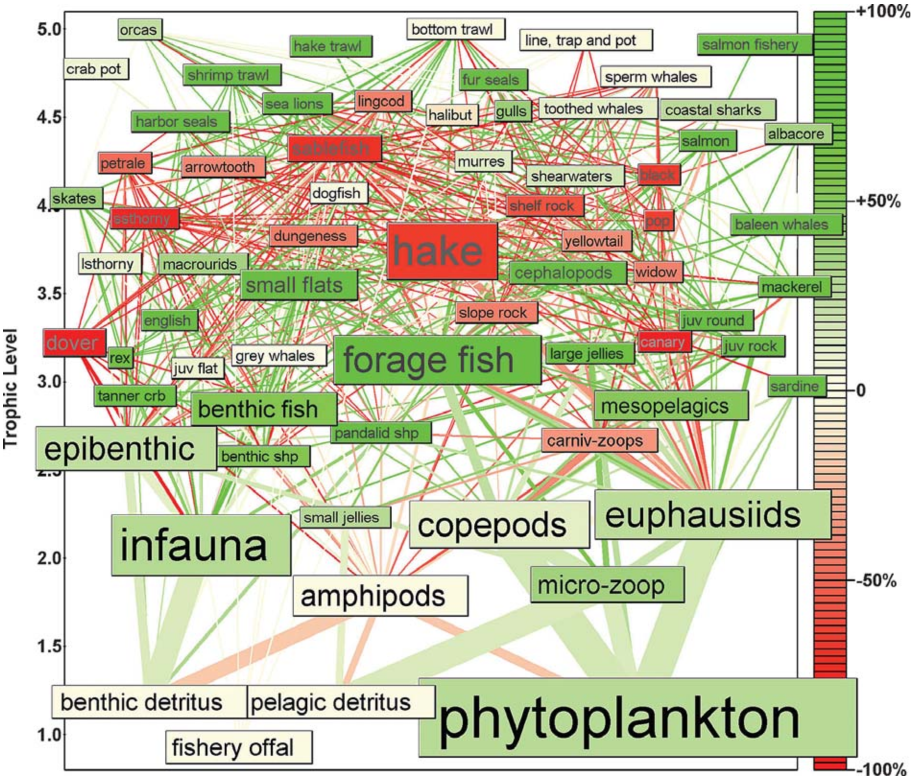

Fig. 10. The significant food web of the NCC (as in Fig. 2), with estimated changes in relative biomass, biomass flows and catches between 2002 (assuming above average primary and secondary production) coded in color as a percentage change from baseline starting values (1960).

production throughout the California Current. Zooplankton is the major food source for many groundfish and for most forage fish, and forage fish in turn comprise at least 10% of the diet for 24 of the components in the model, and over 50% for five of the components. Yet the poor response of the model to direct forcing by the PDO suggests that this influence is complex and non-linear, and the effects may be better quantified by accounting for a variety of physical factors simultaneously, as was done in the coho survival index. Consequently, a scenario that includes both bottom-up and top-down forcing is more consistent with what is known about the system. This is particularly true given the magnitude of bottom-up variability suggested by not only coho survival, but by observations on the interactions between local and basin-scale forcing, and the observed year-to-year variability in secondary production throughout the California Current (Chelton et al., 1982; McGowan et al., 1998; Robinson and Ware, 1999). Another problem is the lack of appropriate time series. If adequate data on the relative abundance and productivity of lower trophic model elements (zooplankton, forage fish, cephalopods) existed with which to compare model behavior, it might be expected that bottom-up forcing could result in significantly better model performance by fitting higher frequency variability. Similarly, because of a lack of age structure in this model, an autocorrelated climate forcer such as the PDO may better represent long term changes in abundance resulting from high frequency variability in recruitment for long-lived species. For those the impacts of climate on abundance and productivity are cumulative over longer time scales. Although the model and the model results discussed here are based on incomplete data, and are highly dependent on simplifying assumptions regarding ecosystem structure and physical dynamics, the results are consistent with what is known about the interactions between the biota in this ecosystem and their environment.

That much of the variability observed in single species models and dynamics can be replicated in this multi-species modeling approach is both encouraging and informative for two key reasons. The first is that model performance can be improved significantly when climate is introduced as a driving force, which is consistent with the observation that climate forcing has been shown to be a critical factor in determining the productivity and dynamics of many individual species in this ecosystem. Secondly, such convergence implies that there are few strong interspecific interactions (predation, competition) between most of these species that might have led to trajectories diverging from those suggested by single species assessments. This is somewhat intuitive for many of the rockfish, roundfish and longer-lived flatfish, where low natural mortality rates are indicative of low predation rates and relatively weak trophic interactions. Stronger interactions were observed in species such as shrimp, salmon, and small flatfish, where high turnover and high predation are coupled with substantial changes in many of their key predators (hake, sablefish, marine mammals) over the last 40 years. For example, the model fit to observed landings of pandalid shrimp improved significantly with both bottom up forcing (consistent with Hannah, 1993) and top-down forcing, consistent with literature describing strong interactions between shrimp and Pacific hake (Gotshall, 1969; Rexstad and Pikitch, 1986; Hannah, 1995). In the case of shrimp in particular, the relative improvement in fit was actually greatest when both the bottom-up (Logerwell) and the top-down (PDO) indices were used to drive the model. This suggests (perhaps not surprisingly) that both bottom-up and top-down factors are of great importance to shrimp abundance and productivity. In a similar modeling exercise focused on Pacific hake, Agostini (2005) used the model described here to assess the direct impact of increasing or decreasing hake biomass on other elements of the ecosystem. Her results suggest that most elements of the model (particularly pandalid shrimp, rockfish, salmon, seabirds and marine mammals) benefited from a reduction in hake biomass as a result of increases in the availability of forage fish and other prey.

Some of the stronger interactions suggested by the model were among several of the slower growing species: sablefish (*Anoplopoma fimbria*), shortspine thornyhead (*Sebastolobus alascanus*), and longspine thornyhead (*S. altivelis*). Several authors have noted that thornyheads are an important prey item of sablefish (Laidig et al., 1997; Buckley et al., 1999), and both sablefish and shortspine thornyheads appear to represent the most significant (known) sources of predation for longspine thornyheads. The baseline model suggests that natural mortality (predation) rates for longspine thornyheads have fallen by nearly fourfold over the past forty years, coincident with the declines in predator abundance (Field, 2004). Since this has been associated with an increase in catches of longspines from the late 1980s to the late 1990s, the increased fishing mortality may have been largely offset by declines in predation mortality. Moreover, total mortality has declined to very low levels in recent years associated with reductions in fishing effort. While the 1996 stock assessment, assuming a constant natural mortality rate, predicted declines in longspine abundance beginning in the early 1990s, the reductions of their major predators suggest that the biomass should have been largely stable, or increasing (as suggested by Figs. 4–7). The lack of any discernable trend in the slope survey data, except for a possible increase in abundance in recent years, lends support to this potential interaction.[5] At a minimum, this is a consideration that could be taken into account, qualitatively if not quantitatively, both in stock assessments and in future consideration of the impacts of fishing on community structure.

It must be acknowledged that the aggregation of many species and assemblages, and lack of size, age, and ontogenetic life history structure in the model may mask additional potentially significant interactions. For example, Yoklavich et al. (2000) show dramatic changes in the community composition of heavily fished rocky reef habitats, where piscivorous species such as lingcod, bocaccio, yelloweye, and cowcod (*Ophiodon elongates*, *Sebastes paucispinis*, *S. ruberrimus*, and *S. levis*, respectively) have been substantially depleted (all of these species are currently listed as overfished by the Pacific Fisheries Management Council). In these reefs, the abundance of smaller, faster growing, and less commercially important species such as greenstripe, rosethorn, splitnose, and pygmy rockfish (*S. elongates*, *S. helvomaculatus*, *S. saxicola*, and *S. wilsoni*, respectively) was considerably greater. By contrast, isolated and presumably lightly fished reefs with higher concentrations of piscivorous species were associated with much lower concentrations of such smaller, planktivorous species. Similarly, Walters and Kitchell (2001) demonstrated the potential for strong interactions among the adults of higher trophic level piscivores and their prey, such that adults crop down forage species that may be potential predators or competitors of their own juveniles, with non-linear negative impacts on piscivore stocks when

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[5] Based on the data collected on Alaska Fisheries Science Center West Coast Slope Surveys in Lauth (1999, 2000a,b), as well as unpublished data from the Northwest Fisheries Science Center, Fisheries Resource Analysis and Monitoring Division slope surveys conducted between 1998 and 2004 (Helser et al., NWFSC, unpublished manuscript).

adult abundance is reduced by fishing. Despite the recognized importance of trophic ontogeny in these and other species in the NCC, the lack of adequate abundance and age or size-specific diet data for most species makes modeling such potential interactions extremely challenging.

Future modeling efforts will benefit greatly both from assessing ecosystem behavior under a range of modeling approaches, as well as from integrating traditionally distinct modeling approaches to couple more realistic physical forcing mechanisms with multispecies and ecosystem interactions across multiple trophic levels. For example Fulton et al. (2004) found that combining hydrographic and biological submodels that incorporated functional groups and processes into reasonably complex food webs resulted in the ability to replicate the behavior of a large, temperate bay ecosystem in South Australia. In another example, Aydin et al. (2005) linked a food web model based on Ecopath with Ecosim with nutrient–phytoplankton–zooplankton (NPZ) model to drive seasonal variability in production and a bioenergetics model for pink salmon (*Oncorhynchus gorbuscha*), illustrating the significance of seasonal and ontogenetic prey switching for this key species in the Alaskan subarctic gyre ecosystem. As baseline knowledge and modeling abilities increase, the integration of multiple modeling approaches is likely to hold considerably more promise for successfully identifying the processes and mechanisms of ecosystem change in the future than any individual modeling approach alone. In achieving such objectives, the results of this paper should be considered a stepping-stone, rather than an end product.

Perhaps the most vexing characteristic of the Ecosim model is that model behavior is constrained by equilibrium processes, such that a perturbed model will always return to equilibrium, following the removal of perturbations such as changes in fishing mortality or bottom up forcing (given sufficient time). Although this is not entirely true when modeling under very high vulnerability scenarios, which can lead to erratic and at times chaotic behavior (users are cautioned against setting vulnerability values too high), even then the usual result is a return to starting conditions after long time periods. Walters et al. (2000) identified this as a weak, albeit necessary, characteristic of the model, particularly as this equilibrium generally precludes the possibility of prey switching by predators. Hollowed et al. (2000) noted that these constraints reduce the utility of such models in evaluating the consequences of species outbreaks, as well as the introduction of exotic species. Similarly, Rice (2001) attacks this stability by arguing that an alternative form of interaction, which he describes as scramble competition, occurs when resource availability changes abruptly for reasons other than usage by consumers, and when all individuals simultaneously experience either a sudden shortage or a sudden abundance of food or other resources. Such variability is often an integral feature of coastal upwelling ecosystems, for example, which are characterized by variability in physical conditions and productivity over multiple time scales. By driving population dynamics with climate information both from the bottom-up and the top-down, we begin to move slowly away from such equilibrium assumptions. However, the model by design has retained its equilibrium qualities, such that all species will eventually return to their starting values if perturbations (changes in bottom-up productivity, fishing) are removed; a quality that could be unrealistic in the face of possible "flips" of ecological states.

The need to move beyond traditional equilibrium-based approaches in both modeling and management has been well recognized for decades, yet because such movement pushes us into unfamiliar territory, there remains substantial reluctance to proceed (Gunderson et al., 1995; Levin, 1998; Rice, 2001). For example, Holling and Meffe (1996) argue that the key to maintaining resilience in natural resource management is to facilitate existing processes and variability, rather than attempt to alter and control them, and McEvoy (1996) advises that "the best that fisheries managers can do is to monitor and adjust the interaction between a volatile ecology, a creative economy, and society's understanding and control as they go along." From a socio-ecological perspective, Berkes et al. (2002) argue that resilience is a function of the livelihood security of stakeholders (be they individuals or groups), as defined by entitlements and access to resources. For example, Hanna (1992) found that the diversification of fishing strategies between groundfish, shrimp, and crab, benefited fishermen in the NCC by virtue of reducing the variability of landings and earnings during changes in resource abundance, suggesting that socio-ecological resilience is in part dependent upon access to a range of resources.

Pikitch et al. (2004) have reiterated the often-made point that there remains a need to derive and develop community and system-wide standards, reference points, and control rules analogous to single species criteria, particularly evaluations of ecosystem productivity relative to the requirements of other ecosystem components and removals by fisheries. Quantitative ecosystem models offer a valuable vehicle for doing so (Pauly et al., 1998; Jarre-Teichmann and Pauly, 1998; Fulton et al., 2005). Furthermore, where trophic interactions between exploited species seem clear, dynamic modeling can offer valuable information regarding the likely or potential trade-offs between harvest strategies, and provide a template to evaluate both the magnitude and some measure of reasonable consequences of removals of either predators or prey in the system of interest (Christensen and Walters, 2004b; Walters et al., 2005).

Although quantitative modeling of significant trophic interactions in the NCC may not lead to substantive changes in harvest or management strategies in the near term, it may enhance understanding of variations in population trends, and will contribute to a more holistic understanding of ecological connections and interactions. By far the most important feature of these models is that, if based on reasonable knowledge and presented with appropriate skepticism, they serve as a stimulus and focus for initiating dialogues and discussions with regard to both past ecosystem dynamics and plausible ecosystem futures. Ecosystem models can complement the insights gained from single species models through a more holistic evaluation of past and current abundance and productivity, and offer a means to evaluate plausible expectations of future system trade-offs among management decisions. Admittedly, however, the challenges of distilling the insights gained from these simulations into concrete management advice remain substantial.

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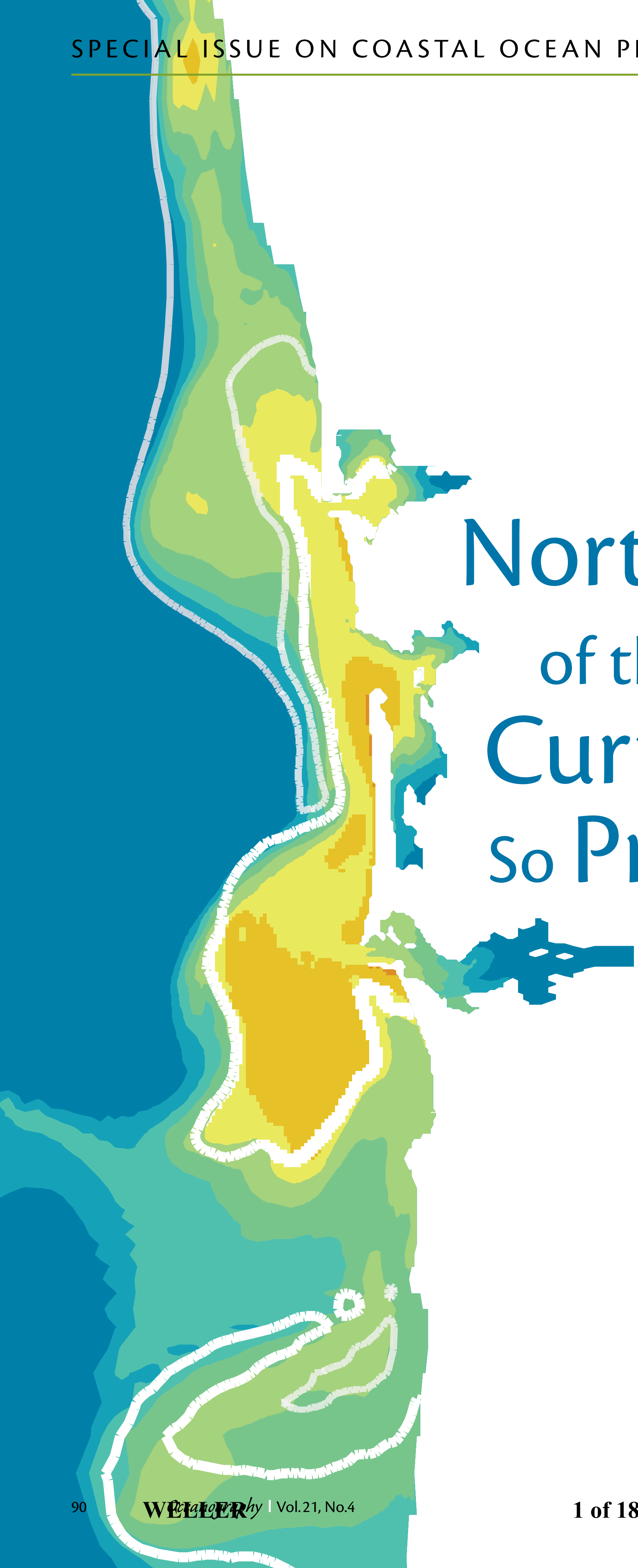

Why is the Northern End of the California Current System So Productive?

BY BARBARA M. HICKEY
AND NEIL S. BANAS

ABSTRACT. Although scientists have long believed that, in an eastern boundary current system, alongcoast wind stress is responsible for the upwelling of deep nutrients that initiates phytoplankton blooms, the California Current System (CCS) presents a challenge to this idea. Seasonally averaged chlorophyll concentrations are several times higher along the Washington/southern British Columbia coast than off northern California, where alongcoast wind stress is several times greater. The high chlorophyll concentration is reflected in higher trophic levels, such as zooplankton and fish density in the northern CCS. This article discusses potential reasons for this apparent paradox. The analysis suggests that the northern CCS has several mechanisms that can produce upwelled nutrient concentrations comparable to those in regions with much greater wind stress, including a persistent nutrient supply through the dynamics of the Strait of Juan de Fuca and local upwelling enhancement by submarine canyons. Large-scale upwelling resulting from coastal-trapped waves forced in the areas with stronger wind stress is also likely an important factor, as is iron input by the Columbia River. In addition, in contrast to other parts of the CCS, the high-productivity northern latitudes have numerous physical features that give phytoplankton blooms time to develop fully and to be retained on the shelf, including wide shelves, coastlines without large capes, a large bank, wind intermittency, and density fronts related to the Columbia River.

DOES PRODUCTIVITY DIFFER ACROSS REGIONS IN THE CALIFORNIA CURRENT SYSTEM?

Overall biological productivity in the California Current System (CCS), a system of currents that flow along the western boundary of the United States and southern Canadian Pacific coast (Figure 1), is generally attributed to seasonal upwelling of nutrient-rich deep waters to the continental shelf, as in other eastern boundary systems (Hill et al., 1998). This upwelling is caused primarily by the stress of winds blowing equatorward on the ocean's surface next to the coastal boundary. When the deeper water with higher nutrient concentration upwells, phytoplankton in the upwelling layers are exposed to light and begin to grow, resulting in a "bloom" (a high concentration of phytoplankton) (MacIsaac et al., 1985). It might be expected that overall productivity along any eastern boundary coast would be correlated with the strength of the alongcoast wind stress at a given location. In the CCS, this relationship does not hold: seasonally averaged coastal chlorophyll concentrations increase fivefold from northern California to southern Vancouver Island, counter to the magnitude of the alongshelf wind stress, which decreases by a factor of eight over this region (Figure 2; see also Hickey and Banas, 2003; Ware and Thomson, 2005). High chlorophyll concentrations in the northern CCS are reflected in higher trophic levels, such as zooplankton biomass and fish stocks ("bottom-up control"), in the Washington/British Columbia region (Ware and Thomson, 2005; Figure 3).

One important oceanic difference among regions in the CCS is the degree of influence of freshwater (i.e., water input by rivers and estuaries and energetic tidal currents associated with these features; Figure 1). These freshwater sources affect stratification, light, circulation, nutrient supply, and phytoplankton retention in coastal waters. Juvenile salmon are generally more highly concentrated in regions affected by river plumes (Figure 4). The distribution of the annual return of bird colonies to sites along the Washington coast suggests that birds may find areas most influenced by freshwater most attractive. Near the Juan de Fuca Strait, as well as farther south near the plume from the Columbia River, colonies returned in most years studied (80–100% colony return; Figure 5). This paper explores the potential causes of the large-scale alongcoast chlorophyll gradient in the CCS in light of two recent observational programs that studied the regions most influenced by freshwater: River Influences on Shelf Ecosystems (RISE, a Coastal Ocean Processes [CoOP] project) focused on the Columbia River; and Ecology and Oceanography of Harmful Algal Blooms Pacific Northwest (ECOHAB PNW) focused on the Strait of Juan de Fuca effluent.

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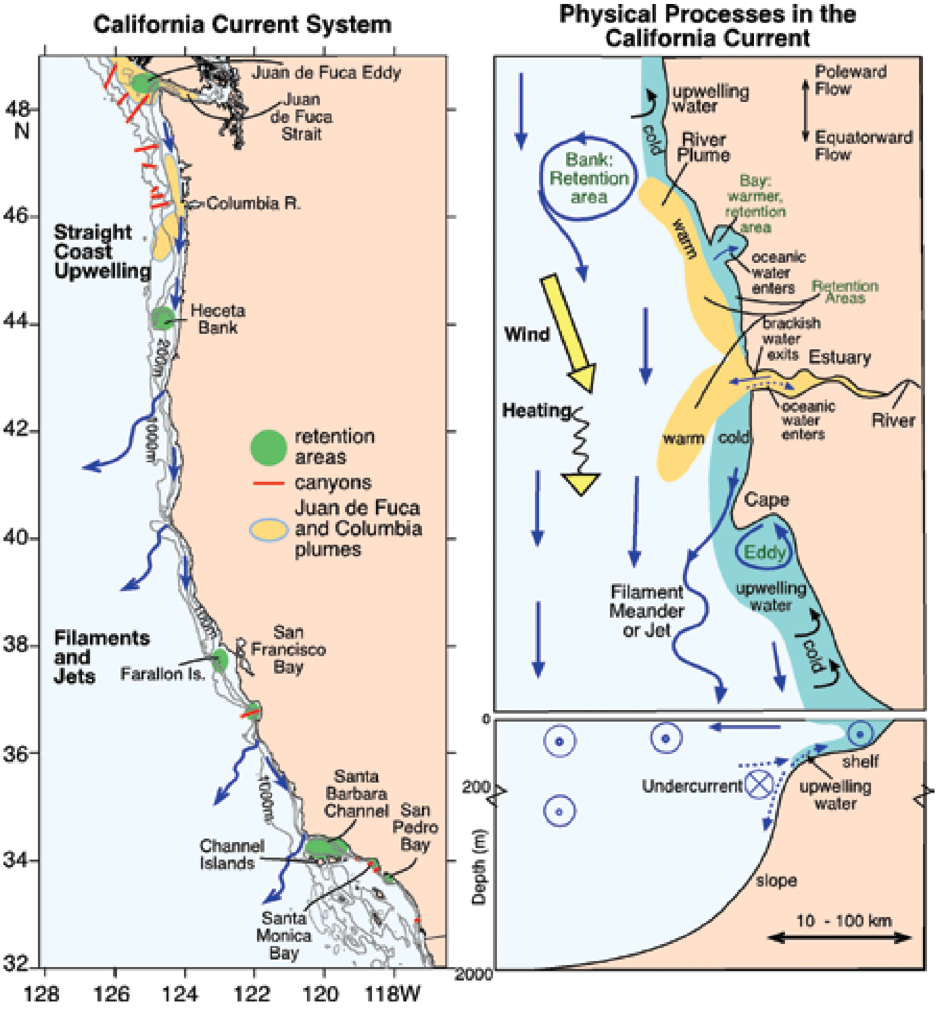


Figure 1. Primary physical processes in the California Current System (CCS) in summer. (Left) A map of the CCS with bottom topography and typical surface currents (blue arrows), showing the location of submarine canyons (red), regions with longer than average residence times (green, "retention areas"), and primary sources of freshwater (yellow, the Strait of Juan de Fuca and the Columbia River). The Columbia River plume is depicted in the bi-directional pattern frequently seen in the summer season. Regions where upwelling is primarily two dimensional ("straight coast upwelling") are differentiated from those farther south that are more three dimensional ("filaments and jets"). (Right) A cartoon showing typical circulation patterns for an arbitrary subregion of the CCS in plan view (upper) and cross section (lower). In the cross section, circles with dots indicate equatorward flow; circles with crosses indicate poleward flow. Retention areas over banks, behind capes, and within bays and estuaries are noted in green text. Upwelling water next to the coast is shown as darker blue. Note that river plumes are generally warmer than coastal waters in summer.

THE CCS AND LOCAL WIND-DRIVEN UPWELLING

The California Current is a ~ 1000-km-wide, sluggish current that forms the eastern limb of the North Pacific gyre, spanning the Pacific coast from ~ 20°N to ~ 50°N (Hickey, 1979, 1998). Superimposed on that mean flow, narrower equatorward jets induced by the equatorward alongshelf wind stress develop seasonally on the shelf, spreading seaward over the shelf and slope as the season progresses (Strub and James, 2000). Isopycnals begin to tilt upward toward the coast following the "spring transition" (Huyer et al., 1979; Huyer, 1983; Strub and James, 1988), resulting in the upward movement of deeper, nutrient-rich water, and this upward movement continues throughout the season (Hickey et al., 2006) (Figure 1). Thus, nutrients, which have higher concentrations deeper in the water column, are lifted to upper layers of the continental shelf where they can be used by phytoplankton. Recent measurements show that in addition to vertical movement of nutrients due to upwelling, vertical mixing can enhance nitrate flux into the euphotic zone by as much as 25% (Hales et al., 2005). A poleward undercurrent (the "California Undercurrent") develops over the continental slope as upwelling continues (Figure 1, lower right panel). The development of the undercurrent is important in that once it is present, flow in the bottom boundary layer (~10 m from the bottom) changes from onshore (in which it can provide nutrient-rich water to the shelf) to offshore (in which it can remove nutrient-depleted water from the shelf).

These seasonal patterns are interrupted or their amplitudes modified at intervals of 2–20 d when the wind along the shelf reverses direction (Hickey, 1998; Barth et al., 2007). The frequency of interruption changes significantly along the coast, from almost no interruptions (i.e., steady equatorward winds) off California to frequent interruptions off Washington (Figure 6d, showing the percentage of days with equatorward winds as a function of latitude). The seasonal coastal jet over the middle and outer shelf and upper slope rarely

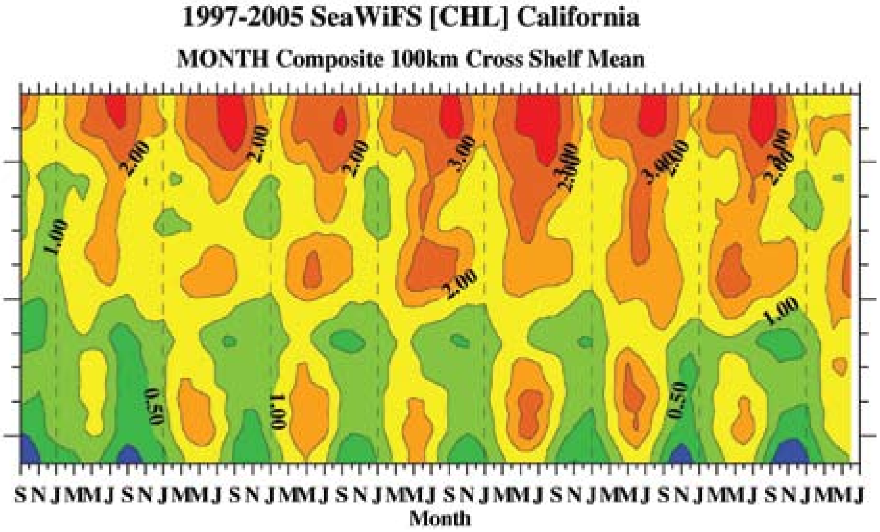


Figure 2. Seasonal and interannual variation of coastal chlorophyll concentration versus latitude in the CCS. Data were derived from several years of SeaWiFS satellite data and averaged from the coastline seaward to 100 km. This averaging distance captures the majority of seasonal chlorophyll variability (Henson and Thomas, 2007). The figure depicts the strong latitudinal gradients that are the focus of this paper: higher chlorophyll concentrations are observed in the northern CCS. Contours are 0.25 (dark blue), 0.5, 1.0, 2.0, 3.0, and 5.0 (red) mg chl m^{-3}. Maximum chlorophyll is located well north of the Columbia River entrance, and the Strait of Juan de Fuca has a low particulate load, so that coastal particulates are not expected to have significantly biased these patterns. The patterns as well as magnitudes in the northern CCS (3–6 mg m^{-3}) are consistent with extensive historical in situ chlorophyll measurements (Landry et al., 1989). *Figure courtesy of Andrew Thomas, University of Maine; see also Legaard and Thomas, 2006*

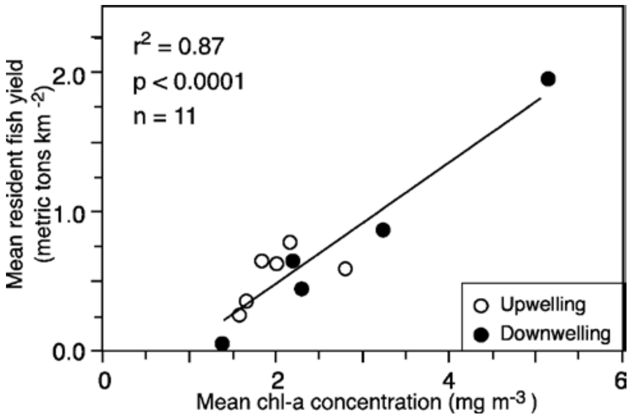


Figure 3. Demonstration of large-scale "bottom up" trophic linkage. The mean annual chlorophyll *a* concentration and the long-term annual yield of resident fish are strongly correlated along the British Columbia coast. Solid circles denote upwelling periods. Open circles denote downwelling periods. *Figure adapted from Figure 2 in Ware and Thomson (2005)*

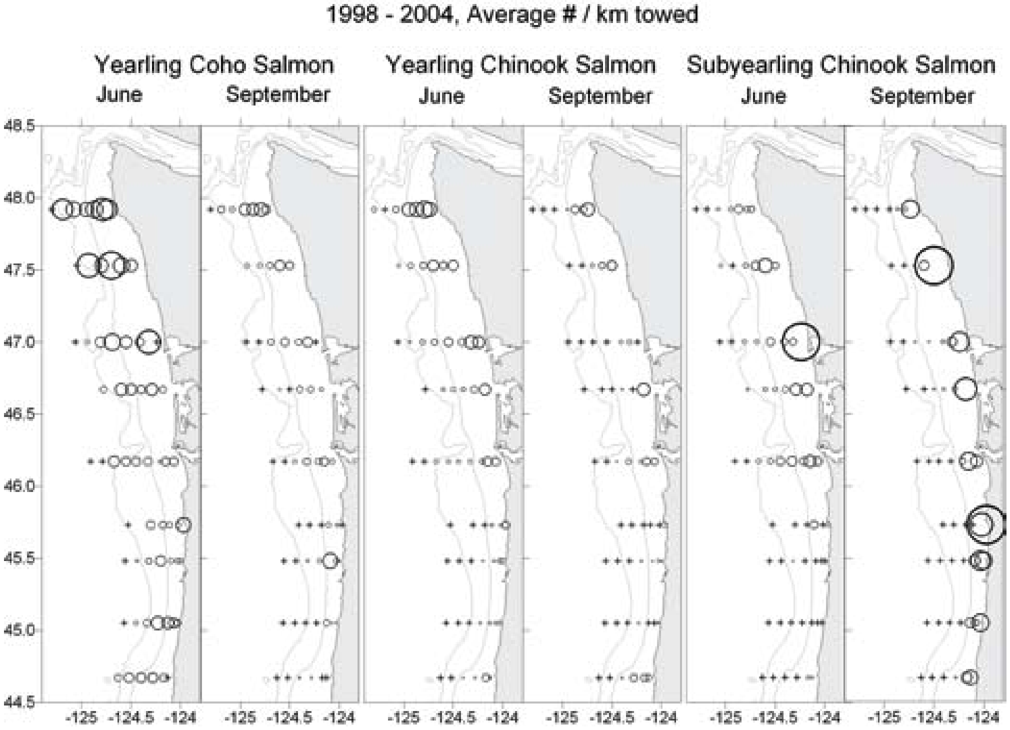
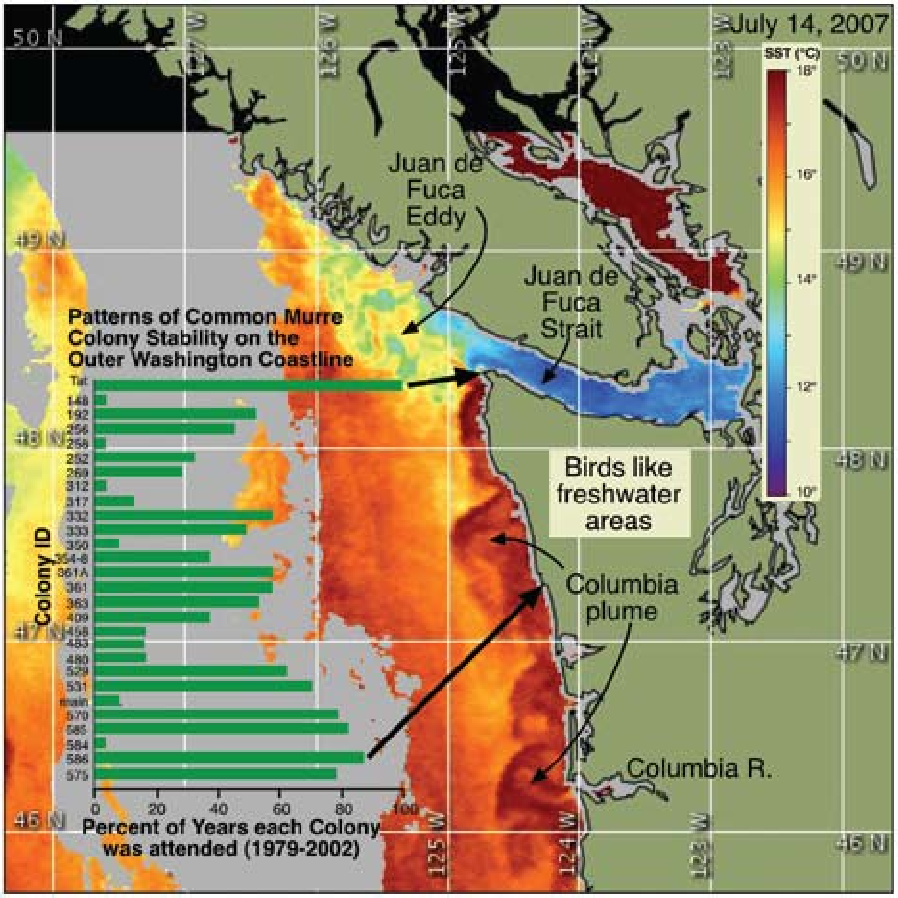


Figure 4. Average number of juvenile salmon per km towed during seasonal cruises over a six-year period. The fish were using a 100-m-long NORDIC 246 Rope Trawl with a 20 m x 30 m mouth opening. The size of the circles is proportional to the number of fish caught per km towed. The largest circle indicates >26 fish per km; the + sign indicates that no fish were caught in the tow. The illustration indicates that most young salmon prefer more northern habitat; in particular, they prefer the region north of the Columbia River entrance (just north of 46°N), a region frequently occupied by the Columbia plume in spring and early summer. Fall Chinook are an exception. *Figure courtesy of Bill Peterson and Ed Casillas; data in part from Fisher et al. (2007)*

Figure 5. Patterns of colony stability for the Common Murre along the northern Washington coast (data are from the region between the black arrows), plotted on a satellite-derived image of sea surface temperature for July 4, 2007. The freshwater plume from the Strait of Juan de Fuca is seen as a cold feature emanating from the Strait; the plume from the Columbia River is seen as a warm feature all along the Washington/Oregon coast. The Columbia River plume on this date extends much farther along the coast than is typical for this month. The highest percent of colony occupation occurs near or at the two ends of the region sampled, suggesting a relationship between colony stability and location of freshwater plumes. Satellite AVHRR data are from the NOAA Coastwatch program. *Unpublished bird colony data courtesy of Julia Parrish and the US Fish and Wildlife Service, Washington Outer Coast Refuge*



reverses direction from equatorward to poleward during the upwelling season (Huyer et al., 1979; MacFadyen et al., 2008), although its amplitude is modified by local wind dynamics. The jet is controlled by pressure differences due to sloping isopycnals and sea surface height, and the Coriolis force (Earth's rotational tendency). In contrast, currents on the inner shelf (~ 30 m bottom depth or less), which are controlled by surface and bottom friction, reverse from equatorward to poleward a few hours after the wind reverses. In the northern reaches of the CCS, much of the variability in alongshelf currents over the middle and outer shelf is a result of propagating disturbances generated by winds south of a given location (Battisti and Hickey, 1984). Near the sea surface and near the seafloor at all locations across the shelf and slope, friction is also important. Surface frictional currents change direction from onshore to offshore when winds change from poleward ("downwelling-favorable") to equatorward ("upwelling-favorable").

If winds blow equatorward along a straight coastline, at equilibrium, the depth at the source and the amount of upwelled water should be roughly proportional to the strength and duration of the winds divided by the Coriolis parameter (two times Earth's rotation rate times the sine of the latitude) and density (Hill et al., 1998). As mentioned above, alongshelf winds are not constant along the coast: maximum wind stress magnitude occurs off northern California and the alongcoast difference between Washington (~ 48°N) and northern California (~ 42°N) is about a factor of eight (Figure 6a). The factor of eight might possibly be mitigated in northern latitudes by the duration of upwelling winds if those winds were more persistent. But in spring off the Washington coast, upwelling winds typically occur only one-half to two-thirds of the time, and actual downwelling winds also occur (Figure 6d).

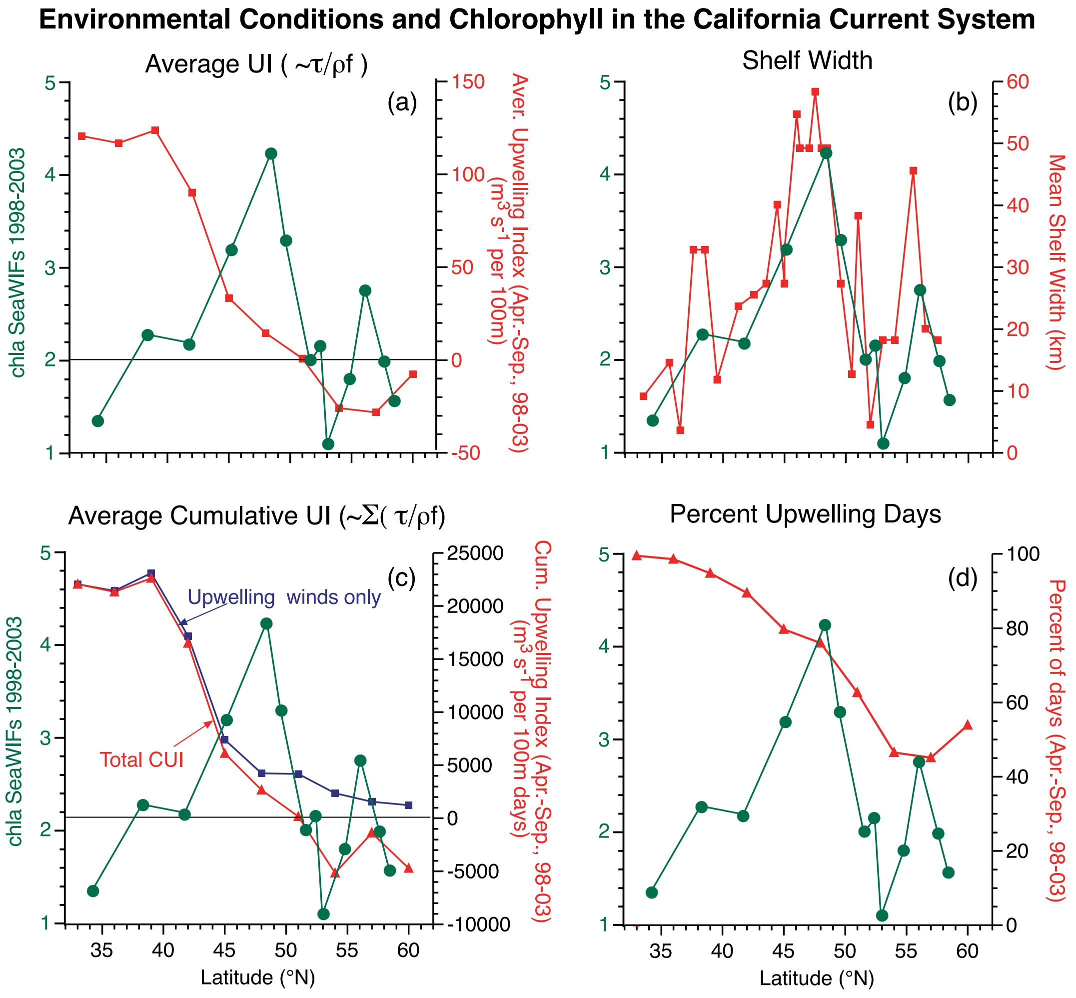


Figure 6. Mean chlorophyll concentration along the coast (from Ware and Thomson, 2005) and (a) Spring-to-summer average (Apr. 1–Sep. 30, over 1998–2003) coastal upwelling index (Bakun, 1973); (b) shelf width averaged manually over one-degree intervals; (c) spring-to-summer average cumulative coastal upwelling index for all winds (CUI) and for just upwelling winds; and spring-to-summer average percentage of days with upwelling-favorable winds. The figure shows that chlorophyll concentration is a maximum at mid latitudes, in a region of declining upwelling wind stress magnitude (panels a and c) and increasing degree of upwelling intermittency (panel d). The alongcoast chlorophyll pattern is well correlated only with shelf width (panel b).

IS NITRATE SUPPLY FOR PRIMARY PRODUCTIVITY SIMILAR OVER THE CCS?

In spite of these alongcoast differences in wind forcing, nitrate supplied to the sea surface is indeed similar over the CCS from California to Vancouver Island. (In the CCS, nitrate, silicate, and phosphate have very similar spatial and temporal seasonal patterns as shown in Figures 1.14–1.22 in Landry et al. [1989]. We use "nutrients" to describe the macronutrients nitrate, nitrite, silicate, and phosphate; we use "nitrate" to describe nitrate and nitrite together.) Values of 20–25 µM nitrate are typically reported in waters upwelled to the surface over the inner shelf by early summer (see MacFadyen et al., 2008, for Washington/Vancouver Island values; see Huyer et al., 2005, for central Oregon and northern California). Minimum temperatures of shelf bottom water over this latitudinal range are essentially identical as well (Geier et al., 2006).

HOW IS NITRATE SUPPLY ABLE TO OVERCOME A FACTOR OF EIGHT DIFFERENCE IN WIND STRESS OVER THE CCS?

Remote Wind Forcing

Seasonal changes in water properties can propagate poleward from the region where winds caused the disturbance ("remote wind forcing") as a baroclinic (density-related) wave (McCreary et al., 1987). In support of this model-generated idea, observational studies have attributed the spring transition in part to remote wind forcing (Strub et al., 1987; Hickey et al., 2006). Analyses of seasonal changes in the northern CCS in 2005 provide convincing evidence that remote wind forcing continues to be important for large-scale upwelling of water properties in the northern CCS throughout the upwelling season (Hickey et al., 2006; Pierce et al., 2006).

Still, these analyses provide, at most, a partial answer to the question. Although remote wind forcing might be sufficient to ensure that the source depth of water that upwells to the northern shelves is similar to that in regions with stronger and more persistent local wind forcing, this mechanism does not necessarily result in delivery of the deeper water and associated nutrients to the euphotic zone where the nutrients can be used by the phytoplankton. Figure 6d shows that local upwelling winds are intermittent at northern latitudes and thus isopycnals are upwelled to the surface near the coast only intermittently. Also, the presence of large amounts of freshwater increases stratification at northern latitudes much of the time, further inhibiting upwelling (Hickey et al., 2005). Fortuitously, the northern CCS has other mechanisms, such as estuarine and tidal dynamics, that help move nutrients to the euphotic zone.

Major estuaries and associated river plumes in the CCS occur in its northern end (Figure 1). River plumes can alter nutrient supply as a *conduit* of land-derived nutrients from watersheds to the ocean, like the Mississippi River. Alternately, they can act as a *facilitator*, entraining coastal upwelling-derived nutrients into the euphotic layer and distributing them out over the continental shelf or slope in the plume (Figure 7). The northern CCS has two

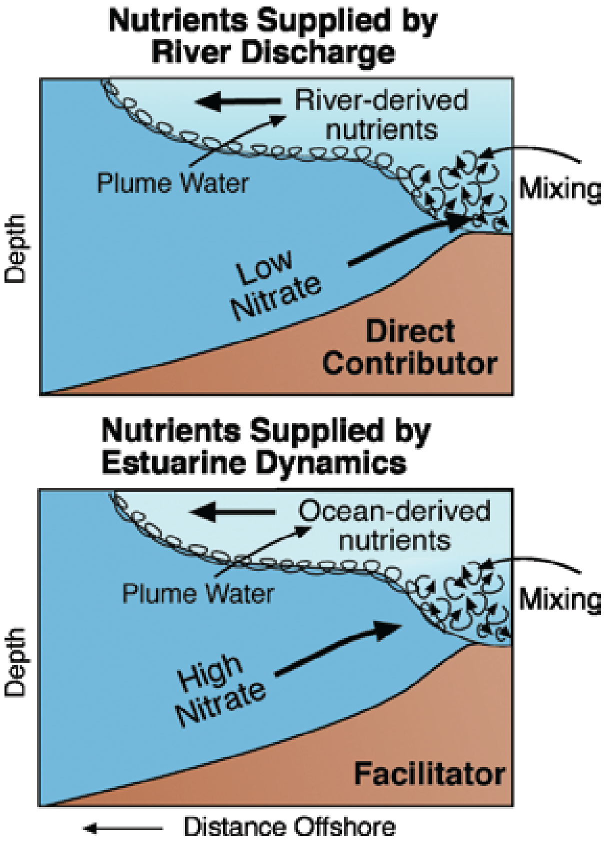


Figure 7. Cartoon depicting how freshwater plumes (lighter blue) interact with the coastal ocean (darker blue). Fresher water may contain land-derived nutrients (plume as "conduit"), such as occurs generally with the Mississippi River plume. Alternately, if upwelling is occurring, the intense mixing with ocean water near the plume lift-off region mixes nutrient-rich upwelled water into the plume, which then carries the rich water seaward (plume as "facilitator").

massive freshwater sources: the effluent from the Strait of Juan de Fuca, whose freshwater originates in the Fraser River and the rivers of Puget Sound, and the Columbia River, the second largest river in the continental United States. The Columbia outflow is half an order of magnitude smaller than the outflow from the Strait of Juan de Fuca (1.4 x 10^4 m^3 s^{-1} vs. 10^5 m^3 s^{-1}; Hickey et al., 1991, 2008). However, the salinity deficit of the freshwater transferred to the coastal ocean is much larger than that of the strait (~ 10–20 vs. 31.5 practical salinity units [psu]; Hickey et al., 2005, 2008); thus, effects of the Columbia River on local stratification and circulation (but not necessarily on macronutrients) can exceed those of the strait. During the delayed spring transition of 2005, relatively high values of chlorophyll were observed in the vicinity of both these freshwater features, in contrast to other regions (Figure 8d).

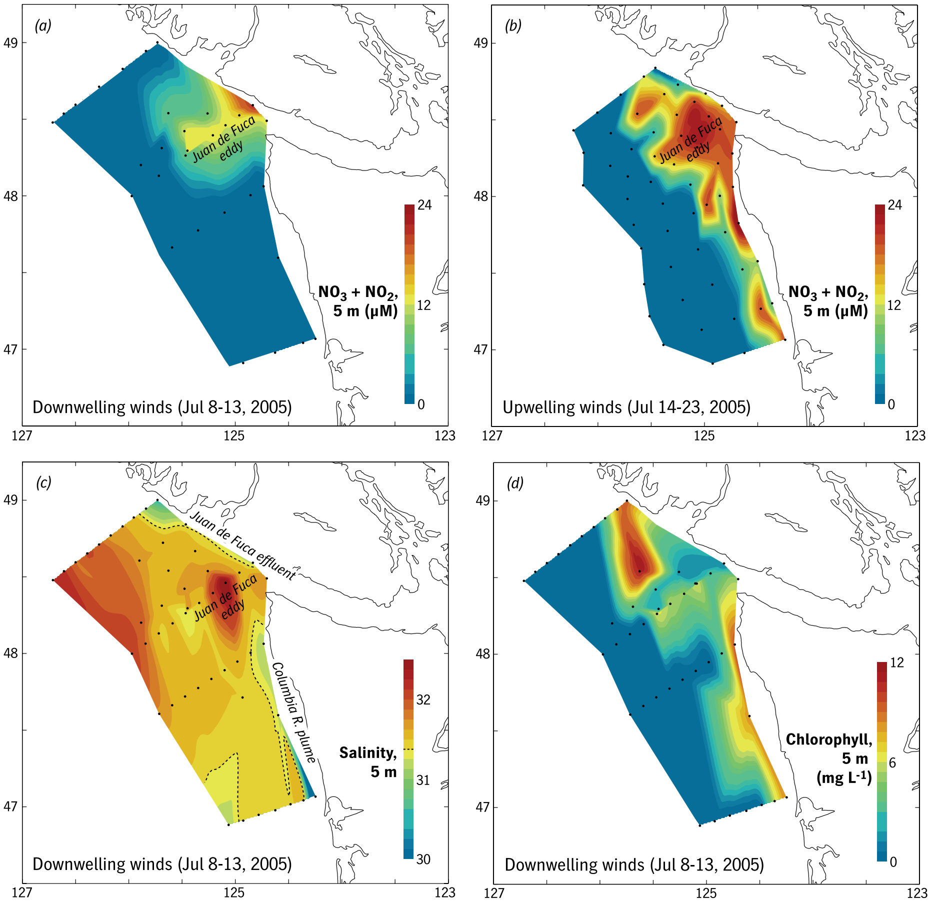


Figure 8. Upper panels compare contoured maps of nitrate plus nitrite during downwelling-favorable (a) and subsequent upwelling-favorable (b) winds along the southern Vancouver Island/Washington coast at a depth of 5 m. Station locations are indicated with black dots and no smoothing has been done. The contrast between the nitrate supply along the open coast, which disappears during periods of downwelling winds, and in the Juan de Fuca region, where supply is governed by estuarine/strait dynamics, is shown explicitly. In addition to a more persistent nutrient supply, the nutrients are transported offshore by the strait effluent and the offshore Juan de Fuca eddy, a distance several times greater than by wind-driven transport in the coastal upwelling zone. Lower panels compare 5-m salinity (c) and chlorophyll *a* (d) during a period of downwelling in early July 2005. Chlorophyll concentration is elevated in the two regions most influenced by freshwater (dark blue areas, offshore of the strait and in the Columbia River plume) even though winds were downwelling-favorable. Nitrate concentration remained high offshore of the strait as shown in Figure 8a. This was the period of delayed upwelling when chlorophyll, primary productivity (Kudela et al., 2006), and other marine populations (e.g., Mackas et al., 2006; Newell and Cowles, 2006) failed in some regions. *Unpublished nitrate and chlorophyll-a data from Bill Cochlan, San Francisco State University, ECOHAB PNW program. See MacFadyen et al. (2008) for more details.*

The Juan de Fuca Strait Outflow

Nutrients exiting the Juan de Fuca Strait are essentially all derived from the same water source that is upwelled in the rest of the CCS (Mackas et al., 1980). The water is drawn up the Juan de Fuca canyon and enters the strait to compensate for the loss of mass of the outflowing water, because the strait is an estuary. This nutrient-rich water is subsequently entrained into outflowing strait water and thus provides a massive, relatively steady nutrient source to the northern CCS (Mackas et al., 1980; Denman et al., 1981; MacFadyen et al., 2008). The difference between nitrate supplied by straight-coast, wind-driven upwelling and by the Juan de Fuca Strait can be seen by comparing surface nitrate during a period of downwelling and subsequent upwelling (Figures 8a and 8b). Nitrate continues to emerge from the strait but is absent along the coast during the period of downwelling winds (see also MacFadyen et al., 2008). The Juan de Fuca region has three other unique advantages as a nutrient source over regions supplied by upwelling along a straight coastline. First, its strong currents transport nutrients offshore at least four times farther than water upwelled at the coast (~ 60 km vs. 15 km offshore). Second, it retains them locally due to the

Table 1. Order of magnitude estimates of nitrate input to the southern Vancouver Island/Washington shelf by a variety of sources.

Type of Upwelling	Spring (Apr–Jun) x 10^9 kg	Full Season (Apr–Sep) x 10^9 kg	Comments
Strait of Juan de Fuca	0.2 0.3	0.5 0.6	Strait alone Doming enhancement added
Coastal	0.2	0.4	WA coast
Canyon Enhancement	0.2–0.5	0.2–0.5	No input after undercurrent develops; H = 10m
Columbia, Downwelling (conduit)	0.02	0.02	Input only in spring
Columbia, Upwelling (facilitator)	0.02	0.04	Mean value from Bruland et al., 2008

Juan de Fuca eddy (Figures 1 and 8), a major topographic feature in this area (see later discussion of retention). These physical advantages are enhanced by diminished utilization by phytoplankton as water emerges from the strait (MacFadyen et al., 2008). The source waters for phytoplankton in the strait are always deep (100–200 m) so that plankton density is low, in contrast to phytoplankton upwelled close to the coast on the wide, highly retentive northern shelves. While transiting the strait, phytoplankton are light limited due to vigorous vertical mixing, so that growth is minimal. Thus, several days are required to initiate blooms that significantly draw down nutrients. The third advantage is that because the outflow from the strait occurs over the upper 100 m (Hickey et al., 1991), high nutrient concentrations (nitrate > 25 µM; MacFadyen et al., 2008) are provided much deeper in the water column than occurs with the ~ 10–20-m-thick offshore surface Ekman layer produced by wind-driven upwelling. Local usage of these nutrients usually depletes the upper 10 m of the water column. However, the remainder of the water column is exported equatorward to Washington and Oregon in the coastal jet, providing a rich source of nutrients to the ecosystems of those shelves.

To obtain an order of magnitude seasonal estimate of nitrate input by the Strait of Juan de Fuca, we used a flux of 50 kg nitrate s^{-1} (Mackas et al.,1980). The flux was multiplied by the appropriate number of days in the April to June period (spring) and for the full April through September upwelling season (upper value in Table 1). As the season progresses, doming beneath the Juan de Fuca eddy is itself a source of upwelling to the base of the pycnocline (MacFadyen et al., 2008). To include that effect, estimates were increased by 25%, using the estimates of cross-isopycnal nitrate flux derived from microstructure measurements off Oregon (Hales et al., 2005) (lower value in Table 1).

For comparison, we estimated nitrate contributed by upwelling due to local winds along the Washington coast by assuming a two-dimensional balance such that the wind-driven offshore flux in the surface layer is balanced by an onshore upwelling flux (as in Denman et al., 1981). A cumulative upwelling index was used to compute the mass input over spring alone and over the full season (as seen in Figure 6). Following Hickey et al. (2006), only upwelling-favorable wind stress values were included because wind reversals do not appear to reverse currents in the bottom boundary layer over the middle and outer shelf. The upwelling distance used was the entire coast from the Columbia River to the Strait of Juan de Fuca. For a conservative estimate, the upwelling nitrate concentration was assumed to be 30 µM (see nitrate time series in Hickey et al., 2006).

Results show that in spring, nitrate supplied by outflow from the ~ 20-km-wide Strait of Juan de Fuca contributes roughly the same (or more) nitrate to the 220-km-long southern Vancouver Island/Washington shelf as local coastal upwelling, a doubling of available nitrate. The significance of nitrate output by the strait is consistent with Crawford and Dewey (1989), who showed that the strait was the dominant source of nutrients for the Vancouver Island coast.

Nitrate provided by the strait is thus substantial, and would allow phytoplankton to continue blooming when nitrate is depleted in regions without this alternate nitrate source, as occurs during periods of persistent downwelling winds such as in spring 2005.

The Columbia River Plume

The Columbia River plume was historically reported to be oriented southwest of the river mouth in summer (Barnes et al., 1972). However, recent work shows that the plume is present more than 50% of the time north of the river mouth, and frequently has branches both north and south of the river mouth at the same time in summer (Figure 1) (Garcia-Berdeal et al., 2002; Hickey et al., 2005, 2008). The plume from the Columbia River can be both a nutrient conduit and a facilitator (Figure 7). Most nutrients derived from local watersheds are used inside the Columbia River estuary in the summer growing season and are not exported out to the continental shelf (Conomos et al., 1972). However, in spring and early summer during periods of high rainfall, moderate concentrations of nitrate (~ 5–18 μM) can be supplied directly to the coastal ocean (Bruland et al., 2008). This nutrient supply may help sustain local ecosystems during periods of weak or no upwelling, or late transitions to spring conditions, as occurred in 2005 (Figure 8d).

Significant entrainment of shelf water occurs where the plume separates from the bottom (the plume "lift off" region) and exits the river mouth, and also occurs just inside the estuary (Figure 7) (McCabe et al., 2008; Bruland et al., 2008). If upwelling has been occurring on the nearby shelf, the nutrient-rich upwelled shelf water is mixed or entrained into the outflowing Columbia River water, similar to the process that entrains much deeper nutrients into Juan de Fuca Strait. Model results (Banas et al., in review; MacCready et al., 2008) suggest that the amount of nitrate mixed into the coastal water exceeds that which would be upwelled by wind-driven upwelling along a coast without a plume or an estuary. This result is captured in a plot showing the difference in total nutrients (biomass plus nitrate) as well as nitrate and chlorophyll maps on selected dates between two model runs, one with, and one without the Columbia River estuary and its plume (Figure 9). During a period of weak or intermittent upwelling (July 12–18), nitrate is much higher near the river mouth when the riverflow and estuary are included in the model (Figure 9d); total nitrate shows a ~10 μM increase in the plume area throughout this period. The enhanced nitrate supply is due to a combination of freshwater and tidal dynamics; note the smaller, corresponding positive anomaly in nitrate at the mouth of the estuary just north of the Columbia estuary (Figure 9d, July 18), which has strong tides but negligible summer river input (set to zero in the model).

During the modeled downwelling event July 18–20 (Figure 9a), the excess plume-facilitated nitrate supports a phytoplankton bloom near the Columbia mouth and along the Washington coast (Figure 9b, July 20), whereas in the no-river case, nitrate and biomass both decline quickly during downwelling (Figures 9b and 9d, July 20). These plume effects are strongest under weak-to-moderate upwelling; during periods of strong, sustained upwelling-favorable winds (July 21–26), the plume is blown offshore and southwest, and nitrate supply varies little between model cases (Figure 9d, July 26).

The presence of a river plume over a shelf does not always increase local nitrate or total nutrient supply. The increased stratification can impede upwelling of new nitrate from deeper layers (Hickey et al., 2005), as shown in model runs. During weak, variable upwelling (July 12–17), the plume partially caps nutrient supply and reduces primary production along the Washington coast in comparison with the no-river case, causing a deficit in biomass (Figure 9b, July 14) and total nitrogen (Figure 9c).

For comparison with other sources in Table 1, seasonal nitrate input by the Columbia River plume was estimated both for downwelling-favorable winds, in which entrainment into the plume was ignored but watershed-derived nitrate exiting the estuary was counted, and for upwelling-favorable winds, in which riverine nitrate was assumed to be zero but the nitrate from upwelled water on the shelf is mixed or entrained into the outward moving plume near its lift off location. Ranges for nitrate obtained on RISE cruises were taken from Bruland et al. (2008): 5–18 μM in river water during downwelling periods and ~ 20 μM in plume water during upwelling periods. Values were multiplied by the typical spring riverflow (~ 10^4 m^3 s^{-1}) and by the number of days of downwelling or upwelling, respectively. Because river input of nitrate only occurs under substantial storms, we assumed that no direct river contribution occurs after June.

Perhaps surprisingly, nitrate supply

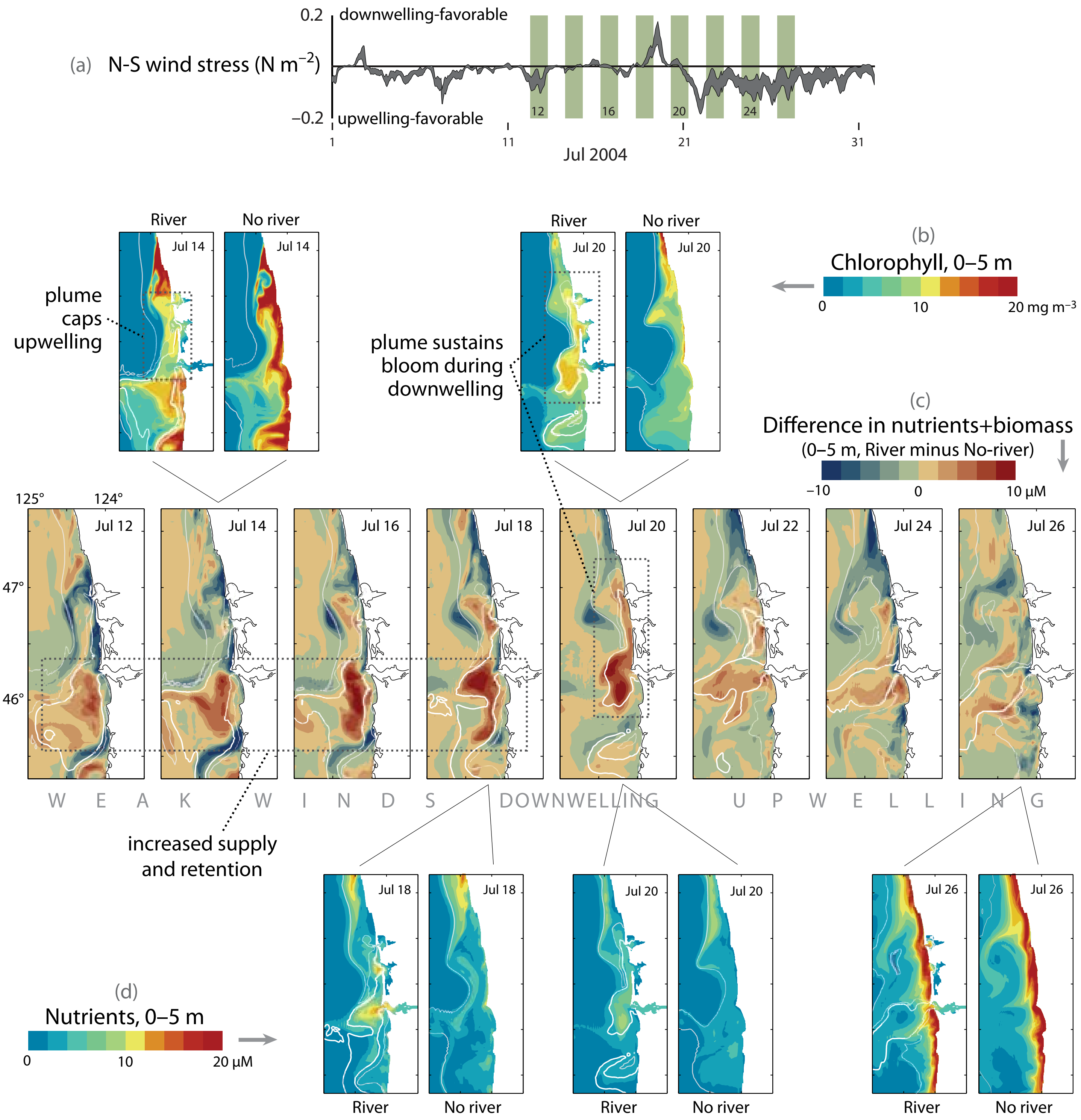


Figure 9. Timeline of nutrients and biomass in the surface layer (0–5-m average) from July 2004, from an ecosystem model case (see Banas et al., in review; MacCready et al., 2008) with the Columbia River plume included ("River"), and a "No-river" case in which riverflow = 0 and the Columbia River estuary and Washington small bays are replaced with an unbroken coastline. River nitrate is set to zero. Each snapshot is a 25-h tidal average. Contours of salinity are shown in white (thicker, 30 practical salinity units [psu]; thinner, 31.5 psu) to mark the location of the plume. North-south wind stress is given in (a). The main timeline (c) shows the difference between model cases in nutrients + biomass (both in nitrogen units); snapshots of chlorophyll (b) and nutrients (d) are also shown to highlight key features. During weak, variable upwelling (July 12–17), the plume partially caps nutrient supply and primary production along the Washington coast, causing a deficit in biomass (b, July 14). At the same time, however, the plume also causes increased supply and retention of nutrients in the plume south of the river mouth during this period (c, July 12–18; d, July 18). During the downwelling event July 18–20 (a), the excess plume-derived nutrients support a phytoplankton bloom near the Columbia mouth and along the Washington coast (b, July 20), whereas in the no-river case, nutrients and biomass both decline quickly during downwelling (b, d, July 20). These plume effects are strongest under weak-to-moderate upwelling: during strong, sustained upwelling (July 21–26), the plume is blown offshore and the nutrient supply varies little between model cases (d, July 26).

by the Columbia River and its plume, both as a conduit from the river itself and as a facilitator of upwelling-supplied nitrate, is an order of magnitude smaller than that from all other sources (Table 1) for the region as a whole. If we restrict our attention to the river mouth, the nitrate supplied by mixing of upwelled water into the plume at lift off (Bruland et al., 2008) suggests a half order of magnitude enhancement over straight coast upwelling (2.5 vs. 0.5 kg s^{-1}, for a Columbia River mouth width of 4 km). This estimated enhancement is also consistent with patterns shown in Figure 9. The small overall contribution of the Columbia River in comparison with, for example, the Strait of Juan de Fuca, is due primarily to the small river and plume volumes, in comparison to the other sources. Still, despite the relatively small contributions on a seasonal basis, the Columbia River can be important as a local source during periods of downwelling or weak upwelling winds.

Iron is vital for phytoplankton blooms in an upwelling system, and iron supply may contribute to productivity differences along the CCS (Chase et al., 2005). Recent measurements indicate that even off the Oregon coast, phytoplankton growth is not iron limited (Chase et al., 2005), although iron can be a limiting nutrient off California (Hutchins and Bruland, 1998). RISE studies show that iron is never limiting on the Washington coast (Bruland et al., 2008). Not only is the plume from the Columbia River heavily laden with iron, but iron from the Columbia plume is also deposited in sediment along both the Washington and Oregon coasts. The iron-laden sediment can be mixed into bottom water and thus added to the already nitrate-rich water.

Submarine Canyons

Like river plumes, submarine canyons are not distributed uniformly over the CCS—the majority of canyons occur in the northern CCS (Figure 1). Upwelling is enhanced on the southern sides of these canyons (Allen, 1996; Hickey, 1997; She and Klinck, 2000), forced by the cross-shelf pressure gradient associated with the equatorward flowing coastal jet. This enhancement would not be expected once the poleward undercurrent sets up seasonally. Although the water originating in canyons does not break the sea surface locally, this upwelled water moves onshore in the bottom boundary layer over the shelf as it moves equatorward in the shelf jet (Crawford and Dewey, 1989). This water reaches the coast at some location south of a particular canyon, where it would require local wind forcing to upwell it into the euphotic zone.

We estimated the seasonal contribution by submarine canyons to nitrate over the shelf bottom using results in Hickey (1997) to scale the thickness (~10 m), temperature (7–7.5°C), and velocity (~ 10 cm s^{-1}) of the upwelling layer. Temperature was converted to nitrate (~ 35 μM in this temperature range) using a relationship obtained from multiple ECOHAB PNW and RISE cruises ($r^2 = 0.8$). The length of the downstream (equatorward) side of each canyon was measured manually. To provide a range of possible input, estimates were made for two coastline intervals: all canyons between 46°N and 50°N, and canyons south of Juan de Fuca canyon only (Juan de Fuca canyon is open ended and thus has unique canyon dynamics). Input was estimated to occur only from April to June, before the poleward undercurrent develops, and only during upwelling periods, because the currents that impinge on the canyon at canyon depth may reverse to poleward during downwelling events (Hickey, 1997). Therefore, resulting values were multiplied by the average number of days of upwelling in each month.

Results suggest that in spring, nitrate supplied to the shelf bottom due to upwelling enhancement by canyons is roughly the same as (or more than) the amount that local coastal upwelling supplies to the southern Vancouver Island/Washington shelf (Table 1). The canyon enhancement is also comparable to the nutrient supply by the Strait of Juan de Fuca.

IS RETENTION/CONCENTRATION OF PHYTOPLANKTON A MAJOR FACTOR IN EXPLAINING ALONGCOAST PRODUCTIVITY STRUCTURE?

The preceding discussions demonstrate that the northern CCS has delivery methods to the euphotic zone that ensure nutrient concentrations required for primary production at levels similar to other areas in the northern CCS. But chlorophyll concentrations at the sea surface are about five times higher in the northern CCS than off northern California (Figure 2). This observation suggests that retention of phytoplankton blooms plays an important role in producing alongcoast chlorophyll patterns. Indeed, the northern CCS is endowed with a massive eddy persistently supplied with nutrients, retentive river plume fronts, a coastline with no major promontories such as cause offshore jets and meanders farther south in the CCS

(Strub et al., 1991; Barth and Smith, 1996), and wide shelves (see Figure 1).

Surface drifters deployed in summer in the high-chlorophyll northern end of the CCS under a variety of wind conditions (Figure 10) demonstrate that the Washington shelf is indeed extremely retentive to surface water movement. There is little evidence of offshore movement in surface Ekman layers during periods of upwelling-favorable winds; drifter pathways, once free of the Juan de Fuca eddy at the northern end, are controlled primarily by the baroclinic coastal jet. In this region, fronts from the Columbia River are common (Hickey et al., 2005), and these fronts are generally oriented along the shelf. In general, water is retained on the Washington shelf for at least 10 days under moderate upwelling wind conditions (MacFadyen et al., 2008).

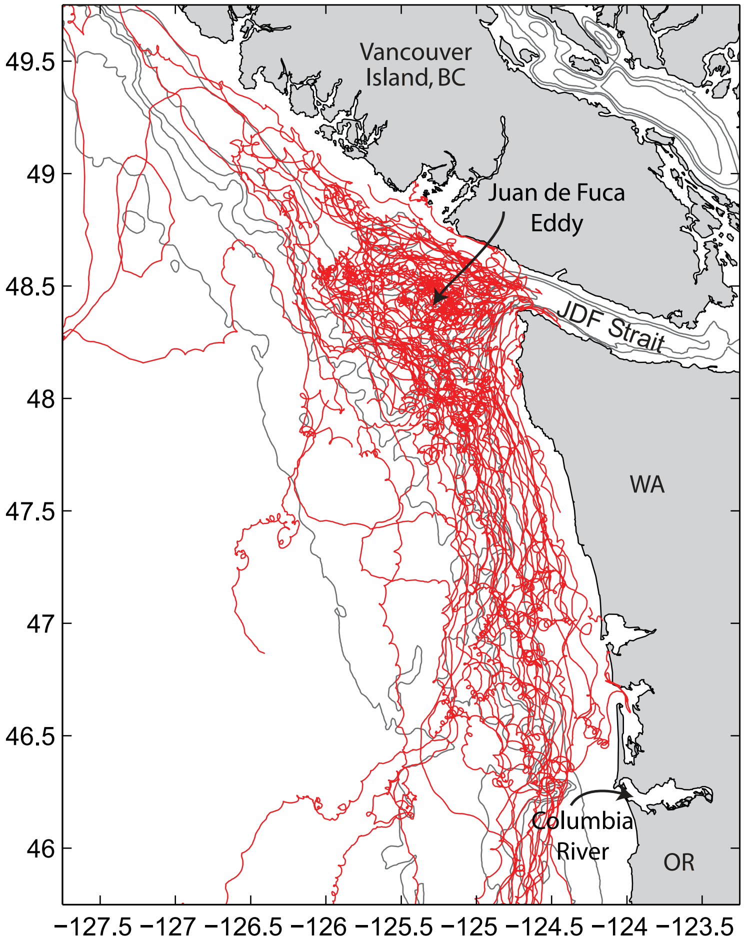


Figure 10. An illustration of particle retention on the southern Vancouver Island/Washington coast. Tracks of 68 surface drifters deployed in summer 2003–2006 during the ECOHAB PNW study. Most drifters were deployed in the Juan de Fuca eddy, the region with dense tracks just offshore of the Strait of Juan de Fuca. Contour intervals are 100, 150, 250, 500, 1000, and 2000 m. Drifters show little evidence of offshore transport in the surface frictional layer. Transit time from the eddy to the Columbia mouth is about 10 days in moderate upwelling winds. Few drifters leave the shelf; the few exceptions occur at the northwest end of the region under downwelling wind conditions, or at the south end of the region where drifters encountered the plume from the Columbia.

Retention is particularly long (up to 32 days have been observed) just offshore of the Strait of Juan de Fuca, in the Juan de Fuca eddy (Figure 10; Freeland and Denman, 1982; MacFadyen et al., 2005, 2008; Foreman et al., 2008). Although bloom concentration is important, we note that bloom maintenance during retention is perhaps more important—blooms require an ongoing source of nutrients in order to maintain high chlorophyll concentrations. The Juan de Fuca eddy region has an almost steady supply of nutrients, as noted previously. Escape from the eddy occurs primarily under upwelling-favorable wind conditions; in the near surface frictional layer, the geostrophic constraint is broken by frictionally dominated currents. Filaments with high chlorophyll have been observed emanating from the eddy region equatorward along the outer Washington shelf and slope along pathways like those shown in Figure 10 (MacFadyen et al., 2008; Trainer et al., in press). The Juan de Fuca eddy region likely provides much of the chlorophyll observed on the Washington shelf. Just below the surface layer, nutrients follow pressure surfaces, flowing generally equatorward in the shelf break jet whether winds are upwelling- or downwelling-favorable. These waters provide a high-nutrient environment that can sustain subsurface phytoplankton blooms, features commonly observed on the Washington shelf (Landry et al., 1989). They also are likely the source of waters upwelled along the

Washington/Oregon coasts in later parts of the upwelling season.

Heceta Bank, off central Oregon, is another retentive region in the northern CCS (Gan and Allen, 2005) where chlorophyll concentrations are relatively high (Landry et al., 1989; Spitz et al., 2005; Henson and Thomas, 2007). Although Heceta Bank and the Juan de Fuca eddy region may have similar retentive properties, Heceta Bank does not have the persistent strait-generated nutrient supply of the more northern feature.

The Columbia River plume also plays a significant role in retention on the southern Washington/northern Oregon shelf. Drifter pathways become more convoluted at about the latitude of the Columbia River mouth, a result of eddies spun off from the recirculating region near the mouth and offshore-tending fronts due to the southwest Columbia plume that develops during periods of upwelling-favorable winds (Figure 10; Banas et al., 2008). Model results (Figure 9) show that the plume can concentrate both nitrate and biomass, thus retaining the total resource over the shelf in a localized area much longer than if no plume were present. This concentration effect occurs during periods when winds change intermittently from downwelling- to upwelling-favorable.

Comparison of modeled surface particle tracks with and without a river plume included shows that surface particles originating on the inner shelf can be episodically retained on the inner shelf in the presence of the Columbia plume (Figure 11). At other times in the upwelling-downwelling cycle, the plume appears to enhance cross-shelf export instead (Banas et al., 2008). Model

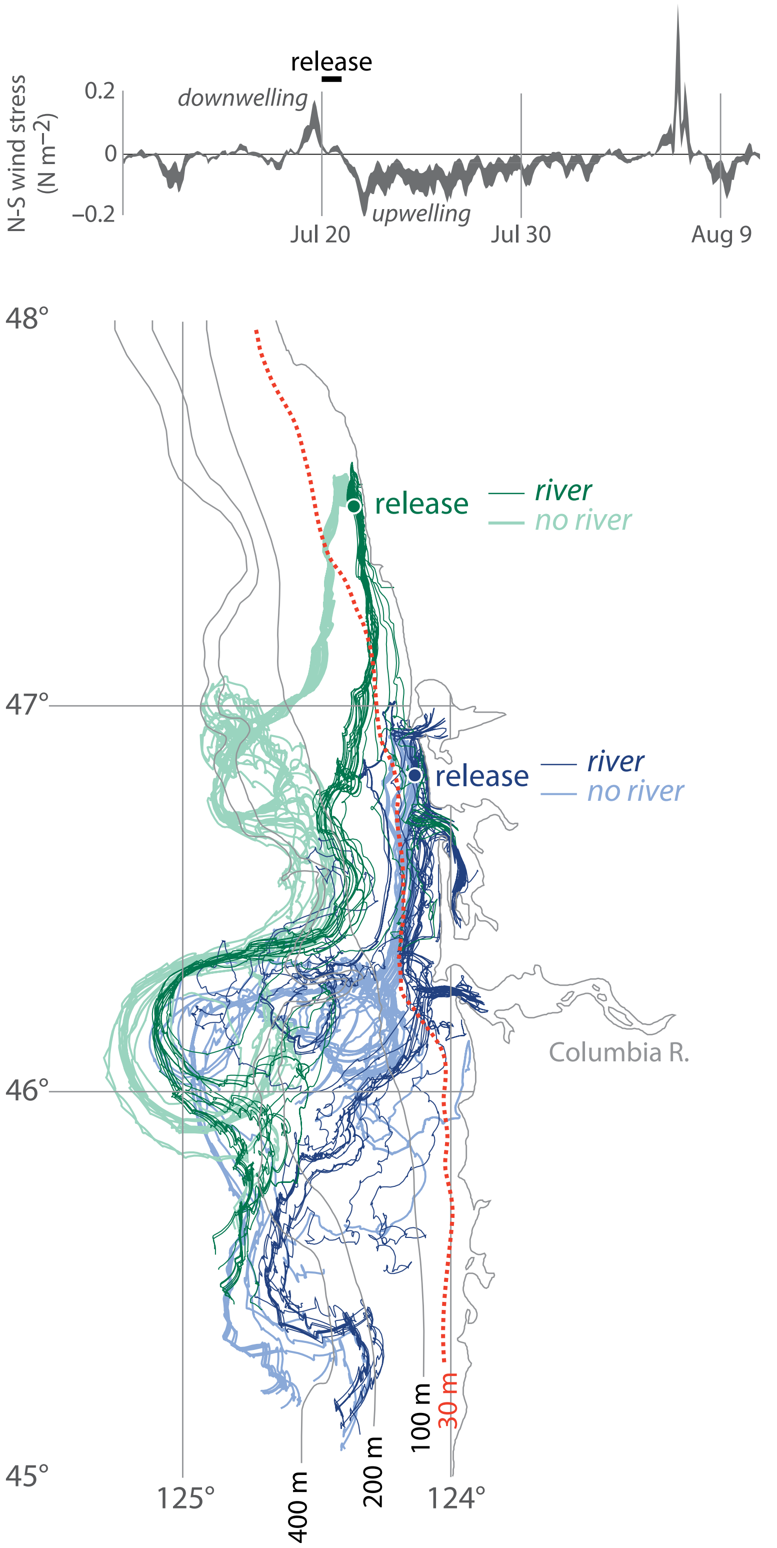


Figure 11. An example of nearshore retention caused by a river plume. The fate of water found on the Washington inner shelf during the onset of a sustained upwelling event, July 20, 2004, shown for two model cases: a base case with the Columbia River included (darker lines) and a case in which the Columbia is turned off and the estuary replaced by unbroken coastline. Particles were released at two locations (47.5°N, 46.83°N) over 25 h on July 20 and tracked using surface velocity fields for 20 d. During this transition from downwelling to upwelling, particles are retained on the inner shelf (landward of the 30-m isobath, dotted red line) several days longer in the presence of the plume.

studies also suggest (Banas et al., 2008) that interactions between the plume and variable winds episodically retard the equatorward advection of biomass from the Washington shelf, so that the plume acts as a retention feature in an alongcoast sense as well. Note that all these types of plume-driven retention occur in part as a result of wind intermittency: if the winds were upwelling-favorable only, we would expect the plume to result in excess offshelf transport to the southwest. Nevertheless, as downwelling-favorable winds occur over 30% of the time in this region in an average year (Figure 6d), inner shelf retention of phytoplankton, and resulting changes of patterns of microzooplankton, have important effects on the local ecosystem.

Last, we note that chlorophyll concentration is strongly related to shelf width along the coast (Figure 6b). The width of the shelf decreases equatorward from ~ 60 km at more northern latitudes to ~ 10 km off much of California (Figure 6b). Data in Lentz (1992) and in Hickey (1989) show that wind-driven flow in the near surface layers is similar at most locations: ~ 0.1 m s^{-1}. As winds blow harder, mixed layer depth increases (Lentz, 1992) and flow is distributed over a greater vertical distance. Thus, for the same wind stress along the coast, the residence time of material on the shelf should vary linearly roughly with shelf width. For a typical wind stress, surface residence time would be a week off the Washington coast, but one or two days off northern California in regions with a straight coastline; again, northern regions are favored for bloom retention.

OTHER ISSUES AFFECTING ALONGCOAST CHLOROPHYLL CONCENTRATIONS

Shelf Shape and Depth of Upwelled Water

In general, shelves are broader and flatter at northern latitudes (Figure 6b); note that width and steepness are strongly correlated by their geology. Allen et al. (1995) show that the depth from which shelf water is derived during upwelling depends critically on bottom slope and the width of the shelf. Over steeper shelves (e.g., off California), much of the flow that compensates for the wind-driven offshore flow in the surface frictional layer (the "return flow") originates from the central water column rather than from the bottom boundary layer. Because nutrients increase with depth in the water column, water originating deeper in the water column would tend to have higher nutrient concentrations than that originating from shallower depths. We might therefore expect water upwelled in the compensating flow over broader, steeper shelves (such as occur off Washington and southern British Columbia) to originate deeper and thus to have higher nutrient concentration than upwelled water over narrower, steeper shelves (such as occur off much of Oregon and California). Although the Allen et al. (1995) modeling result described above suggests a mechanism to help explain the correlation between shelf width and chlorophyll seen in Figure 6b, the modeled cross-shelf circulation pattern is not supported by field observations. In particular, the majority of the return flow in upwelling regions occurs well above the bottom boundary layer independent of shelf morphology as shown by Smith (1981) for both the CCS and the Peruvian upwelling systems. Off the Washington shelf, the strongest return flow is typically observed at a depth of about 10–15 m (Hickey, 1989).

Bloom Time Scales Versus Wind Intermittency

Intermittency is a critical component of resulting biological patterns. Off central California, maximum phytoplankton productivity is observed when wind variability matches phytoplankton bloom time scales, with three to seven days of relaxation being optimal and diatoms dominating the population (Wilkerson et al., 2006; Botsford et al., 2006). When winds are stronger, new production is less than the theoretical maximum, consistent with substantial export from the shelf as well as increased mixed layer depth and reduced light exposure (Dugdale et al., 2006). Stronger winds reduce transit time across the shelf to fewer than five days so that blooms cannot fully develop before they are exported offshelf and coastal waters are increasingly influenced by detritus (Kudela et al., 2006). Because the duration and strength of upwelling-favorable winds decreases poleward over the CCS (Figure 6d), wind time scales again are most optimal for growth in the northern CCS.

SUMMARY AND DISCUSSION

Chlorophyll concentration along the CCS is strongly correlated with shelf width (Figure 6b). If retentive banks are included in the wide shelf category, shelf width likely is more important overall than river plumes for retention in the northern CCS, and comparable in effect to the absence of large coastal promontories. Yet no chlorophyll would collect on a wide shelf if the appropriate nutrients were not available to fuel a bloom. Thus, in addition to a wide shelf and no large capes, to attain high productivity, nutrients must be upwelled onto the northern CCS shelf in concentrations comparable to or exceeding those in the central and southern CCS. Moreover, those nutrients need to be injected into the euphotic zone to be used by the phytoplankton, and ultimately, to affect higher trophic levels.

The discussion presented in this article suggests that these two requirements are met by different processes in the northern and southern CCS. Upwelling of deep isopycnals occurs in all parts of the CCS to distances more than 100 km from the coast and depths greater than 200 m from the sea surface. In northern latitudes, this large-scale upwelling is likely forced at least in part by the winds off northern California, with the disturbance traveling poleward as a wave, and is enhanced by submarine canyon upwelling. Nutrients upwelled into bottom waters by these processes as well as by local wind upwelling are moved into surface layers by estuarine dynamics and enhanced tidal mixing near estuaries, each of which inputs nitrate at levels comparable to local coastal upwelling. The Strait of Juan de Fuca and canyon upwelling provide nitrate at levels comparable to or exceeding that of local wind-driven coastal upwelling, almost an order of magnitude greater than nitrate supplied by the Columbia River plume. The nutrient supply from the strait is more persistent, extends farther offshore, and extends deeper in the water column than nutrients supplied by traditional coastal upwelling. However, during periods with significant downwelling, contributions from the Columbia River supply sufficient nitrate to fuel the ecosystem until upwelling conditions return. Off northern and central California, where upwelling-favorable winds are strong and persistent, upwelling forced by local winds near the coastline brings the needed nutrients to the euphotic zone. Our recipe for understanding and/or modeling the CCS ecosystem includes the following as essential elements:

- The Strait of Juan de Fuca with its tidal dynamics and its freshwater
- The Columbia River with its tidal dynamics, nutrients, and freshwater
- Submarine canyons with high topographic resolution
- Alongcoast wind structure to capture remote wind forcing

These conclusions can be used to speculate on potential effects of global warming in the northern CCS. For example, as air temperature rises, we might expect less riverflow in both the Fraser and Columbia Rivers, because the summer effluent in both rivers is derived from snowmelt. A decline in Fraser River outflow would cause a decline in the outflow from the Strait of Juan de Fuca, and hence a decline in turbulent mixing in the strait. Both effects would suggest a decline in nutrient supply to the northern CCS and perhaps a decline in the strength of the eddy offshore of the Strait of Juan de Fuca, hence less local retention of both nutrients and phytoplankton. Thus, the upstream source of nutrients and phytoplankton for the Washington/Oregon shelf could be substantially diminished. Weaker Columbia River outflow would cause the Columbia plume to contribute less to both nutrient supply and retention on the Washington shelf, reducing its usefulness as a buffer for the local ecosystem during spring periods of intermittent winds.

A final caveat: our predictions are based on the best existing information and synthetic knowledge. These predictions should be viewed only as a beginning. Much work clearly remains to be done to provide a more realistic basis for predicting changes in the productivity of the CCS over the next several decades.

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Developing the California Current Integrated Ecosystem Assessment, Module I: Select Time-Series of Ecosystem State

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Developing the California Current Integrated Ecosystem Assessment, Module I: Select Time-Series of Ecosystem State

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EXECUTIVE SUMMARY

(1) The California Current Large Marine Ecosystem (CCLME) spans approximately 3,000 km of latitude from northern Vancouver Island, British Columbia, Canada to Punta Eugenia, Baja California, Mexico.
(2) Based on latitudinal variation in physical forcing and biological communities, 3 "eco-regions" can be defined within the CCLME. We present preliminary evidence of linkage and interconnections among eco-regions ("sub-ecosystems"). In no one eco-region are all biological indicators available for ecosystem-based approaches to management.
(3) Herein, we present select biological observations as indicators of ecosystem state at multiple time scales.
(4) Based largely on NOAA's previous sentinel species program, we compiled time-series representing ecosystem "productivity". We have not attempted to integrate these indicators in this report.
(5) In recent years, the CCLME experienced unusual "ocean climate" as shown by the Pacific Decadal Oscillation index (PDO) and multivariate El Niño/Southern Oscillation index (MEI). There have also been obvious changes in the seasonal cycle of upwelling in the northern and central eco-regions.
(6) This variation in ocean climate has led to significant changes in food webs, as shown by: (i) higher copepod diversity and lower copepod and euphausiid (krill) biomass, (ii) reduced market squid (*Loligo opalescens*) abundance, and (iii) reduced and/or altered distribution and abundance of northern anchovy (*Engraulis mordax*), Pacific sardine (*Sardinops sajax*) and a suite of age-0 rockfish (*Sebastes* spp.).
(7) Vertebrate predators responded to these changes in the food web. Coho salmon (*Oncorhynchus kisutch*) survival has been very low and many seabirds experienced below normal breeding success, with unprecedented breeding failures of the dominant planktivorous species (Cassin's Auklet, *Ptychoramphus aleuticus*) in 2005 and 2006.
(8) Recent observations are best viewed in the context of long-term ecosystem fluctuations. Since the late 1980s/early 1990s, there have been signs of increasing system variability, diminishing ecosystem productivity, and declines in species with "sub-arctic" bio-geographic affinities. Some top predators are showing opposing changes. There has been increasing production of a dominant marine mammal (California sea lion, *Zalophus californianus*) and apparent decreasing production of large predatory fishes (e.g., Pacific hake *Merluccius productus*).
(9) The causes of these changes are not well understood, but possible mechanisms of change include (a) increased ocean stratification which may limit the efficacy of upwelling and primary productivity, (b) reduced advection and transport of cold, sub-arctic water and organisms to the ecosystem, or (c) ecosystem effects due to other human activities such as fishing.

INTRODUCTION

What is an Integrated Ecosystem Assessment?

An Integrated Ecosystem Assessment (IEA) is a dynamic, decision-support tool for management of living marine resources. Fluharty et al. (2006) include the following specific objectives for IEAs to be developed for each large marine ecosystem (LME) in the U.S.:

- To compile relevant data sets for the ecosystem (e.g., physical oceanography, atmospheric, climatological and weather observations, human use patterns and statistics, abundance and distribution of biological resources),

- To report on current conditions and trends in relevant data time series of physical, biological and human uses,

- To synthesize time series data to link important ecological outcomes to changes in relevant climate and human use drivers (i.e., forecasting),

- To evaluate data time series; provide suites of key indicators of ecosystem state (status); propose reference levels for safe and for desired states of the ecosystem,

- To forecast relationships between state indicators and pressure indicators (e.g., pollution, climate change, fishing-related removals, coastal development, etc.) to inform management, and

- To provide periodic ecosystem assessment updates to inform managers, stakeholders and the public on the state of the ecosystem.

For the California Current LME (CCLME), there are many physical and biological components that warrant observation and understanding, from a mechanistic perspective, to derive factors affecting key ecosystem form, function, and control, and the population dynamics of the top vertebrate marine predators (fish, seabirds, sea turtles, and marine mammals) of significant management concern. In this document, we present records (time-series) of key biological organisms, describe these data in the context of recent and long-term changes in the ecosystem, identify apparent gaps in knowledge, and outline possible future directions for CCLME IEA development. We emphasize that this *initial* [biological indicator] approach to development of a CCLME IEA should be complemented by other approaches (e.g., ecosystem modeling) and that the indicators shown herein are not comprehensive. Nonetheless, we suggest that the species and parameters selected are useful for understanding the population biology of species of management concern, and are therefore of great value to state and federal authorities in the CCLME.

The California Current Large Marine Ecosystem: Form, Function, and Controls

The CCLME is a large, dynamic and spatially heterogeneous marine environment in the eastern North Pacific Ocean off the west coast of North America (Duda and Sherman 2002). It spans nearly 3,000 km of latitude, from approximately the northern tip of Vancouver Island, British Columbia, Canada to Punta Eugenia, Baja California, Mexico (Figure 1). Several major physical oceanographic processes, all linked to variability in atmospheric circulation and the flow of dominant currents in the region, determine ecosystem form and function. These include *local effects* through coastal upwelling, effects of meso-scale structures (e.g., fronts and eddies) formed by jets and meanders of upwelling plumes and the California Current itself, and influences of *basin-scale* winds on sub-arctic and sub-tropical water mass intrusions. From an oceanographic perspective, the CCLME is under influence from the northern and western Pacific, as well as the tropical eastern North Pacific.

Atmospheric Considerations

The strength and juxtaposition of the North Pacific High relative to the Continental Low in summer and Aleutian Low in winter determines the phasing and amplitude of winds which force coastal upwelling and the strength of the California Current (Hickey 1979, Chelton et al. 1982). However, winds, currents, and upwelling within the CCLME are not homogenous; there is substantial latitudinal variation in physical forcing mechanisms. In the north, the CCLME is dominated by strong seasonal variability in winds and upwelling, whereas in the south there is less of a “seasonal cycle” in these parameters, meaning that winds and upwelling are more constant.

Habitat Considerations

There are numerous regions of elevated primary and secondary productivity, including seamounts, capes and coastal promontories (Figures 1 and 2). These highly productive “hotspots” offer favorable habitat for juvenile salmonids, and serve as spawning and feeding grounds for important small pelagic fish such as sardines, anchovies, and smelts. These also provide dynamic locations for trophic interactions, including foraging opportunities for a diverse, abundant suite of vertebrate predators. Many of these species are highly-migratory, visiting the CCLME from breeding grounds in Alaska (e.g., fur seals, northern fulmars), Baja California (e.g., gray whales), the Western Pacific (e.g., bluefin tuna, leatherback turtles), and as far as the southern hemisphere (e.g., several shearwaters and petrels). These living marine resources support vast societal interests, including commercial and recreational fishing and ecotourism.

Variability

Despite being diverse and productive, the CCLME is highly variable. Natural variability is exemplified by the Pacific Decadal Oscillation (PDO; Figure 3) and the El Niño/La Niña phenomena (Figure 4). These basin-scale environmental fluctuations have significant physical oceanographic (Bograd et al. 2003) and ecological effects, altering primary productivity and food webs (zooplankton: McGowan et al. 2003, Brinton and Townsend 2003; forage fish: Chavez et al. 2003). This variation in turn affects top predators (Ainley et al. 1995, Veit et al. 1997, Sydeman and Allen 1999, Sydeman et al. 2001, Hyrenbach and Veit 2003). Therefore, temporal environmental variability presents a fundamental challenge to management as population changes must be viewed from the perspective of normal ecosystem fluctuations (Botsford et al. 1997).

Human Impacts

Anthropogenic stressors, such as fishing, coastal development, pollution and global climate change affect the CCLME. These human impacts may act synergistically with natural ecosystem variability if they occur at the same time and place. For example, the west coast population of Pacific sardine (*Sardinops sagax*) was driven to low levels (and economic extinction) by extensive fishing during a period of adverse climatic conditions for this species (Chavez et al. 2003). Thus, understanding the potential interactions between natural and anthropogenic impacts is central for management of the CCLME.

Sub-ecosystem structure

The California Current is formed as the eastern leg of the North Pacific Gyre. The intensity of the transport in the California Current varies by season, year, and decade. It fluctuates, in part, relative to the position and strength of the North Pacific Current/West Wind Drift, which traverses the sub-arctic North Pacific Ocean and bifurcates between southern British Columbia and northern Oregon into the Alaska Current and California Current. While Washington and southern British Columbia may be considered a “transition zone,” we define the northern boundary of the CCLME as the northern tip of Vancouver Island, B.C., due to frequent upwelling along this section of the coastline in spring and summer (Allen et al. 2001, Whitney et al. 2005). Based on physical and biological attributes, U.S. GLOBEC (1992) subdivide the CCLME into three distinct “eco-regions” or sub-ecosystems: (1) southern British Columbia, Washington and Oregon to Cape Blanco; (2) Cape Blanco, southern Oregon, to Point Conception, California; and (3) southern California and Baja (Figure 5). Due to seasonal and longer-term climate variability, it is recognized that the boundaries of these broad eco-regions are dynamic and shift under varying oceanographic conditions.

RESULTS

Long-Term Research in the CCLME

Several long-term research projects investigating the CCLME have been conducted, with coverage spanning the entire ecosystem and 3 eco-regions (Table 1); at least three projects have over 20 year of data (Figure 2, Goericke et al. 2007). Data from several of these projects will be shown and discussed.

Recent Status of the CCLME

Basin-scale environmental indices

The PDO index (Figure 3) and Multivariate El Niño index (MEI; Figure 4) have both been in a positive (i.e., warm eastern North Pacific) state more or less continuously since late 2002. From late 1998 to early 2002, these indices were negative after nearly a decade in the 1990s of consistently positive anomalies.

Temperature and Upwelling

According to many studies, sea-surface temperature (SST) in the CCLME has increased by 0.5^{o}C to 1.0^{o}C over the past 50 years. Upwelling, however, has been variable, with an apparent general increase in NOAA's west coast upwelling index (Schwing and Mendelssohn 1997). Interannual variability in upwelling has been substantial, especially in recent years. In 2005, upwelling was delayed and/or interrupted and sea surface temperatures (SST) were ~2˚-6˚C warmer than normal (GRL 2006). In 2006, weak upwelling was noted in the central eco-region, while strong upwelling occurred in the north. The situation in the southern eco-region was different in both years, as average upwelling and SST was apparent (Peterson et al. 2006).

Zooplankton

Biologically, these unusual oceanographic conditions resulted in numerous changes in key ecosystem indicators. Off Oregon, copepod species richness was elevated with below-average abundance of northern-boreal species, particularly in 2005 (Figure 6). Copepod biomass in 2005 was the lowest on record, whereas it returned to near average in 2006 (Figure 7). It is hypothesized that when advection of waters from the Gulf of Alaska is strong, northern-boreal copepods are more abundant, copepod biomass is higher, and copepods species richness declines (Figure 8). These conditions apparently favor a more productive sub-arctic ecosystem off Oregon.

Off southern California, the seasonally-derived "small plankton volume" index (copepods and euphausiids) based on the California Cooperative Oceanic Fisheries Investigation (CalCOFI) program (Figure 2c) was slightly (though not significantly) below average in 2005 or 2006 (Figure 9). Average or slightly elevated zooplankton biomass was noted in the southernmost limits of the CCLME, off Baja California, in these years as well (Peterson et al. 2006).

The abundance of the euphausiid *Thysanoessa spinifera* in the diets of fish off Vancouver Island, Canada, was also below average in 2005 and 2006 (and continuing during winter 2007; Figure 10). Similarly, the abundance of euphausiids in the diet of a planktivorous seabird (Cassin's Auklet, *Ptychoramphus aleuticus)* off central California was anomalously low in 2005 (Figure 11). These euphausiids are keystone species in the coastal food webs of the CCLME.

Squid

Market squid (*Loligo opalescens*) in the southern eco-region were below-normal in 2005 and 2006 as evidenced by both landing data and California sea lion (*Zalophus californianus*) diet (Figure 12).

Forage fish indices

Northern anchovy (*Engraulis mordax*) and Pacific sardine egg counts in spring (April) 2005 and 2006 were very low, especially in comparison with 2001 – 2003 period (Figure 13). The relative increases and decreases in anchovy versus sardine eggs between years may be attributed to temperature and upwelling (Lluch-Belda et al. 1991, Jacobson and MacCall 1995).

The abundance of juvenile age-0 rockfish (*Sebastes* spp.) was exceptionally low in 2005. Essentially, complete recruitment failure in the central eco-region was observed (Figure 14). Juvenile rockfish were also conspicuously absent from the diet of a piscivorous seabird (Common Murre, *Uria aalge*) in 2005 and 2006 (Figure 15).

Vertebrate predators

Coho salmon (*Onchorhynchus kisutch*) returns to hatcheries (the Ocean Production Index [OPI]) were below average in 2005 and 2006 (Figure 16), pointing to poor ocean conditions in 2004 and 2005, the years of ocean entry. These years, though demonstrating reduced returns, were not as poor as during the mid 1990s (Peterson and Schwing 2003). Juvenile coho salmon growth off of the west coast of Vancouver Island in 2005 was the lowest on record since 1998 (DFO 2006).

Breeding success for most seabirds in the central eco-region was below average in 2005 and 2006, including complete breeding failure by the obligate planktivore (Cassin's Auklet) in both years (Sydeman et al. 2006, Figure 17). The two most common euphausiid species, *Euphausia pacifica* and *Thysanoessa spinifera*, were found in anomalously low proportions in Cassin's Auklet diet in 2005 (Figure 11).

The abundance of California sea lions (indexed by the anomaly in pup production from a rookery in the Channel Islands) was high and continuing an increasing trend since the mid 1980s (Figure 18), with the exception of the 1998 El Niño/Southern Oscillation (ENSO).

DISCUSSION

Up-scaling

There are regional differences within the CCLME in climate forcing and ecosystem response (Figures 5 and 19). Therefore, an assessment of the southern California Current region (eco-region 3) may vary from that for the northern California Current (eco-region 1). When considering an overall IEA for the CCLME, it may prove most useful to evaluate each eco-region/"sub-ecosystem" separately. But, in no single region are all the physical, chemical, and especially biological attributes available for comprehensive analyses. Therefore, to understand ecosystem form, function, and control, we must combine information between regions.

A simple mechanistic example for co-variation

The northern CCLME is dominated by strong seasonal variability in winds, temperature, upwelling, and plankton production. In addition to weak, delayed or otherwise ineffectual upwelling, warm-water conditions in this region could result from either onshore transport of offshore subtropical water or northward transport of subtropical coastal waters (Figure 8). Low copepod species richness and high abundance of northern-boreal copepods (Figure 6) is apparently associated with cold, sub-arctic water masses transported to the northern CCLME from the Gulf of Alaska. Therefore, copepod community composition may be used as an indicator of this physical oceanographic process.

Preliminary evidence suggests co-variation between eco-regions. When fatty, sub-arctic northern-boreal copepods are present in the northern CCLME during cool-water conditions, the productivity of the planktivorous Cassin's Auklet, in the central sub-region, increases (Figure 19a). Conversely, when the less fatty subtropical copepods dominate the system in warm-water years (i.e., a higher southern copepod Index), Cassin's Auklet breeding success is reduced (Figure 19b).

Area-based management?

As noted previously, there are regional differences in oceanography and biology. Moreover, within each region, there are differences in habitats that may be related to bathymetry and geology (Figure 20). Understanding the relationships between topography, oceanography, and species distributions will promote better management of CCLME resources spatially, as well as temporally. The relationships between bottom topography and ecosystem productivity are not well known, but so-called "benthic-pelagic" coupling is likely to be important for top predators. Identification and assessment of locations of high trophic interaction may be key to future management and conservation decisions in the CCLME.

Effects of global warming?

Ocean temperatures have increased, and are likely to continue to increase for the foreseeable future. Land is expected to heat faster than the ocean and these contrasts in temperatures may result in higher wind speeds (Bakun 1990, Snyder et al. 2003). Warmer waters are also increasing stratification (Roemmich and McGowan 1995, McGowan et al. 2003). The effects of stronger winds and increased stratification on upwelling, temperature and primary productivity in the CCLME are not well known (but see Schwing and Mendelssohn 1997, Mendelssohn and Schwing 2002), but clearly will have ecosystem consequences.

The timing of the seasonal cycle of productivity is changing (GRL 2006). Just as terrestrial biological systems are experiencing earlier phenology (IPCC 2007), we may observe an earlier (or later) start to the upwelling season in the CCLME, and this may vary by eco-region. If upwelling occurs earlier, we may observe an earlier seasonal cycle, from earlier phytoplankton blooms, to earlier peaks in zookplankton abundance. In contrast, as noted previously, if the efficacy of upwelling is weakened and/or delayed by increased water stratification, the seasonal cycle of different organisms may be offset, leading to mismatches between trophic levels in the abundance or availability of prey.

With these contrasting scenarios in mind, the potential for increased variability in the CCLME is probable. A more volatile climate with more extreme events will impact biological systems of the CCLME. Notably, by 2030, the minimum value of the PDO is expected to remain above the mean value for the 20th century. In addition, evidence of variability and declines in biological systems in the CCLME since ~1990 has already been shown. Such changes and others (e.g., range shifts in species' distributions) are likely to continue.

Data gaps and some future directions

We have many gaps in the long-term datasets that need to be identified and filled. For example, there has been extensive work in Monterey Bay, California on changes in phytoplankton community structure (e.g., a ratio of diatoms to dinoflagellates), and new work is commencing in Oregon (B. Peterson, personal communication). The ratio of diatoms to dinoflagellates appears to be an important index for food web development. Having this type of information available for other locations in the CCLME would be extremely valuable.

The species and parameters we have chosen are representative of different trophic levels, and known to be linked by trophic relationships, and have been considered in other ecosystem reports (Peterson et al. 2006, Goericke et al. 2007). No doubt, there will be other variables to consider, but this suite of parameters will be critical to any IEA developments for this system.

Importantly**,** we have not addressed the human dimension (fishing, development, pollution, etc.) on ecosystem dynamics. As intended, this report has focused on long-term observations (Table 1) and some key biological indicators. We have not considered socio-economic data and other human-related data, though this has been put forth as key to the IEA concept overall (Fluharty et al. 2006). Incorporating this information could advance an IEA for the CCLME.

One of the goals of IEA is to forecast future conditions for the ecosystem under consideration. This is difficult, but it is essential to consider how to best develop forecasting capabilities. Part of the solution may be to integrate, statistically, what is known and previously summarized. Integration of these indicators is therefore a primary goal of future IEA developments, which should also include modeling components. Coupling complementary field observations with spatially explicit ecosystem modeling, while beyond the scope of this document, is clearly needed to answer key ecological and management questions as well as to evaluate the efficacy of various CCLME monitoring programs.

Table 1. Summary of select long-term (10 years or longer) research projects of the CCLME.

Project name and coordinators	Region	Years covered	Description
Line P, Department of Fisheries and Oceans Canada (DFO) & others	1	1949 – present	Oceanographic sampling began on ships used for enhanced weather forecasting off British Columbia, Canada. Since then, vessels from the DFO have followed the same ~1,500 km cruise track from Vancouver Island (48.51°N, 124.81°W) to Ocean Station Papa (50.0°N, 145.0°W) 2-3 times each year (Figure 7a). Hydrography, nutrients and lower trophic level productivity is measured. Seabirds and marine mammals are also surveyed.
Rockfish Recruitment Survey, NOAA-NMFS-SWFSC & others	2	1983 – present	NOAA-NMFS and other collaborators have conducted annual surveys in the greater Gulf of the Farallones (Monterey Bay to Bodega Bay) region off central California (Figure 7b). Hydrography and estimates of recruitment for young-of-the-year (age-0) *Sebastes* are priories for this survey. Seabirds and marine mammals are also surveyed.
CalCOFI, NOAA-NMFS, California Department of Fish and Game, Scripps Institution of Oceanography & others	3	1949 – present	The California Cooperative Oceanic Fisheries Investigations (CalCOFI) has been monitoring ecosystem dynamics since 1949. In its current form, the CalCOFI survey grid consists of six parallel transects, ranging in length from 470 (northernmost) to 700 (southernmost) km (Figure 7c). This study area encompasses over 300,000 km^2 of the Pacific Ocean, ranging from 30° to 35° N, and seaward from the southern California coast to 124° W. Hydrography and icthyoplankton surveys are priorities for this program. Seabirds and marine mammals are also surveyed.
Southeast Farallon Island Seabird Ecology, U.S. Fish and Wildlife Service & PRBO	2	1971 – present	The Farallon Islands National Wildlife Refuge, managed by United States Fish and Wildlife Service (USFWS), host the largest marine bird and mammal colonies in the contiguous United States. Under contract with USFWS, PRBO Conservation Science monitors and studies the ecology of 12 seabird species and 5 pinniped species at this site. Daily measurements of SST, salinity, and weather are also made.
Channel Islands Seabird Ecology, Channel Islands National Park, California Center Environmental Studies	3	1968 - present	The California Center for Environmental Studies initiated research on Brown Pelicans (*Pelicanus occidentalis*) in the Channel Islands in the late 1960s. In 1985, the Channel Islands National Park initiated long-term studies of a variety of seabirds at Santa Barbara, Anacapa, and Prince (San Miguel) islands. This time series (not illustrated in this report) shows substantial interannual variability in seabird productivity and trends related to both the recovery of seabirds from DDT contamination of the marine environment and climate variability and change.
Vancouver Island Zooplankton, Department of Fisheries and Oceans, Canada	1	1979 - present	Since 1979, Fisheries and Oceans Canada has measured zooplankton and hydrographic conditions on the Vancouver Island continental margin. The zooplankton time series (not illustrated in this report) shows very strong interannual variability in community composition. Large copepods have shown strong shifts of the seasonal life history timing, becoming progressively earlier from the late 1970s to the present, with variation.
Newport Hydrographic Line, NOAA-NMFS-NWFSC	1	1996 – present (1969-1973)	Biweekly surveys of this line are conducted off Newport, Oregon. Priorities for this survey include hydrography and zooplankton (copepods and euphausiids). This time series augments similar data collected along the same transect in 1969-1973. Seabird observations have recently been added to this program.
Oregon and Washington	1	1998 - present	Hydrography, nutrients, chlorophyll-a, zooplankton and pelagic forage fish are sampled at six stations along each of eight

Forage Fish, NOAA-NMFS			transects ranging from Newport, Oregon to the Washington-Canadian border.
Winds to Whales – Monterey Bay, UC Santa Cruz	2	1996 - present	This interdisciplinary project organized by the Center for Integrated Marine Technologies (UCSC-CIMT) collects data on physical (winds, currents, SST), chemical (nutrients, trace metals, etc.) and biological (phytoplankton, zooplankton, marine mammals, etc.) processes in nearshore Monterey Bay.
Monterey Bay Time Series, Monterey Bay Aquarium Research Institute	2	1989 - present	Monthly shipboard surveys conducted to collect data on physical, chemical and biological properties in Monterey Bay. In1997, the surveys were conducted quarterly and became known as the Studies of Ecological and Chemical Responses to Environmental Trends (SECRET) project.
Tatoosh Island Seabird Ecology, University of Washington	1	1990 – present	Studies of the breeding success and diet of seabirds that inhabit Tatoosh Island, WA, focused on Common Murre (*Uria aalge*), began in 1990.
Triangle Island Seabird Ecology, Canadian Wildlife Service and Simon Fraser University	1	1994 - present	Studies of the breeding success and diet of the seabirds that inhabit Triangle Island. Focus on Rhinoceros Auklet (*Cerorhinca monocerata)* and Cassin's Auklet (*Ptychoramphus aleuticus*). Studies complement previous work conducted by CWS at this site in the late 1970s.
Groundfish Surveys, NOAA-NMFS-NWFSC & Fisheries and Oceans Canada	1	1977 - present	Triennial midwater/acoustic surveys of groundfish, with an emphasis on Pacific hake, are conducted from central British Columbia (Dixon Entrance) to central California (Monterey Bay). Measurements of hydrographic conditions and abundance of fish are priority measurements.

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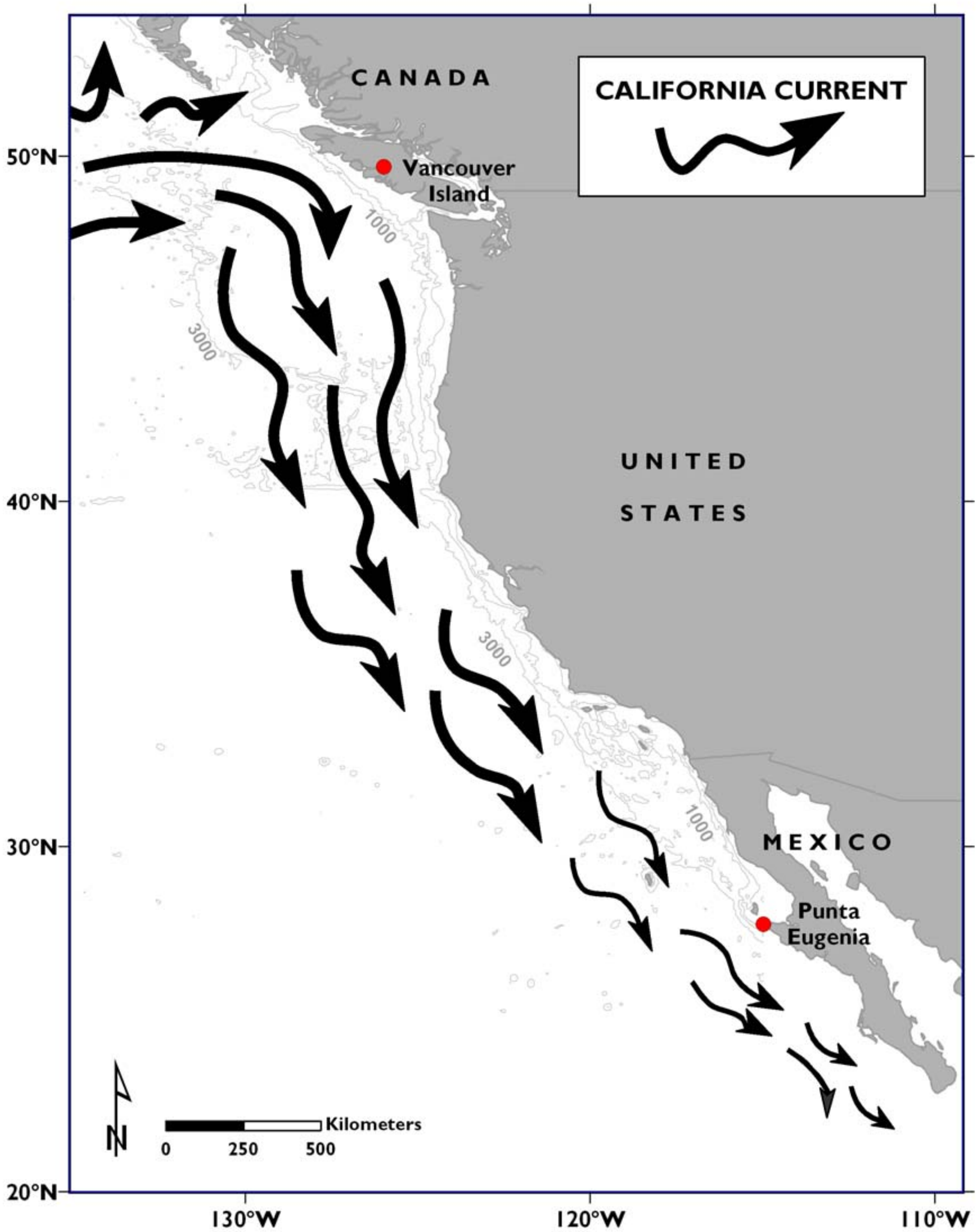


Figure 1. Conceptual map of the California Current Large Marine Ecosystem (CCLME). The geographic scope of this IEA is from Vancouver Island, Canada to Punta Eugenia, Mexico and offshore. Mangroves are found south of Punta Eugenia, but not to the north. The North Pacific Current (West Wind Drift) splits into the California Current and Alaska Current roughly at Vancouver Island.

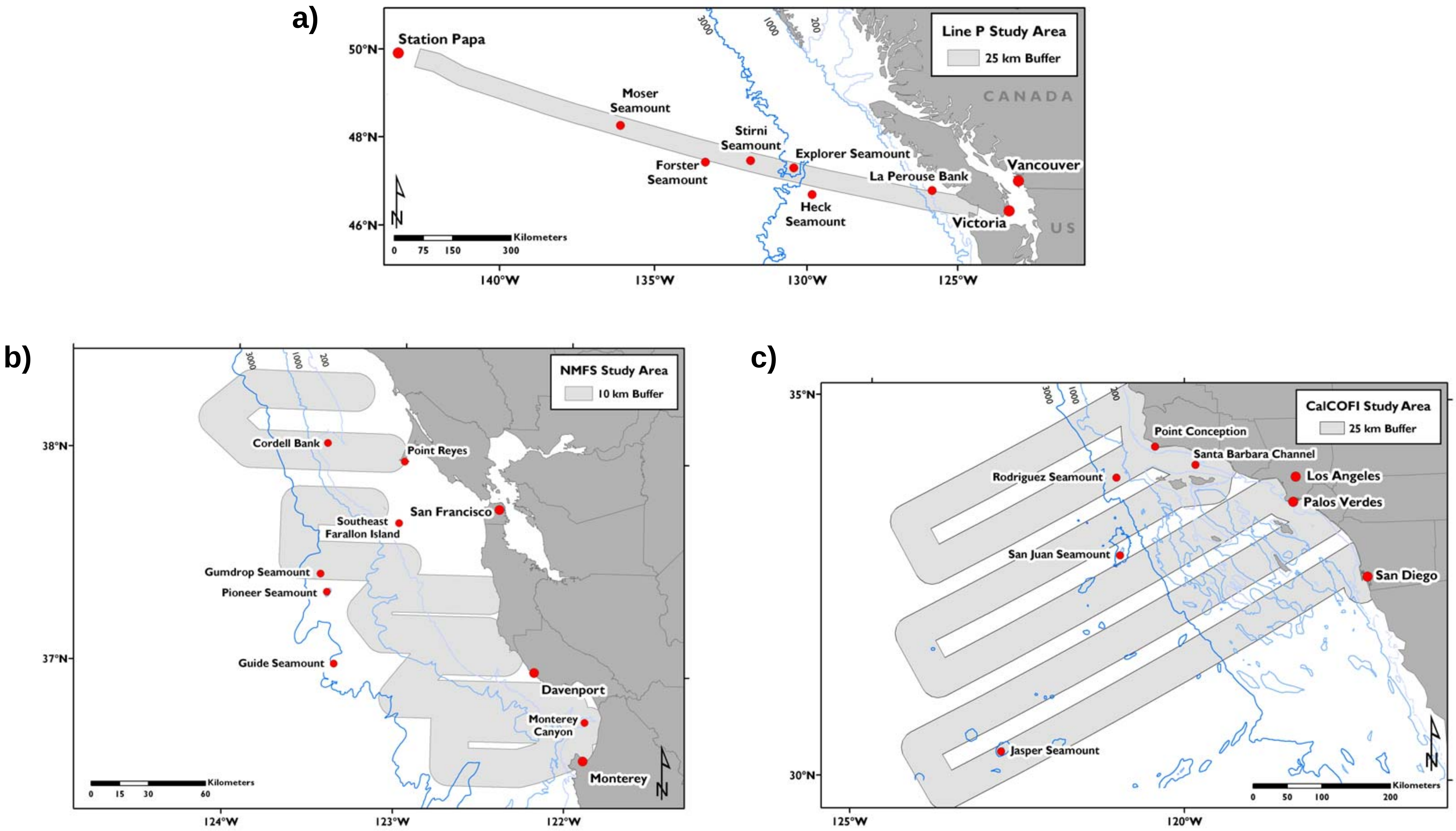


Figure 2. Examples of three (3) long-term oceanographic research programs within the CCLME. Each of these programs has been in operation for over continuous 20 years: (a) the Department of Fisheries and Oceans, Canada, "Line P" project; (b) the National Marine Fisheries Service "Rockfish Recruitment Survey"; and, (c) the "California Cooperative Oceanic Fisheries Investigation" run by a consortium of National Marine Fisheries Service, California Department of Fish and Game, and Scripps Institution of Oceanography. Some shallow-water topographies (offshore seamounts) are illustrated.

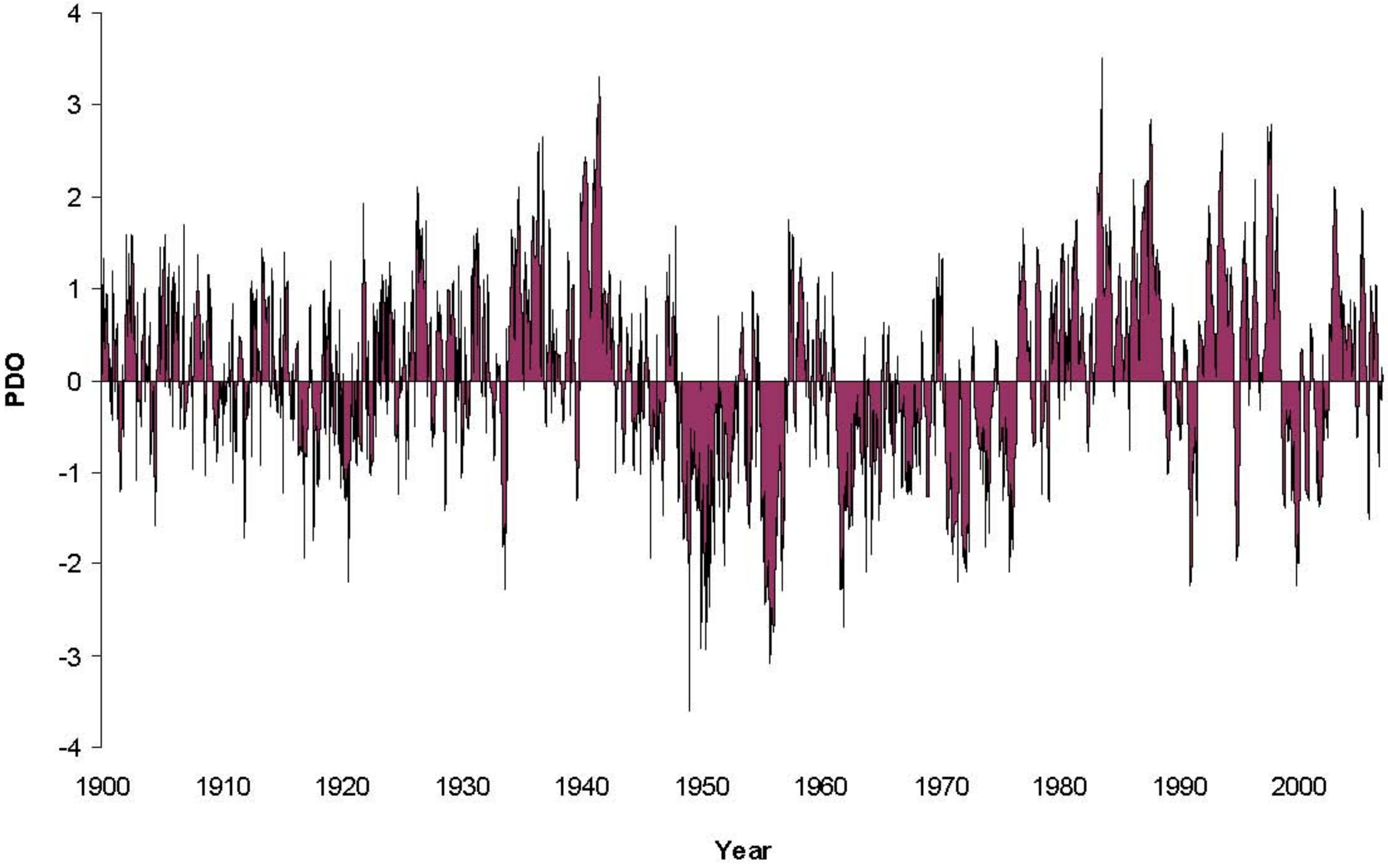


Figure 3. The Pacific Decadal Oscillation (PDO) index (1900-2006). Data courtesy Nate Mantua (Joint Institute for the Study of the Atmosphere and Ocean, UW). Positive values indicate warm eastern North Pacific SST, whereas negative values indicate cool temperatures. The long-term ocean warming signal has been removed to illustrate interannual and interdecadal SST variation. http://jisao.washington.edu/pdo/PDO.latest

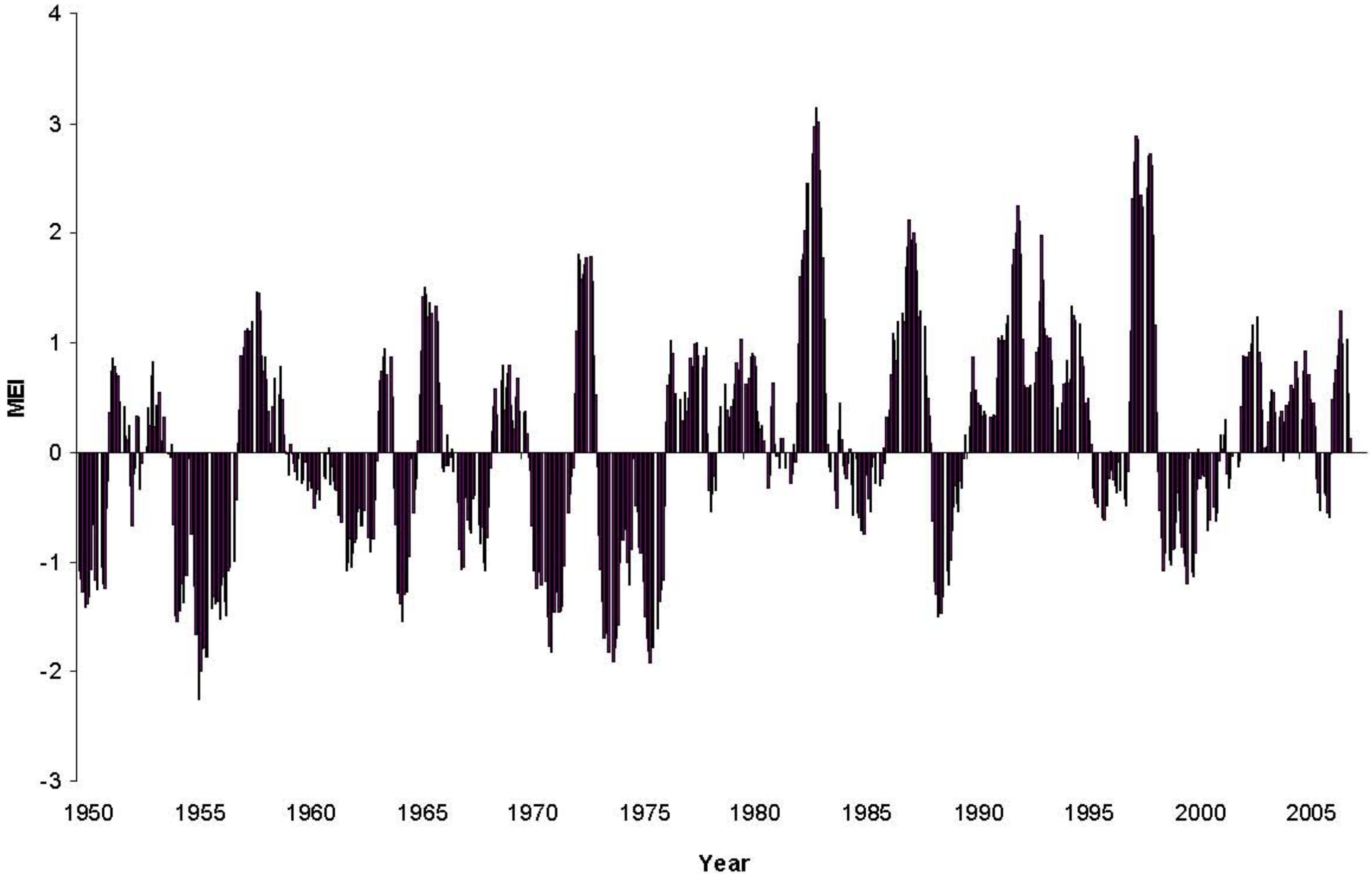


Figure 4. The Multivariate El Niño Index (MEI), 1950-2006. Data courtesy Klaus Wolter (NOAA-Earth System Research Laboratory). Positive values reflect El Niño events whereas negative values indicate La Niña. The MEI is a composite index constructed using 7 environmental variables. http://www.cdc.noaa.gov/people/klaus.wolter/MEI/table.html.

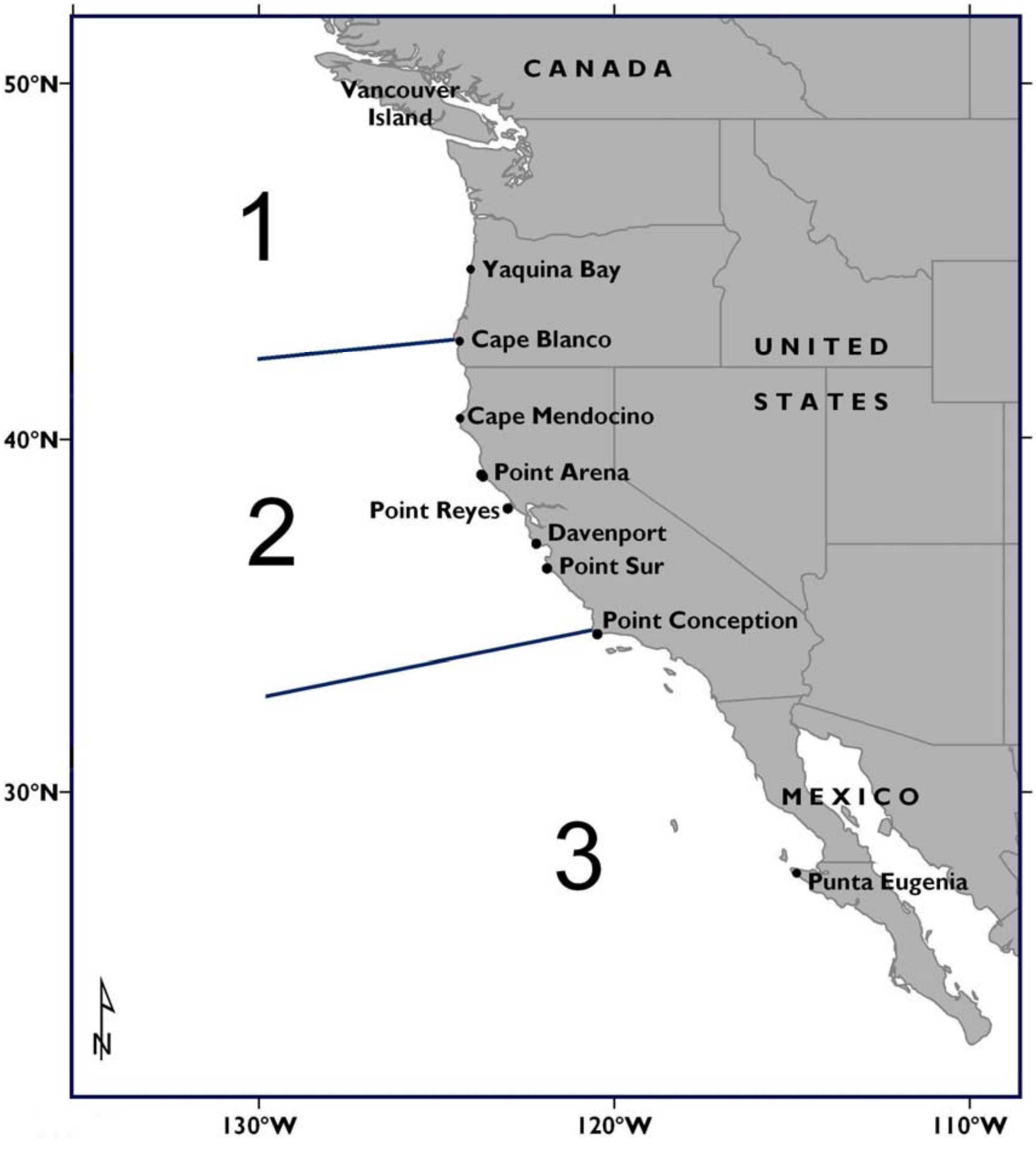
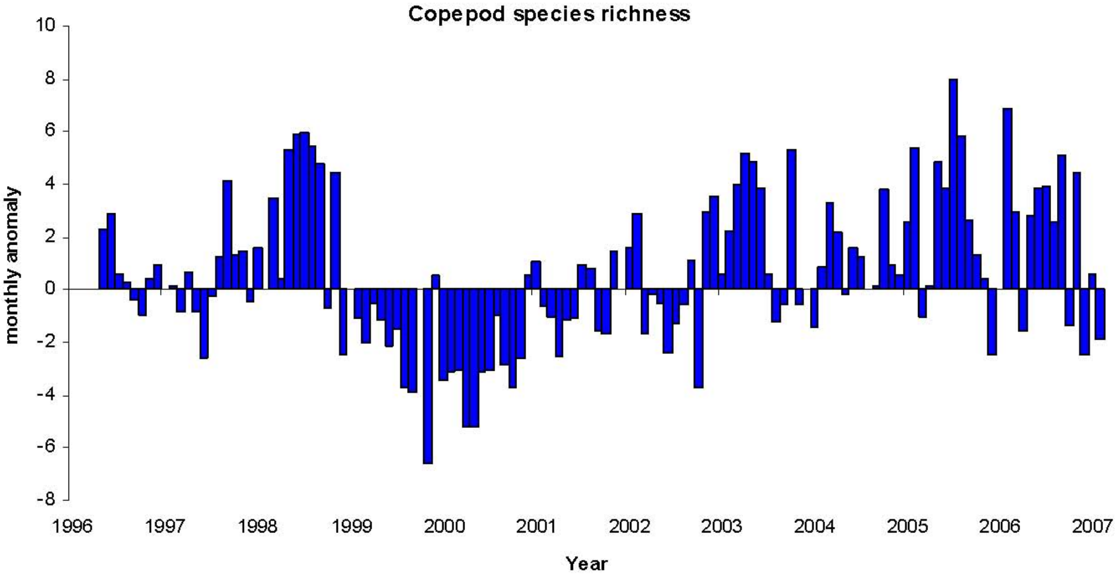


Figure 5. Eco-regions of the CCLME as defined by U.S. GLOBEC (1992). Physical oceanography and biological attributes of the ecosystem vary by region. The degree to which each "sub-ecosystem" co-varies with climate variability and change will be developed in future IEA reports.



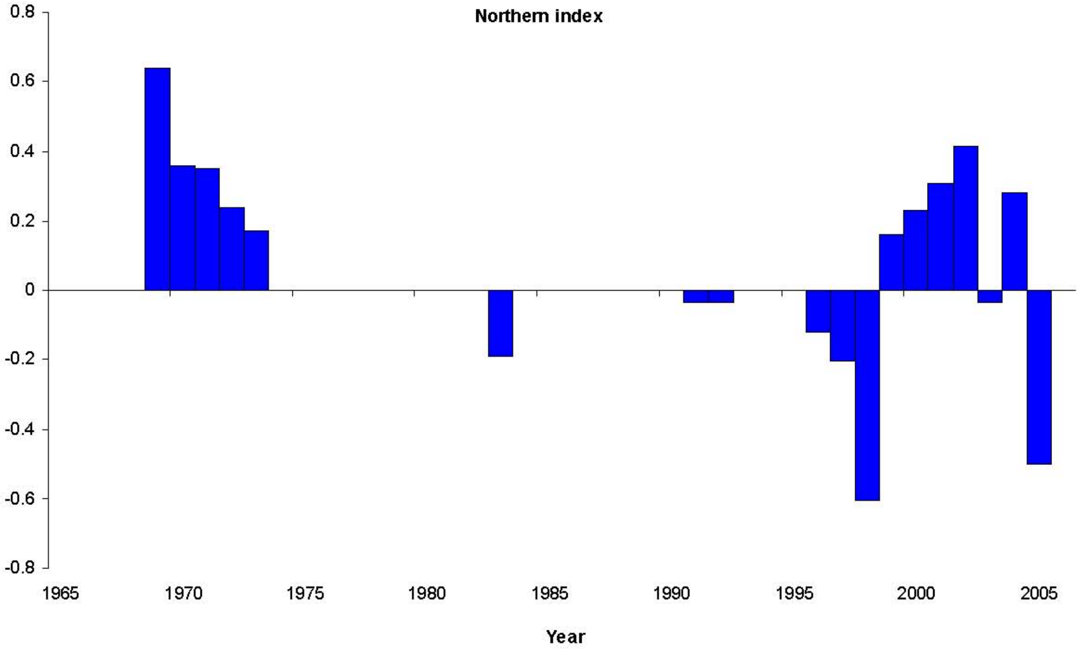


Figure 6. Copepod species richness index (1996-2006), and the "boreal" copepod index (1965-2005) from Newport, Oregon. Note that the time scales differ between the two plots. Data courtesy Bill Peterson (NOAA Fisheries, NWFSC).

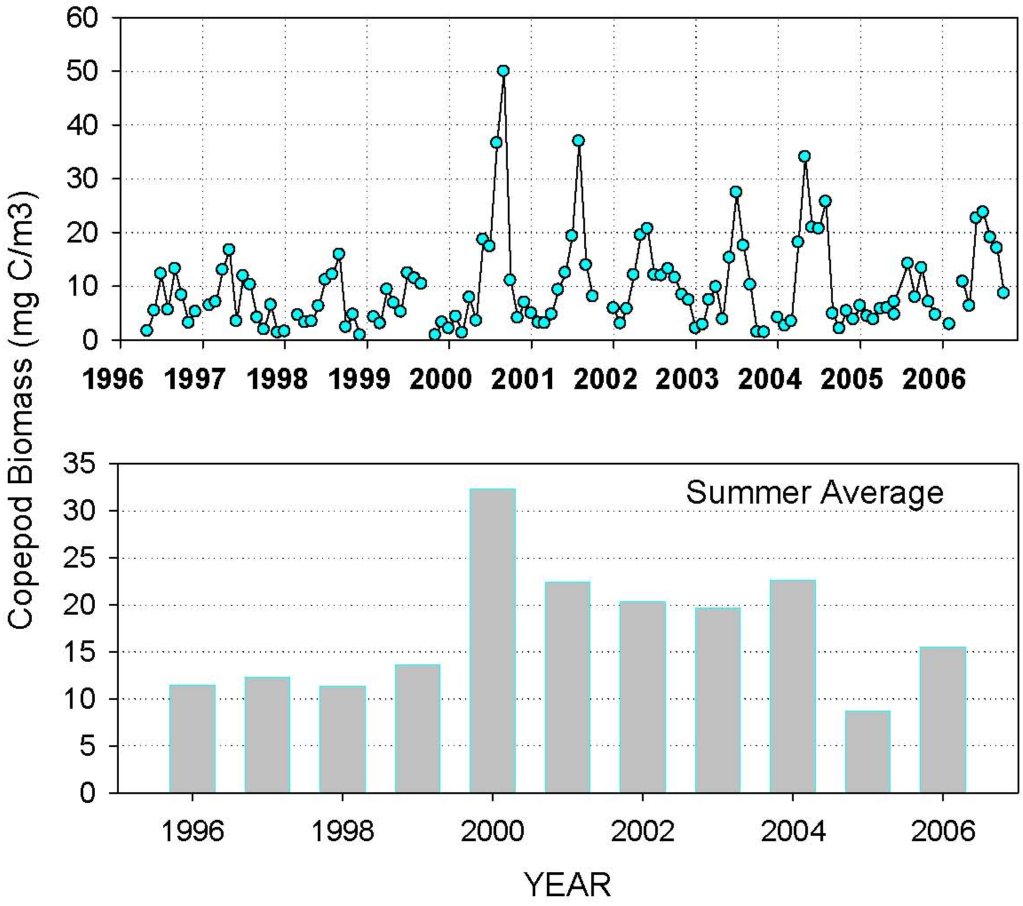
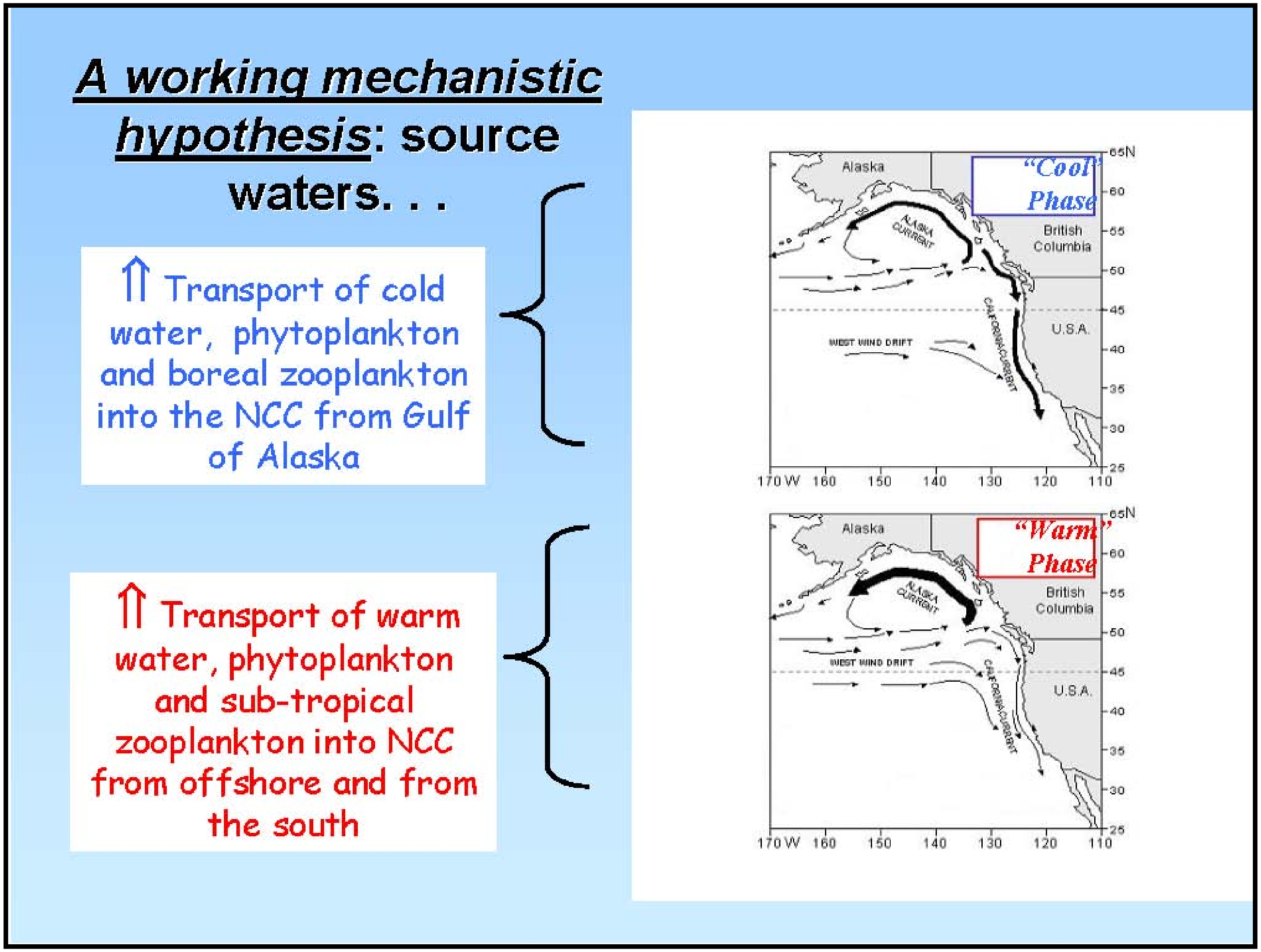


Figure 7. Copepod biomass index from Newport, Oregon (1996-2006). Monthly copepod biomass values (top panel) and average summer biomass values (bottom panel). Data courtesy Bill Peterson (NOAA Fisheries, NWFSC).



A working mechanistic hypothesis: source waters. . .

⇑ Transport of cold water, phytoplankton and boreal zooplankton into the NCC from Gulf of Alaska

⇑ Transport of warm water, phytoplankton and sub-tropical zooplankton into NCC from offshore and from the south

Figure 8. Hypothesized mechanism for variation in copepod indices off Newport, Oregon. Figure courtesy Bill Peterson (NOAA Fisheries, NWFSC). Transport of organisms from the north and south is proposed to explain these indices.

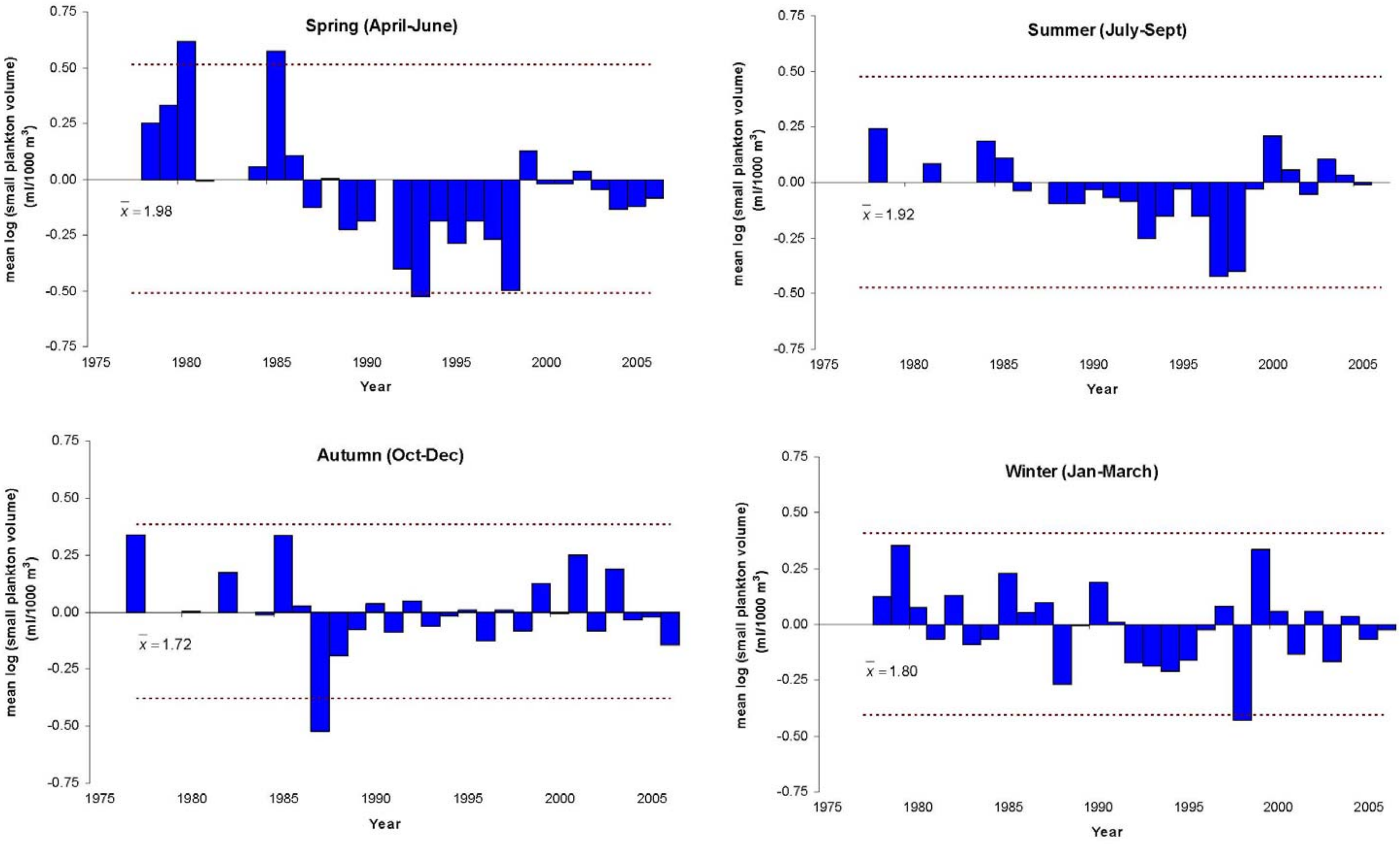


Figure 9. The southern California small plankton volume (SPV) index from CalCOFI (1977 - 2006). SPV includes all plankton with a displacement volume of < 5mL, representing copepods and euphausiids. Anomalies show the deviation of each annual seasonal value from the long-term seasonal mean. Dotted lines represent 1 standard deviation above/below the long-term seasonal mean. Data courtesy Rich Charter (NOAA-Fisheries Resources, SWFSC).

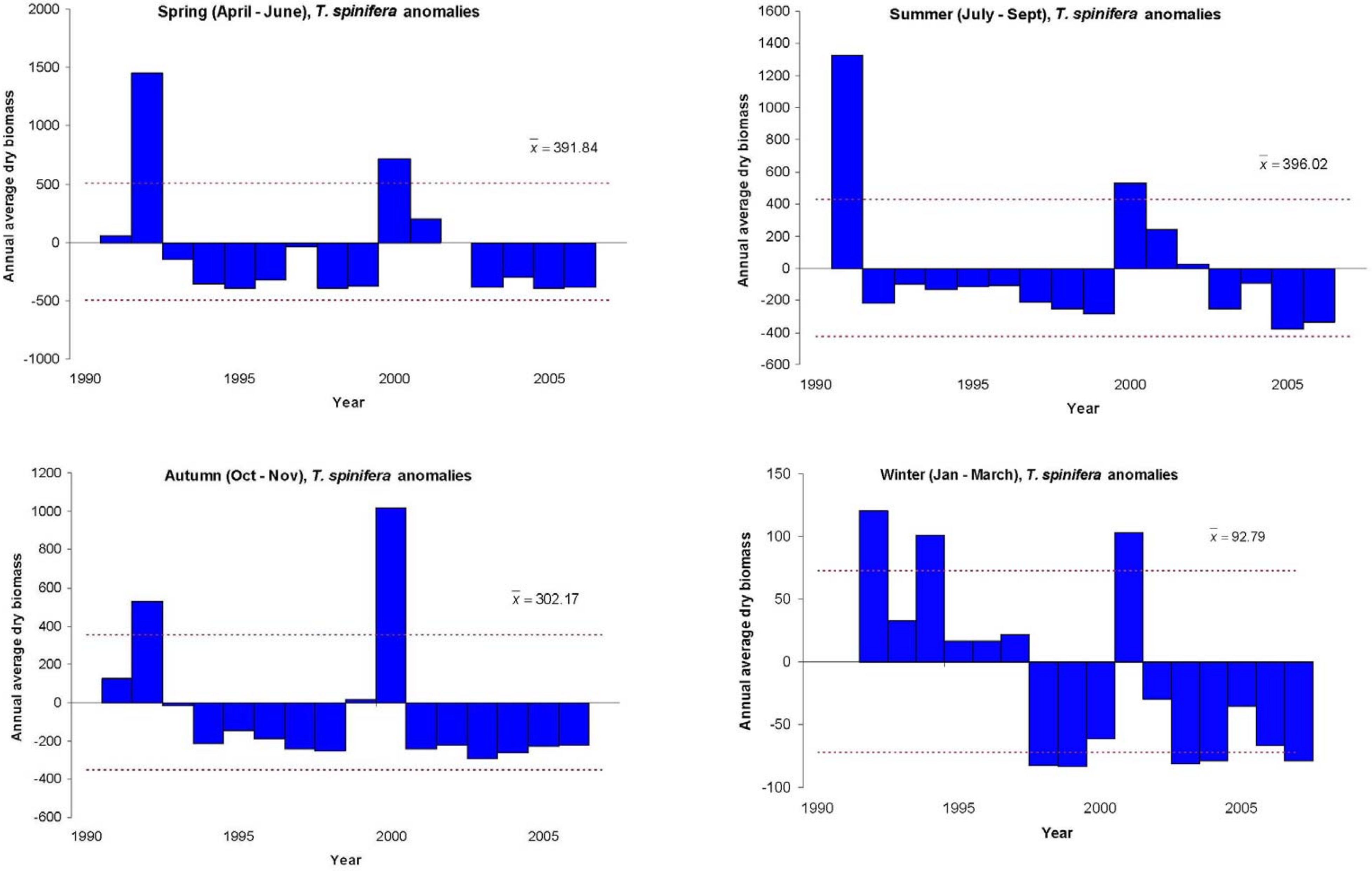


Figure 10. Vancouver Island, Canada, the euphausiid *Thysanoessa spinifera* index based on standardized net samples. Data courtesy Ron Tanasichuk (Department Fisheries and Oceans, Canada).

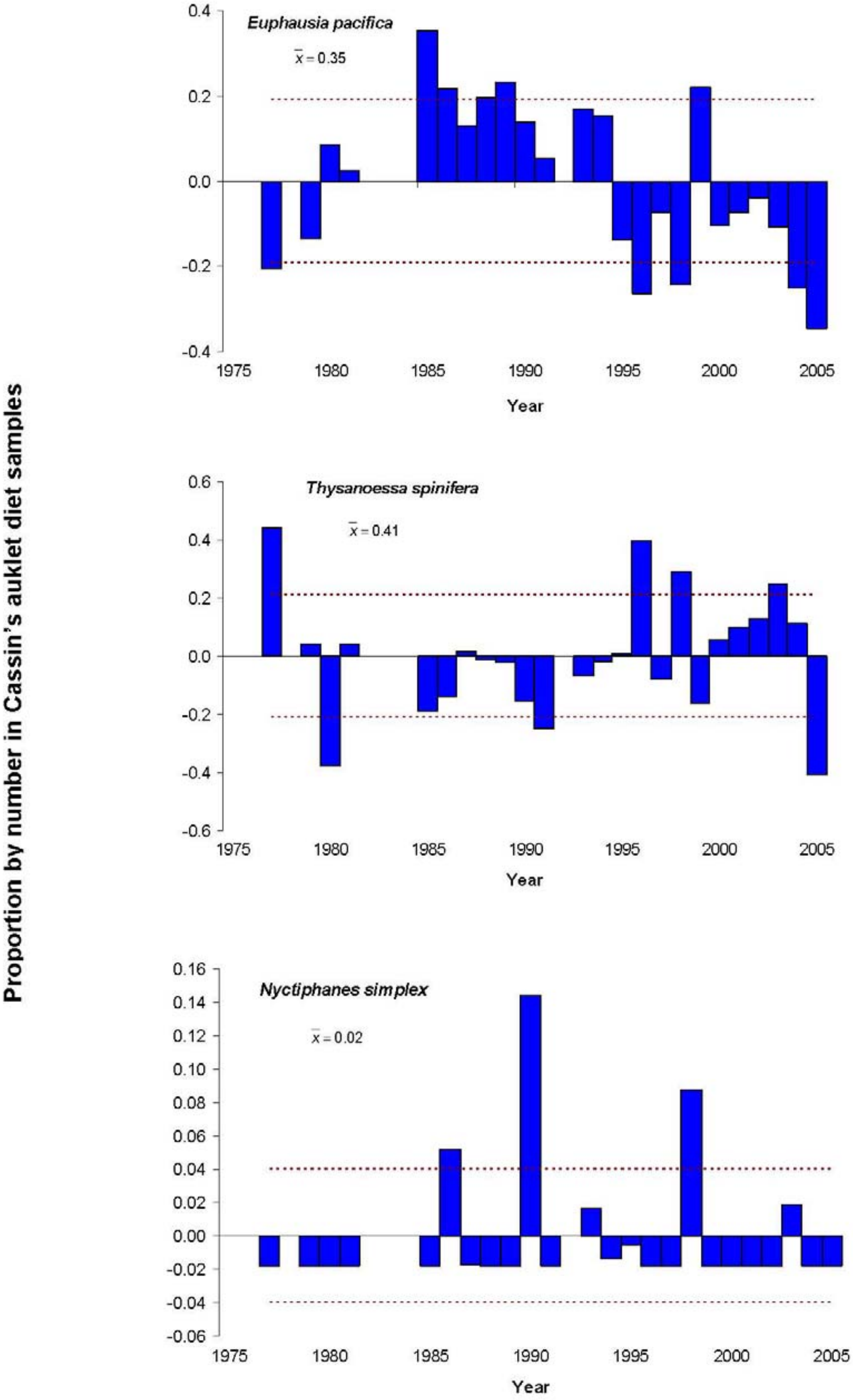
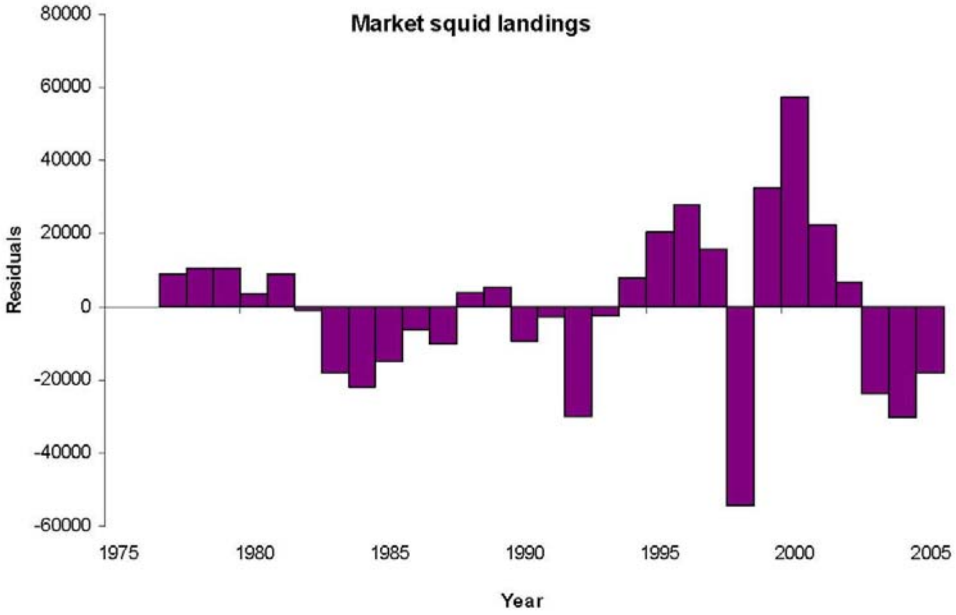


Figure 11. Indices for three euphausiid species (*Euphausia pacifica*, *Thysanoessa spinifera* and *Nyctiphanes simplex)* based on seabird predator (Cassin's Auklet, *Ptychoramphus aleuticus*) diet samples on Southeast Farallon Island, California (1977-2005). Data courtesy Christine Abraham (PRBO Conservation Science).

a)



b)

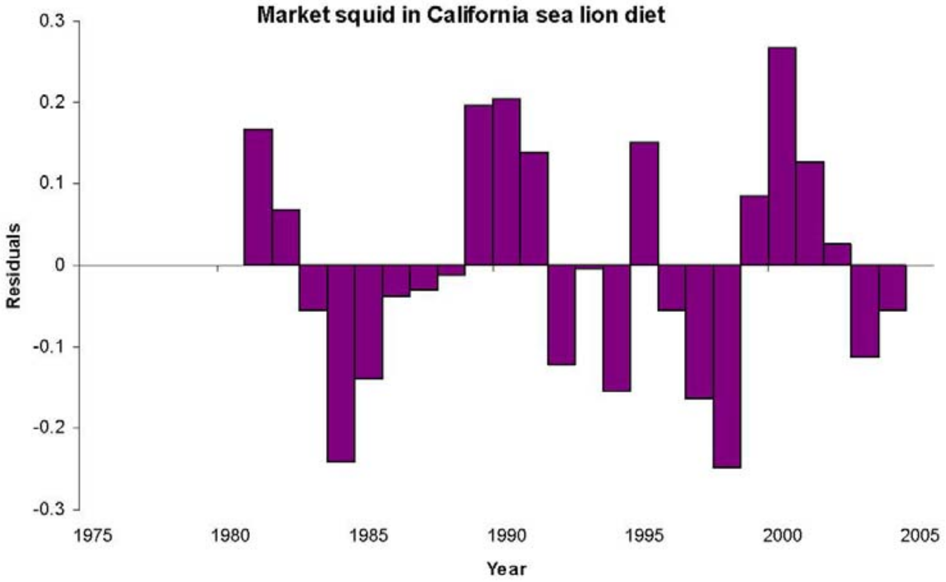
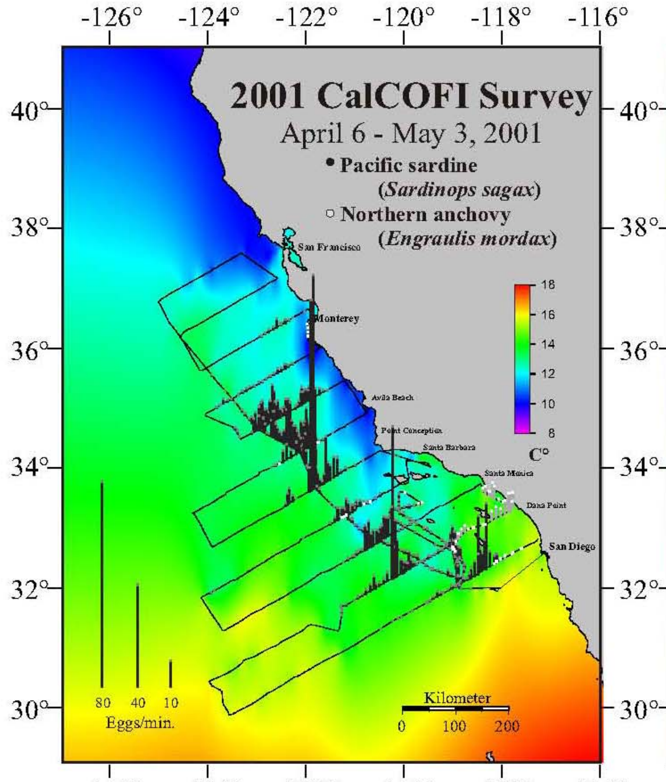
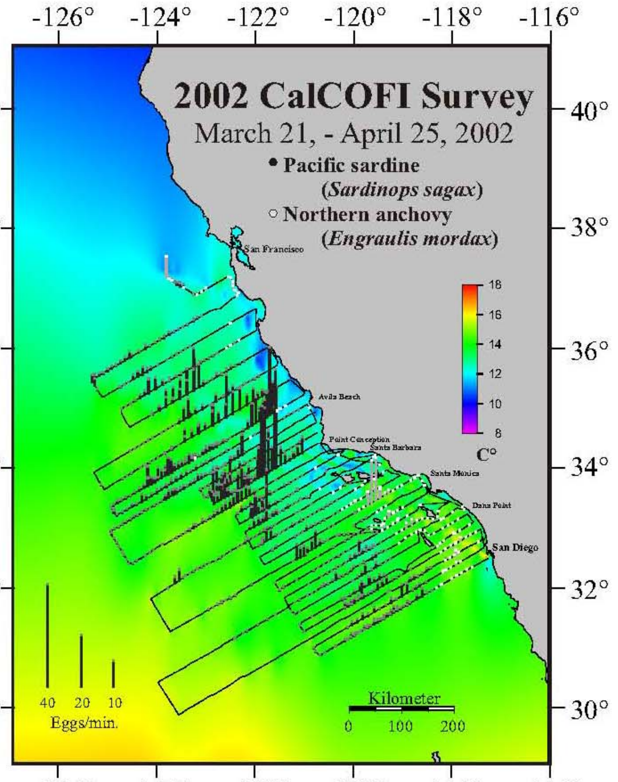


Figure 12. Market squid (*Loligo opalescens)* indices from catch data, and the diet of a marine mammal (California sea lion) Note: the trend of increasing catch due to increasing fishing effort has been removed by quadratic regression. Bars represent residuals after detrending. Catch data courtesy Dale Sweetnam (CDFG). Marine mammal data courtesy Mark Lowry (NOAA-NMFS, SWFSC).


2001 CalCOFI Survey
April 6 - May 3, 2001
● Pacific sardine
(Sardinops sagax)
○ Northern anchovy
(Engraulis mordax)
San Francisco
Monterey
Avila Beach
Point Conception
Santa Barbara
Santa Monica
Dana Point
San Diego
18
16
14
12
10
8
C°
80
40
10
Eggs/min.
Kilometer
0
100
200
-126°
-124°
-122°
-120°
-118°
-116°
40°
38°
36°
34°
32°
30°


2002 CalCOFI Survey
March 21, - April 25, 2002
● Pacific sardine
(Sardinops sagax)
○ Northern anchovy
(Engraulis mordax)
San Francisco
Avila Beach
Point Conception
Santa Barbara
Santa Monica
Dana Point
San Diego
18
16
14
12
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C°
40
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Eggs/min.
Kilometer
0
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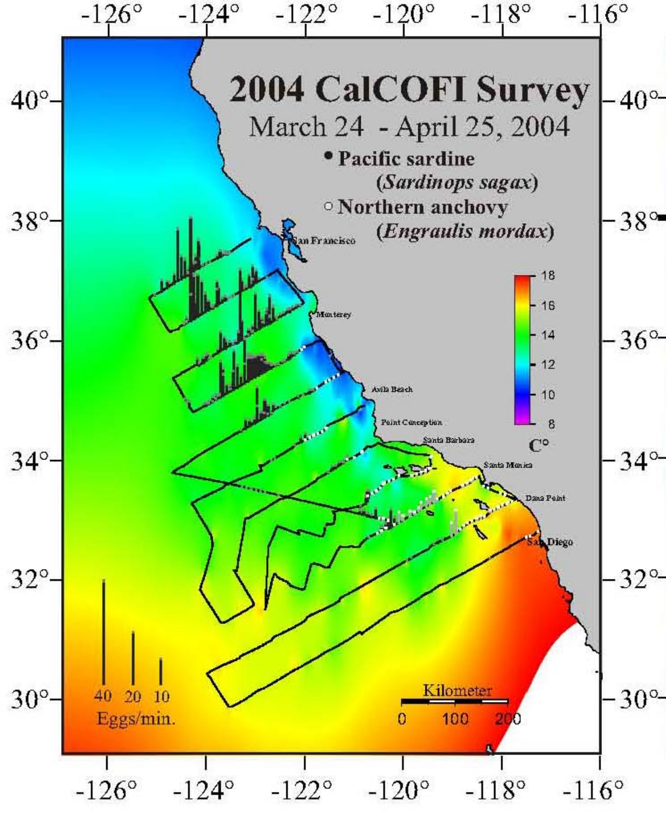
2004 CalCOFI Survey
March 24 - April 25, 2004
● Pacific sardine
(Sardinops sagax)
○ Northern anchovy
(Engraulis mordax)
San Francisco
Monterey
Avila Beach
Point Conception
Santa Barbara
Santa Monica
Dana Point
San Diego
18
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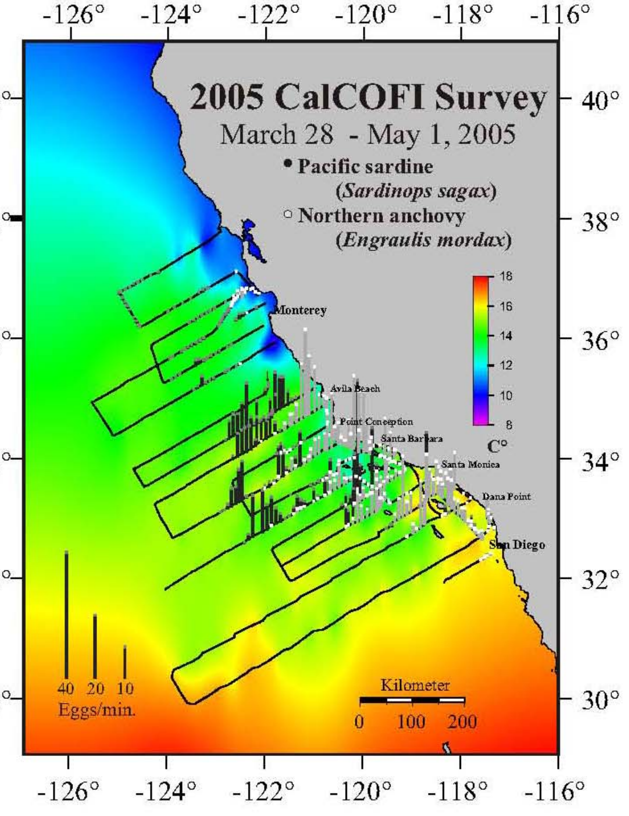
2005 CalCOFI Survey
March 28 - May 1, 2005
● Pacific sardine
(Sardinops sagax)
○ Northern anchovy
(Engraulis mordax)
Monterey
Avila Beach
Point Conception
Santa Barbara
Santa Monica
Dana Point
San Diego
18
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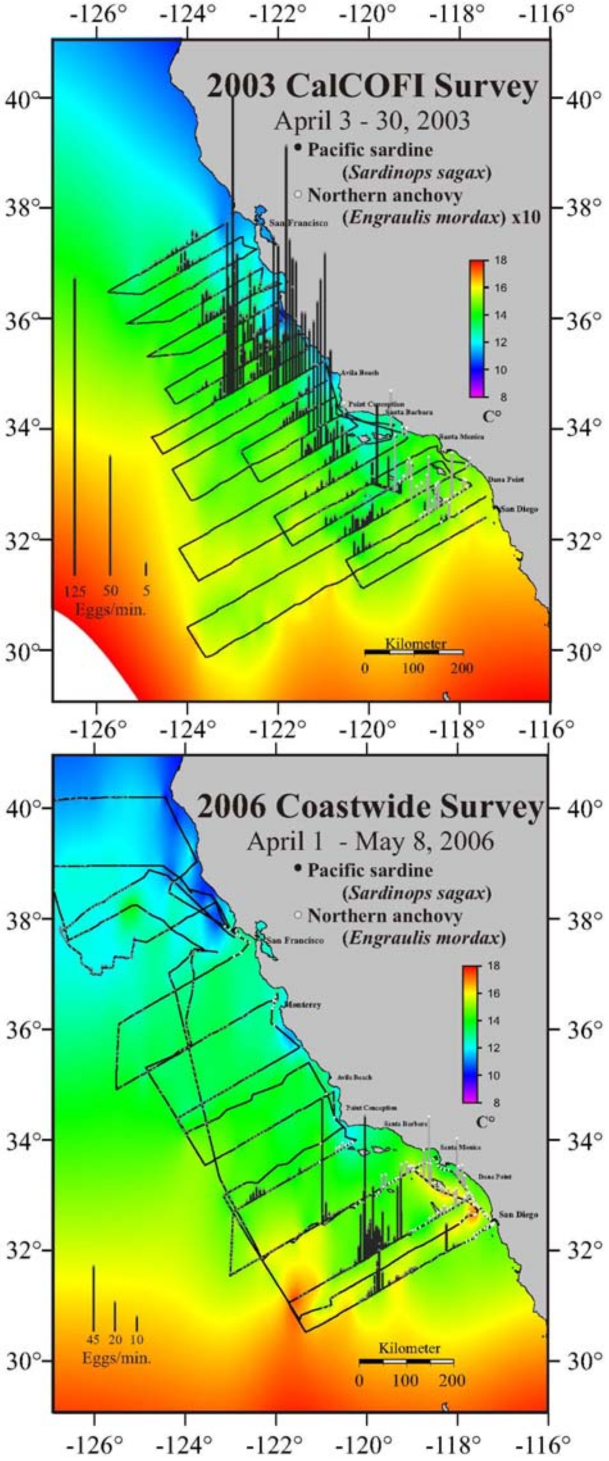
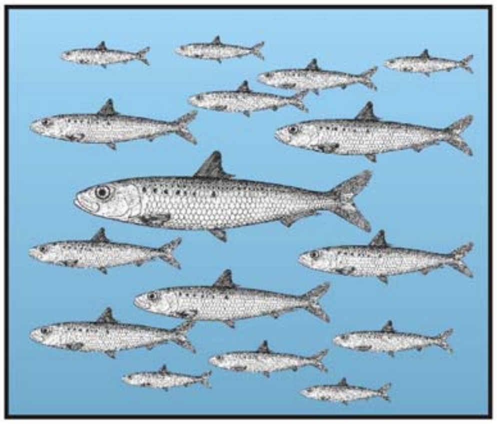
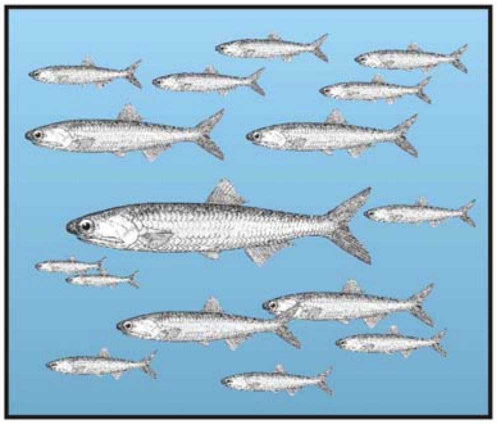


Pacific Sardine and Northern anchovy egg counts collected by CUFES (Continuous underway fish egg sampler) for the CalCOFI (California Cooperative Oceanic Fisheries Investigations) Spring quarter surveys.



Pacific sardine
(Sardinops sagax)



Northern Anchovy
(Engraulis mordax)

Figure 13. Pacific sardine (*Sardinops sagax*) and northern anchovy (*Engraulis mordax*) egg counts from Southern California CalCOFI cruises (2001-2006). Figure courtesy Dave Griffith, Rich Charter, and Roy Allen (NOAA-NMFS, SWFSC). Note shifting distributions and abundances.

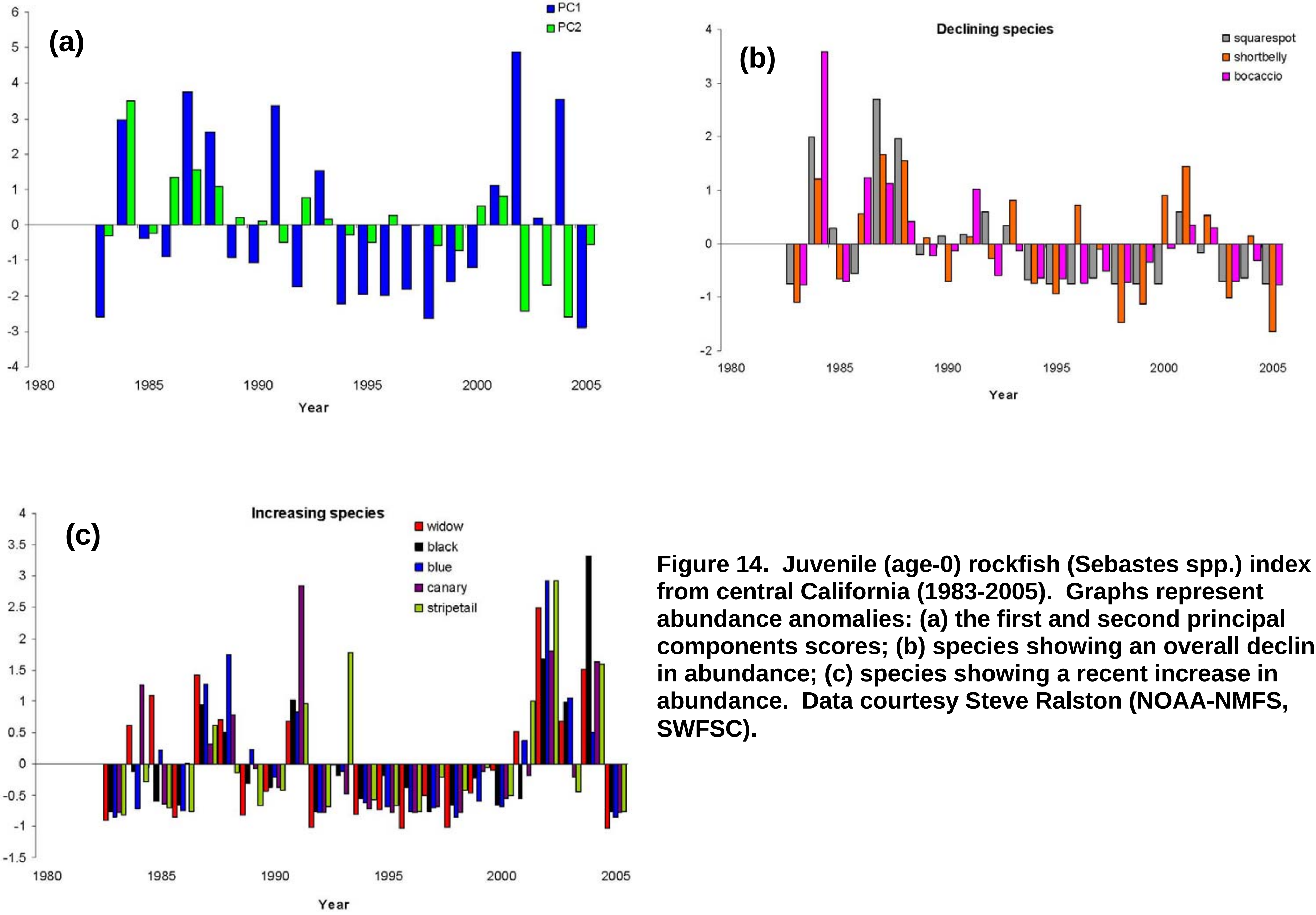


Figure 14. Juvenile (age-0) rockfish (Sebastes spp.) index from central California (1983-2005). Graphs represent abundance anomalies: (a) the first and second principal components scores; (b) species showing an overall decline in abundance; (c) species showing a recent increase in abundance. Data courtesy Steve Ralston (NOAA-NMFS, SWFSC).

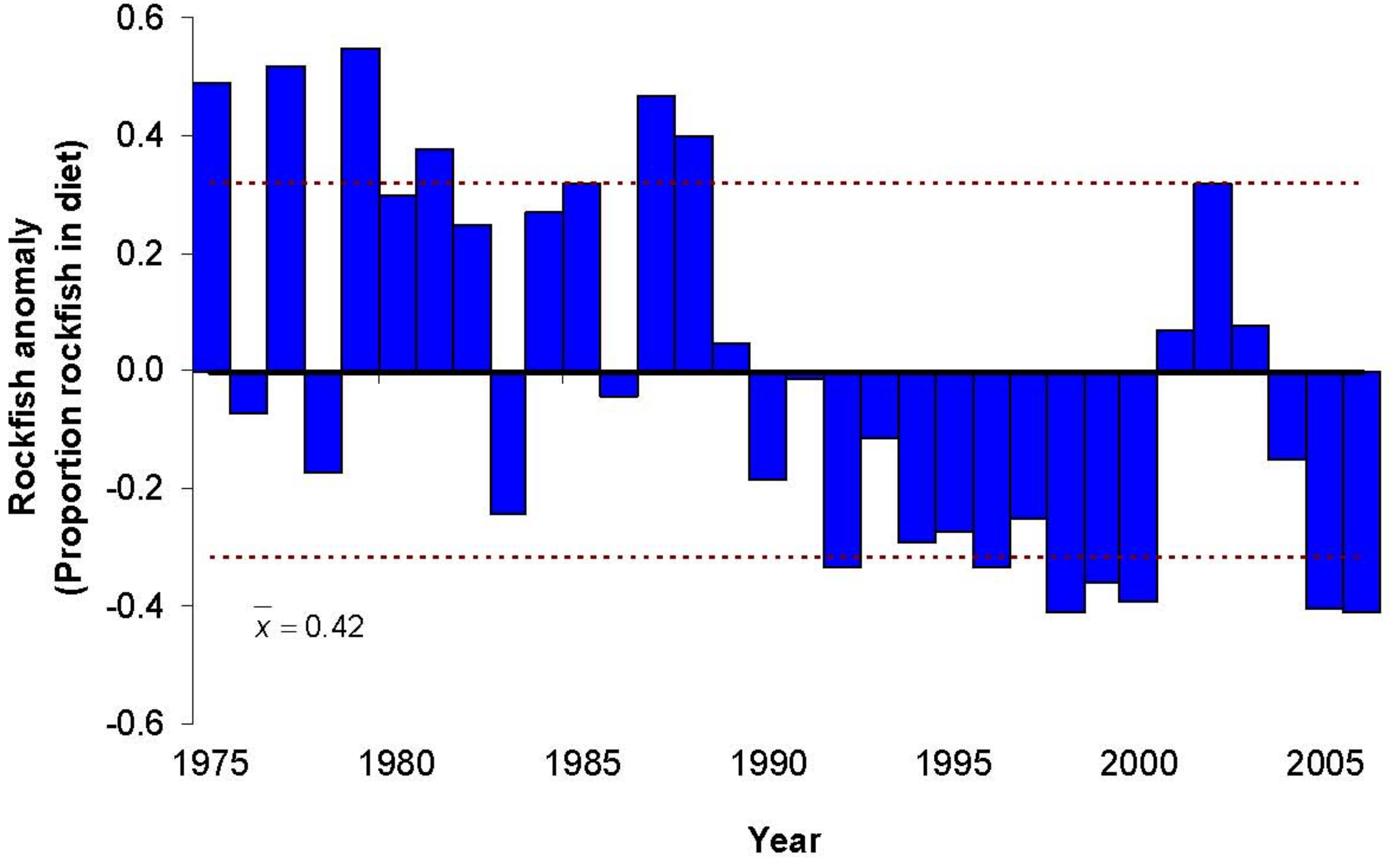


Figure 15. Juvenile (age O) rockfish (*Sebastes* spp.) index based on the diet of a seabird (Common Murre, *Uria aalge*), in central-northern California (1975 – 2006). Data courtesy Pete Warzybok (PRBO Conservation Science).

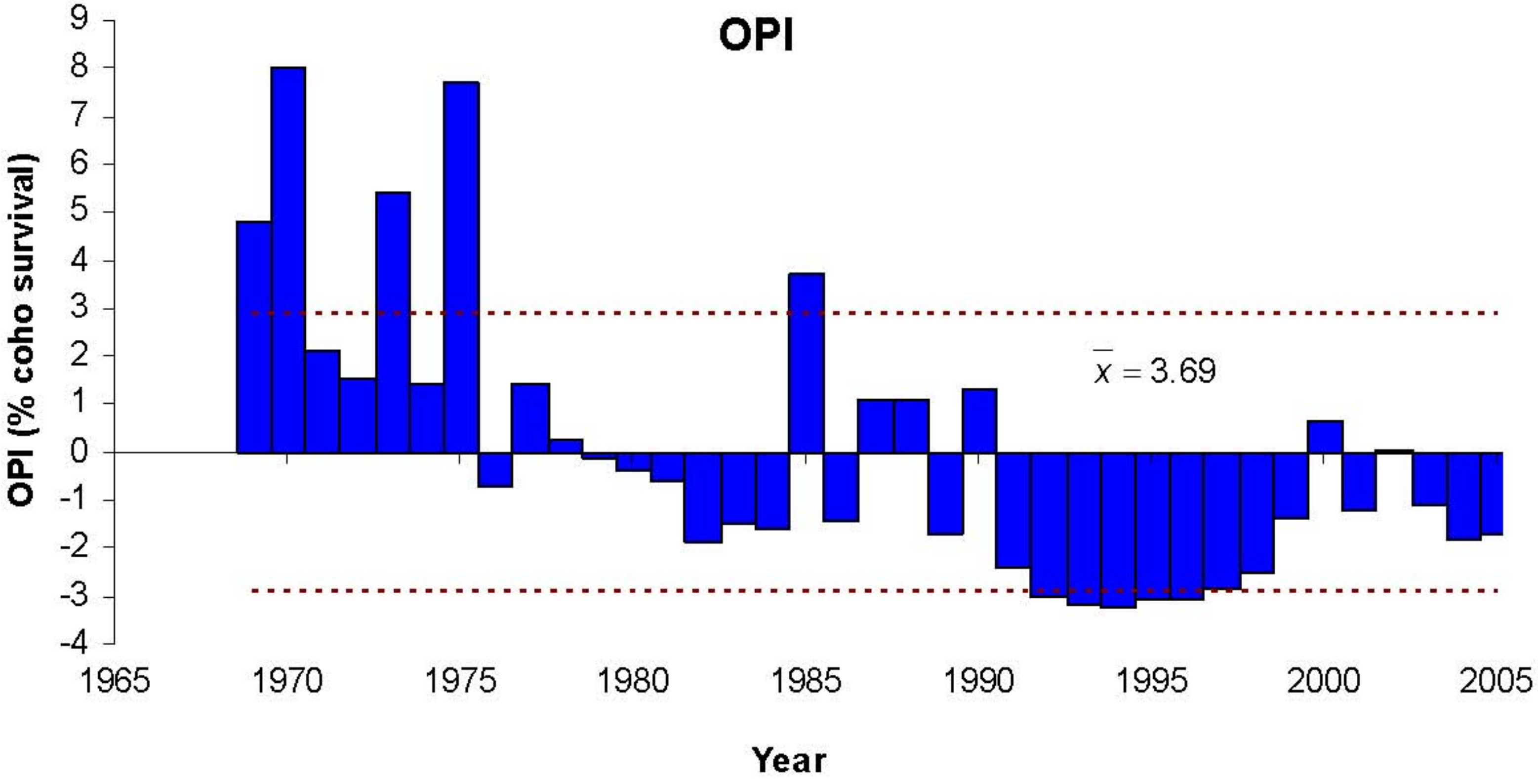


Figure 16. Coho salmon survival at sea as represented by the OPI (Ocean Production Index) anomalies, 1969-2006. Year shown is survival of coho salmon plotted against the year that the fish went to sea (1.5 y before spawning in their natal hatcheries). The 0-line on the y-axis represents the long-term mean (value also shown in graph), and anomalies represent the deviation of each annual value from the long-term mean. Hatched lines represent 1 ± standard deviation from the long-term mean. Data courtesy Bill Peterson (NOAA Fisheries, NWFSC).

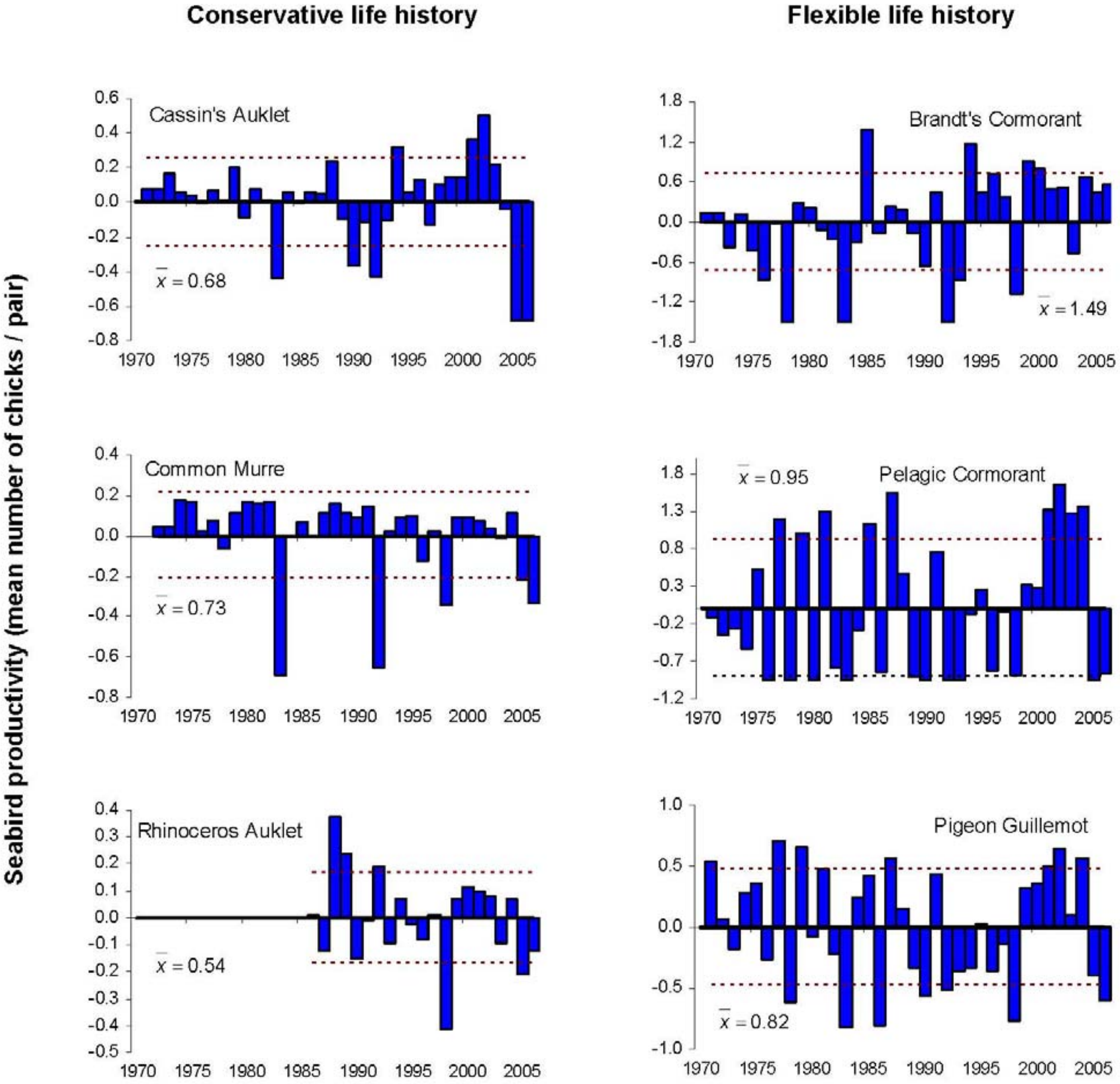


Figure 17. The Farallon seabird productivity index, 1971 - 2006. Data courtesy U.S. Fish and Wildlife Service and PRBO Conservation Science. The annual reproductive success anomalies for 6 species showing varying life history strategies are shown. Auklets and murres lay a single egg per breeding attempt and have great longevity, whereas the cormorants and guillemot lays multi-egg clutches and less longevity. Only the Brandt's Cormorant shows an increase in productivity through time. Data courtesy Russ Bradley, Pete Warzybok, and Bill Sydeman (PRBO).

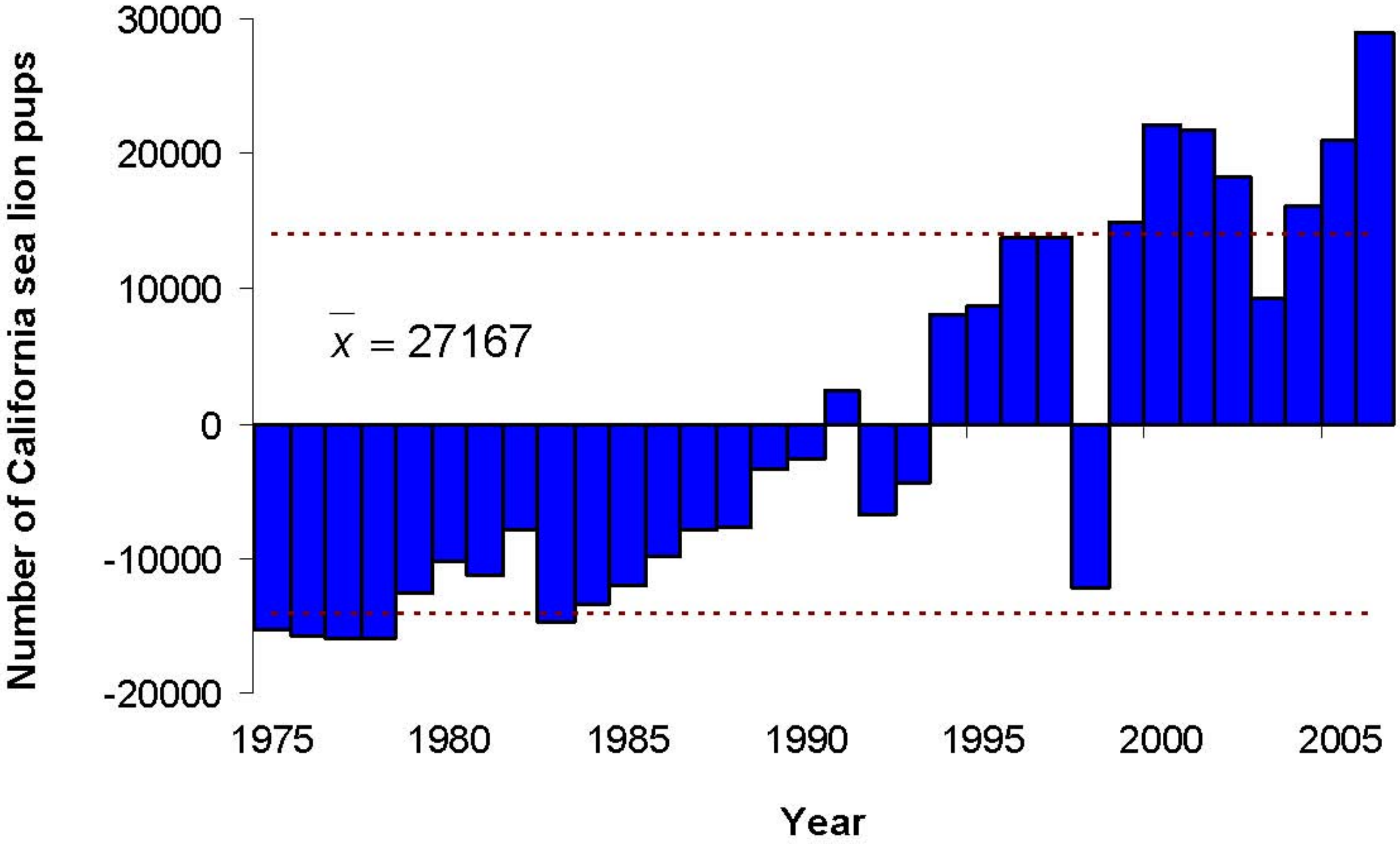


Figure 18. California sea lion production index (number pups) from Southern California (1975 – 2006). Data courtesy of Mark Lowry (NOAA-NMFS, SWFSC).

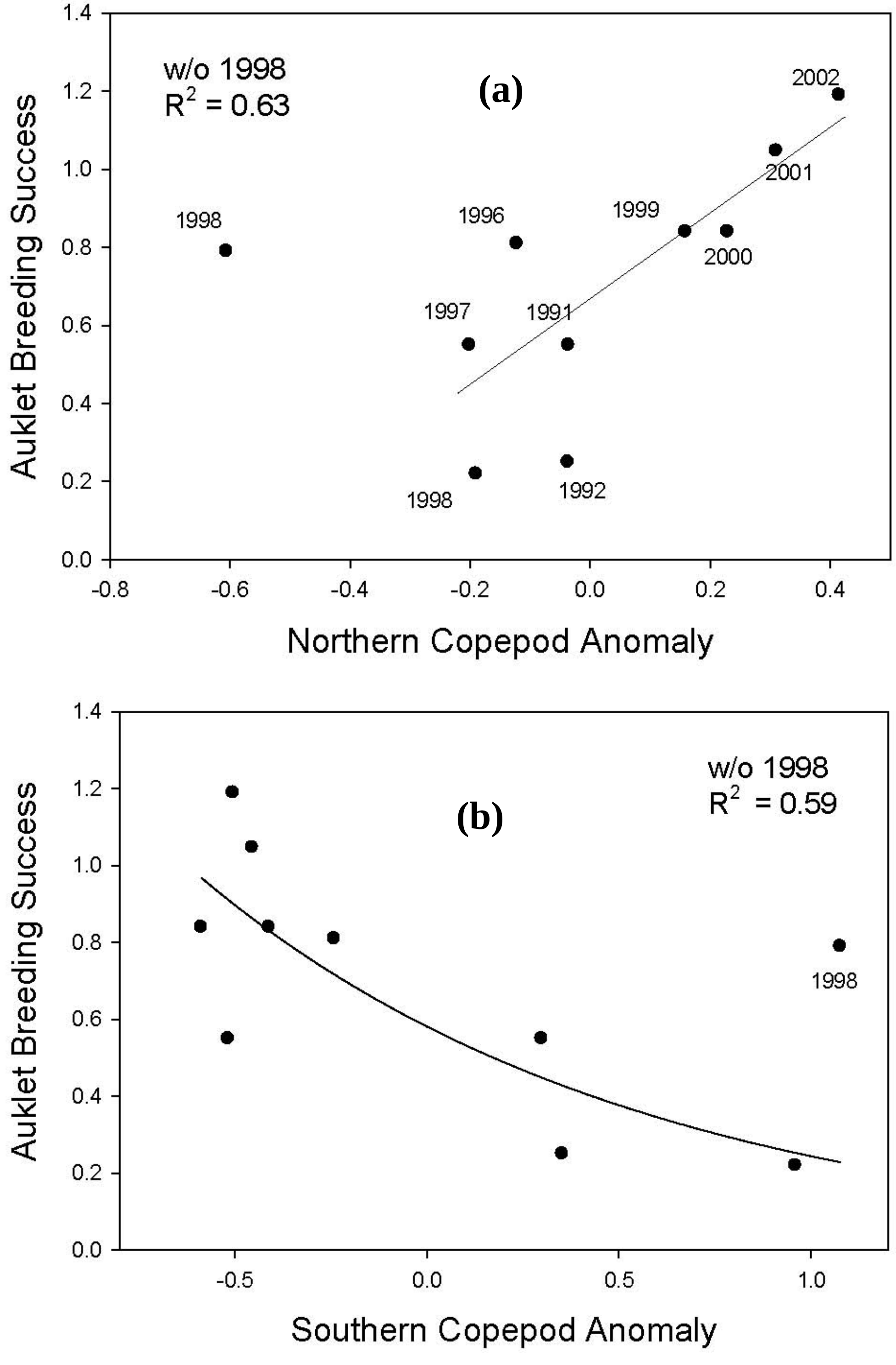


Figure 19. Oregon copepod indices against central-northern California planktivorous seabird productivity. (a) Seabird productivity is positively related to the "northern-boreal" copepod index, and (b) negatively related to the "southern-sub-tropical" copepod index, suggesting co-variation between the northern and central ecoregions illustrated in Figure 5. Figures and data courtesy Bill Peterson (NOAA Fisheries, NWSFC) and Bill Sydeman (PRBO).

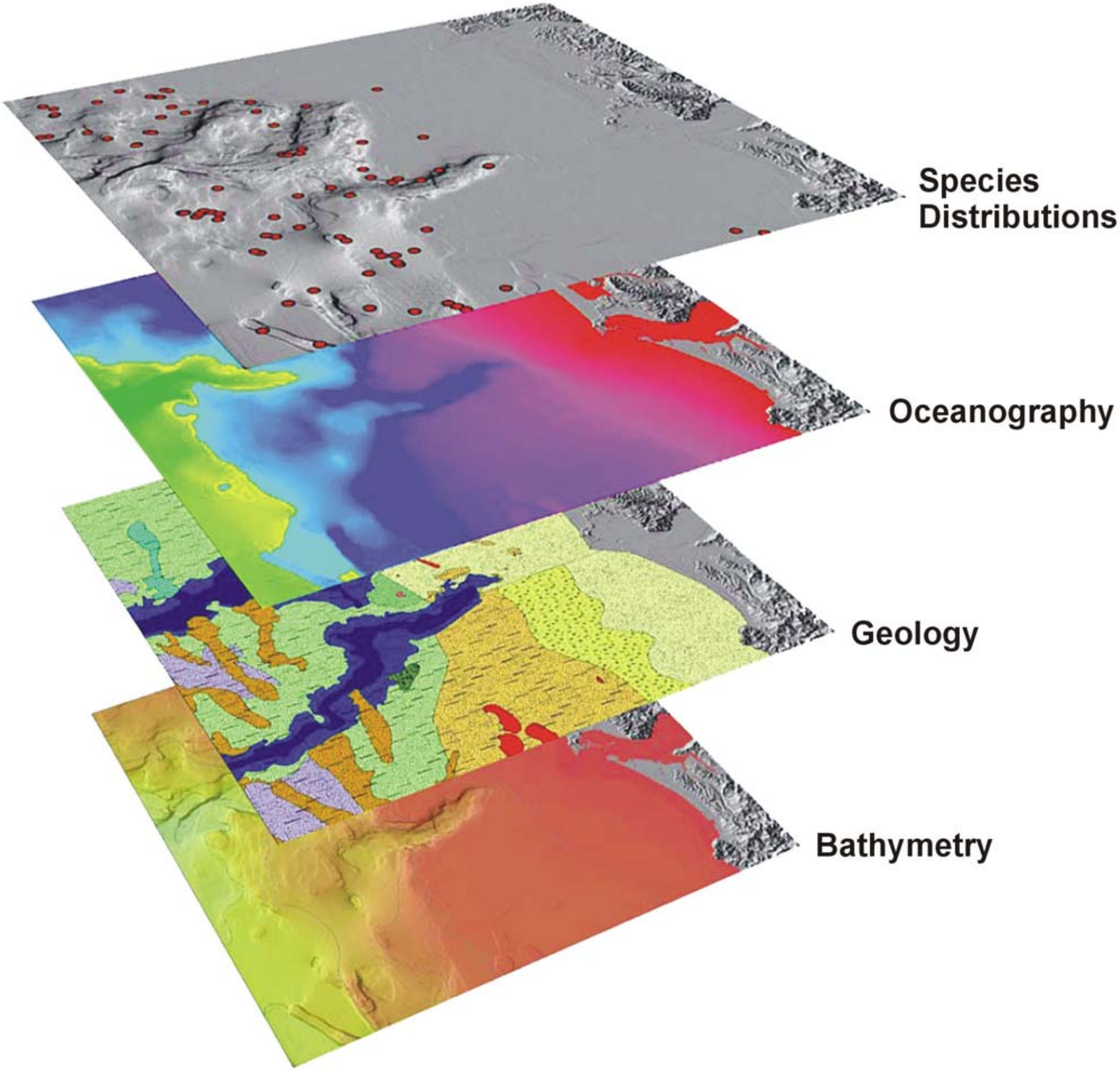


Figure 20. Spatial variability in the CCLME should be evaluated in developing IEA. Strata of ocean properties, including bathymetry, geology, oceanography and species distributions will be considered in future IEA reports. Reproduced with permission from the Pacific Coast Ocean Observing System Science Plan (2004).

NOAA Technical Memorandum NMFS-NWFSC-139

Ecosystem Status Report of the California Current for 2017:

A Summary of Ecosystem Indicators Compiled by the California Current Integrated Ecosystem Assessment Team (CCIEA)

https://doi.org/10.7289/V5/TM-NWFSC-139

November 2017

U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Northwest Fisheries Science Center

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November 2017

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NOAA Technical Memorandums NMFS-NWFSC are available at the Northwest Fisheries Science Center website, https://www.nwfsc.noaa.gov/index.cfm.

Reference this document as follows:

Harvey, C., N. Garfield, G. Williams, K. Andrews, C. Barceló, K. Barnas, S. Bograd, R. Brodeur, B. Burke, J. Cope, L. deWitt, J. Field, J. Fisher, C. Greene, T. Good, E. Hazen, D. Holland, M. Jacox, S. Kasperski, S. Kim, A. Leising, S. Melin, C. Morgan, S. Munsch, K. Norman, W. T. Peterson, M. Poe, J. Samhouri, I. Schroeder, W. Sydeman, J. Thayer, A. Thompson, N. Tolimieri, A. Varney, B. Wells, T. Williams, and J. Zamon. 2017. Ecosystem Status Report of the California Current for 2017: A Summary of Ecosystem Indicators Compiled by the California Current Integrated Ecosystem Assessment Team (CCIEA). U.S. Department of Commerce, NOAA Technical Memorandum NMFS-NWFSC-139. https://doi.org/10.7289/V5/TM-NWFSC-139

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Executive Summary

This document is a companion to the ecosystem status report (ESR) provided by the California Current Integrated Ecosystem Assessment team (CCIEA) to the Pacific Fishery Management Council (PFMC) in March of 2017. The CCIEA team provides such reports annually, as one component of the overall CCIEA goal of providing quantitative, integrative science tools, products, and synthesis in support of ecosystem-based management of marine resources in the California Current.

The indicators summarized in this report represent our best understanding of environmental, ecological, and socioeconomic conditions in the California Current Ecosystem approximately through 2016, though some time series are slightly more up-to-date and others slightly less so depending on the time required for data processing. The indicators have been codeveloped by the CCIEA team and the PFMC through an iterative process since the inception of the CCIEA project in 2009.

Oceanographic and climate-related indicators revealed a shift relative to the previous several years. Following the unprecedented warm anomaly of 2013–16 and the major El Niño event of 2015–16, most large-scale climate indices for the Northeast Pacific (the Oceanic Niño Index, the Pacific Decadal Oscillation, and the North Pacific Gyre Oscillation) returned to relatively neutral values. Coastal upwelling was relatively weak in the northern California Current throughout 2016; upwelling along the central coast was initially weak, but strengthened by summer, while upwelling on the southern coast was average to above-average. Snowpack rebounded from the extremely low levels of 2015, although much of the 2016 snow melted rapidly, leading to low streamflows; precipitation was well above average in early 2017.

Ecological indicators are expected to lag, to varying degrees, behind the shift in oceanographic and climate patterns. Copepod biomass off Newport, OR, was dominated by relatively energy-poor species as of fall 2016, similar to observations from the last several years. The spring/summer pelagic forage community was once again highly diverse in 2016. Surveys experienced poor catches of sardine (*Sardinops sagax*), market squid (*Doryteuthis opalescens*), and euphausiids. However, surveys had high but patchy catches of juvenile rockfish (*Sebastes* spp.), juvenile Pacific hake (*Merluccius productus*), and anchovy (*Engraulis mordax*). Chinook salmon (*Oncorhynchus tshawytscha*) escapements through 2014–15 varied by region and life-history type. Environmental conditions appear to have been poor for Chinook and coho salmon (*O. kisutch*) that went to sea over the past several years. California sea lions (*Zalophus californianus*) at the San Miguel Island colony experienced very poor foraging conditions to support pups in the 2015 cohort, though preliminary evidence suggests better conditions for the 2016 pups.

Socioeconomic indicators are primarily focused on fishing activity and on human wellbeing in fishery-dependent coastal communities. Commercial fishing landings and revenues declined markedly in 2015, driven mainly by drops in the harvest of Pacific hake, coastal pelagic species, and crabs. The diversification of commercial fishery landings continued the long-term declining trend at all scales (i.e., by state, vessel size, and ex-vessel revenue levels). An index of social vulnerability suggested that several commercial fishing-dependent coastal communities have disproportionately high social vulnerability, and therefore may be heavily impacted by shocks to commercial fishing revenues.

Introduction

Ecosystem-based management of fisheries and other marine resources has emerged as a priority in the U.S. (Ecosystem Principles Advisory Panel 1999, Fluharty et al. 2006, McFadden and Barnes 2009, NMFS 2016) and for many marine resource management agencies worldwide (Browman et al. 2004, Sainsbury et al. 2014, Walther and Möllmann 2014, Long et al. 2015). According to its official policy statement, the NOAA National Marine Fisheries Service (NOAA Fisheries) defines ecosystem-based fisheries management (EBFM) as "*a systematic approach to fisheries management in a geographically specified area that contributes to the resilience and sustainability of the ecosystem; recognizes the physical, biological, economic, and social interactions among the affected fishery-related components of the ecosystem, including humans; and seeks to optimize benefits among a diverse set of societal goals*" (NMFS 2016). This definition includes considerations of interactions within and among fisheries, protected species, aquaculture, habitats, and human communities that depend upon fisheries and related marine ecosystem services. It also includes consideration of the direct and indirect impacts of fisheries on other ecosystem components. An EBFM approach is intended to improve upon traditional fishery management practices that primarily are focused on the level of individual fished stocks.

Successful implementation of EBFM requires a considerable amount of effort and coordination, due to the formidable amount of information required and uncertainty involved. Research on marine systems and adjacent, associated systems amasses tremendous amounts of data from numerous disciplines. These data represent a wide range of processes and are expressed in currencies ranging from physical or chemical units to species biomass estimates to revenue streams or sociological measures. Assimilating this volume of diverse information into synthesis products is inherently difficult. Furthermore, even the best modern monitoring programs are still confronted with uncertainties because of the technical, logistical, and financial challenges of measuring statuses and changes in large, complex, and highly variable systems like the ocean and the human societies that depend upon and interact with it.

In response to this complexity and uncertainty, scientists throughout the world have developed many frameworks for organizing science and information in order to clarify and synthesize this overwhelming volume of data into science-based guidance for policymakers. NOAA Fisheries has adopted a framework called Integrated Ecosystem Assessment (IEA; Levin et al. 2008, Levin et al. 2009), which can be summarized in five progressive steps (Figure 1):

1. Identifying and scoping ecosystem goals, objectives, targets and threats.
2. Assessing the status and trends of the ecosystem through the use of valid ecosystem indicators.
3. Assessing the risk of key threats and stressors to the ecosystem.
4. Analyzing management strategy alternatives and identifying potential tradeoffs.
5. Implementing selected actions, and monitoring and evaluating management success.

As implied by Figure 1, this approach is iterative. Following the implementation of management actions, all other steps in the IEA loop must be revisited in order to ensure that a) evolving goals and objectives are clearly identified, b) monitoring plans and indicators are appropriate for the management objectives in mind, c) existing and emerging risks are properly prioritized, and d) management actions are objectively and regularly evaluated for success.

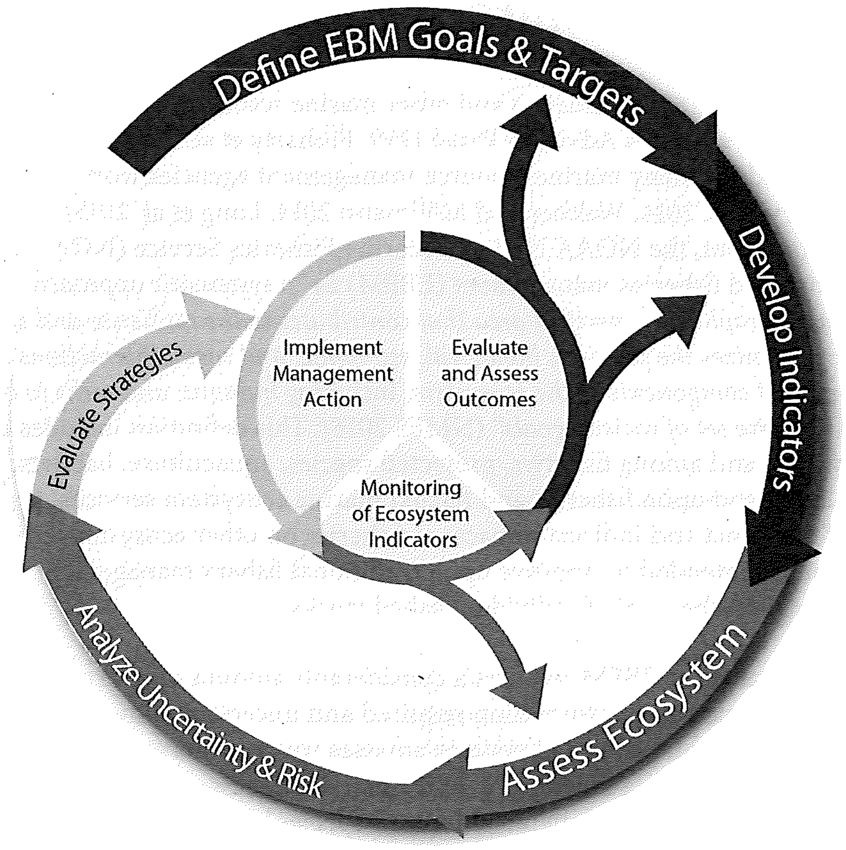

Figure 1. Loop diagram of the five progressive steps in iterations of the integrated ecosystem assessment (IEA) process. From Samhouri et al. (2014).

As the IEA framework was adopted at the national level, regional teams began implementing the IEA approach in different large marine ecosystems in U.S. waters. In 2009, NOAA line offices along the U.S. West Coast initiated the California Current Integrated Ecosystem Assessment (CCIEA). The CCIEA team focused on the California Current, a major current system oriented north–south at the eastern boundary of the northeast Pacific Ocean. The California Current flows along the West Coast of North America from central Vancouver Island, Canada, in the north, to Punta Eugenia, Mexico, in the south. Since its inception, and in keeping with the principles of ecosystem-based management, the CCIEA team has recognized that the California Current Ecosystem (CCE) is a dynamic, interactive, social–ecological system with multiple levels of organization and diverse goals and endpoints from the natural and social sciences (Figure 2). The challenging task of assembling and interpreting information from this broad range of disciplines, locations, and time frames engages over 50 scientists from NOAA's Northwest and Southwest Fisheries Science Centers, other NOAA offices, and colleagues from other agencies, academia, and nongovernmental entities. Information on CCIEA research efforts, tools, products, publications, partnerships, and points of contact is available on the CCIEA website.[1]

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[1] http://www.integratedecosystemassessment.noaa.gov/regions/california-current-region/index.html

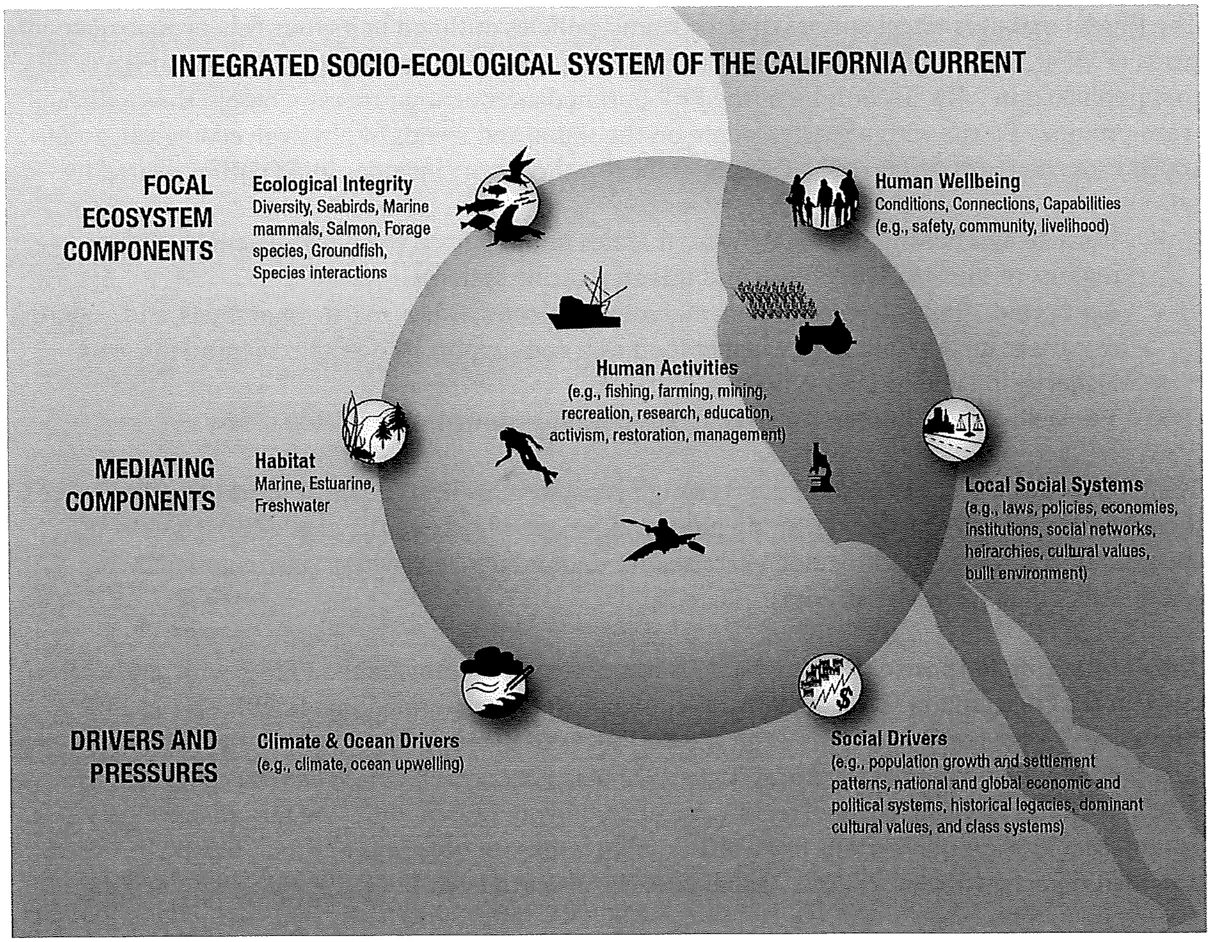

Figure 2. Conceptual model of the California Current social–ecological system. The model represents the complex and inextricable connections between natural components (left) and human components (center and right). These components are arranged in three tiers: 1) focal ecosystem components, which are often associated with broad objectives such as ecological integrity and human wellbeing; 2) mediating components, such as habitat and local social systems; and 3) drivers and pressures, which are generally external forces on the ecosystem. Human activities are placed at the center to emphasize their broad extent and because they are where management actions are directly implemented in order to achieve objectives elsewhere in the system. From Levin et al. (2016).

The primary management partner of the CCIEA team to date has been the Pacific Fishery Management Council (PFMC),[2] made up of representatives from California, Oregon, Washington, and Idaho; a representative of the West Coast indigenous tribes; four at-large members; one NOAA Fisheries member; and five nonvoting members representing key state and federal partners. The PFMC is the regional fishery management council that oversees federally managed fisheries and implementation of the Magnuson–Stevens Fishery Conservation and Management Act in the Exclusive Economic Zone off the U.S. West Coast.

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[2] http://www.pcouncil.org

The PFMC manages target species directly under policies outlined in its four fishery management plans (FMPs), and may incorporate nonbinding guidance from its Fishery Ecosystem Plan (FEP),[3] first published in 2013. Section 1.4 of the FEP outlined a reporting process wherein the CCIEA team provides PFMC with a yearly update on the status and trends of physical, ecological, and social ecosystem attributes of the CCE. Specifically, the report includes information related to:

- Climate and oceanographic drivers, at scales ranging from the North Pacific basin to regions of the U.S. West Coast and inland riverine systems.
- Key species groups (e.g., plankton, macroinvertebrates, fishes, marine mammals, and seabirds) that make up the California Current food web and support its overall ecological integrity.
- Fisheries-related human activities.
- The wellbeing of humans in coastal communities along the U.S. West Coast.

The report tracks ecosystem attributes through ecosystem indicators, most of which were derived through a rigorous indicator screening process developed by Kershner et al. (2011); details of specific CCIEA indicator screening exercises are documented elsewhere (Levin and Schwing 2011, Levin et al. 2013, Harvey et al. 2014).

The overarching purpose of the ecosystem status reports is to provide the PFMC with a general sense of the condition of the ecosystem, as context for its decisionmaking. In 2015–16, an FEP "initiative" was enacted to further align the indicators in the reports to the needs of the PFMC (see Supplemental Ecosystem Workgroup Report 2).[4] Since 2012, the CCIEA team has provided the PFMC with five ecosystem status reports, most recently in March 2017. The reports have previously been available as online sections of PFMC briefing books for meetings at which the CCIEA team provided reports (November 2012, March 2014–17; also available at CCIEA Publications: Reports[5]).

This Technical Memorandum is a companion document to the ecosystem status report delivered by the CCIEA team to the PFMC in March 2017, representing the status and trends of ecosystem indicators in the CCE through 2016 and, in some cases, early 2017 (Harvey and Garfield 2017a,b). It is intended to be the first in an ongoing annual series of Technical Memorandums that will provide a more thorough ecosystem status report of the CCE than the one we present to the PFMC. We will continue to provide the annual report to the PFMC, and this Technical Memorandum series will largely be based on that report. However, as this series evolves, the Technical Memorandums will incorporate more indicators and analyses, covering a broader range of ecosystem attributes. This is because the CCIEA team looks to support other management partners in addition to the PFMC, and our goal over the next several years is for our annual ecosystem status report to feature information in support of ecosystem-based management (EBM) in other sectors and services in addition to fisheries (Slater et al. 2017). The Technical Memorandum format should therefore enable increased information content, contributions from a broader range of authors, and value to a wider range of audiences than the reports produced to date. It is our hope that these improvements will lead to greater dialogue with potential partners and stakeholders; such dialogue and engagement is at the heart of the initial step of the IEA process (Figure 1), and is essential to each other step in all iterations as well.

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[3] http://www.pcouncil.org/ecosystem-based-management/fep/

[4] http://www.pcouncil.org/wp-content/uploads/2016/09/D1a_Sup_EWG_Rpt2_SEPT2016BB.pdf

[5] http://www.integratedecosystemassessment.noaa.gov/regions/california-current-region/publications.html

Notes on Interpreting Time Series Figures

Throughout this report, many data figures will follow one of two common formats, time series plots or quad plots, both illustrated with sample data in Figure 3; see figure caption for details. Time series plots generally contain a single dataset, whereas quad plots are used to summarize the recent averages and trends for multiple time series in a single panel, as when we have time series of multiple populations that we want to compare in a reasonably simple manner. Where possible, we also include estimates of error or uncertainty in the data. Generally, error estimates are standard deviations or standard errors in the observations. In coming years, we will include model fits to time series data where appropriate; model fits will most likely be derived from Multivariate Auto-Regressive State Space (MARSS) models, as has been recommended to the CCIEA team by the PFMC Scientific and Statistical Committee's Ecosystem Subcommittee (SSCES).

Sampling Locations

Figure 4 shows the CCE and major headlands that demarcate potential biogeographic boundaries, in particular Cape Mendocino and Point Conception. We generally consider the region north of Cape Mendocino to be the "Northern CCE," the region between Cape Mendocino and Point Conception the "Central CCE," and the region south of Point Conception the "Southern CCE."

Figure 4a also shows sampling locations for much of the regional climate and oceanographic data (see Regional Climate Indicators) presented in this report. In particular, many of the physical and chemical oceanographic data summarized in this document are collected on the Newport Line off Oregon and the California Cooperative Oceanic Fisheries Investigations (CalCOFI) grid off California. Physical oceanography sampling is further complemented by basin-scale observations and models.

Freshwater habitats worldwide can be spatially grouped into "ecoregions" according to the designations of Abell et al. (2008); see also Freshwater Ecoregions of the World, FEOW[6]). The freshwater ecoregions in the CCE are shown in Figure 4b (derived from FEOW), and are the basis by which we summarize freshwater habitat indicators relating to streamflow and snowpack (see Hydrologic Indicators).

The map in Figure 4c represents sampling for most biological indicators, including copepods (Northern Copepod Biomass Anomaly), forage species (Regional Forage Availability), California sea lions (Marine Mammals), and Seabirds. Not shown is groundfish bottom trawl sampling (see Groundfish), which covers most trawlable habitat on the shelf and upper slope (depths of 55–1,280 m) in U.S. waters; the blue and green polygons in Figure 4c roughly approximate the areal extent of the NOAA Fisheries West Coast groundfish bottom trawl survey (Keller et al. 2017).

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[6] http://www.feow.org

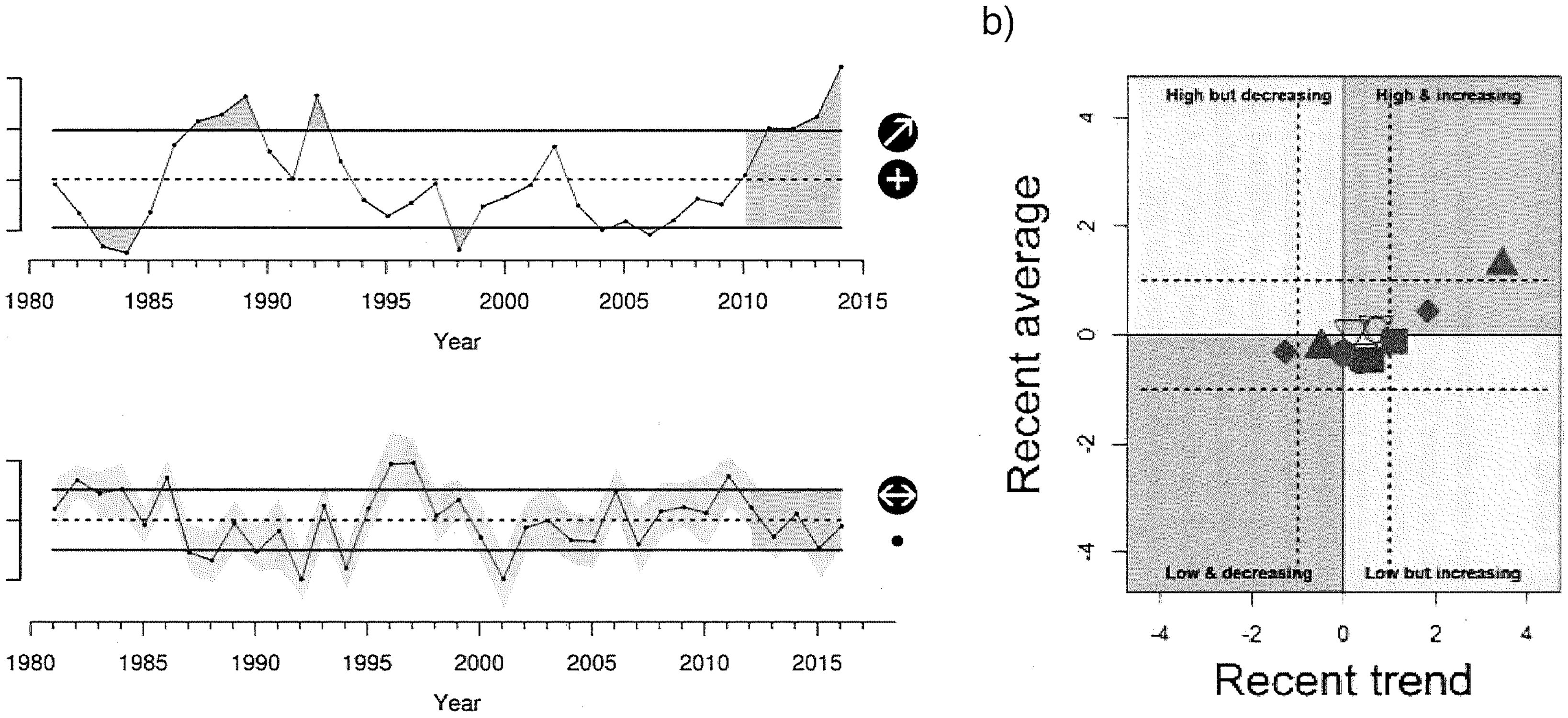

Figure 3. a) Sample time series plots, with indicator data relative to mean (dashed line) and ±1 SD, standard deviation (solid lines), of the full time series. Arrow at right indicates if the trend over the most recent 5 years (shaded green) is positive (↗), negative (↘) or neutral (↔). Symbol at lower right indicates if the recent mean was greater than (+), less than (–), or within 1 SD (·) of the long-term mean. When possible, time series include 95% confidence intervals (gray shading, lower panel). b) Sample quad plot. Each point represents one normalized time series. The position of a point indicates if the recent years of the time series are above or below the long-term average, and if they are increasing or decreasing; quadrants are "stoplight" colored to highlight the status of the indicator condition (where green = improving conditions, yellow = neutral, and red = declining conditions). Dashed lines represent ±1 SD of the full time series.

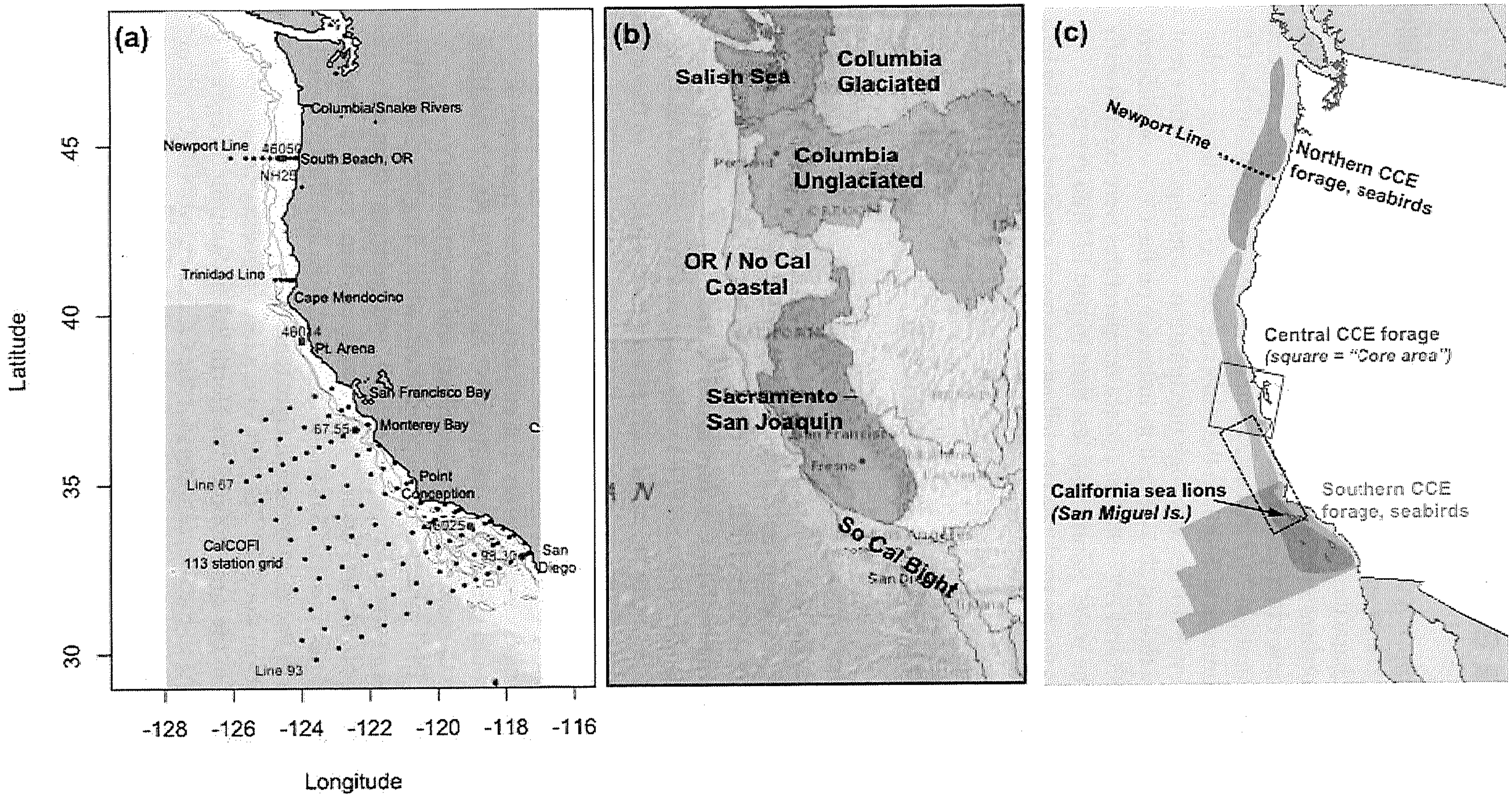

Figure 4. Maps of the California Current Ecosystem (CCE) and sampling areas. a) Key geographic features and oceanographic sampling locations. b) Freshwater ecoregions, where snowpack and streamflow indicators are measured. c) Biological sampling areas for copepods (Newport Line), pelagic forage species, seabirds, and California sea lions. Solid box = the "core" sampling area for forage in the Central CCE. Dotted box approximates the foraging area for adult female California sea lions from the San Miguel colony.

Climate and Ocean Drivers

Climate and ocean processes determine important ecosystem characteristics in the CCE, including water and air temperature, winds, currents and mixing of ocean waters, water chemistry, and precipitation. These environmental characteristics are important drivers of ecological processes and human activities. Overall, the northeastern Pacific Ocean has experienced exceptional climate variability in recent years, reaching new extremes for many indicators related to climate and ocean drivers. After a series of events beginning in 2013 that caused unprecedented warming in the CCE, conditions have changed since the summer of 2016 into the winter of 2016–17, producing cooler coastal waters and a succession of winter storms with high precipitation. A strong El Niño event peaked in the tropical Pacific in the winter of 2015–16, but its influence on the CCE was different than strong El Niño events of 1982–83 and 1997–98. Sea surface temperatures were exceptionally high, but the extent of heating into the water column was less than in past El Niño events (Figure 5). Late winter upwelling was not as weak, and upwelling was much stronger leading into the spring. The following sections provide in-depth descriptions of basin-scale, regional-scale, and hydrologic indicators of climate and ocean variability in the CCE.

Basin-Scale Indicators

The CCE is driven by atmosphere–ocean energy exchange that occurs on many temporal and spatial scales. To capture large-scale variability, the CCIEA team tracks three indices: the status of the equatorial El Niño–Southern Oscillation (ENSO), described by the Oceanic Niño Index (ONI); the Pacific Decadal Oscillation (PDO); and the North Pacific Gyre Oscillation (NPGO). Positive ONI and PDO values and negative NPGO values usually denote conditions that lead to low CCE productivity, whereas negative ONI and PDO values and positive NPGO values are associated with periods of high CCE productivity. These indices vary independently, so there is a wide range of observed variability in the CCE.

ENSO events impact the CCE by modifying the jet stream and storm tracks, deepening the nearshore thermocline, and generating coastal currents that enhance poleward transport of equatorial and subequatorial waters (and species). A positive ONI indicates El Niño conditions, which usually means more storms to the south, weaker upwelling, and lower primary productivity in the CCE. A negative ONI means La Niña conditions, which usually lead to higher productivity. The PDO is related to sea surface temperature (SST), and is derived from sea surface temperature anomalies (SSTa) in the Northeast Pacific, which often persist in "regimes" that last for many years. In positive PDO regimes, coastal SSTa in the Gulf of Alaska and the CCE tend to be warmer, while those in the North Pacific Subtropical Gyre tend to be cooler. Positive PDOs are associated with lower productivity in the CCE. The NPGO is a low-frequency variation of sea surface height, indicating variations in the circulation of the North Pacific Subtropical Gyre and the Alaskan Gyre, which in turn relate to the source waters for the CCE. Positive NPGO values are associated with increased equatorward flow, along with increased surface salinities, nutrients, and chlorophyll-*a*. Negative NPGO values are associated with decreases in such values, implying fewer subarctic source waters and generally lower productivity.

This past year saw the ONI shift from El Niño to neutral and even La Niña conditions, the PDO switch from strongly positive to neutral, and the NPGO move from strongly negative to neutral (Figure 6). Each of these indices would suggest a return to conditions of higher productivity. However, the Northeast Pacific and the CCE continued to show the aftereffects of the very anomalous conditions experienced during 2013–16. The large marine heat wave, a.k.a. "the Blob" (Bond et al. 2015), dissipated in fall 2016 in the Northeast Pacific, but anomalously warm surface waters were present in the Gulf of Alaska and immediately along the North American west coast during the winter (Figure 7). Summer SSTa showed no lasting influence of the El Niño event, with anomalies average to slightly below-average along the coast from Vancouver to San Diego. However, temperatures in subsurface waters of the Northeast Pacific remained warm, with anomalies >1°C down to 160 m and >0.5°C down to below 200 m (Harvey and Garfield 2017b). This deep warming is interpreted as a remnant effect of the marine heat wave.

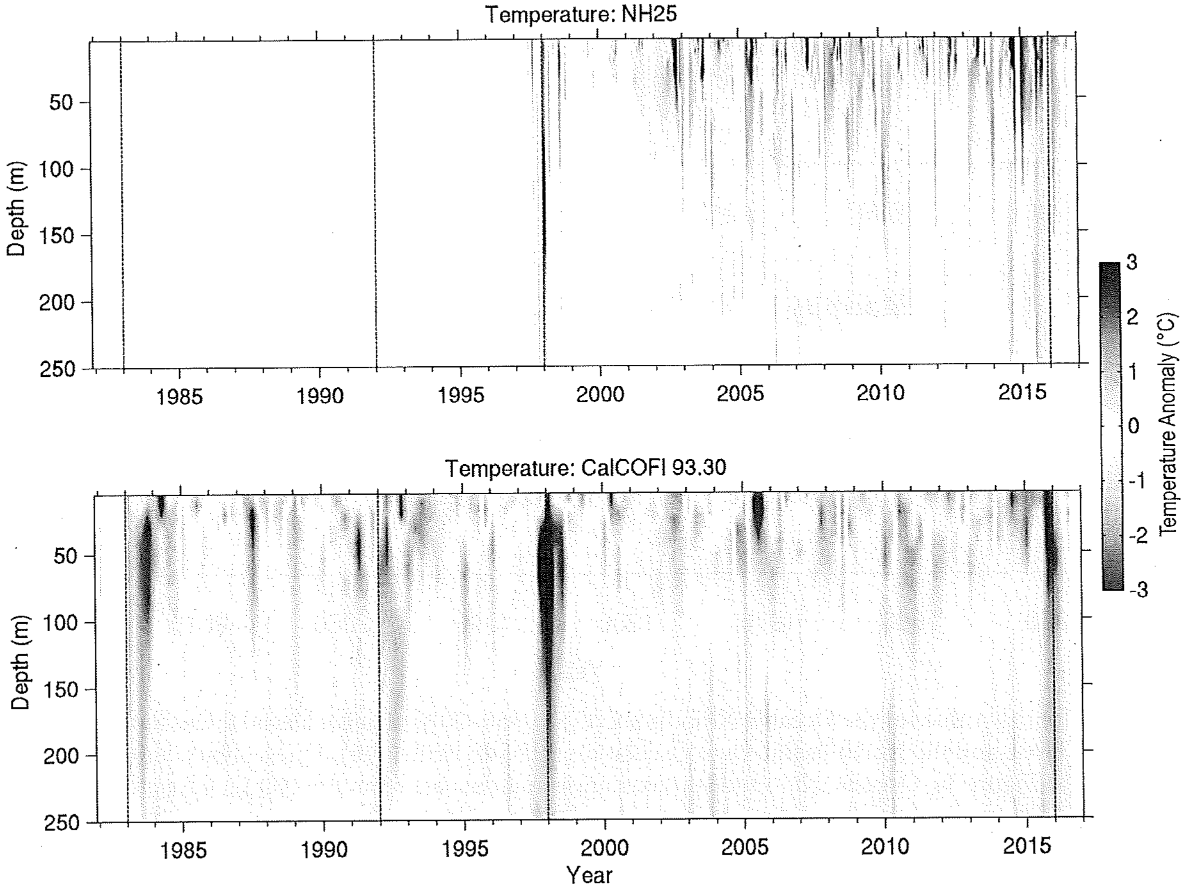

Figure 5. Time–depth temperature contours from nearshore stations NH25 and CalCOFI 93.30 (see Figure 3a). Vertical lines mark El Niño events. Newport Hydrographic (NH) line temperature data are from Dr. Bill Peterson (NOAA). CalCOFI hydrographic line data are from the CalCOFI website.* CalCOFI data before 2016 are CSV format files from the Access database, while 2016 data are preliminary CSV files from the CTD (conductivity, temperature, depth) database.

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* http://calcofi.org/data.html

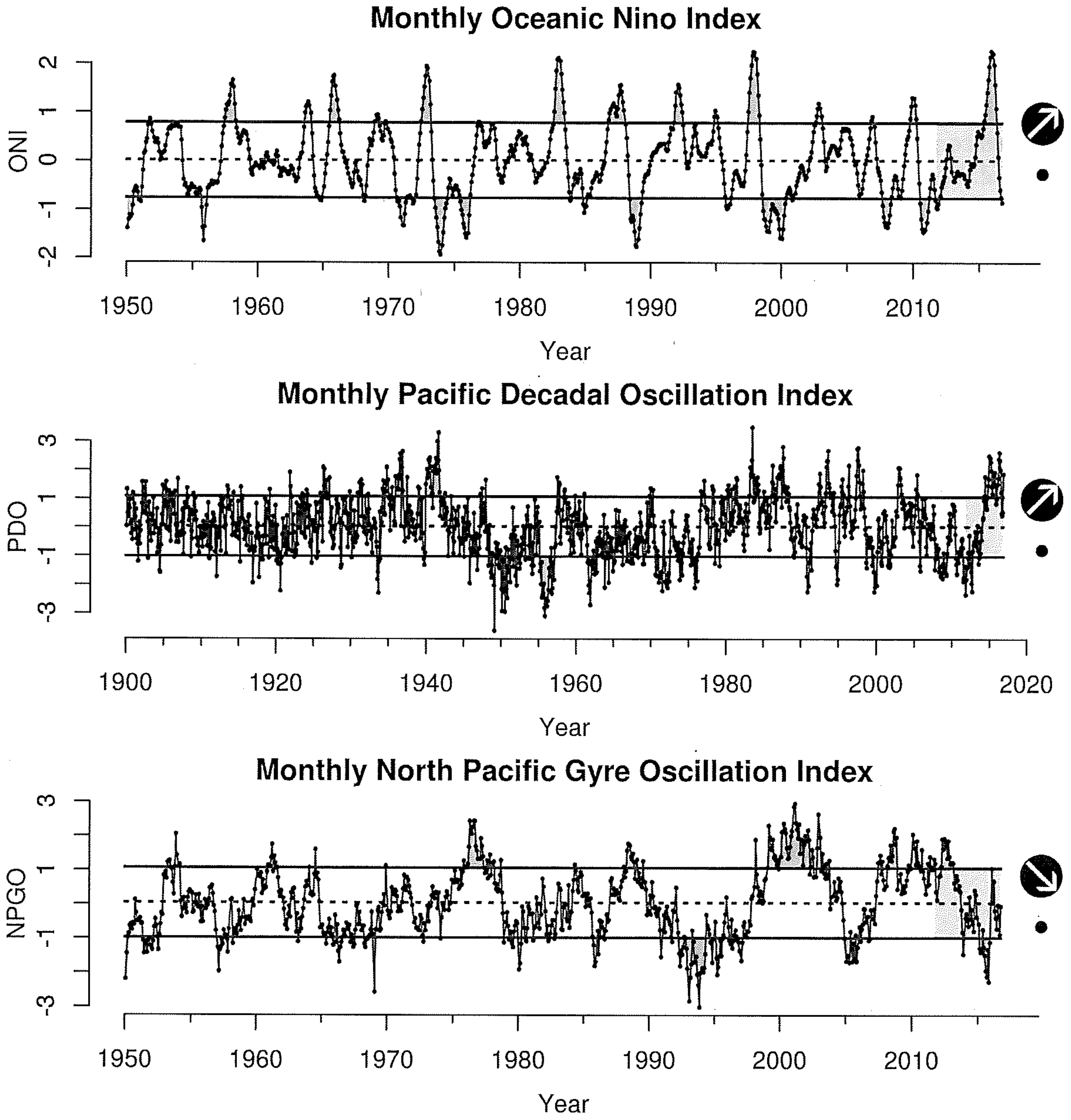

Figure 6. Monthly values of the Oceanic Niño Index (ONI; 1950–2016), Pacific Decadal Oscillation (PDO; 1900–2016), and the North Pacific Gyre Oscillation (NPGO; 1950–2016). Lines, colors, and symbols are as in Figure 3a. Oceanic Niño Index information and data are from the NOAA Climate Prediction Center.* Pacific Decadal Oscillation data are from Dr. Nate Mantua (NOAA) and are served by the University of Washington Joint Institute for the Study of the Atmosphere and Ocean (JISAO).† North Pacific Gyre Oscillation data are from Dr. Emanuele Di Lorenzo (Georgia Institute of Technology).‡

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[*] http://www.cpc.ncep.noaa.gov/products/analysis_monitoring/ensostuff/ONI_change.shtml

[†] http://research.jisao.washington.edu/pdo/

[‡] http://www.o3d.org/npgo/

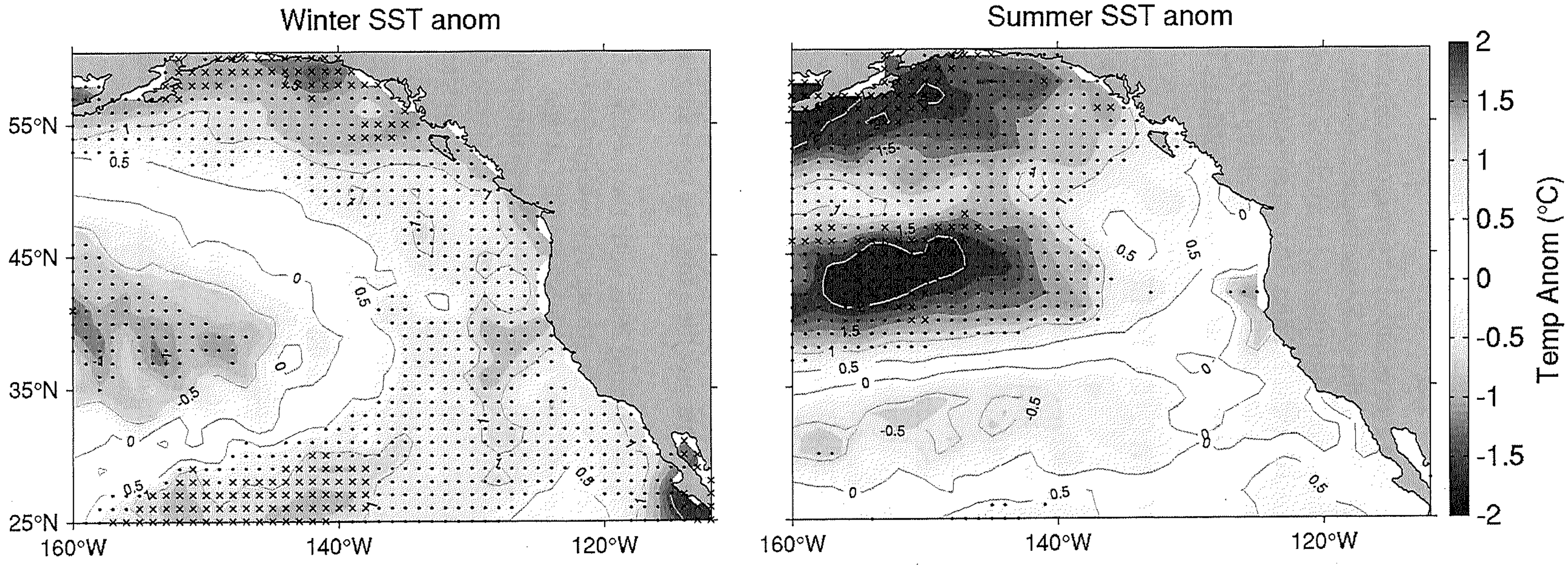

Figure 7. Sea surface temperature anomalies (SSTa) in winter (Jan–Mar, left) and summer (Jul–Sep, right), 2016. The time series at each grid point began in 1982. Positive anomalies of the marine heat wave and El Niño are seen in the Gulf of Alaska in winter and summer, and off Baja California in winter. Black circles mark cells where the anomaly was >1 SD above the long-term mean. Black Xs mark cells where the anomaly was the highest of the time series. Sea surface temperature maps are optimally interpolated remotely-sensed temperatures (Reynolds et al. 2007). The daily optimal interpolated Advanced Very High Resolution Radiometer (AVHRR) SST can be downloaded from the NOAA SWFSC Environmental Research Division Data Access Program (ERDDAP).*

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* http://upwell.pfeg.noaa.gov/erddap/griddap/ncdcOisst2Agg.html

Another marine heat wave formed off Baja California in 2014 and strengthened in 2015, keeping nearshore SSTs >0.5°C above normal. This event was likely caused by weaker atmospheric forcing in the Southern California Bight and along the Mexican coast (Leising et al. 2015, McClatchie et al. 2016). By summer 2016, SSTs in this region dropped to near-average values (Figure 7).

In summary, while the 2015–16 El Niño was one of the largest ever recorded in terms of equatorial warming and the ONI, the large-scale environmental response of the CCE was dominated in the north by the lingering impacts of the marine heat wave, with only moderate influence from the El Niño, whereas in the south, the CCE was more strongly influenced by the El Niño. Thorough summaries of these dynamics are in Leising et al. (2015) and McClatchie et al. (2016). These large-scale forces help explain the dynamics of some biological indicators in Focal Components of Ecological Integrity, below.

Regional Climate Indicators

Seasonal high pressure over the Gulf of Alaska and low pressure over the U.S. Southwest drive the upwelling-favorable winds that fuel the high spring–summer productivity that is typical of the CCE. Upwelling is a physical process of moving cold, nutrient-rich water from deep in the ocean up to the surface, and is forced by strong, northerly alongshore winds. Upwelling is critically important to productivity and ecosystem health in the CCE, as it is local coastal upwelling that allows the primary production at the base of the food web. The most common metric of upwelling is the Bakun Upwelling Index (UI), which is a measure of the magnitude of upwelling anywhere along the coast. The timing, strength, and duration of upwelling in the CCE are highly variable by region and by year. The cumulative upwelling index (CUI) is one way to display this variability. The CUI provides an estimate of the net influence of upwelling on ecosystem structure and productivity over the course of the year. The CUI integrates the onset date of upwelling-favorable winds (the "spring transition"), a general indication of the strength of upwelling, relaxation events, and the end of the upwelling season.

Upwelling strength displayed significant regional variability during 2016, with the least favorable conditions in the Northern CCE. At lat 45°N (near Newport, OR), strong downwelling from January through March was followed by average upwelling from April to July; CUI at this latitude was much lower than the strong upwelling of 2015 (Figure 8), and similar to the reduced upwelling of the 1998 El Niño event (McClatchie et al. 2016). At lat 39°N (near Point Arena, CA), the spring transition to upwelling began weakly in mid-March and strengthened in May, leading to above-average upwelling by July and comparable CUI to 2015 by August. In the Southern California Bight (lat ~33°N), the CUI was close to the long-term mean during the beginning of the season, and above average after June. This is in stark contrast to the reduced upwelling seen throughout the year in 1998 following that year's comparably large El Niño. Additional upwelling information for 2012–16 is summarized in Harvey and Garfield (2017b).

Although CUI was stronger in the south than the north in 2016, productivity did not increase concomitantly as one might expect. This is likely because of increased stratification and a deeper thermocline in this region, due to the lingering effects of the marine heat wave, plus the influence of the 2015–16 El Niño event (McClatchie et al. 2016).

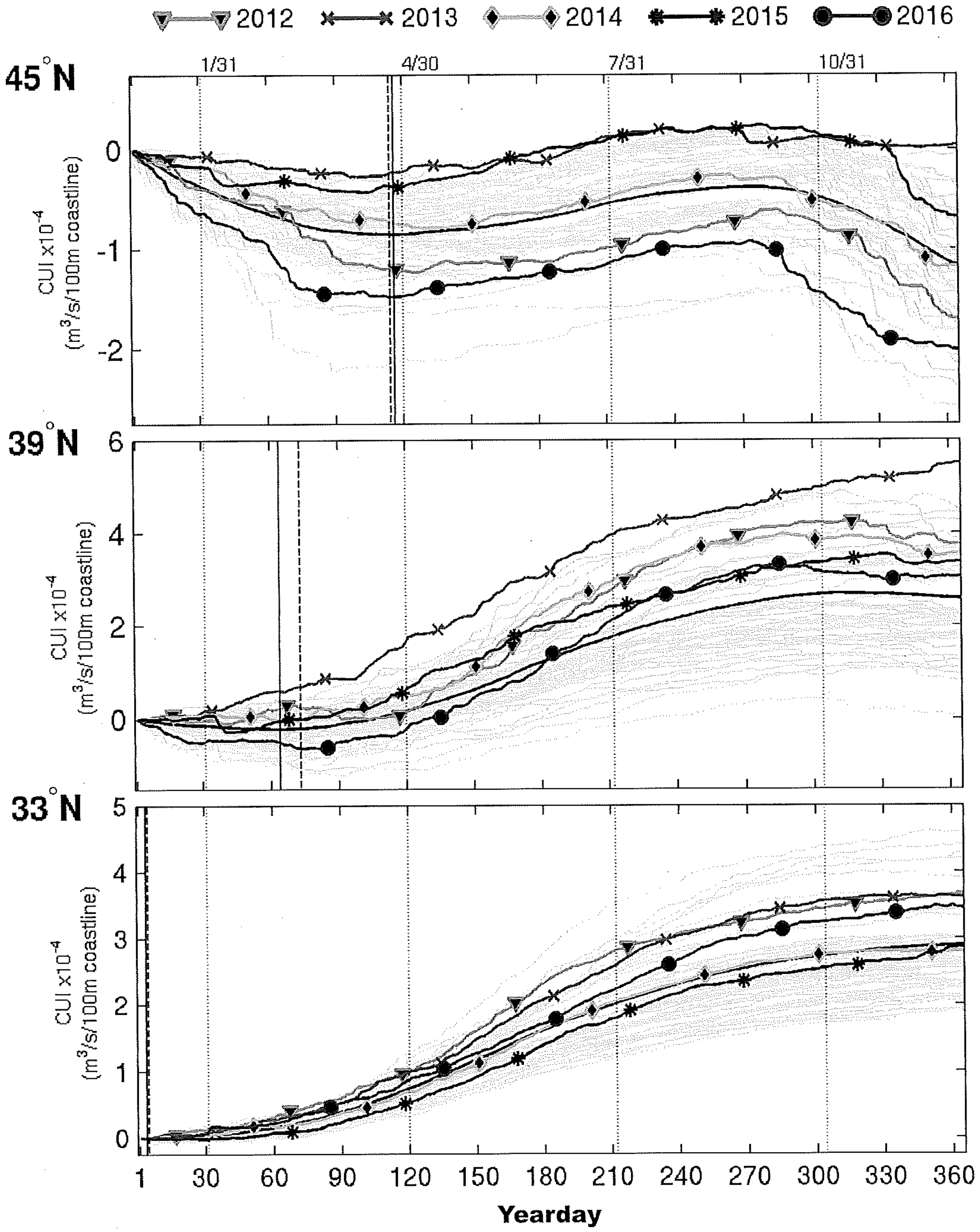

Figure 8. Cumulative Upwelling Index (CUI) at three latitudes, 1967–2016. Black trend = long-term mean; gray trends = 1967–2011; colored trends = 2012–16. Black vertical lines mark the 2016 spring transition date (dashed) and long-term mean spring transition date (solid). Dotted red vertical lines mark the ends of January, April, July, and October. Cumulative Upwelling Index curves are calculated from the six-hourly upwelling index product.*

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* http://upwell.pfeg.noaa.gov/erddap/tabledap/erdUI216hr.html

Hypoxia and Ocean Acidification

Nearshore dissolved oxygen (DO) levels and ocean acidification (OA) are related to the strength of coastal upwelling. DO is required for organismal respiration, and DO levels are dependent on a number of physical and biological processes, including circulation, air–sea exchange, and community-level production and respiration. Waters with DO levels below 1.4 ml/L (2 mg/L) are considered to be hypoxic. Low DO can compress habitat and cause stress or even die-offs for sensitive species. OA is caused by increased levels of anthropogenic CO_2 in seawater, which impacts the chemical environment of marine organisms by reducing both pH and carbonate ion concentrations. A key indicator of OA effects is aragonite saturation state, a measure of how corrosive seawater is to organisms with shells made of aragonite (a form of calcium carbonate). Values <1.0 indicate corrosive conditions that have been shown to be stressful for many CCE species, including oysters, crabs, and pteropods. Upwelling, which drives primary production in the CCE, also transports hypoxic, acidified waters onto continental shelves, where increased community-level respiration can further reduce water-column DO and exacerbate OA (Chan et al. 2008, Feely et al. 2008).

At the three stations shown here, DO was seasonally variable, with peaks in the winter, but all measurements were consistently above the hypoxia threshold of 1.4 ml/L in 2016 (Figure 9). The five-year annual trend at each site has been stable, but there is evidence of seasonal increases in DO. Briefly, station NH25 off Newport, OR, has experienced increasing winter DO over the past five years. At the nearshore station 93.90 off southern California, DO has declined since 1984, driven mainly by winter values, and was ~1 SD below the mean in winter 2016. However, the recent trend is stable and possibly increasing based on seasonal averages. At the offshore station 90.90, summer DO has increased in recent years. Nearshore DO values are almost always lower than those offshore (93.30 vs. 90.90 in Figure 9). Additional data are summarized in Harvey and Garfield (2017b).

In nearshore waters off Newport, OR (station NH5), aragonite levels at 40 m depth are typically saturated (>1.0) during the winter and spring, and then fall below 1.0 in the summer and fall; this was the case again in 2016 (Figure 10). Further offshore (station NH25) at 150 m depth, aragonite saturation state follows the same seasonal cycle but across a narrower range, and aragonite levels at this area and depth are almost always <1.0. However, aragonite levels were elevated slightly in the anomalous conditions of the past two years. In fact, according to seasonal data, winter aragonite levels have increased over the past five years at both stations (Harvey and Garfield 2017b).

Hydrologic Indicators

Freshwater conditions are critical for salmon populations and for estuarine habitats that support many marine species. The freshwater indicators presented here focus on snowpack and streamflow, and are summarized by freshwater ecoregion (Figure 4b). Snow-water equivalent (SWE) is the total water content in snowpack, which provides a steady source of freshwater into the summer months. Maximum streamflows in winter and spring are important for habitat formation, but can cause scouring of salmon nests. Minimum streamflows in summer and fall can restrict habitat for in-stream juveniles and migrating adults. All three indicators are influenced by climate and weather patterns, and will be affected as the effects of climate change intensify.

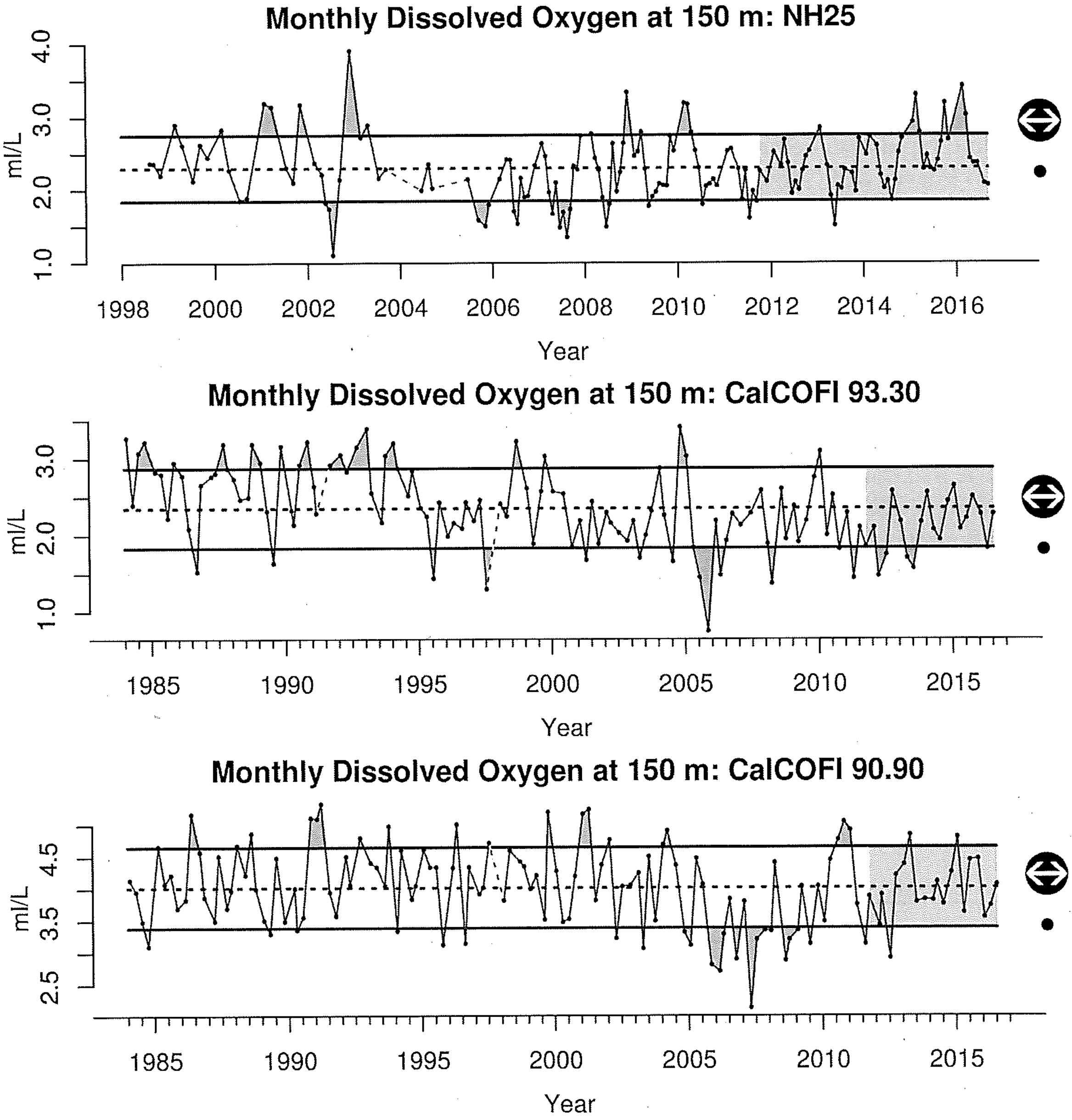

Figure 9. Dissolved oxygen (DO) at 150 m depth off Oregon and southern California through 2016. Stations NH25 (Newport, OR) and 93.30 (Southern CA) are <50 km from shore; station 90.90 (Southern CA) is >300 km from shore. Lines, colors, and symbols are as in Figure 3a; dashed red lines indicate data gaps >6 months. Newport Hydrographic (NH) line DO data are from Dr. Bill Peterson (NOAA). CalCOFI hydrographic line data are from the CalCOFI website. Note: CalCOFI data before 2016 are from the bottle data CSV database, while 2016 data are preliminary data from the CTD CSV database.

After years of steady declines and a historic low in 2015, SWE returned to average levels in all ecoregions in 2016 (Figure 11). However, despite the rebound of SWE in early 2016, high spring and summer air temperatures resulted in rapid snowmelt. These factors led to an increase in maximum flows in 2016, although not to levels considered dangerous to most salmon stocks. The early and rapid melt helped contribute to worsening trends in minimum flow in most of the ecoregions (Harvey and Garfield 2017b). SWE in 2017 was on pace to exceed 2016 following a series of winter storms earlier this year (Harvey and Garfield 2017b).

We summarized streamflow using quad plots that compile recent status and trends in flow anomalies at the finer spatial scale of individual Chinook salmon (*Oncorhynchus tshawytscha*) evolutionarily signifcant units (ESUs, sensu Waples 1995). Here, high and increasing maximum flows are regarded as undesirable (i.e., the red quadrant of the max flow plot in Figure 12) due to the potential for scouring redds; low and decreasing minimum flows are also undesirable (the red quadrant of the min flow plot) because of the potential for stress related to temperature, oxygen, or space. The maximum flow events are within ±1 SD of long-term averages and generally lack signficant trends, although four ESUs indicate a recent increase (Figure 12, left). On the other hand, miminum flow anomalies have worsening trends for many ESUs, particularly those sensitive to low-flow conditions, such as the Sacramento winter run and the Klamath/Trinity ESUs (Figure 12, right).

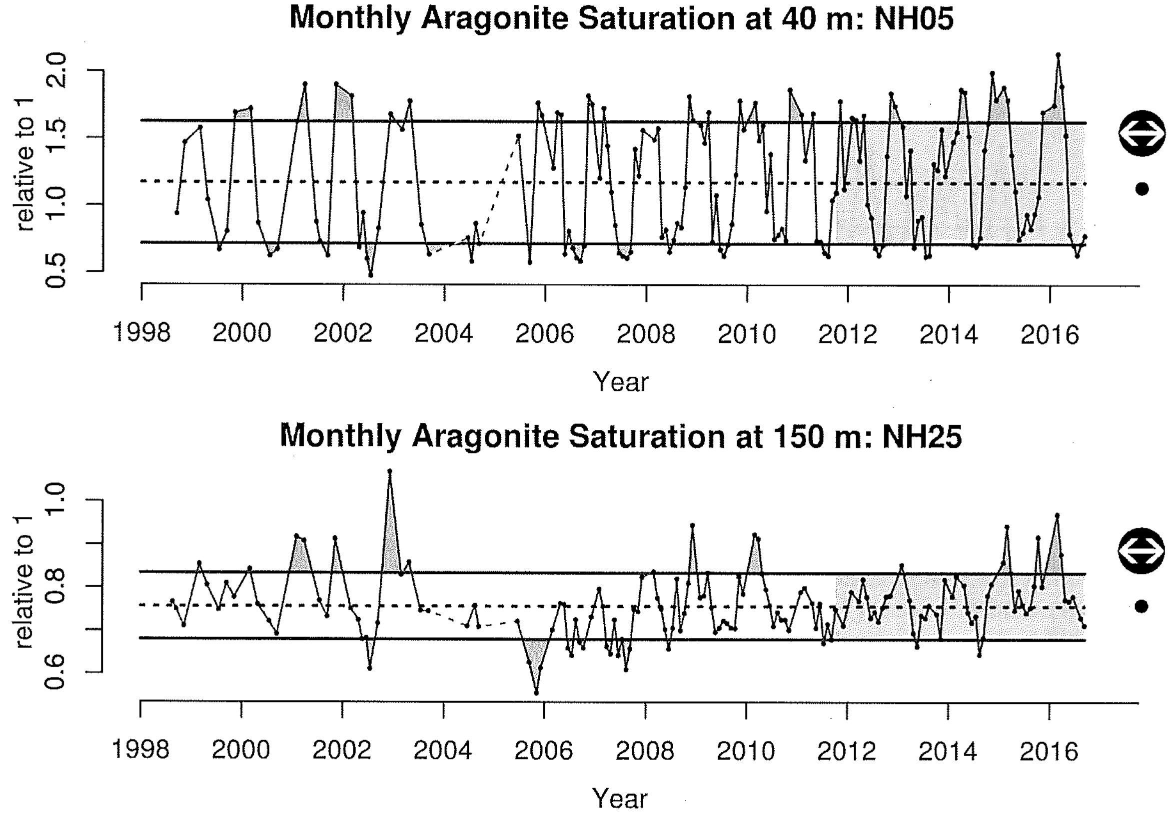

Figure 10. Monthly aragonite saturation values off of Newport, Oregon, 1998–2016. Lines, colors, and symbols are as in Figure 3a; dashed red lines indicate data gaps >6 months. Aragonite saturation state data were provided by Dr. Bill Peterson (NOAA).

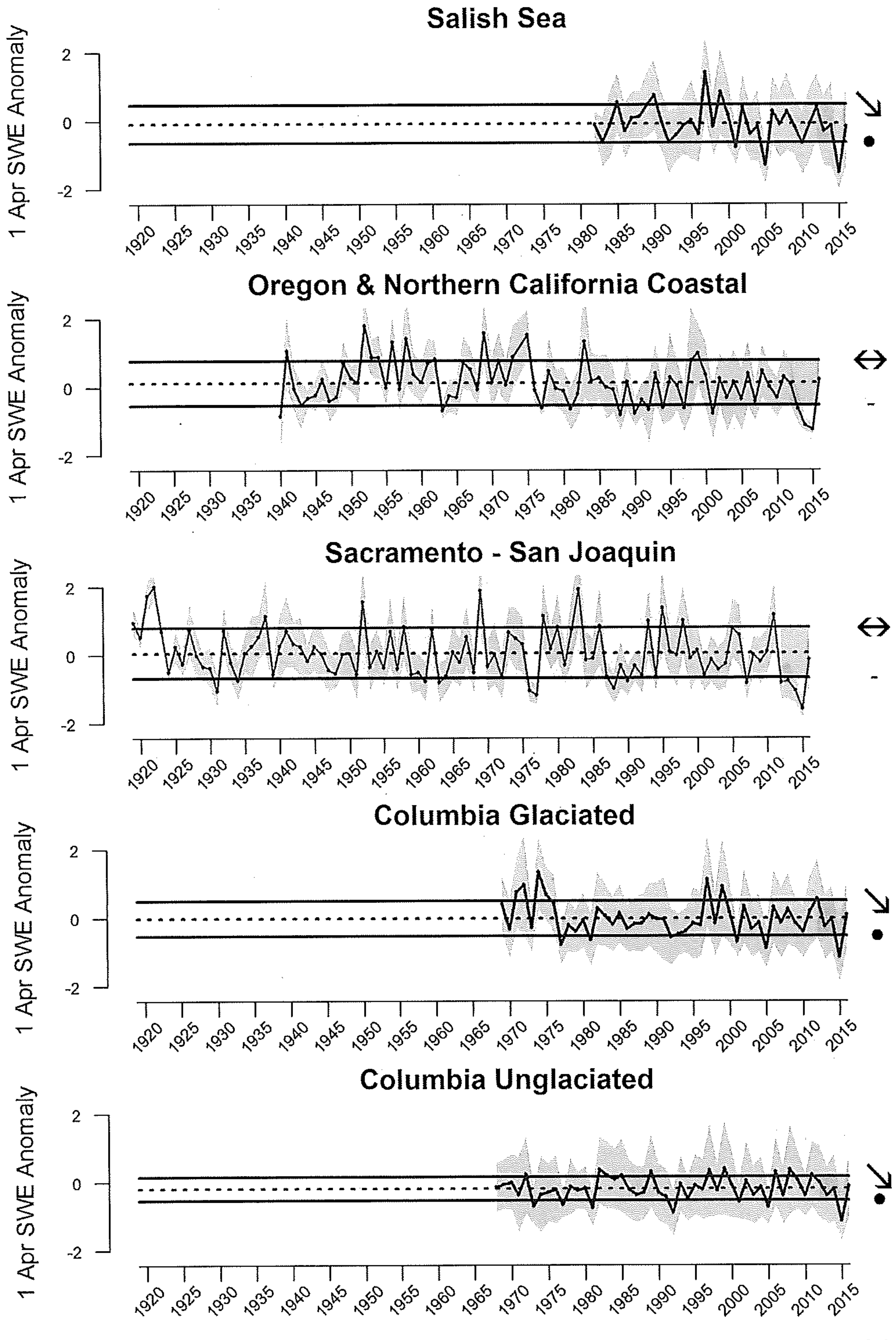

Figure 11. Anomalies of April 1st snow-water equivalent (SWE) in five freshwater ecoregions of the CCE through 2016. Lines, symbols, and colors are as in Figure 3a. Ecoregions are mapped in Figure 4a. SWE data are from the California Data Exchange Center's Resources snow survey* and the Natural Resources Conservation Service's SNOTEL sites† in WA, OR, CA, and ID.

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* http://cdec.water.ca.gov/snow/current/snow/index.html

† http://www.wcc.nrcs.usda.gov/snow/

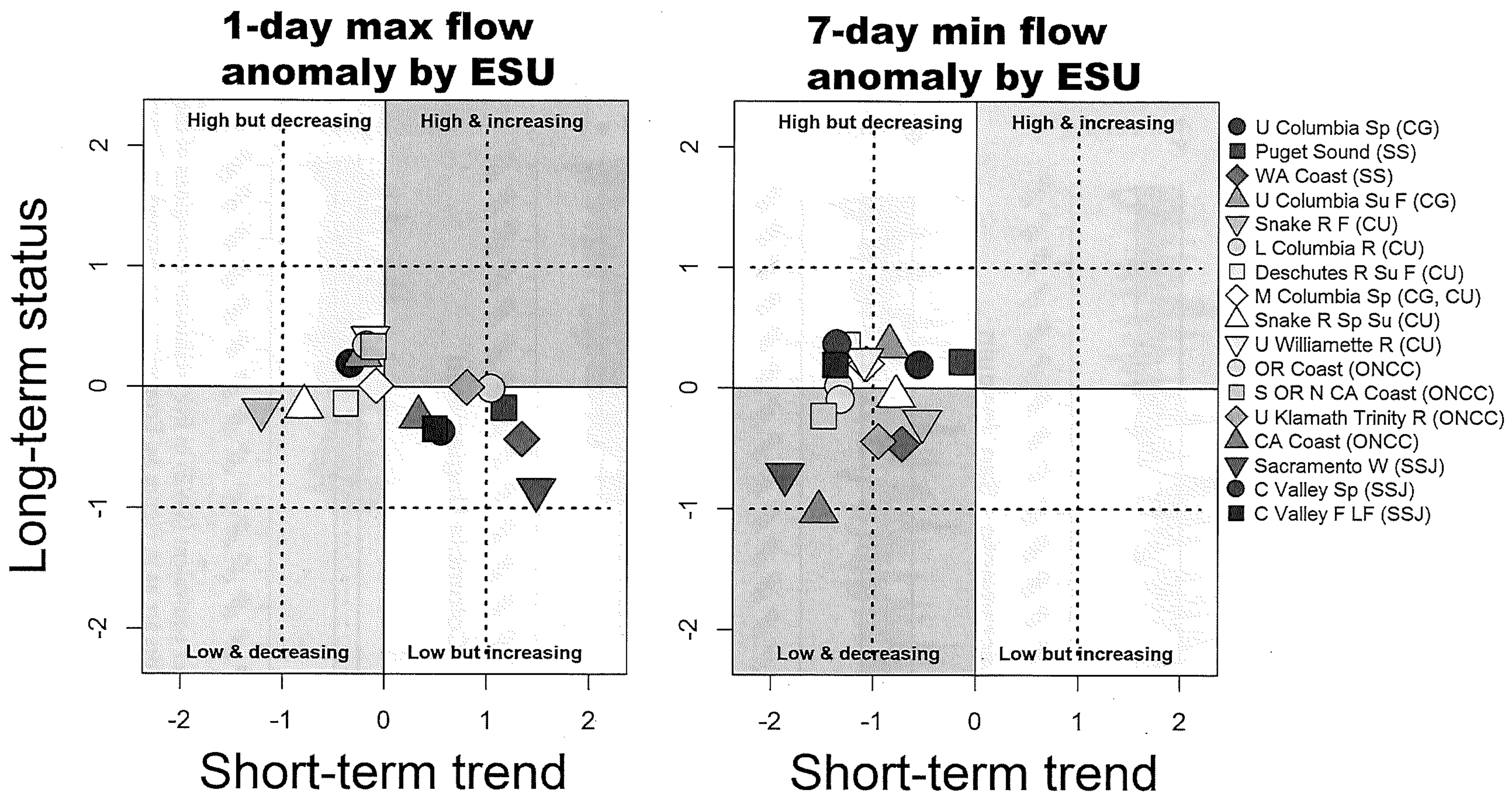

Figure 12. Quad plots of status and trends of maximum and minimum flow in 17 Chinook salmon evolutionarily significant units (ESUs) in the CCE through 2016. The five-year status and trends of flow for each ESU are divided into green (improving conditions), yellow (neutral), and red (declining conditions). Symbols of ESUs are color-coded from north (blue) to south (red). Quad plot lines and base colors are as in Figure 3b. Minimum and maximum streamflow data were provided by the U.S. Geological Survey.*

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* http://waterdata.usgs.gov/nwis/sw

Focal Components of Ecological Integrity

The CCIEA team examines many indicators related to the abundance and condition of key species, the dynamics of community structure, and ecological interactions. Many CCE species and processes respond very quickly to changes in ocean and climate drivers, while other responses may lag by many years. These dynamics are challenging to predict. Over the last several years, many ecological integrity metrics have indicated conditions of poor productivity at low trophic levels and poor foraging conditions for many predators. In 2016, we also continued to observe unexpected community structure in pelagic waters throughout the CCE. It remains to be seen how different populations have been affected, or whether 2017 will represent a shift away from the unproductive conditions observed since 2014.

Northern Copepod Biomass Anomaly

Copepod biomass anomalies represent interannual variation in biomass of two groups of copepod taxa: northern copepods (e.g., *Pseudocalanus mimus*, *Acartia longiremis*, and *Calanus marshallae*), which are "cold-water" species rich in wax esters and fatty acids that appear to be essential for pelagic fishes, and southern copepods (e.g., *Acartia tonsa*, *Calanus pacificus*, *Calocalanus* spp.,

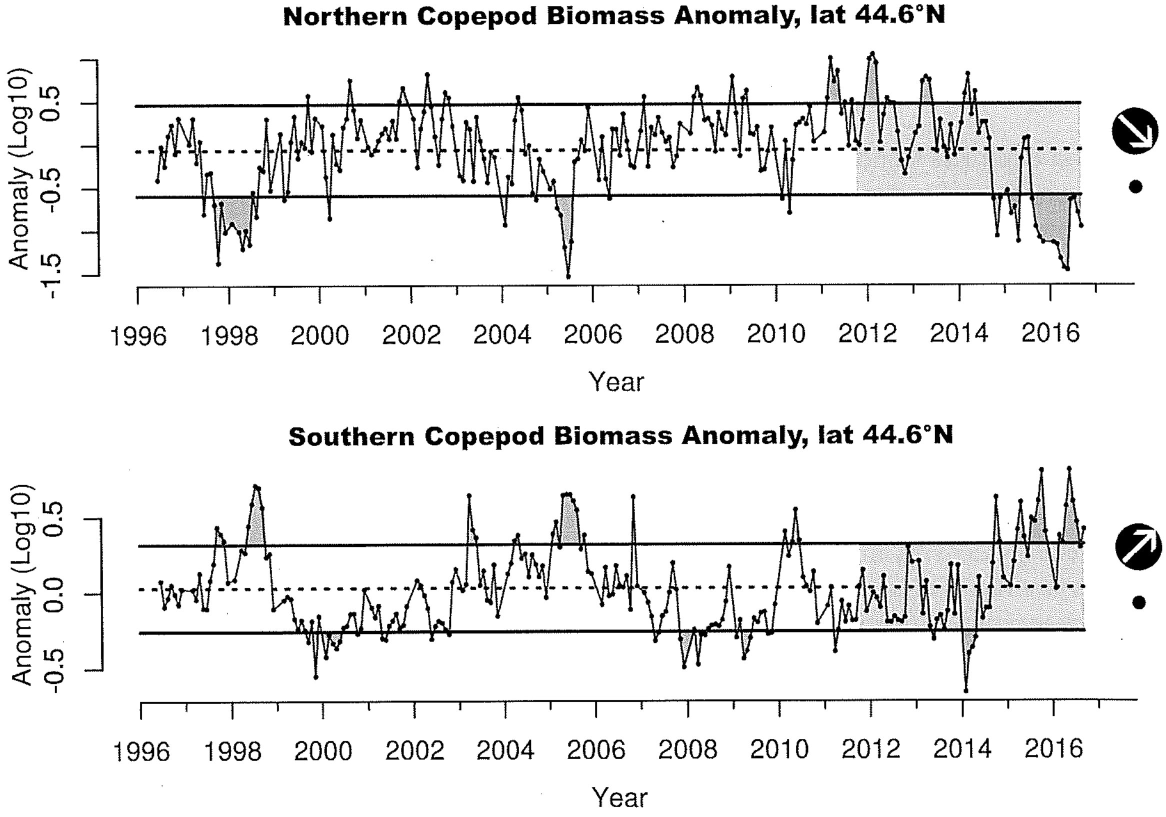

Figure 13. Monthly northern (top) and southern (bottom) copepod biomass anomalies from 1996–2016 in waters off Newport, OR. Lines, colors, and symbols are as in Figure 3a. Copepod biomass anomaly data were provided by Dr. Bill Peterson (NOAA).

Clausocalanus spp., *Corycaeus anglicus, Ctenocalanus vanus, Mesocalanus tenuicornis,* and *Paracalanus parvus*), which are "warm-water" species that are generally smaller and have lower lipid content and nutritional quality. In summer, northern copepods usually dominate the coastal zooplankton community as represented by collections along the Newport Line (see Figures 4a and 4c), while southern copepods dominate the community during winter. This pattern is often altered during El Niño events and/or when the PDO is positive, leading to higher biomass of southern copepods (Keister et al. 2011, Fisher et al. 2015). Threshold values for the anomalies have not been set, but positive values of northern copepods in summer are correlated with stronger returns of Chinook salmon to Bonneville Dam, and values >0.2 are associated with better survival of coho salmon (*Oncorhynchus kisutch*; Peterson et al. 2014).

With the exception of a brief period during summer 2015, the northern copepod anomaly has remained >1 SD below the long-term mean since the autumn of 2014 (Figure 13, top). During this same period, the southern copepod biomass anomaly increased significantly and was strongly positive in much of 2016 (Figure 13, bottom). These anomaly patterns are consistent with warm surface waters and poor feeding conditions for pelagic fishes, and reflect a sustained departure from the generally productive ocean conditions for much of 2011–14. Moreover, 17 species of copepods have been collected since autumn 2014 that had not been observed in these waters previously. It appears that many of these exotic copepod species were offshore, central Pacific species, not the typical southern species that are often transported northward to the Newport Line during major El Niño events.

Regional Forage Availability

This section describes trends in forage availability, based on spring/summer research cruises that have been conducted independently in three different regions (Figure 4c) for decades. The species shown below represent a substantial portion of the available forage in the regions sampled by the cruises. *We consider these regional indices of relative forage availability and variability, not indices of absolute abundance of coastal pelagic species* (CPS). Absolute abundance estimates should come from stock assessments and comprehensive monitoring programs, which these surveys are not. Moreover, the regional surveys that produce these data use different methods (e.g., gear selectivity, timing, frequency, and survey objectives); thus, the amplitudes of each time series are not necessarily comparable among regions.

The CCE forage community is a diverse portfolio of species and life history stages, varying in behavior, energy density, and availability to predators. Years with abundant pelagic fish, market squid (*Doryteuthis opalescens*), and krill (e.g., *Euphausia pacifica* and *Thysanoessa spinifera*) are generally associated with cooler waters, strong upwelling, and higher productivity (Santora et al. 2014, McClatchie et al. 2016). Here, we present the forage indicators in quad plots analogous to Figure 3b; time series data are summarized elsewhere (Harvey and Garfield 2017b).

Northern CCE

The Northern CCE survey targets juvenile salmon in June in surface waters, but also catches juvenile and adult pelagic fishes, market squid, and gelatinous zooplankton. Except for jack mackerel (*Trachurus symmetricus*), recent average catch-per-unit-effort (CPUE) of most forage species were within 1 SD of the long-term mean and showed no discernable short-term trends (Figure 14). Sardine (*Sardinops sagax*) and anchovy (*Engraulis mordax*) CPUEs remained near the lowest levels observed in this survey's time series (Harvey and Garfield 2017b). The two main species of gelatinous zooplankton were within the long-term mean range, although the small water jelly *Aequorea* sp. declined from 2015 and the large sea nettle *Chrysaora* was relatively uncommon. Anecdotally, a related survey in this region, which uses different methods and only began in 2011, caught many adult anchovy near the Columbia Plume, and saw evidence of anchovy spawning off Oregon in 2015 and 2016. The related survey also showed a steep drop in krill in 2015 and 2016, concurrent with an increase in gelatinous salps. The survey also found young-of-the-year (YOY) rockfish (*Sebastes* spp.) and Pacific hake (*Merluccius productus*) more abundant in 2016 than previous years.

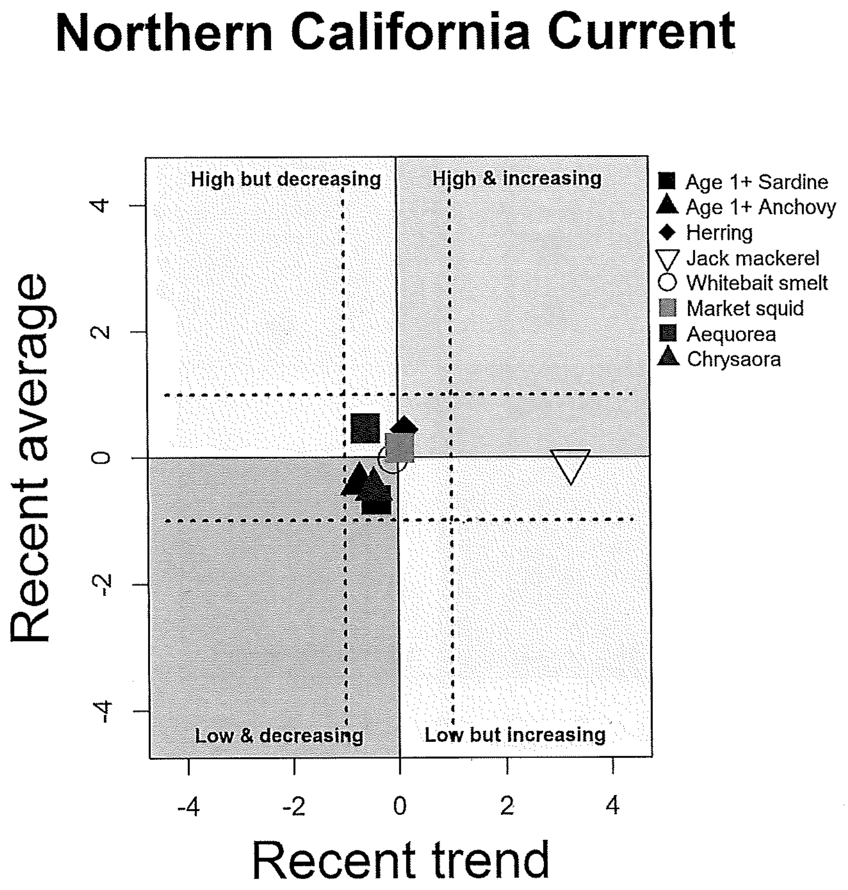

Figure 14. Means and trends of CPUE for key forage in the Northern CCE. Means and trends are from 2012–16 and normalized relative to the full time series (1999–2016). Lines, colors, and symbols are as in Figure 3b. Pelagic forage data from the Northern CCE were provided by Dr. Ric Brodeur (NOAA) and were derived from surface trawls conducted as part of the Bonneville Power Authority Plume Survey.

Central CCE

Data presented here are from the "core area" of a survey (see Figure 4c) that targets YOY rockfishes, but also samples other forage fishes, market squid, and zooplankton. The Central CCE forage community in 2016 exhibited many of the anomalous catch levels and trends observed in recent years. Adult sardine and anchovy CPUEs remained relatively low, whereas YOY rockfish CPUE was above average for the fourth year in a row (Figure 15; see also Harvey and Garfield 2017b). YOY Pacific hake CPUE also maintained its recent increase, and YOY sanddabs (*Citharichthys* spp.) remained above the long-term mean. Krill and market squid CPUE have declined in recent years, particularly squid since 2014. *Chrysaora* jellyfish also declined, though that may be due to avoidance of sites where *Chrysaora* has fouled sampling gear in the past. However, salps were relatively abundant, as were warm-water species such as pelagic crabs (*Pleuroncodes planipes*; data not shown).

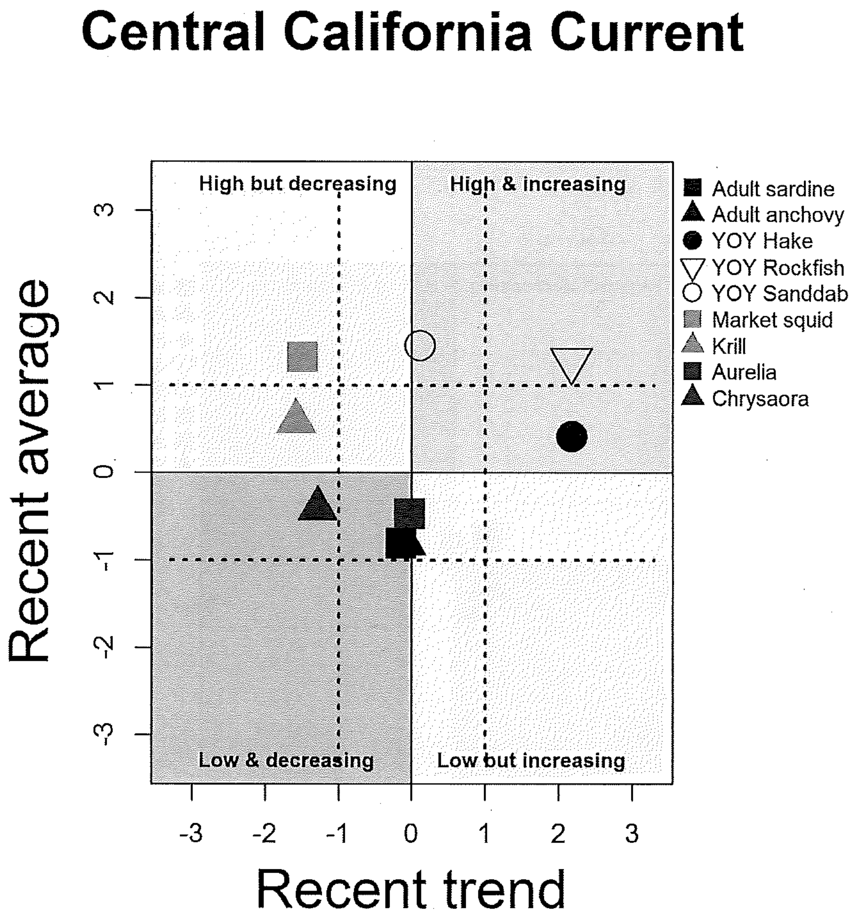

Figure 15. Means and trends of CPUE for key forage in the Central CCE (core area). Means and trends are from 2012–16 and normalized relative to the full time series (1990–2016). Lines, colors, and symbols are as in Figure 3b. Pelagic forage data from the Central CCE were provided by Dr. John Field (NOAA) from the SWFSC Rockfish Recruitment and Ecosystem Assessment Survey.*

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* https://swfsc.noaa.gov/textblock.aspx?Division=FED&ParentMenuId=54&id=20615

Southern CCE

The forage abundance indicators for the Southern CCE come from larval fish surveys conducted by CalCOFI. The larval biomass is assumed to correlate with the spawning stock biomass (SSB) of forage species such as sardine, anchovy, market squid, shortbelly rockfish (*Sebastes jordani*), and some mesopelagic species. Recent CPUE for the four species that have been analyzed through 2016 were within ±1 SD of their long-term means, but anchovy showed a significant increasing trend while market squid show a recent decline (Figure 16). The increase in larval anchovy CPUE in recent years is consistent with anecdotal nearshore observations of large schools of adult anchovy in the Southern California Bight.

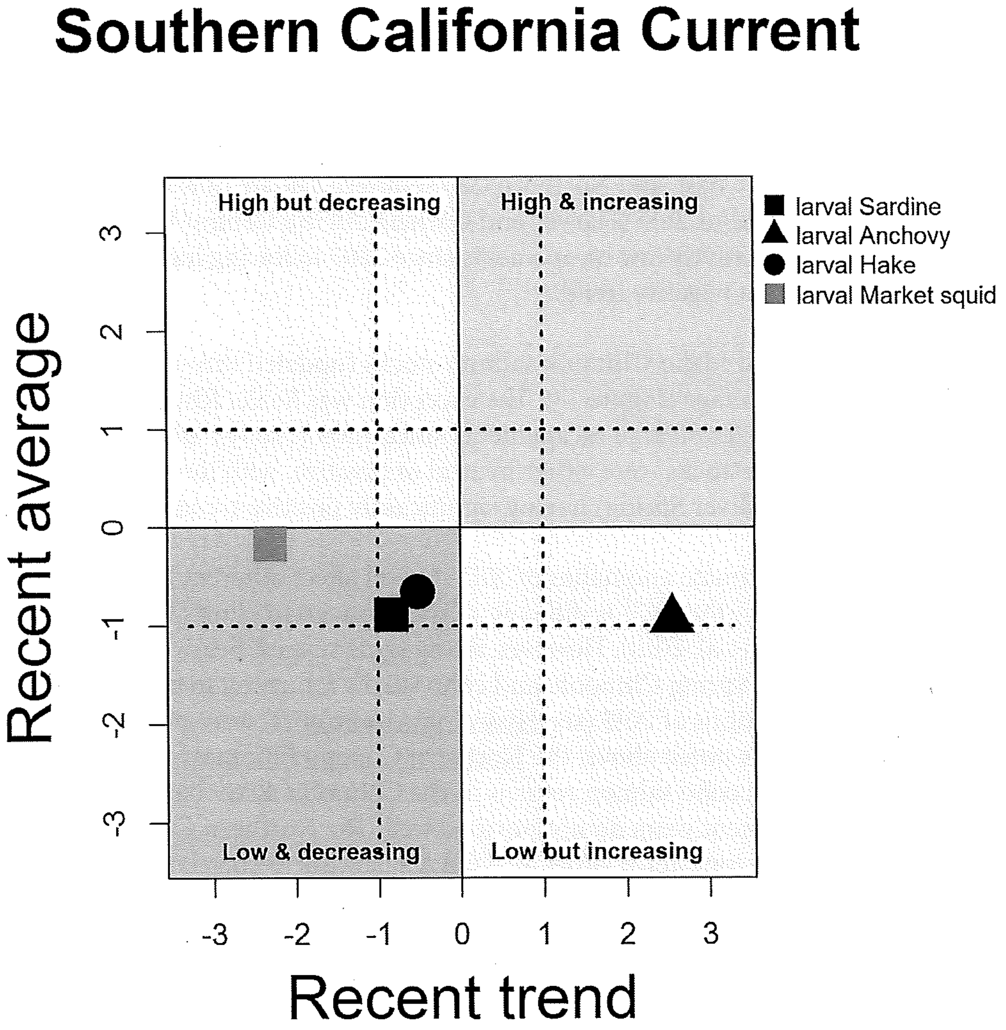

Figure 16. Means and trends of CPUE for key forage in the Southern CCE. Means and trends are from 2012–16 and normalized relative to the full time series (1990–2016). Lines, colors, and symbols are as in Figure 3b. Pelagic forage data from the Southern CCE were provided by Dr. Andrew Thompson (NOAA) and were derived from spring CalCOFI surveys.

Salmon

For indicators of the abundance of Chinook salmon populations, we compare the trends in natural spawning escapement along the CCE to evaluate the coherence in production dynamics, and also to get a more complete perspective of their status across the greater portion of their range. When available, we use escapement time series back to the 1970s; however, some populations have shorter time series (for example, Central Valley Spring starts in 1995, Central Valley Winter starts in 2001, and Coastal California starts in 1991). Here, we present the Chinook salmon escapements in quad plots; time series data for specific populations are summarized elsewhere (Harvey and Garfield 2017b).

Due to data limitations, California Chinook salmon escapements are updated only through 2015. Generally, California Chinook salmon escapements were within 1 SD of their long-term averages (Figure 17), although 2015 escapements were generally near the low end of the normal range (Harvey and Garfield 2017b). Most California stocks have neutral trends over the last decade, which is a noteworthy change from our last report: trends that had been positive for Central Valley Fall, Klamath Fall, California Coast, and Northern CA/Southern OR are now neutral after poor escapements in 2013, 2014, and/or 2015 (Harvey and Garfield 2017b). Central Valley Winter Run Chinook salmon have had relatively low escapements since 2007 following high escapements in 2005–06, leading to the recent negative trend.

For Oregon, Washington, and Idaho Chinook salmon stocks (updated through 2014), most recent escapements were close to average (Figure 17). The exception was Snake River Fall Chinook, which have experienced a series of large escapements since 2009 (Harvey and Garfield 2017b). Ten-year trends for northern stocks were either neutral or positive, with three (Lower Columbia, Snake River Fall, and Snake River Spring) having significantly positive trends from 2005–14.

Predicting exactly how the climate anomalies of 2013–16 will affect different brood years of salmon from different parts of the CCE is difficult, despite concerted efforts by many researchers (e.g., Burke et al. 2013, Wells et al. 2016). However, many signs suggest below-average returns may occur for Fall Chinook, Spring Chinook, and coho stocks returning to the Columbia Basin. The poor hydrological conditions of 2015 (see Hydrologic Indicators) were problematic for both juvenile and adult salmon. As noted above, the Northern Copepod Biomass Anomaly is positively associated with Chinook and coho salmon returns in the Columbia River basin (Peterson et al. 2014), and its low levels in recent years do not portend well. The Northern Copepod Biomass Anomaly is just one part of a long-term effort by NOAA scientists to correlate oceanographic conditions and pelagic food web structure with salmon productivity (e.g., Burke et al. 2013). Their assessment is that physical and biological conditions for smolts that went to sea between 2013 and 2016 are generally consistent with poor returns of Chinook and coho salmon to much of the Columbia Basin in 2017, as depicted in the "stoplight chart" in Table 1.

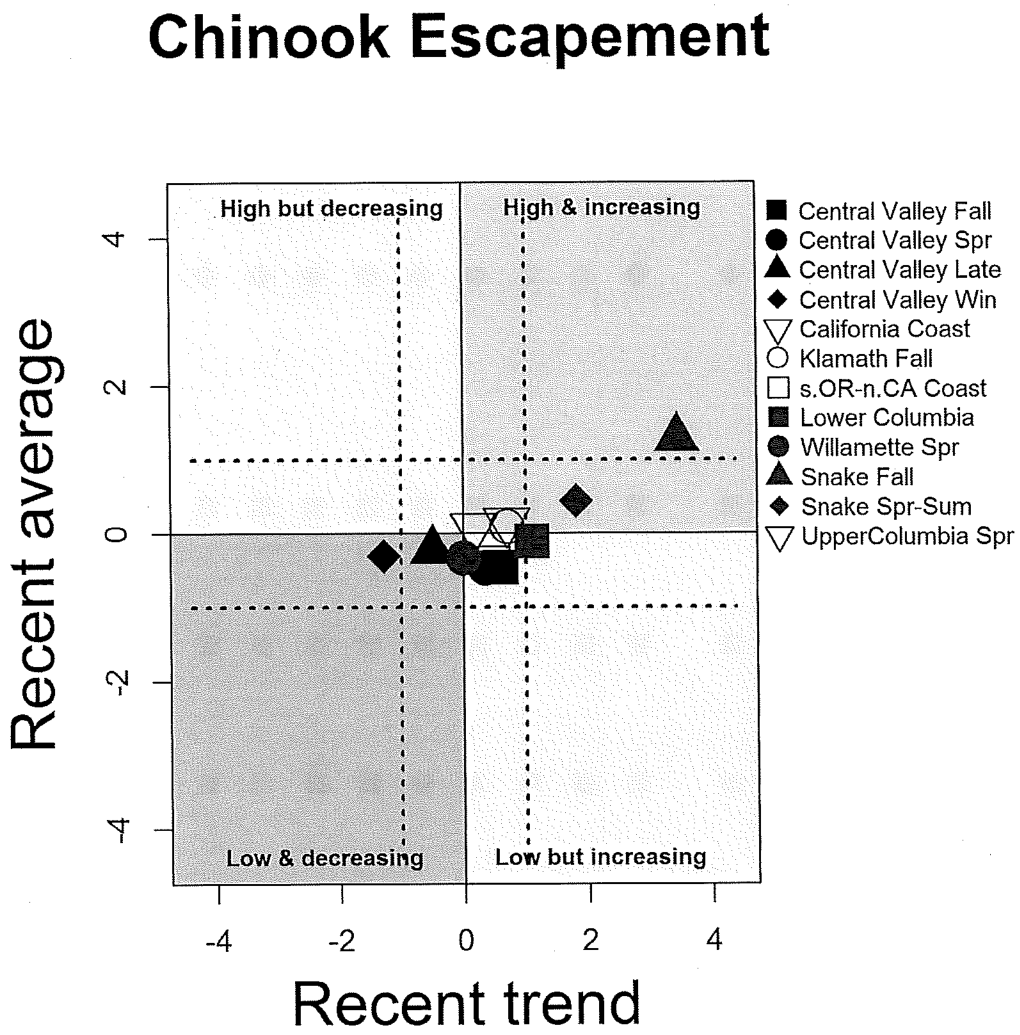

Figure 17. Chinook salmon escapement anomalies through 2015. "Recent average" is mean natural escapement (includes hatchery strays) from 2006–15 relative to the mean of the full time series. "Recent trend" indicates the escapement trend from 2006–15. Base colors and lines are as in Figure 3b. Chinook salmon escapement data were derived from the California Department of Fish and Wildlife,* from Pacific Fishery Management Council preseason reports,† and from NWFSC's "Salmon Population Summary" database.‡

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* http://www.dfg.ca.gov/fish/Resources/Chinook/CValleyAssessment.asp

† http://www.pcouncil.org/salmon/stock-assessment-and-fishery-evaluation-safe-documents/preseason-reports/2016-preseason-report-i/

‡ https://www.webapps.nwfsc.noaa.gov/sps

Table 1. "Stoplight" table of basin-scale and local–regional conditions for smolt years 2013–16 and likely adult returns in 2017 for coho and Chinook salmon that inhabit coastal Oregon and Washington waters in their marine phase. Green = improving conditions, yellow = neutral, and red = declining conditions; these are based on rankings of all years sampled, e.g., if a parameter in a given year ranks among the top third most favorable years recorded, it is green, but if it ranks among the top third least favorable years, it is red. Courtesy of Dr. Bill Peterson (NWFSC).

	Smolt year				Adult return outlook	
Scale of indicators	**2013**	**2014**	**2015**	**2016**	**Coho, 2017**	**Chinook, 2017**
Basin-scale						
PDO (May–Sept)	□	□	■	■	◆	◆
ONI (Jan–Jun)	□	□	■	■	◆	◆
Local and regional						
SST anomalies	□	□	■	■	◆	◆
Deep water temp	■	■	■	□	◇	◆
Deep water salinity	■	■	□	□	◇	◇
Copepod biodiversity	▨	□	■	■	◆	◆
Northern copepod anomaly	▨	▨	■	■	◆	◆
Biological spring transition	▨	■	■	■	◆	◆
Winter ichthyoplankton biomass	□	■	▨	▨	◈	◈
Winter ichthyoplankton community	□	□	■	■	◆	◆
Juvenile Chinook catch (Jun)	▨	□	■	□	◆	◆
Juvenile coho catch (Jun)	▨	□	□	□	◇	◇

Groundfish: Stock Abundance and Community Structure

The CCIEA team regularly presents the status of groundfish biomass and fishing pressure based on the most recent stock assessments. About one-third of the species in the groundfish Fishery Management Plan (FMP) have been formally assessed since 2007. Two key indicators derived from these stock assessments are summarized here. The first indicator describes how close groundfish population abundances are to biomass targets or limits, including being in "overfished" status. It is expressed on the x-axis of Figure 18 in terms of the spawning output (SO) of the mature population biomass. Specifically, it is the ratio of SO in the terminal year of the assessment ($SO_{terminal}$) to the target SO that supports maximum sustainable yield (SO_{MSY}) for that stock. For flatfishes, SO_{MSY} is assumed to be 25% of the theoretical SO of an unfished population; for other groundfishes, SO_{MSY} is assumed to be 40% of unfished SO. The target reference point (TRP) for $SO_{terminal}/SO_{MSY}$ is 1.0. If $SO_{terminal}/SO_{MSY}$ falls below the established limit reference point (LRP; 0.5 for flatfishes, 0.6 for all other groundfishes), then the stock is designated to be overfished, and a rebuilding plan with various management measures will be implemented.

The second key groundfish indicator describes the fishing rate and whether or not "overfishing" (i.e., fishing greater than the target fishing rate) is currently occurring on assessed stocks. Overfishing technically occurs when catches exceed overfishing limits (OFLs), but not all assessed stocks are managed by individual OFLs. Our best alternative was to compare fishing rates to proxy fishing rates at maximum sustainable yield (F_{MSY}), which are used to set OFL values. The y-axis of Figure 18 is therefore not a direct measure of overfishing, but rather a measure of whether fishing rates are above proxy-MSY fishing rates ($F_{30\%}$ for flatfishes, $F_{50\%}$ for other groundfish). This occurs when the ratio of $F_{terminal}/F_{MSY}$ is >1.0, i.e., above the horizontal dashed line in Figure 18.

Most of the recently assessed groundfish species are near or above the biomass LRPs, and are thus not in an overfished status (Figure 18). Only two stocks (Pacific ocean perch [*Sebastes alutus*] and yelloweye rockfish [*S. ruberrimus*], both last assessed in 2011) remained below the rockfish LRP as of their most recent assessment. Only two stocks (black rockfish [*S. melanops*] stocks in California and Washington, both assessed in 2015) were being fished above F_{MSY} in their most recent assessments.

Because 2017 was a year in which many stock assessments were conducted, the information in Figure 18 will be updated substantially in the 2018 ecosystem status report, as well as in the 2018 iteration of this Technical Memorandum series.

As noted in Regional Forage Availability, YOY rockfish were highly abundant in the Central CCE in 2015 and 2016, and results from both shipboard and scuba surveys also revealed large numbers of pelagic and post-settled juvenile rockfish along the Washington coast in 2016. Given the anomalously warm and unproductive oceanographic conditions of 2013–16, these findings run counter to what we might have expected from conceptual models linking climate and productivity conditions to groundfish populations (Harvey and Garfield 2017b). It will be several years before these fish are large enough to be caught in bottom trawls; thus, we will have to wait to determine how groundfish populations changed following the recent climate anomalies.

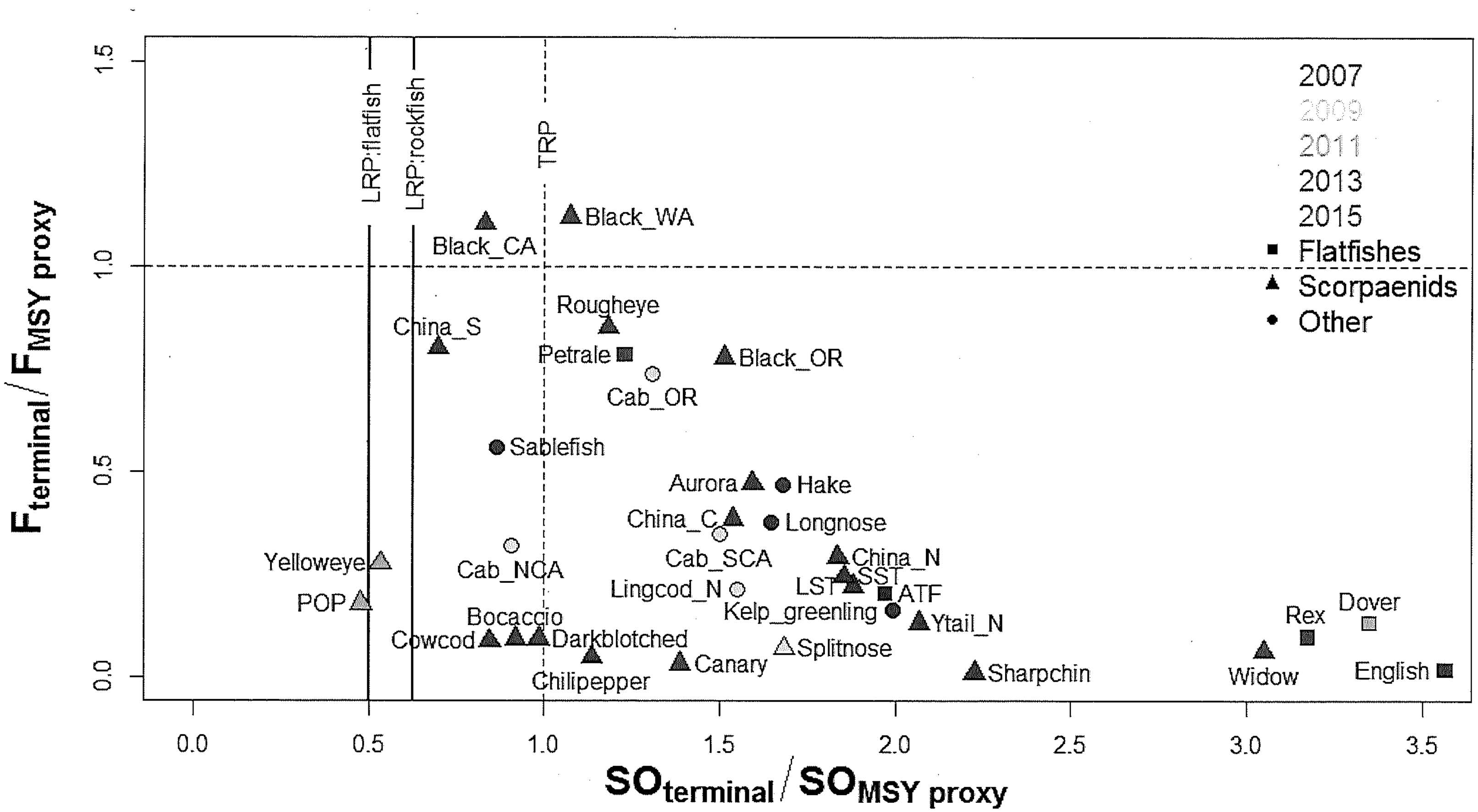
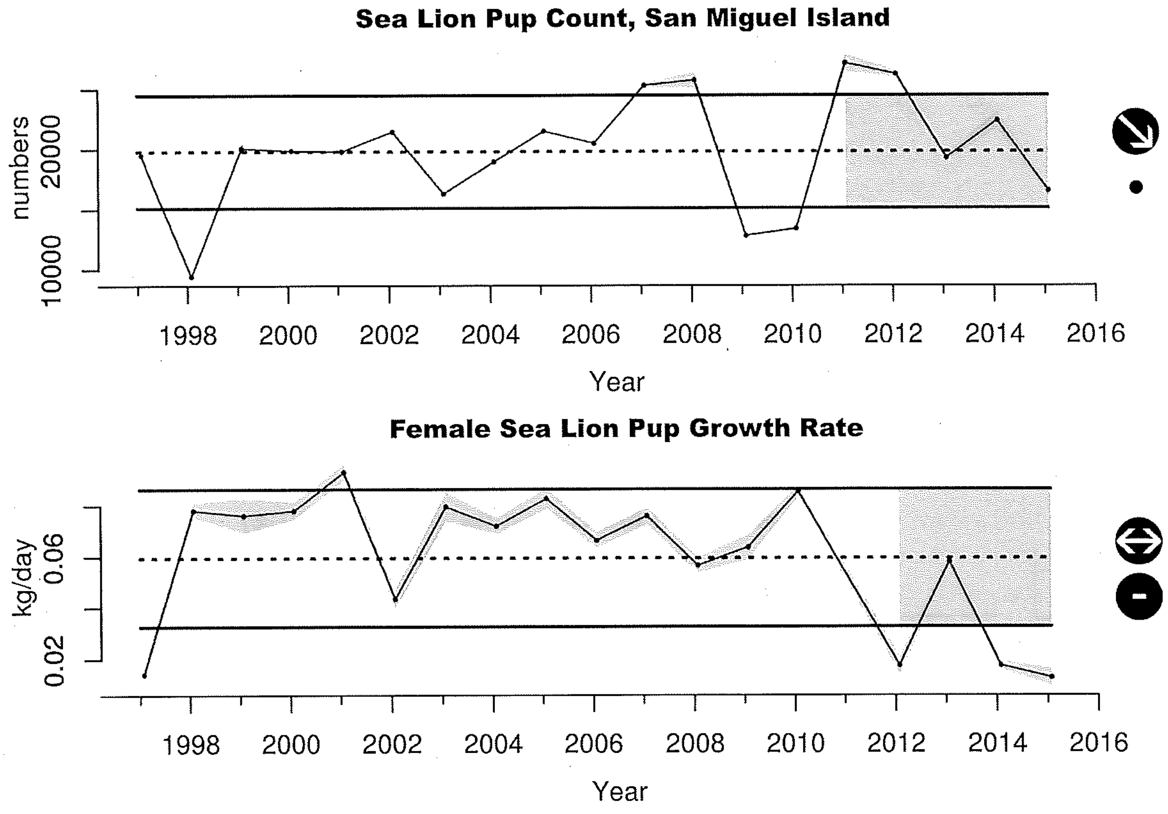


Figure 18. Stock status of CCE groundfish, based on spawning output (SO) and fishing rate (F) from the most recent stock assessment of each stock. The x-axis is an indicator of the biomass of the stock, expressed as SO in the terminal assessment year relative to SO at the theoretical stock biomass associated with maximum sustainable yield (MSY). The y-axis is an indicator of fishing pressure, expressed as F in the terminal assessment year relative to F consistent with MSY. Horizontal dashed line = overfishing rate limit reference. Vertical lines = biomass target reference point (TRP, dashed line) and limit reference points (LRP, solid lines; falling to the left of these lines indicates overfished status for flatfish or rockfish/other groundfish). Symbols indicate groupings of taxa; colors indicate year of most recent assessment. Groundfish stock status data were provided by Dr. Jason Cope (NOAA) and were derived from NMFS stock assessments.

Marine Mammals

California sea lions (*Zalophus californianus*) are permanent residents of the CCE, breeding on the Channel Islands and feeding throughout the CCE, and so are good indicators for the population status of pinnipeds in the system. California sea lions may also be sensitive indicators of prey availability in the Central and Southern CCE: the sea lion pup count in the San Miguel Island breeding colony relates to prey availability for adult females during gestation (October–June), while pup growth is related to prey availability to adult females during the 11-month lactation period (Melin et al. 2012).

Over recent years, California sea lion adult females experienced extremely poor feeding conditions (Figure 19). Pup counts declined from 2011–15, and pup growth was near historic lows in at least three of the last five cohorts. These results, coupled with high rates of springtime pup stranding and mortality in 2013–16, reflect the extent of poor foraging conditions for pinnipeds in the Central and Southern CCE and may foretell a decrease in the California sea lion adult population. Other pinniped species that breed in this region but forage further offshore (Guadalupe fur seals [*Arctocephalus townsendi*] and northern fur seals [*Callorhinus ursinus*]) also experienced poor pup growth in the same time period.


Sea Lion Pup Count, San Miguel Island

Female Sea Lion Pup Growth Rate

Figure 19. California sea lion pup counts at San Miguel Island (top) and estimated mean daily growth rate of female pups from 4–7 months (bottom) for the 1997–2015 cohorts. Lines, colors, and symbols are as in Figure 3a. California sea lion data were provided by Dr. Sharon Melin (NOAA).

Preliminary results suggest that the 2016 cohort of California sea lion pups at San Miguel was more abundant and experienced better early growth than the preceding four cohorts, implying that foraging conditions may have improved.

Seabirds

Seabird species richness data were unavailable for this report, so we instead present regional time series for three key species. Data are derived from visual shipboard surveys during sampling cruises in regions shown in Figure 4c. Sooty shearwaters (*Ardena grisea*) migrate from the southern hemisphere to the CCE in spring and summer to prey on small fish and zooplankton near the shelf break. Cassin's auklets (*Ptychoramphus aleuticus*) and common murres (*Uria aalge*) are resident species that feed over the shelf; Cassin's auklets prey on zooplankton, while common murres target small fish.

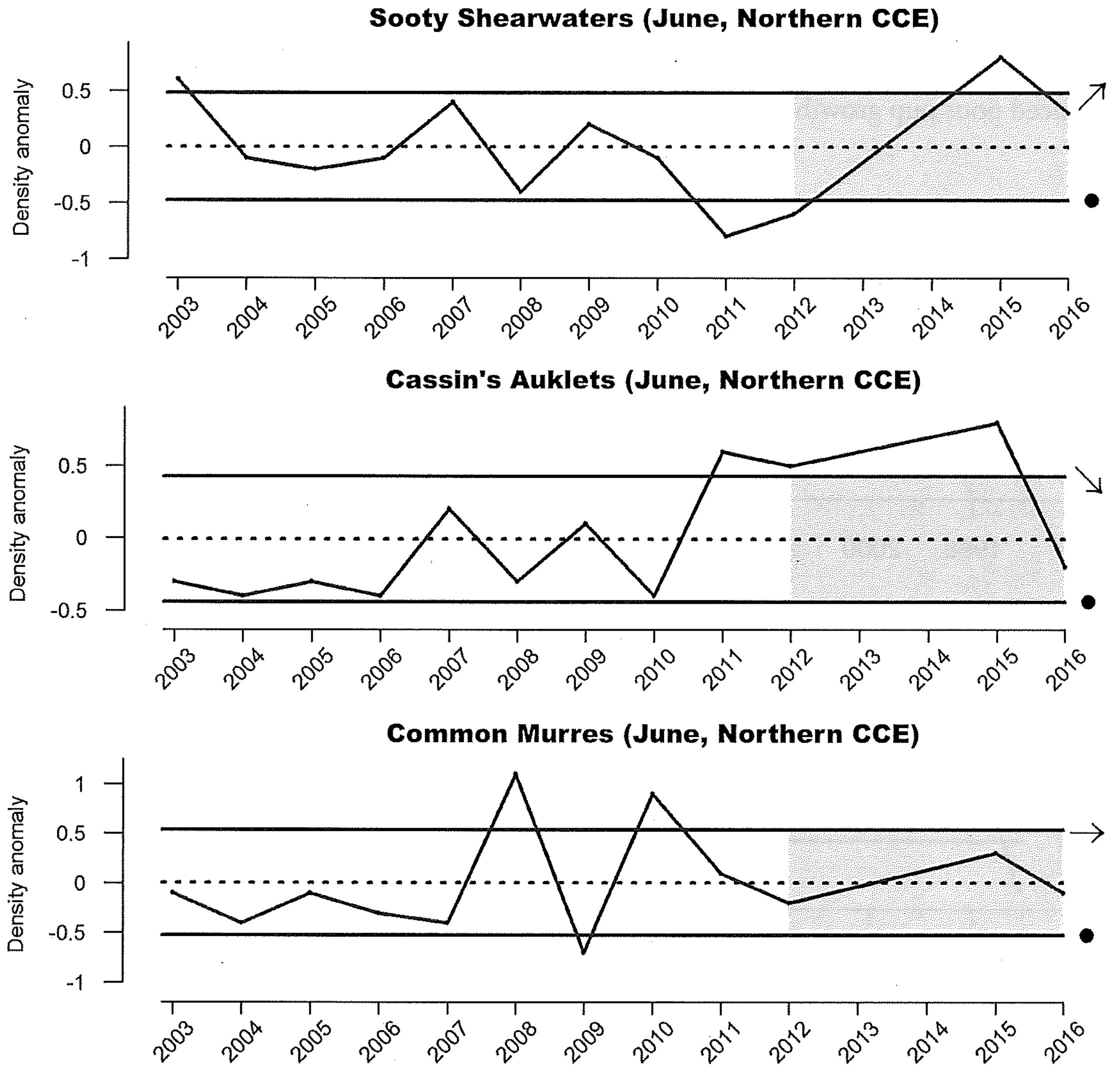
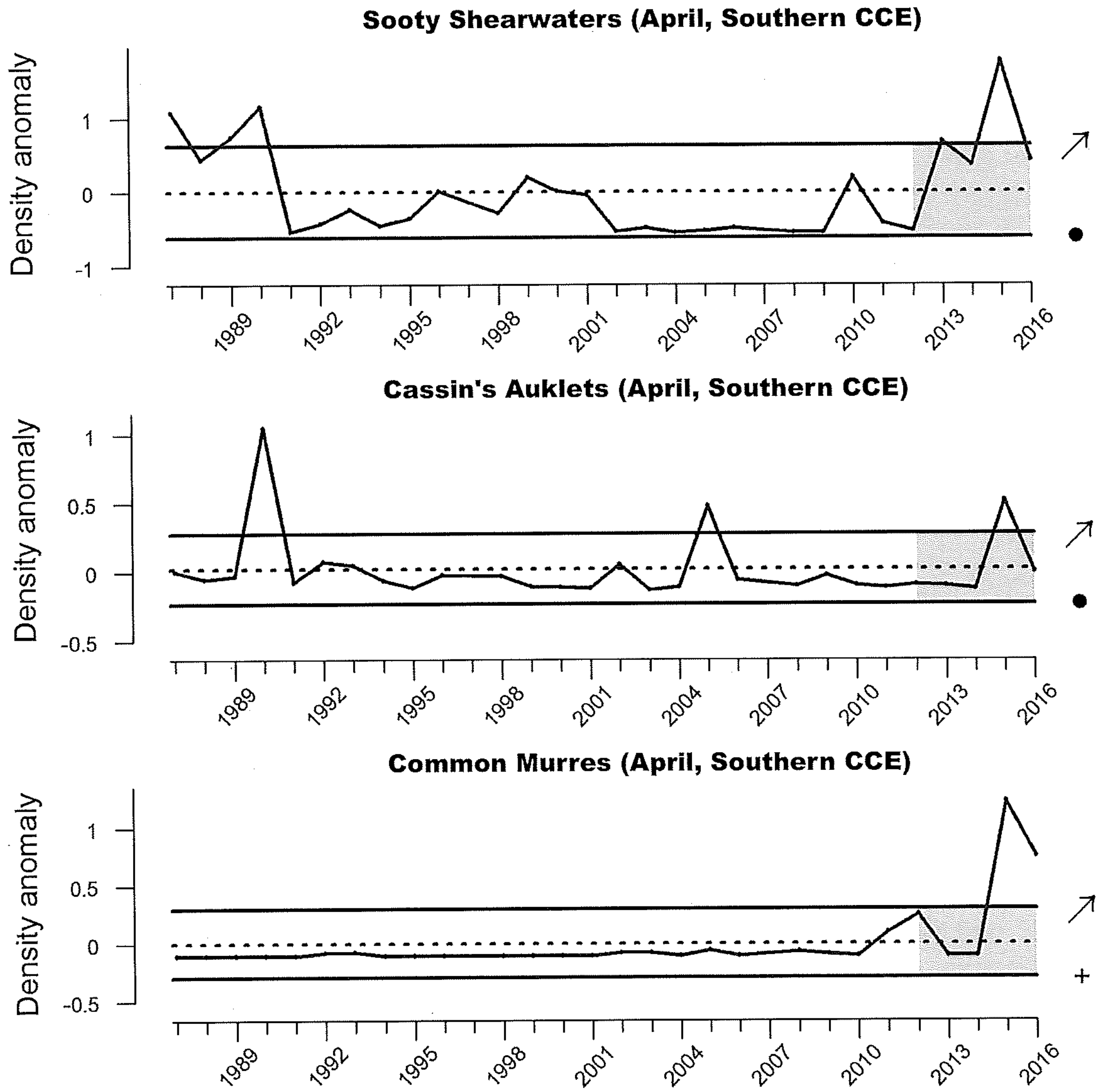


Figure 20. Anomalies in at-sea densities of sooty shearwaters, Cassin's auklets, and common murres in June in the Northern CCE through 2016. Lines, colors, and symbols are as in Figure 3a. Seabird abundance data from the Northern CCE were collected and provided by Dr. Jeannette Zamon (NOAA).

In the Northern CCE sampling area, all three species exhibited temporal variability, particularly since the mid-2000s (Figure 20). Sooty shearwaters have increased in recent years, while Cassin's auklets declined in 2016, possibly related to an exceptional mortality event in 2014–15. Common murre counts showed no trend. (Note: No data were collected in 2013 or 2014.)

In the longer Southern CCE time series, sooty shearwaters had increasing springtime density trends over the past five years (Figure 21), which represents a return to densities observed in the late 1980s. Common murre densities had been minimal since data collection began in 1987 until an uptick in 2011, followed by strongly positive anomalies in 2015 and 2016. By contrast, Cassin's auklets in the Southern CCE have been just below average density over the last 10 years.



Sooty Shearwaters (April, Southern CCE)

Cassin's Auklets (April, Southern CCE)

Common Murres (April, Southern CCE)

Figure 21. Anomalies in at-sea densities of sooty shearwaters, Cassin's auklets, and common murres in April in the Southern CCE through 2016. Lines, colors, and symbols are as in Figure 3a. Seabird abundance data from the Southern CCE are from CalCOFI surveys, courtesy of Dr. Bill Sydeman (Farallon Institute).

The positive density anomalies in recent years are surprising, given the recent and persistent warm conditions. (For example, sooty shearwaters increased despite their cold-water affinities.) These are abundance indicators of long-lived birds, however, and we may need condition indicators like diet, hatching rates, fledgling success, or others to fully understand recent seabird dynamics. To illustrate this, in each of the past several years, at least one seabird species has experienced a "wreck"—anomalously large numbers of dead birds washing up on beaches throughout much of the CCE (e.g., Cassin's auklets in 2014 and common murres in 2015). In the summer of 2016, rhinoceros auklets (*Cerorhinca monocerata*) experienced a wreck, although it was largely confined to the Northern CCE (Harvey and Garfield 2017b).

Human Activities

Coastwide Landings by Major Fisheries

Data for fishery landings are current through 2015. Overall, total landings decreased over the last five years, driven mainly by steep declines in landings of Pacific hake, CPS, and crab in 2015 (Figure 22). Landings of groundfish (excluding hake) were historically low from 2011–15, while hake landings were highly variable. Landings of coastal pelagic fishes and market squid decreased over the last five years. Shrimp landings increased to historic highs, particularly from 2013–15, whereas crab declined sharply from a peak in 2013. Salmon landings were highly variable, while highly migratory species (HMS) landings were relatively consistent; both were within ±1 SD of historic averages. Recreational landings were historically low from 2004–15, and showed no recent trend. Total commercial fishery revenues (in adjusted 2015 dollars) have declined sharply since 2013, driven by declines in landings of crab, market squid, and hake (Harvey and Garfield 2017b). State-by-state commercial and recreational landings and revenue trends are summarized in Harvey and Garfield (2017b).

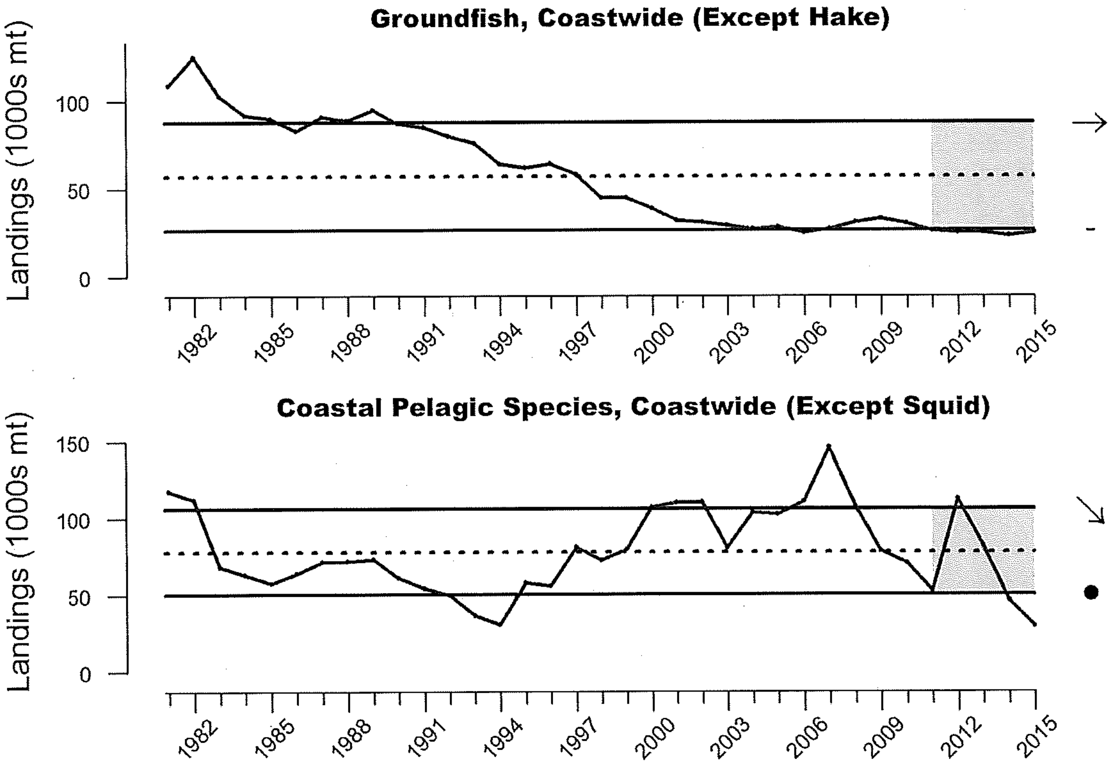


Figure 22. Annual landings of West Coast commercial and recreational fisheries, including total landings across all fisheries from 1981–2015. Lines and symbols are as in Figure 3a. Data for commercial landings are from PacFIN.* Data for recreational landings are from RecFIN.†

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* http://pacfin.psmfc.org/

† http://www.recfin.org/

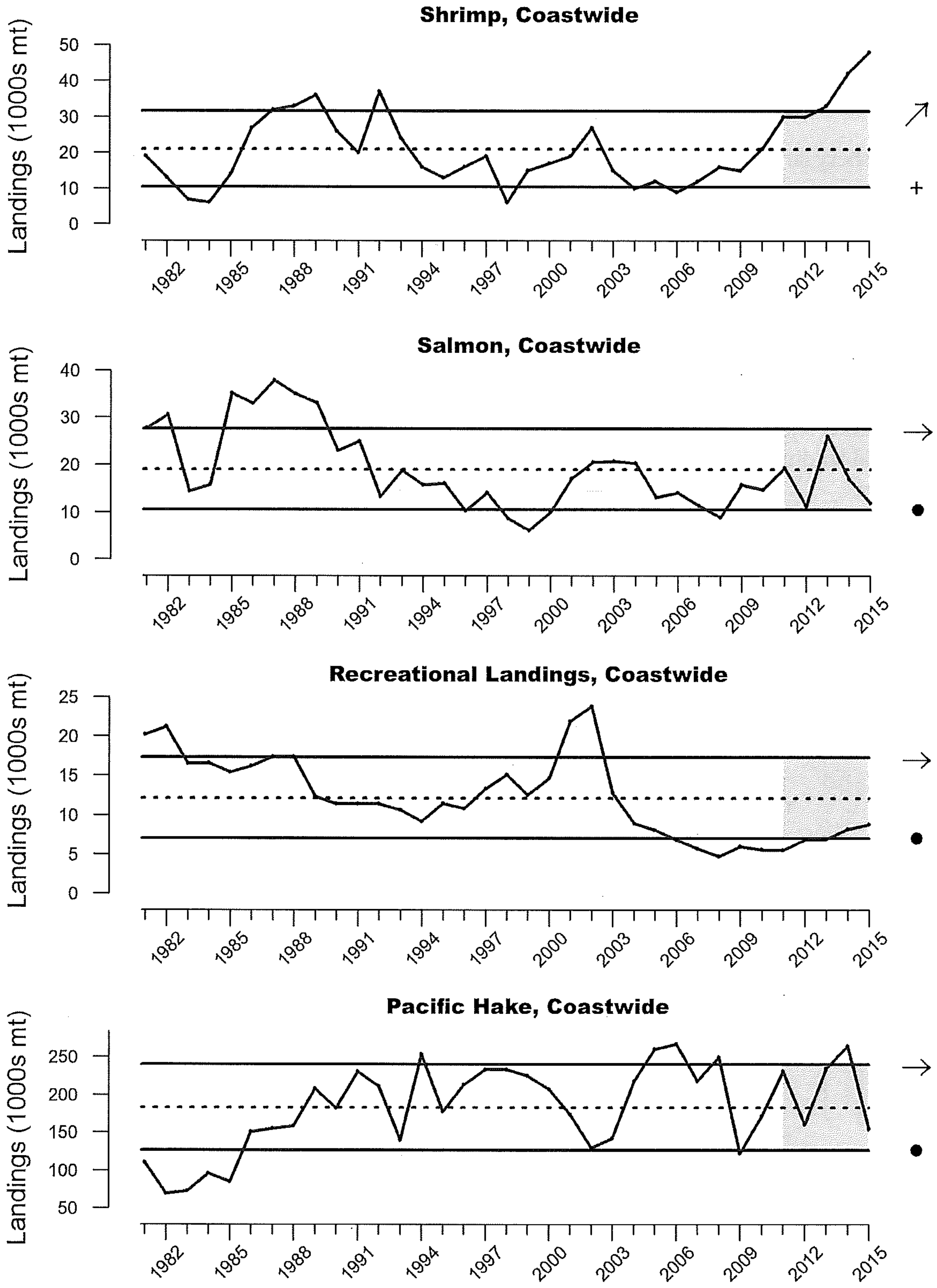

Figure 22 (continued). Annual landings of West Coast commercial and recreational fisheries, including total landings across all fisheries from 1981–2015. Lines and symbols are as in Figure 3a. Data for commercial landings are from PacFIN. Data for recreational landings are from RecFIN.

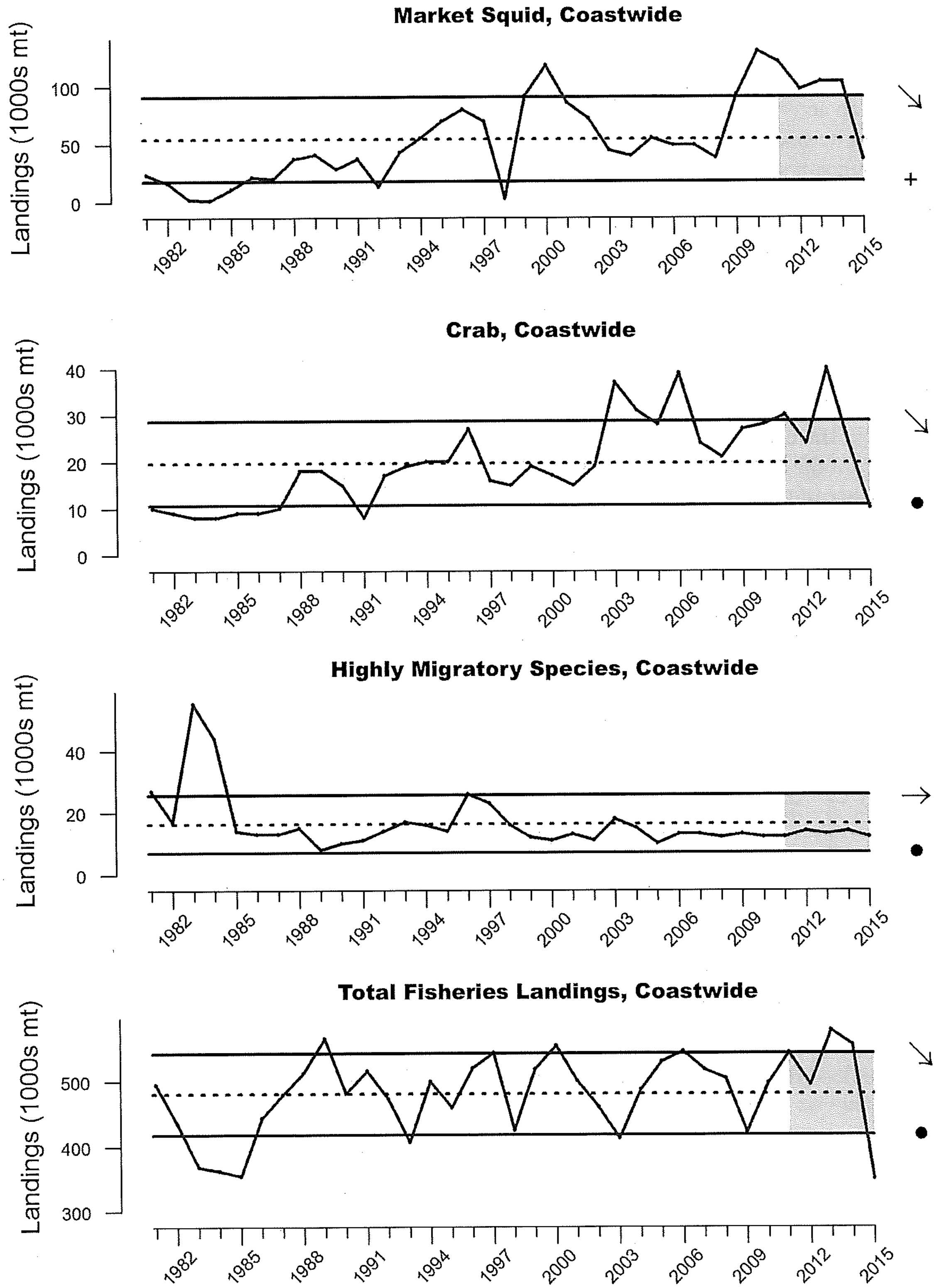

Figure 22 (continued). Annual landings of West Coast commercial and recreational fisheries, including total landings across all fisheries from 1981–2015. Lines and symbols are as in Figure 3a. Data for commercial landings are from PacFIN. Data for recreational landings are from RecFIN.

Gear Contact with Seafloor

Benthic marine species, communities, and habitats can be disturbed by natural processes as well as by human activities (e.g., bottom contact fishing, mining, or dredging). The impacts of fishing likely differ by gear and by habitat type, with hard, mixed, and biogenic habitats needing longer to recover than soft sediments.

We compiled estimates of coastwide distances affected by bottom-contact gear from 1999–2015. Estimates from 2002–15 include bottom trawl and fixed gear, while 1999–2002 includes only bottom trawl data. We calculated trawling distances based on set and haul-back points, and fixed gear distances based on set and retrieval locations of pot, trap, and longline gear. We weighted distances by gear and habitat type, according to sensitivity values described in Table A3a.2 of the 2013 PFMC Groundfish Essential Fish Habitat Synthesis Report[7] (available online only). Gear contact with the seafloor was at historically low levels over the most recent five-year period (Figure 23). The dominant source of seafloor-gear interaction was bottom trawl contact with soft sediments on the shelf and upper slope of the Northern CCE (Harvey and Garfield 2017b). There is uncertainty in the estimation of bottom contact among fixed gear types (e.g., longline vs. pot and trap gear), but this uncertainty is minor compared to the signal from bottom trawl gear.

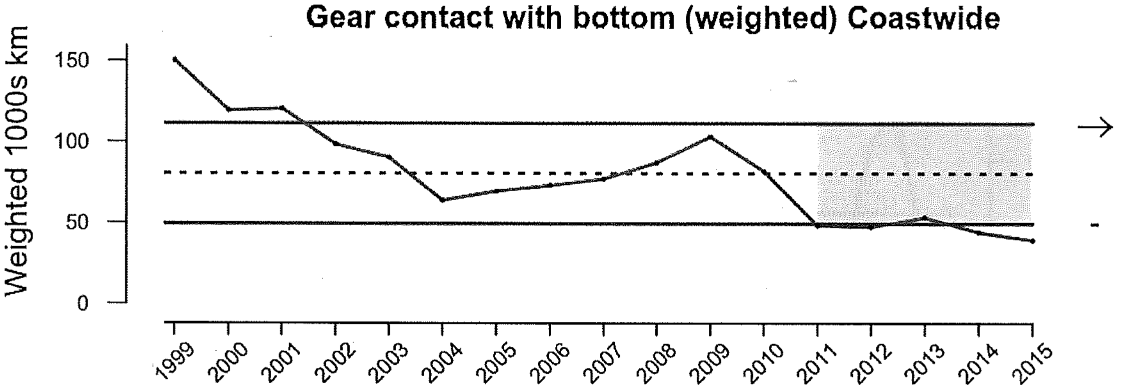

Figure 23. Cumulative weighted distance of fishing gear contact with bottom habitat across the entire CCE, 1999–2015. Lines, colors, and symbols are as in Figure 3a. Data for total benthic habitat distance disturbed by bottom-contact fishing gears were provided by Mr. Jon McVeigh (NOAA). Weightings for benthic habitat sensitivity values come from PFMC's Pacific Coast Groundfish 5-Year Review of Essential Fish Habitat.

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[7] http://www.pcouncil.org/wp-content/uploads/D6b_SUP_NMFS_SYNTH2_APPENDICES_ELECTRIC_ONLY_APR2013BB.pdf

Aquaculture and Seafood Production

Aquaculture activities satisfy some of the demands for seafood and may be related to benefits (e.g., water filtration by bivalves, nutrition, income, or employment) or impacts (e.g., habitat conversion, waste discharge, or species introductions). Shellfish aquaculture production in the CCE has been at historically high levels in recent years (updated through 2014 as of this report), and finfish aquaculture (exclusively Atlantic salmon [*Salmo salar*]) has been near the upper limits of historical averages (Figure 24). Demand for seafood products is increasingly being met by aquaculture, and may be influencing the increases in production.

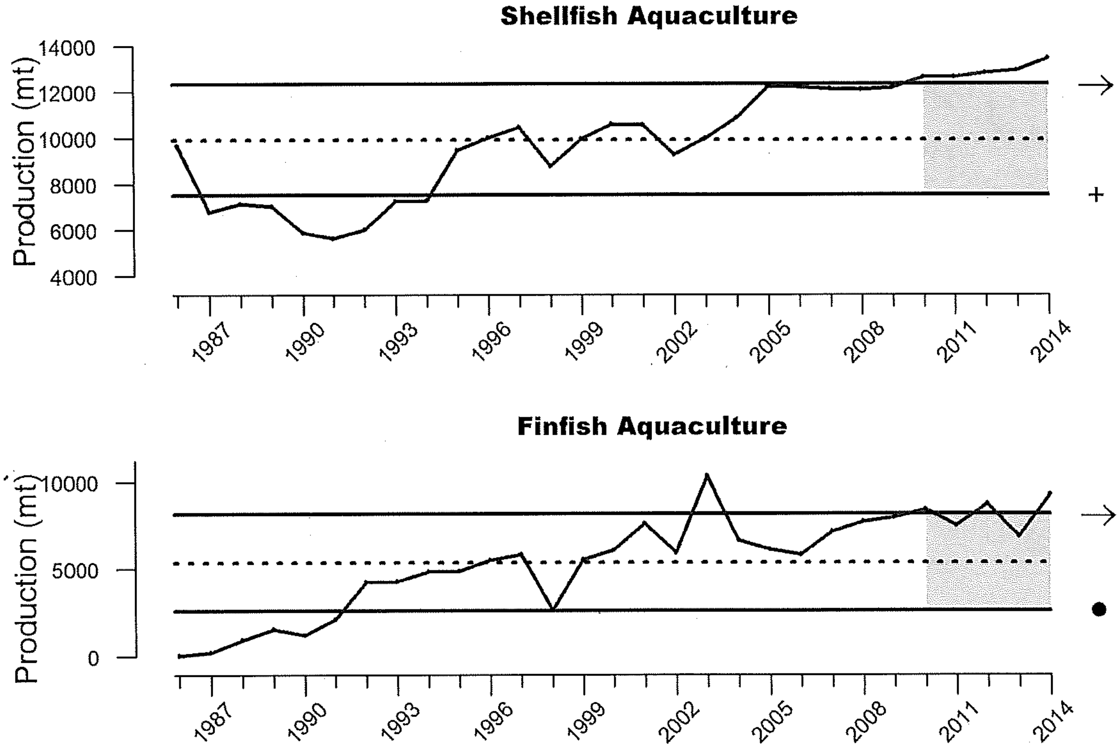

Figure 24. Aquaculture production of shellfish (clams, mussels, oysters) and finfish (Atlantic salmon) in CCE waters. Lines, colors, and symbols are as in Figure 3a. Shellfish aquaculture production data are from the Washington Department of Fish and Wildlife, the Oregon Department of Agriculture, and the California Department of Fish and Game. The only marine net-pen finfish aquaculture operations in the CCE occur in Washington State, and data came from the Washington Department of Fish and Wildlife.

Seafood demand in the U.S. was relatively constant from 2011–15, and had largely recovered from declines late in the previous decade (Figure 25). The recent average total consumption was above historical averages, while per-capita demand was within the historic range. With total demand already at historically high levels, increasing populations, and recommendations in U.S. Dietary Guidelines to increase seafood intake, total demand for seafood products seems likely to continue to increase for the next several years.

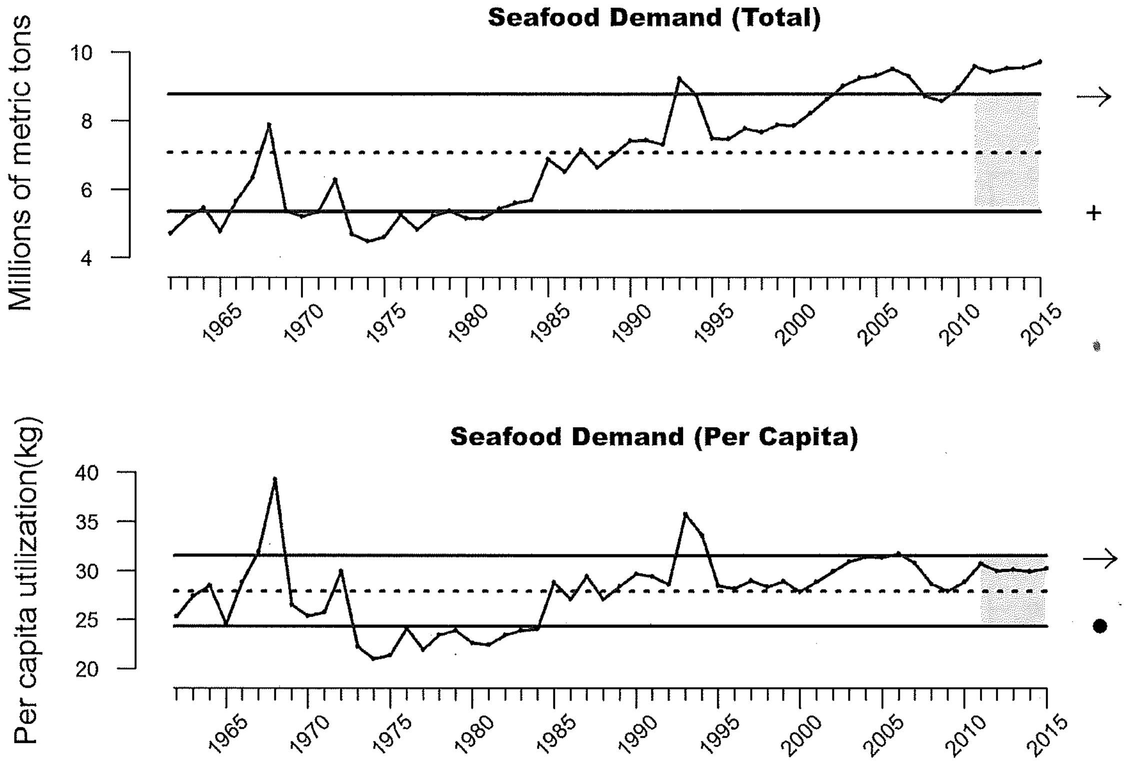

Figure 25. a) Total and b) per-capita use of fisheries products in the U.S., 1962–2015. Lines, colors, and symbols are as in Figure 3a. Data for total (imported and domestic) edible and inedible seafood consumption are from NOAA's Fisheries of the United States[*] annual reports describing the utilization of fisheries products.

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[*] http://www.st.nmfs.noaa.gov/st1/publications.html

Human Wellbeing

Social Vulnerability

Coastal community vulnerability indices are generalized socioeconomic vulnerability metrics for communities involved in commercial fishing. To assess social vulnerability in fishery-dependent communities, we use community-level social data, port-level fish ticket data, and a factor analysis approach to generate composite social vulnerability and commercial fishing indices for 1,139 coastal communities. The Community Social Vulnerability Index (CSVI; Jepson and Colburn 2013) is derived from social vulnerability data (demographics, personal disruption, poverty, housing characteristics, housing disruption, labor force structure, natural resource labor force, etc.). The fishing dependence composite index is based on commercial fishing engagement in a community (including fishery landings, revenues, permits, and processing) and commercial fishing reliance (per-capita enagagement). Figure 26 shows both indices for 25 highly fishing-dependent communities in five regions of the West Coast. Scores are relative to the entire CCE; for example, in 2014, the commercial fishing dependence of Moss Landing was ~33 SD greater than the average community. State-level summaries of CSVI scores are summarized elsewhere (Harvey and Garfield 2017b).

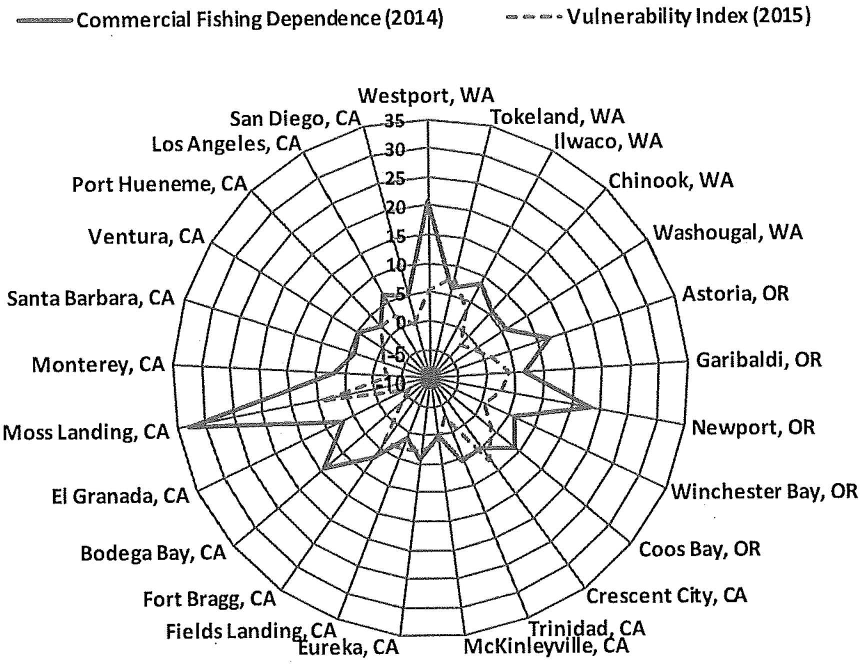

Figure 26. Commercial fishing dependence in 2014 (solid) and social vulnerability index in 2015 (dashed) for the five most fishing-dependent communities in Washington, Oregon, and northern, central, and southern California, expressed as standard deviations relative to all CCE communities. Shaded region is ≤1 SD. Fishery dependence and community social vulnerability index (CSVI) data were provided by Dr. Karma Norman (NOAA) and were derived from the U.S. Census Bureau,* the American Community Survey (ACS),† and PacFIN.

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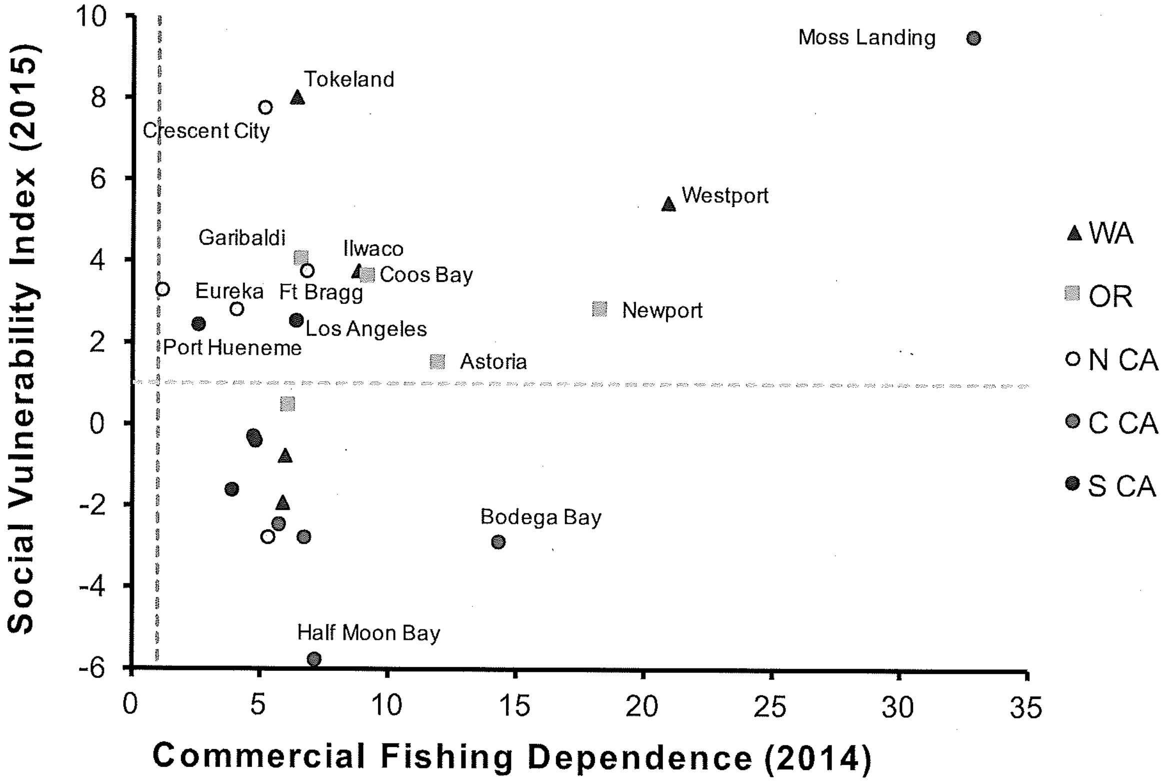
* http://www.census.gov/

† https://www.census.gov/programs-surveys/acs/

Figure 27 shows the two indices in x–y space, allowing us to readily identify fishing-dependent communities with high social vulnerability. Of note are communities like Moss Landing and Westport, which have relatively high commercial fishing dependence (~33 and 21 SD above average) and also a high CSVI (~10 and 5 SD above average). Communities that are strong outliers in both indices may be particularly socioeconomically vulnerable to a downturn in commercial fishing. Exogenous shocks of a management- or ecosystem-related nature may produce especially high individual and community-level social stress in these communities.



time periods as in Figure 26, but as x–y data color-coded by region. Dashed lines indicate 1 SD above the coastwide means, i.e., communities above and right of the two dashed lines have significantly greater social vulnerability and commercial fishing dependence than average communities in the CCE. Fishery dependence and community social vulnerability index (CSVI) data were provided by Dr. Karma Norman (NOAA) and were derived from the U.S. Census Bureau, the American Community Survey (ACS), and PacFIN.

Fleet Diversity Indices

Catches and prices from many fisheries exhibit high interannual variability, leading to high variability in fishers' income. Variability in annual revenue can be reduced by diversifying fishing activities across multiple fisheries or regions (Kasperski and Holland 2013). There may be good reasons for individuals to specialize, however, including reduced costs or greater efficiency. Thus, while diversification may reduce income variation, it does not necessarily promote higher average profitability. We measure diversification with the Effective Shannon Index (ESI). ESI = 1 when revenues are all from a single species group and region. It increases both as revenues are spread across *more* fisheries and as revenues are spread more *evenly* across fisheries. The index has an intuitive meaning: ESI = 2 if fishery revenues are spread evenly across 2 fisheries; ESI = 3 if revenues are spread evenly across 3 fisheries; and so on. If revenue is not evenly distributed across multiple fisheries, the ESI value is lower than the number of fisheries.

As of 2015, the fleet of vessels fishing on the U.S. West Coast and in Alaska was less diverse on average than at any point in the preceding 35 years (Figure 28). Between 2014 and 2015, some categories of vessels showed a small increase in ESI, while others decreased, but absolute changes were minor. The only vessel class to change by >2 SD was vessels 81–125 ft in length, for which ESI increased by about 5%; this change apparently was due to nonparticipation of some less-diversified vessels from West Coast fisheries in 2015. The long-term decrease in ESI from 1981–2015 was due both to entry and exit of vessels and changes for individual vessels. Over time, less-diversified vessels have been more likely to exit, which increases average diversification. However, vessels that remain in the fishery have also become less diversified since at least the mid-1990s, and newer entrants have generally been less diversified than earlier entrants. The overall result is a moderate decline in ESI since the mid-1990s or earlier for most vessel groupings. Notwithstanding these average trends, there are wide ranges of diversification levels and strategies within, as well as across, vessel classes, and some vessels remain highly diversified. It should be noted that increases in diversification from one year to the next may not always indicate an improvement in conditions for the fishing fleet. For example, if a class of vessels was heavily dependent on a single target species with highly variable revenues, such as Dungeness crab (*Metacarcinus magister*), an overall decline in the Dungeness crab fishery might cause ESI to increase. Also, an increase in ESI may be due to the exit of less-diversified vessels. Additional break-downs of diversification are provided in Harvey and Garfield (2017b).

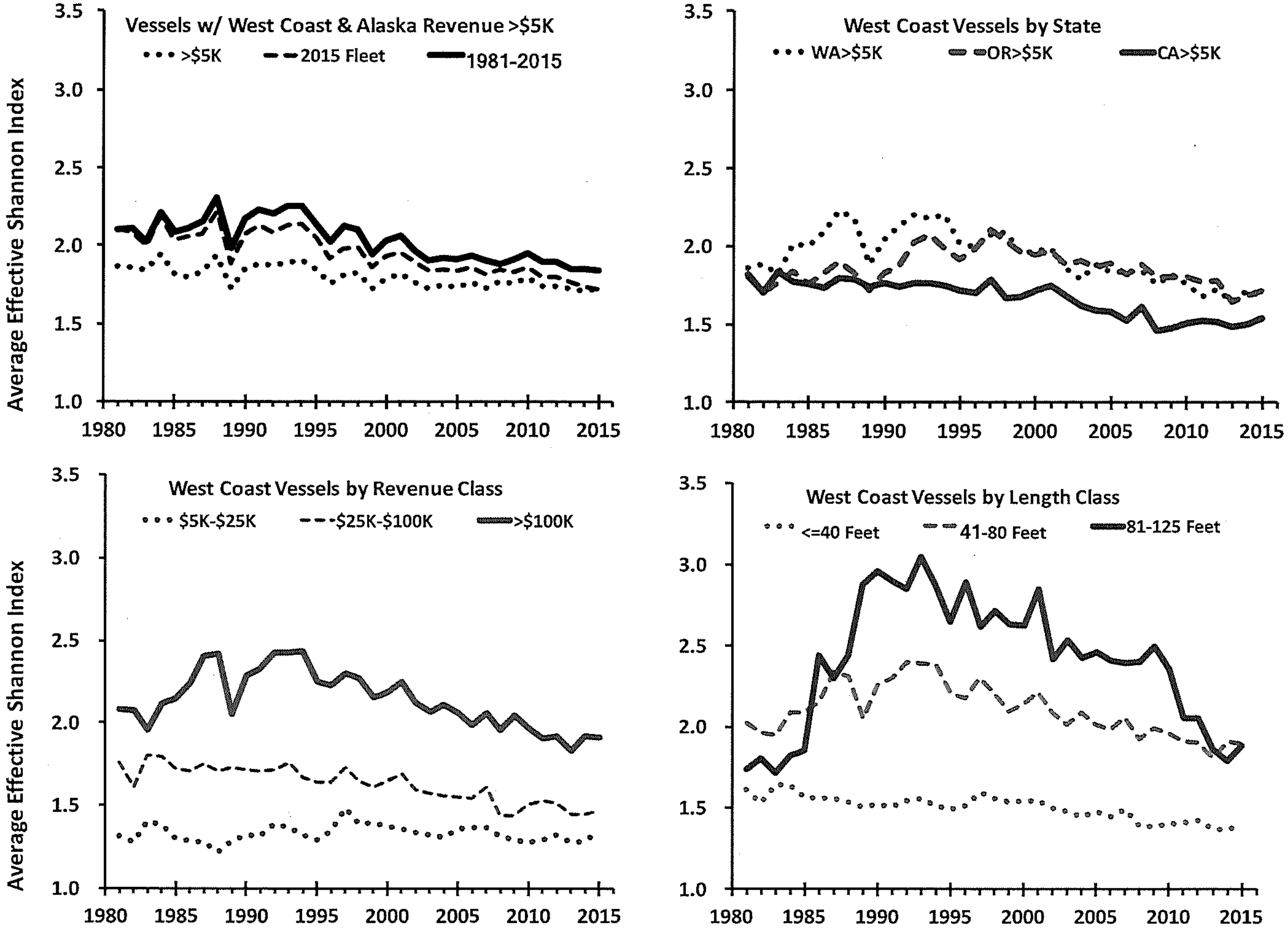


Figure 28. Average fishing vessel diversification for U.S. West Coast and Alaskan fishing vessels with over $5K in average revenues (top left) and for vessels in the 2015 West Coast Fleet, broken out by state (top right), average gross revenue (bottom left), and vessel length (bottom right). Fishery diversification estimates were provided by Dr. Dan Holland and Dr. Stephen Kasperski (NOAA).

CCIEA Team Recommendations for Future Research in the CCE

In March 2015, the PFMC approved FEP Initiative 2, "Coordinated Ecosystem Indicator Review," by which the PFMC, advisory bodies, the public, and the CCIEA team would work jointly to refine the indicators in the annual CCIEA Ecosystem Status Report to better meet PFMC objectives. The Initiative was implemented by an ad-hoc Ecosystem Working Group (EWG). (See PFMC's Decision Summary Document.[8])

As part of the FEP Initiative 2 process, the EWG asked the CCIEA team to summarize their research recommendations in the 2017 ecosystem status report. The six recommendations below reflect our collective assessment of science products that a) we believe are important, b) we could provide to the PFMC in a reasonable time frame (e.g., 1–3 years, including technical review by the SSCES), c) should support regional implementation of the NOAA EBFM Policy and Road Map,[9] and d) would provide added value to the indicators as they relate to management of FMP stocks and protected species.

1. Continue an ongoing scoping process between the PFMC and the CCIEA.

The CCIEA team recognizes the necessity to partner directly with the PFMC on these research recommendations, in order for them to be effective and directly applicable to management. We greatly appreciated the time and effort the PFMC committed to scoping these indicators under FEP Initiative 2. An ongoing scoping process could give the CCIEA team clear direction on PFMC needs, and give the PFMC a clear sense of CCIEA capabilities and capacity. Therefore:

- The Research Recommendations below are based on our current work and interests, but we would appreciate an opportunity to further scope CCIEA work with the PFMC and its advisory bodies, to ensure that our work is aligned with the PFMC's ecosystem science needs.

2. Continue making improvements to indicator analysis.

The CCIEA team benefited greatly from working with the EWG on FEP Initiative 2, and from the complementary support of the SSCES in providing technical review of CCIEA indicators and activities. The CCIEA team recommends that this partnership continue, with emphasis on:

- Continued refining of the existing indicators in this report, to better meet PFMC needs.
- Identifying and prioritizing indicator gaps, such as CPS, HMS, groundfish, diet information, chlorophyll, harmful algal blooms, and socioeconomic data from underreported communities.
- Using MARSS models to estimate trends in our indicators, separate from the observation error inherent in field sampling.
- Analyzing time series to 1) determine if threshold relationships exist between stressors and indicators, thus informing risk assessments, and 2) to detect early-warning indicators of major shifts in ecosystem structure or function.

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[8] http://www.pcouncil.org/wp-content/uploads/2015/03/0315decisions.pdf

[9] https://www.st.nmfs.noaa.gov/ecosystems/ebfm/creating-an-ebfm-management-policy

3. Assess the dynamics of fisheries adaptation to short-term climate variability.

The CCE is highly variable, driven by annual or decadal variations such as El Niño events, PDO shifts, and marine heat waves. The livelihoods of fishers in the CCE are heavily influenced by such variability. As fishers attempt to adapt to variability by switching among fisheries, their actions impact other fishers and fishing communities, and may actively influence ecosystem dynamics. This project will investigate how fisheries management and fishers' fishing strategies combine to affect social and ecological resilience to the short-term climate variability inherent to the CCE. We plan to:

- Analyze how productivity of key species varies with climate/ocean conditions.
- Survey CCE fishers to determine motivations for fishery participation, and use the data from the survey and fish tickets to fit statistical models of individual fishing participation choices.
- Construct an integrated model of several CCE fisheries (e.g., salmon, Dungeness crab, albacore [*Thunnus alalunga*], groundfish, and shrimp) that determines participation and effort in each fishery.
- Model how climate variability affects fisheries both directly, via environmental effects, and indirectly, via participation decisions, and explore what types of fishing portfolios, for individuals or ports, result in lower variation in income and higher quality of life.

4. Assess the vulnerability of communities at sea to long-term climate change.

Long-term climate change has already shifted distributions of marine species in the CCE, but the socioecological impacts of climate change on fishing communities over the next several decades are difficult to anticipate. A major challenge remains in linking vulnerability to predicted long-term changes in the marine seascape upon which each community depends, particularly because both target species and fleets from different ports form spatially and temporally dynamic "communities at sea" (e.g., Colburn et al. 2016). We plan to:

- Develop a composite index of vulnerability for each community at sea as a function of its exposure (changes in target species biomass) and sensitivity (dependence on each target species) to long-term climate change.
- Assess each community at sea's adaptive capacity (e.g., mobility and target switching).
- Set up Environmental Competency Groups throughout the CCE, so that scientists, fishers, and managers can together interrogate information about climate vulnerabilities and impacts, co-develop adaptation strategies, and proactively reveal barriers to adaptation.

5. Explore implementing Dynamic Ocean Management to reduce bycatch in HMS fisheries.

Traditional management measures for bycatch reduction are static in space and time, despite the fact that both marine species and human users rely on dynamic environmental features. Dynamic Ocean Management (DOM) offers an ecosystem-based management approach toward addressing these dynamic issues (Lewison et al. 2015). We define DOM as management of marine systems that can change in space and time with the shifting nature of the ocean and its users. We are exploring DOM for HMS, specifically to maximize swordfish (*Xiphias gladius*) catch in the California drift gillnet fishery while minimizing bycatch of key species including leatherback sea turtles (*Dermochelys* *coriacea*), blue sharks (*Prionace glauca*), and California sea lions; we will extend this to include marine mammals that are hard-cap species, i.e., species that are protected such that capture of a specific number will result in a fishery closure for the rest of the season. Our approach is to:

- Use species-specific bycatch risk profiles to create risk–reward ratios for swordfish vessels.
- Track spatiotemporal changes in risk ratios as a function of management strategies and dynamic environmental conditions in the area of the drift gillnet fishery.

6. Assess the ecological and economic impacts of ocean acidification.

The CCE is characterized by upwelling of deep, cold, nutrient-rich waters that support fish stocks and the human communities that rely on them, but that also make the area particularly at risk of OA. The CCIEA team is leading focused research to identify the species, fisheries, FMPs, and ports most vulnerable to OA. Specifically, we will:

- Apply an Atlantis ecosystem model, which was formally reviewed by a PFMC Methodology Review Panel and the Center for Independent Experts in July 2014, and presented to the full PFMC in November 2014 (Kaplan and Marshall 2016).
- Link the Atlantis model to 1) ensembles of future scenarios for OA, warming, and species range shifts, and 2) updated information about species exposure and sensitivity to OA.
- Identify FMPs, ecoregions, and ports most likely affected by OA, warming, and subsequent range shifts, including both direct and indirect (e.g., food web) effects and impacts on coastal economies, as explored by Marshall et al. (2017).
- Consider impacts on FMPs that result from changes in prey productivity, for instance impacts on rebuilding rockfish stocks.

Conclusions

Conditions in the CCE in 2016–17 suggest a transitional period from several years of anomalously warm temperatures, below-average precipitation, and poor coastal productivity into conditions more representative of long-term averages. Some species already appear to be responding to this shift, although the extent of species responses will require many years to understand: the CCE is a species-rich system, and the many species have developed a wide range of adaptations to deal with the highly variable environmental conditions that characterize the California Current. Some of these adaptations may manifest themselves quickly, but many species in the CCE have highly protracted life histories, which could result in lag times before the environmental effects are known. Many species are also highly mobile or migratory, making it difficult to monitor them and track their responses in real time. Finally, we simply do not fully understand the relationships between many species and their environment, particularly when their environment experiences such extreme anomalies as observed in the California Current from 2013–16.

The CCIEA team will collaborate with colleagues in NOAA and partner agencies and institutions to determine if, in fact, the recent anomalous conditions have resulted in negative impacts on forage species, salmon, and higher predators. We are likely to find unanticipated responses, such as the large numbers of YOY groundfish observed in 2015–16 that suggest favorable conditions for early life stages of those species despite environmental and lower trophic-level indicators to the contrary. We will also continue to study linkages between these dynamics and the equally dynamic human communities that rely on California Current marine resources.

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STATE OF THE CALIFORNIA CURRENT 2016–17: STILL ANYTHING BUT “NORMAL” IN THE NORTH

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THE SHORT VERSION

From: Bill Peterson - NOAA Federal
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Date: Mon, Apr 17, 2017 at 10:09 AM
Subject: Re: CalCOFI report 2016–17
To: Sam McClatchie - NOAA Federal
<sam.mcclatchie@noaa.gov>
Cc: Brian Wells brian.wells@noaa.gov …

Brian, Sam, and Others:

The ocean off Oregon is anything but "normal." Even though SST had cooled down a bit, we still have relatively warm/fresh water at depth as well as strong positive anomalies in copepod species richness and southern copepod biomass—all indicators that we still have a lot of "El Niño water" hanging around. And returns of adult spring Chinook past Bonneville Dam (Columbia River) are 10% of the ten-year average so far. Finally we are seeing small numbers of *Pseudo-nitzschia*. Nothing normal! The only good news is that *Euphausia pacifica* have returned.

Some years ago, we did a "warm in the north, cold in the south" (or was it the opposite title?).

Bill

ABSTRACT

This report examines the ecosystem state of the California Current System (CCS) from spring 2016–spring 2017. Basin-scale indices suggest conditions that would support average to below average coast-wide production across the CCS during this time period. Regional surveys in 2016 sampled anomalously warm surface and subsurface waters across the CCS. Chlorophyll concentrations were low across the CCS in 2016 and, concomitant with that, copepod communities had an anomalously high abundance of subtropical species. Early in 2017 conditions between northern, central, and southern CCS were dissimilar. Specifically, surface conditions north of Cape Mendocino remained anomalously warm, chlorophyll was very low, and subtropical copepods were anomalously abundant. Southern and central CCS surveys indicated that environmental conditions and chlorophyll were within normal ranges for the longer time series, supporting an argument that biophysical conditions/ecosystem states in the southern and central CCS were close to normal.

Epipelagic micronekton assemblages south of Cape Mendocino were generally close to longer-term average values, however the northern assemblages have not returned to a "normal" state following the 2014–15 large marine heatwave and 2016 El Niño. North of Cape Mendocino the epipelagic micronekton was largely composed of offshore and southern derived taxa. We hypothesize that stronger-than-typical winter downwelling in 2017 and a reduced spawning biomass of forage taxa are contributors to the anomalous forage community observed in the north. Also of note, surveys indicate northern anchovy (*Engraulis mordax*) abundance was greater than average (for recent years) and nearer shore in northern regions. Finally, record-low juvenile coho and Chinook salmon catches in the 2017 northern CCS salmon survey suggest that out-migrating Columbia Basin salmon likely experienced unusually high early mortality at sea, and this is further supported by similarities between the 2017 forage assemblage and that observed during poor outmigration survival years in 2004, 2005, and 2015.

Generally, the reproductive success of seabirds in 2016 (the most current year available) was low in the north but near average in central California. At Yaquina Head off Oregon and Castle Rock off northern California some of the lowest reproductive success rates on record were documented. In addition to reduced abundance of prey, there was a northward shift of preferred seabird prey. Seabird diets in northern areas also corroborated observations of a northward shift in fish communities. Nest failure was attributed to a combination of bottom-up and top-down forces. At Castle Rock, most chicks died of starvation whereas, at Yaquina Head, most nests failed (95% of common murre, *Uria aagle*) due to disturbance by bald eagles (*Haliaeetus leucocephalus*) seeking alternative prey. Mean bird densities at sea for the 2017 surveys between Cape Flattery Washington and Newport Oregon were the lowest observed and may indicate continued poor reproductive performance of resident breeders in 2017. South of Cape Mendocino, where forage availability was typical, seabird reproductive success was also below average for most species in 2016, but did not approach failure rates observed in the north. Finally, in 2017, abundances of seabirds observed at-sea off southern California were anomalously high suggesting an improved foraging environment in that area.

Marine mammal condition and foraging behavior were also impacted by the increased abundance and shifting distribution of the northern anchovy population. Increases in the abundance of northern anchovy in the Southern California Bight coincided with improved condition of sea lion (*Zalophus californianus*) pups in 2016. Namely, lipid-rich northern anchovy occurred in great frequencies in the nursing female diet. Increases in northern anchovy nearshore in the central and northern CCS may have also contributed to a shoreward shift in distribution of humpback whales (*Megaptera novaeangliae*) in these regions. These shifts along with recovering humpback whale populations contributed to recent increases in human-whale interactions (e.g., fixed-gear entanglements).

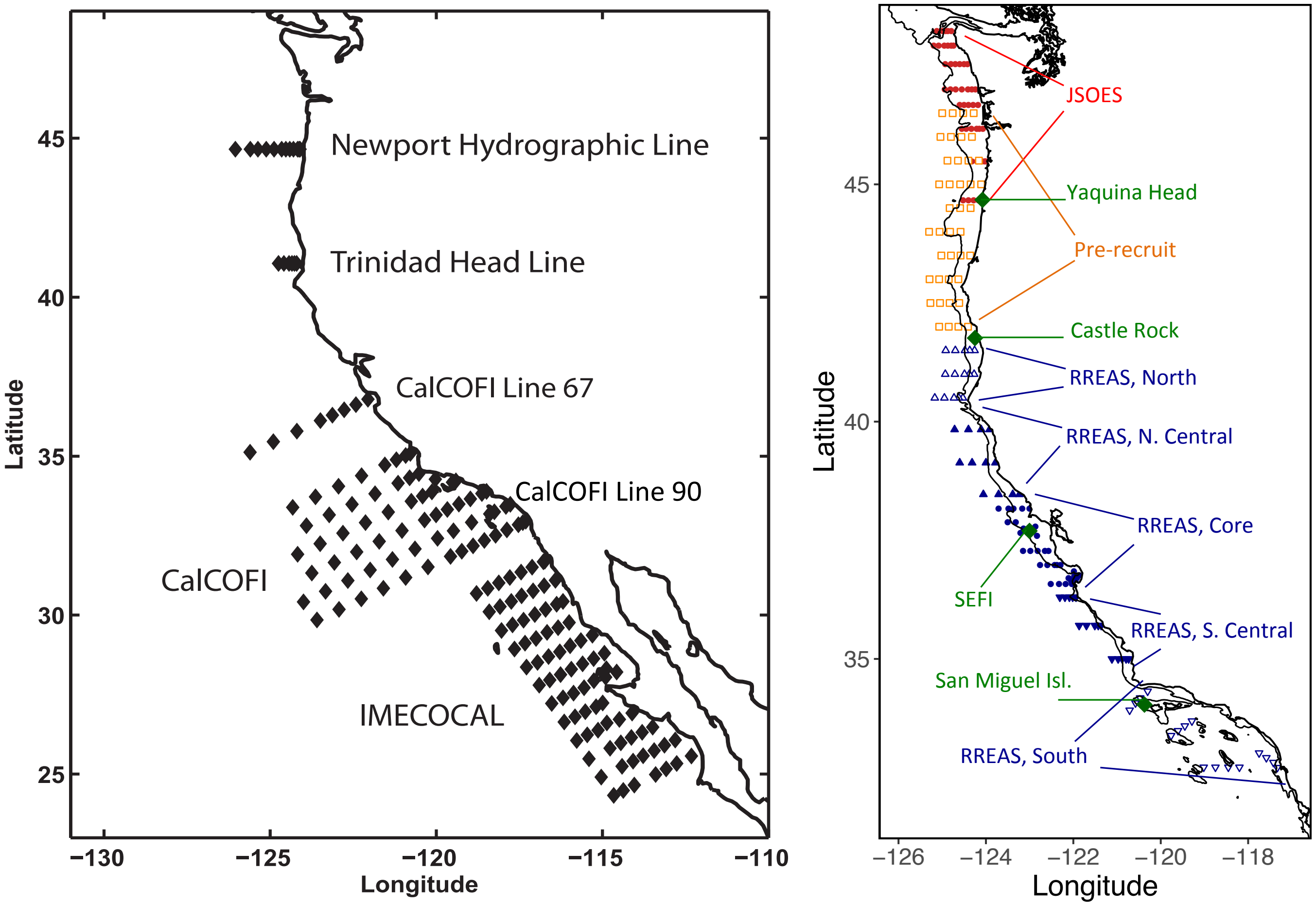

Figure 1. Left) Station maps for surveys that were conducted multiple times per year during different seasons to provide year-round observations in the California Current System. The CalCOFI survey (including CalCOFI Line 67 and 90) was occupied quarterly; the winter and spring CalCOFI survey grid usually extends just north of San Francisco. The IMECOCAL survey is conducted quarterly or semiannually. The Newport Hydrographic Line was occupied biweekly. The Trinidad Head Line was occupied at biweekly to monthly intervals. Right) Location of annual or seasonal surveys, including locations of studies on higher trophic levels, from which data were included in this report. Different symbols and colors are used to help differentiate the extent of overlapping surveys. Surveys used in this report include (Red) Juvenile Salmon and Ocean Ecosystem Survey (JSOES, NOAA/BPA rope trawl), (Orange) NWFSC Pre-recruit midwater trawl survey, and (Blue) SWFSC Rockfish Recruitment and Ecosystem Assessment Survey (RREAS) in five regions. SEFI indicates Southeast Farallon Island.

INTRODUCTION

From 2014 to 2017 the California Current System (CCS) had an unprecedented combination of warm-water conditions that may affect CCS marine life for a number of years, there was a large marine heat wave from 2014–16, influenced in part by anomalously warm conditions in the tropical Pacific that were punctuated by the 2015–16 El Niño (Leising et al. 2015; Jacox et al. 2016; Di Lorenzo and Mantua 2016; McClatchie et al. 2016; Frischkneckt et al. 2017; Peterson et al. 2017). This report revisits these years when applicable to current ecosystem conditions but primarily examines the state from spring 2016–spring 2017; this report is an extension of the previous State of the California Current report (McClatchie et al. 2016). Specifically, following on previous reports, we consolidate environmental and survey data from throughout the California Current (fig. 1). These data include indicators of basin-scale conditions, regional oceanographic conditions, and the food-web from primary production to top-predator foraging behavior, reproductive success, and condition. Although many results are preliminary and encompass dissimilar survey designs, synthesis of these diverse components provides a first approximation of the coast-wide and regional ecosystem conditions. Typical of these reports, we highlight emerging stories as supported by the available data and explore the connections between past, current, and future CCS ecosystem states. This year's report will focus on the clear disparity between ecosystem recoveries following the record 2014–16 warming of the CCS in northern and southern CCS subregions. Specifically, while the southern region trended toward a "normal" ecosystem state in 2016–17, the northern region did not (e.g., there was a persistence of the southern copepod community, limited forage availability, anomalously high salmon mortality,

TABLE 1
**State of various indicators along California Current System (CCS).
The status represents early 2017 unless otherwise stated. Grey font indicates average production/condition, red indicates below average production/condition, and green indicates above average production/condition. Italics represent data cited from elsewhere within this report or preliminary analyses discussed in this report. Abbreviations: Oceanic Niño Index (ONI), Pacific Decadal Oscillation (PDO), North Pacific Gyre Oscillation (NPGO), North Pacific High (NPH), and sea surface temperature (SST).**

Indicator	Basin	Northern CCS	Central CCS	Southern CCS
ONI	Average			
PDO	Above average			
NPGO	Near average			
NPH	Below average			
Upwelling		Below average	Average	Above average
Cumulative upwelling		Average	Below average	Average
SST		Above average	Average	Average
Chlorophyll		Below average	Average	Average
Harmful algal blooms		No	No	Yes
Copepods		Southern derived and rich	—	—
Forage		offshore and southern derived assemblage	Typical assemblage	Typical assemblage along with increased anchovy abundances
Salmon survival		Below average juvenile abundance at sea	*Ecosystem indicators related to salmon suggest average*	—
Seabird productivity (2016)		Reproductive failures	Below/near average	—
Seabird at-sea abundance		Well below average	*Below/near average*	Well above average
Sea lions (2016)		Signs of recovery after the 2013 unusual mortality event		
Whales			Humpback whales distributed shoreward	

unprecedented abundance of pyrosomes, and reduced reproductive success of seabirds) (table 1).

BASIN-SCALE CONDITIONS

North Pacific Climate Indices

The CCS experienced a marine heat wave that featured record-high sea surface temperatures (SST) in 2015, with 2014–16 the warmest 3-year period on record (Jacox et al. 2017). The exceptionally high SST anomalies declined from their peak values in spring/summer 2016. The marine heatwave was first evident in the Gulf of Alaska in late 2013 (Bond et al. 2015) and by the middle of 2014, anomalously high SST anomalies were also observed in the southern CCS as far south as Baja California (Leising et al. 2015).

El Niño/Southern Oscillation (ENSO) is a mode of interannual variability in the equatorial Pacific causing physical and ecological impacts throughout the Pacific basin and CCS, though the links between ENSO and the CCS are complex (Fiedler and Mantua 2017). The Oceanic Niño Index (ONI; http://www.cpc.ncep.noaa.gov/data/indices/), a three-month running mean of SST anomalies averaged over the NINO3.4 region of 5˚S–5˚N and 120˚W–170˚W, had values exceeding the 0.5˚C threshold that signifies an El Niño event from April 2015 through May 2016 (fig. 2). Peak ONI values in 2015–16 rivaled those of the record 1997–98 El Niño event, but this tropical climate event was perhaps not quite as extreme (Jacox et al. 2016). Negative ONI values, indicative of a tropical La Niña event, first appeared during July 2016, but declined only to –0.84˚C indicating a modest intensity La Niña during October–November 2016. By March 2017 the ONI had transitioned to ENSO-neutral conditions, with small positive values below the 0.5˚C threshold. NOAA's Climate Prediction Center[1] has issued a report stating that El Niño neutral conditions were present during the summer of 2017 and they predict that there are growing odds for a tropical La Niña event in winter 2017–18.

The Pacific Decadal Oscillation (PDO) index describes the temporal evolution of dominant spatial patterns of SST anomalies over the North Pacific (Mantua et al. 1997). Positive PDO values are also associated with a shallower upwelling cell in the northern CCS (Di Lorenzo et al. 2008). The PDO values from January 2015 to the spring of 2016 were exceptionally high. By summer of 2016 the PDO values dropped considerably and reached their lowest values since the spring of 2014 (fig. 2). However, the winter 2016–17 PDO values were slightly elevated from these, only to decline to near-zero values in July–August 2017 (fig. 2).

The North Pacific Gyre Oscillation (NPGO) is a low-frequency signal of sea surface height, indicating variations in the circulation of the North Pacific Subtropical Gyre and Alaskan Gyre (Di Lorenzo et al. 2008). Positive values of the NPGO are linked with increased equatorward flow in the California Current, along with increased surface salinities, nutrients, and chlorophyll values in the southern-central CCS (Di Lorenzo et al. 2009). Negative

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[1] http://www.cpc.ncep.noaa.gov

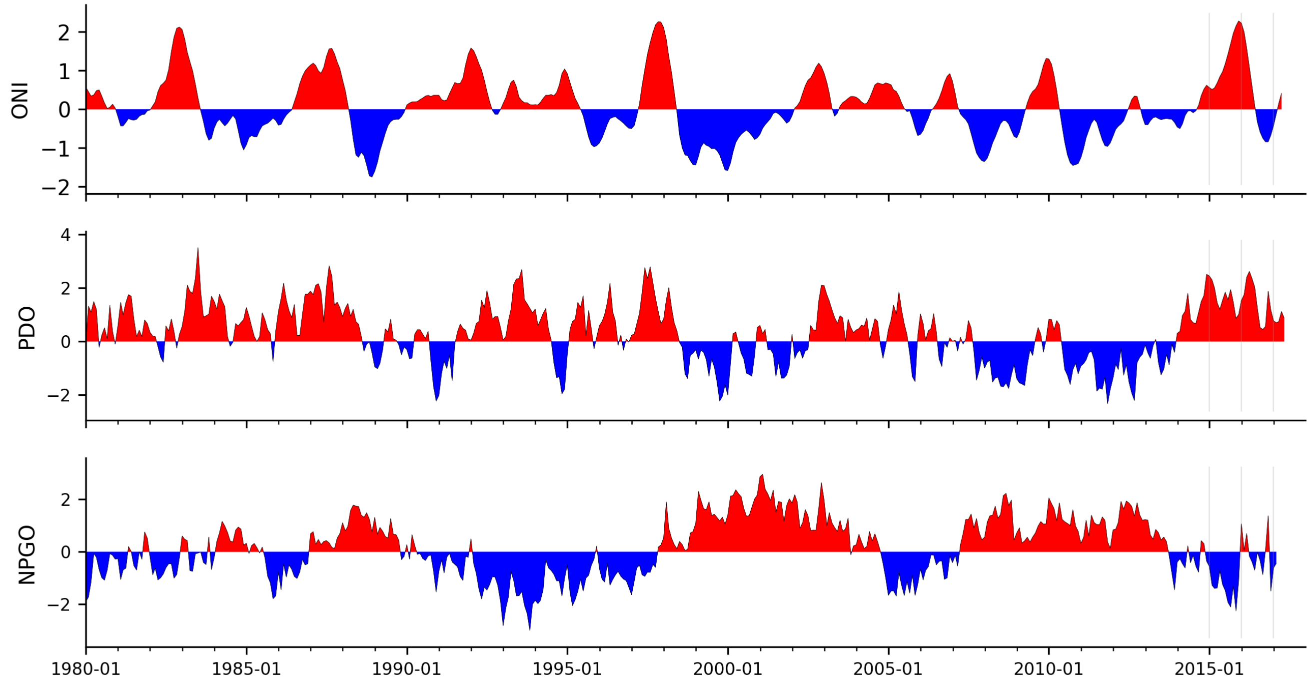

Figure 2. Time series of monthly values for three ocean climate indices especially relevant to the California Current: Oceanic Niño Index (ONI), the Pacific Decadal Oscillation (PDO), and North Pacific Gyre Oscillation (NPGO). Data are shown for January 1980 to July 2017. Vertical lines mark January 2015, 2016, and 2017.

NPGO values are associated with decreases in these variables, inferring less subarctic source waters, fewer nutrients, reduced upwelling and generally lower production in the CCS. The NPGO was negative for the entirety of 2015, with the largest negative values occurring in the fall (fig. 2). During 2016 the NPGO oscillated from positive to negative values that were very small in amplitude. The winter 2016–17 NPGO values were negative with December 2016 having the largest negative value of −1.5. Thus, NPGO index indicated that basin-scale gyre circulation favored low to neutral production across the CCS between spring 2016–spring 2017.

In summary, 2015–16 had extreme positive ONI and PDO index values, and extremely low NPGO index values, all pointing toward increased subtropical influences and reduced subarctic influences in the CCS. Summer 2016 to spring 2017 featured a modest La Niña event and reduced amplitudes in the PDO and NPGO indices, such that these basin-scale patterns were not indicating large fluctuations on the state of the CCS ecosystem over that period.

North Pacific Climate Patterns

A basin-scale examination of SST and surface wind anomalies allows for the interpretation of the spatial evolution of climate patterns and wind forcing over the North Pacific related to trends in the basin-scale and upwelling indices (figs. 3, 4). During July 2016, negative SST anomalies in the central and eastern Equatorial Pacific marked the transition between the El Niño event that peaked in winter 2015–16 and the La Niña event that peaked in winter 2016–17 (fig. 3). Tropical La Niña conditions dissipated by May 2017. During the summer of 2016, SST anomalies exceeding 1˚C were evident in the Bering Sea and the Gulf of Alaska. These positive anomalies persisted into the winter of 2016–17. The SST approached the long-term average by May 2017 in the central and southern CCS but remained warmer than average along the northern CCS.

Wind anomalies over the Bering Sea and Gulf of Alaska were anomalously eastward in July and December 2016 and a large anti-cyclonic pattern was centered at 42˚N, 160˚W due to higher than average sea level pressures during July and December 2016 (fig. 3). High SST anomalies associated with the marine heatwave had dissipated along the west coast of North America by July 2016, with only the Southern California Bight and along the Baja Peninsula showing SST anomalies greater than 1˚C. From December 2016 to May 2017 SST along the West Coast were near the long-term mean, with slightly elevated temperatures along the Washington and Oregon coasts and southern Baja California, Mexico (figs. 3, 4). Alongshore winds were average during July 2016, but strengthened in December 2017. February 2017 winds were anomalously northward, associated with an unusual number of winter storms and excessive rainfall along the West Coast (fig. 3)[2]. Upwelling-favorable (southward) winds resumed by May 2017.

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[2] https://www.ncdc.noaa.gov/sotc/drought/201702

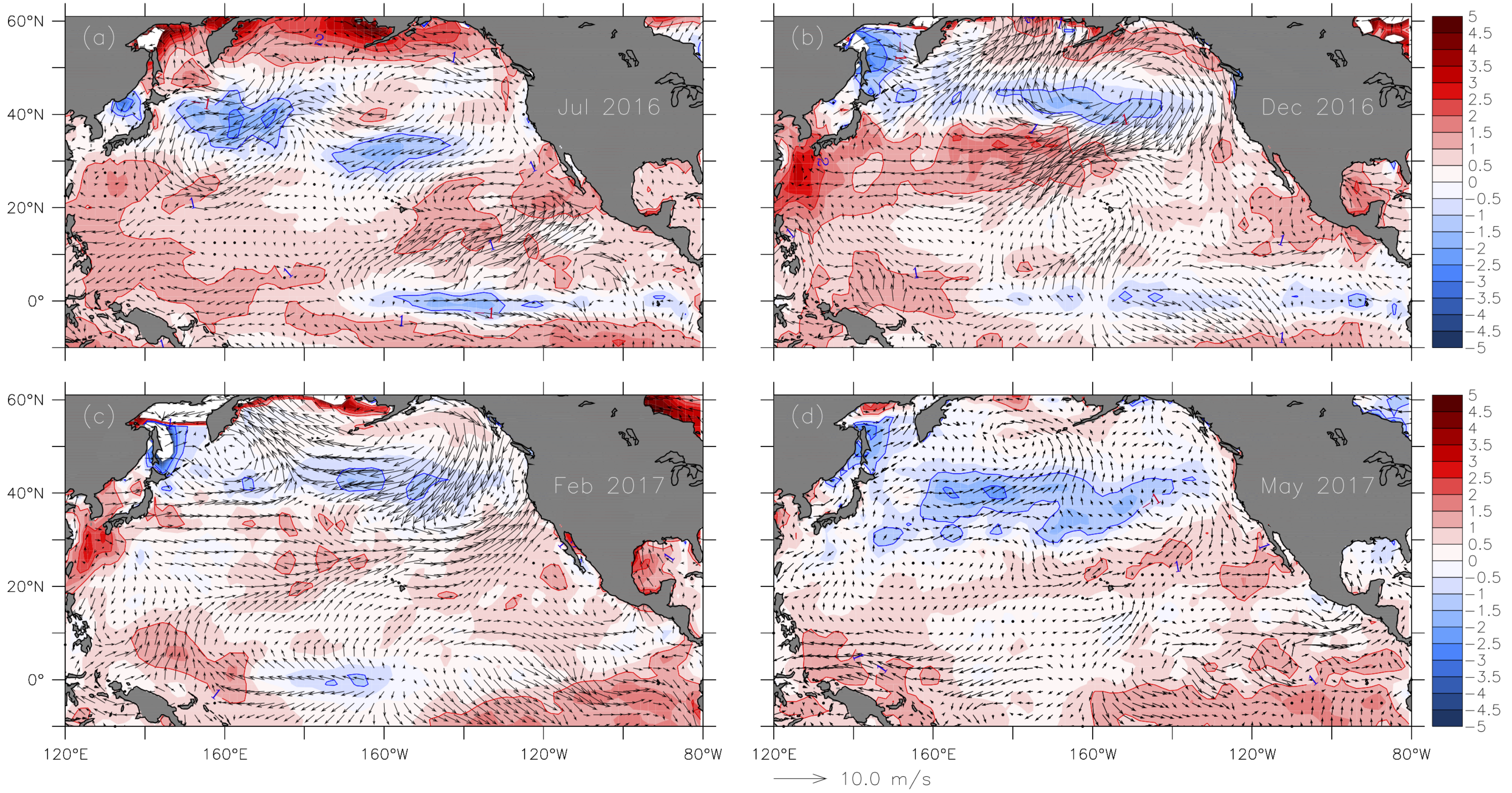

Figure 3. Anomalies of surface wind velocity and sea surface temperature (SST) in the North Pacific Ocean for July 2016, December 2016, February 2017, and May 2017. Arrows denote magnitude and direction of wind anomaly (scale arrow at bottom). Contours denote SST anomaly. Shading interval is 0.5°C and contour intervals of 1 and 2°C are shown. Negative (cool) SST anomalies are shaded blue. Wind climatology period is 1968–96. SST climatology period is 1950–79. Both SST and wind data are from NCEP/NCAR Reanalysis and were obtained from http://www.esrl.noaa.gov.

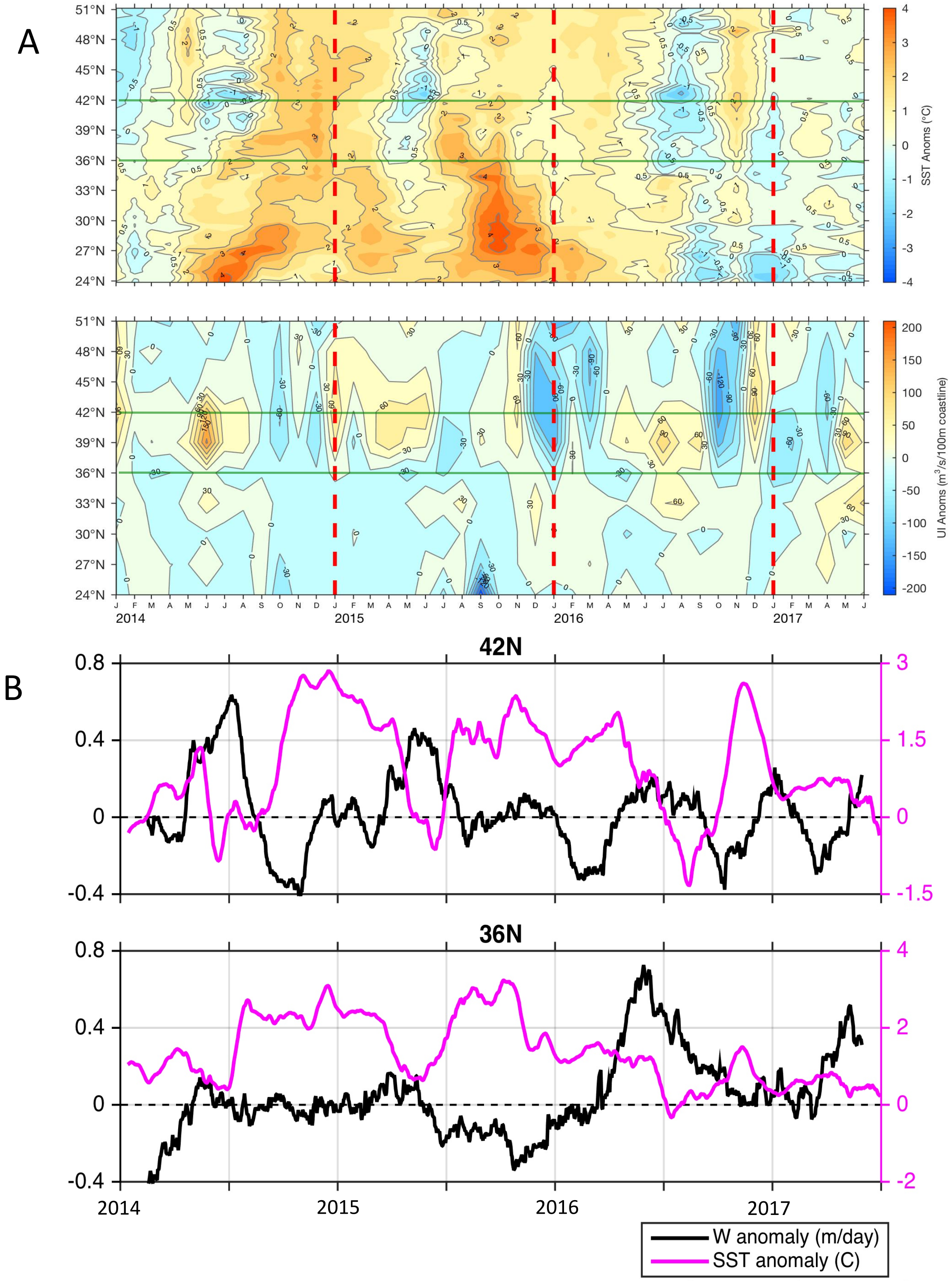

Figure 4. A) Monthly sea surface temperature (SST) anomalies (top) and upwelling index (UI) anomalies (bottom) for January 2014–June 2017. The SST anomalies are averaged from the coast to 100 km offshore. Positive and negative upwelling anomalies denote greater than average upwelling or downwelling (usually during the winter), respectively. Anomalies are relative to 1982–2017 monthly means. Daily optimum interpolation AVHRR SST data obtained from http://coastwatch.pfeg.noaa.gov/erddap/griddap/ncdcOisst2Agg. Six-hourly upwelling index data obtained from http://oceanview.pfeg.noaa.gov/erddap/tabledap/. B) Upwelling anomalies (black) and SST anomalies (magenta) relative to the 1999–2011 climatology, derived from a data assimilative ocean reanalysis of the California Current System (http://oceanmodeling.ucsc.edu/ccsnrt/), are shown at two latitudes off the US West Coast; 36°N and 42°N (indicated by horizontal green lines in A). Values are averaged from the coast to 100 km offshore. SST is smoothed with a 30-day running mean; upwelling, which is much noisier, is smoothed with a 90-day running mean.

COAST-WIDE CONDITIONS

Upwelling in the California Current

Monthly anomalies of SST (averaged from the coast to 100 km offshore) and upwelling are used to examine anomalous coastal upwelling conditions within the CCS from January 2014 to July 2017 (fig. 4). Upwelling estimates come from two sources: the Bakun upwelling index (UI; fig. 4a; Bakun 1973; Schwing et al. 1996), and a data-assimilative regional ocean model (W; fig. 4b; Jacox et al. 2014)[3]. We take this approach as the UI has long been used in studies of the California Current, but in some places, particularly south of 39°N, it is a less reliable indicator of upwelling due to relatively poor estimation of the wind stress and modulation of upwelling by the cross-shore geostrophic flow (Bakun 1973; Jacox et al. 2014). SST anomalies along the coast are driven by upwelling, especially in northern latitudes due to a strong coupling between local winds and SST (Frischknecht et al. 2015). High SST anomalies due to the marine heat wave are evident in 2014 and 2015. Positive SST anomalies (>1°C) during the 2015–16 El Niño event persisted during the winter and spring of 2016 especially for locations north of 42°N. From January to May of 2017, SST anomalies north of 42°N were near the long-term average, with the exception of a few localized periods of ~0.5°C anomalies. UI anomalies from 39° to 45°N were positive during the spring and summer of 2015, but anomalously strong downwelling occurred in the winter of 2015–16 (typical of past El Niño winters). The longest period of sustained positive upwelling anomalies during 2016 occurred from July to September for latitudes between 36° and 42°N. October and November 2016 upwelling anomalies were negative north of 36°N, followed by positive anomalies (weaker downwelling) in December. On the whole, upwelling during 2017 has been about average from 39° to 42°N, weaker than average farther north, and stronger than average farther south.

The cumulative upwelling index (CUI) is the cumulative sum of the daily UI values starting January 1 and ending on December 31, and it provides an estimate of the net influence of upwelling on ecosystem structure and productivity over the course of the year (Bograd et al. 2009). In general, upwelling has been weaker for the last two years, 2016–17, than the previous two years, 2014–15 (fig. 5). During the 2016 winter, upwelling north of 39°N was low due to the El Niño and strong upwelling only began by the summer. South of 39°N, upwelling anomalies were neutral to positive in early 2016, counter to what would be expected from a strong El Niño (Jacox et al. 2015). Upwelling during 2017 was near the long-term average for the whole coast except for the latitudes between 36°–42°N. For these latitudes, the CUI curves during the winter were below the climatological curve and stronger upwelling began by the beginning of May.

Periods of upwelling or, farther north, reduced downwelling during the winter can limit stratification and facilitate introduction of nutrients to the surface acting to precondition the ecosystem for increased production in the spring (Schroeder et al. 2009; Black et al. 2010). The area of the surface atmospheric pressures associated with the North Pacific High (NPH) can be used as an index of this winter preconditioning (Schroeder et al. 2013). Since 2014 there has been a continual weak NPH during the winter (fig. 6). The January–February mean of the NPH area has been very small since the exceptionally large area during 2013, and the 2017 area was the smallest size since 2010.

Coastal Sea Surface and Subsurface Temperatures

SSTs measured by National Data Buoy Center buoys along the West Coast were mostly above long-term averages during summer of 2015 through spring of 2016 (fig. 7). For the northern buoys, this period of warm temperature was briefly interrupted by a decrease in temperatures during August or September that coincided with a strong period of upwelling favorable winds. The decrease in temperatures associated with upwelling was also evident in April and May 2016 for the buoys located off California. For all buoys, warm to exceptionally warm temperatures were recorded during October and November 2016, which decreased greatly in December and January 2017 during a period of strong southward winds. The winter storms that brought excessive rainfall to the West Coast January–February 2017 were accompanied by episodes of strong northward winds lasting approximately a week at a time (fig. 7).

Figure 8 shows January 2014–May 2017 upper ocean temperature anomalies from ROMS averaged from the coast to 100 km offshore at latitudes of 33, 36, 39 and 42°N. From Cape Blanco (42°N) to central California (36°N) near-surface temperature was above average from the summer of 2014 through spring of 2016; yet, at depths greater than ~50 m, cool anomalies were often present. The exception of the warm surface and cool subsurface conditions was during winter 2015–16 when above average temperatures existed throughout the entire water column. This is

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[3] A data-assimilative configuration of the Regional Ocean Modeling System (Shchepetkin & McWilliams 2005; Haidvogel et al. 2008) has been used to produce a reanalysis of the California Current circulation extending back in time to 1980 (Neveu et al. 2016) and continuing to present in near real time (http://oceanmodeling.ucsc.edu/ccsnrt).

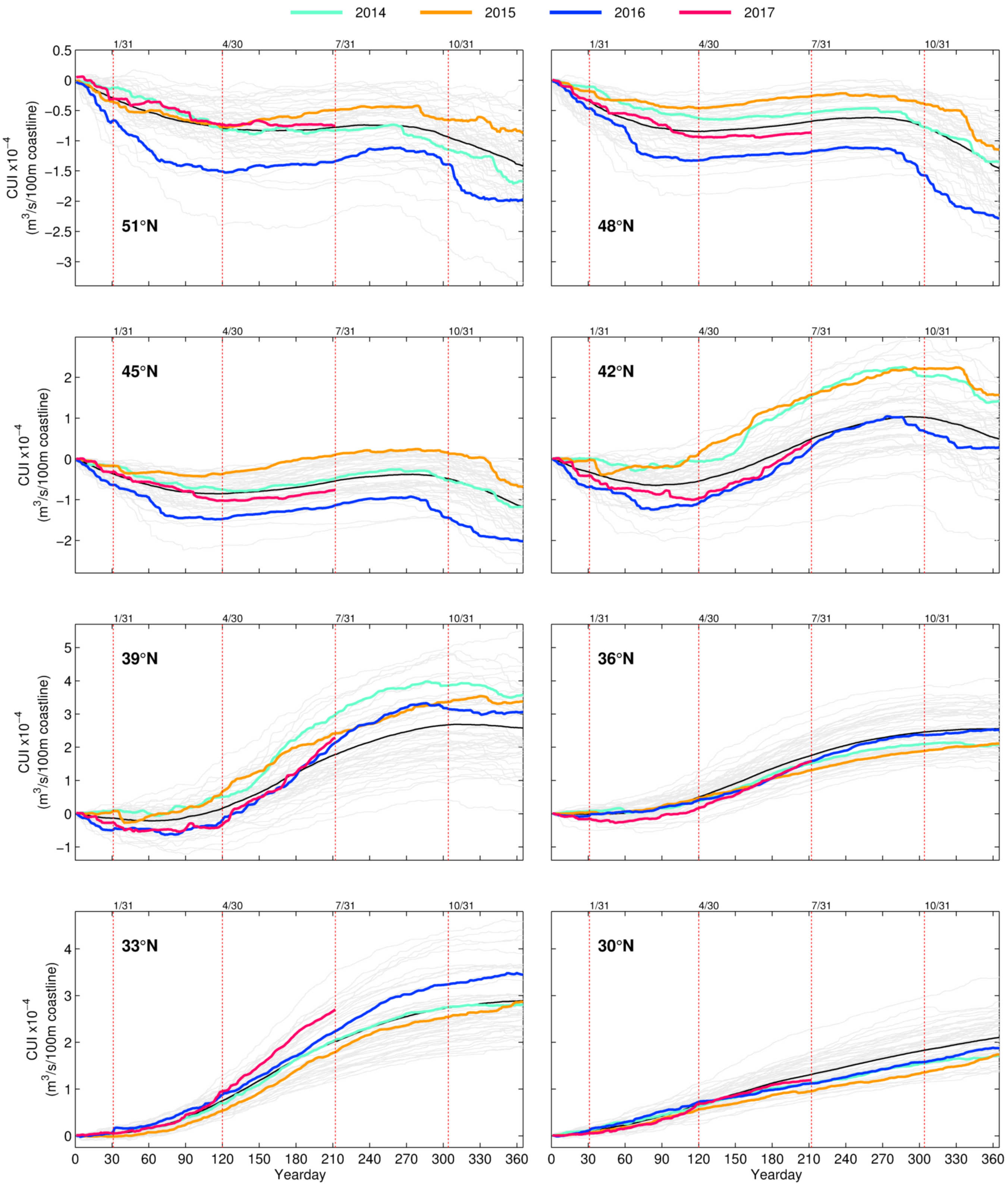

Figure 5. Cumulative upwelling index (CUI) starting on January 1 calculated from the daily upwelling index at locations along the west coast of North America. Grey lines are all yearly CUI for 1967–2016, colored CUI curves are for the years 2014–17. The climatological mean CUI is the black line. The red dashed vertical lines mark the end of January, April, July and October. Daily upwelling index data obtained from http://upwell.pfeg.noaa.gov/erddap/.

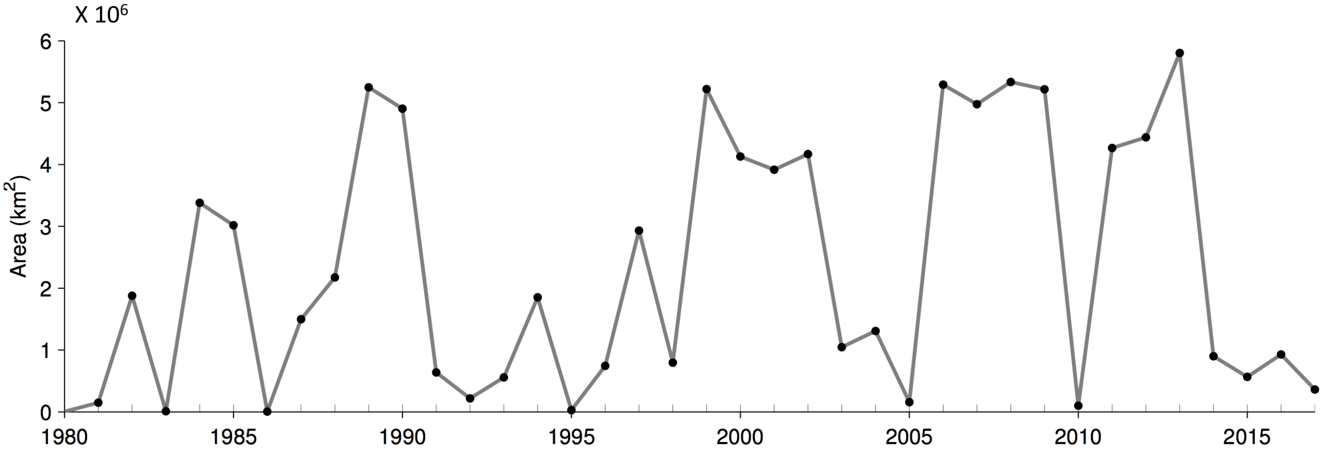

Figure 6. The area of high atmospheric pressure of the North Pacific High averaged over January and February each year (Schroeder et al. 2013). The area is the areal extent of the 1020 hPa isobar located in the eastern North Pacific.

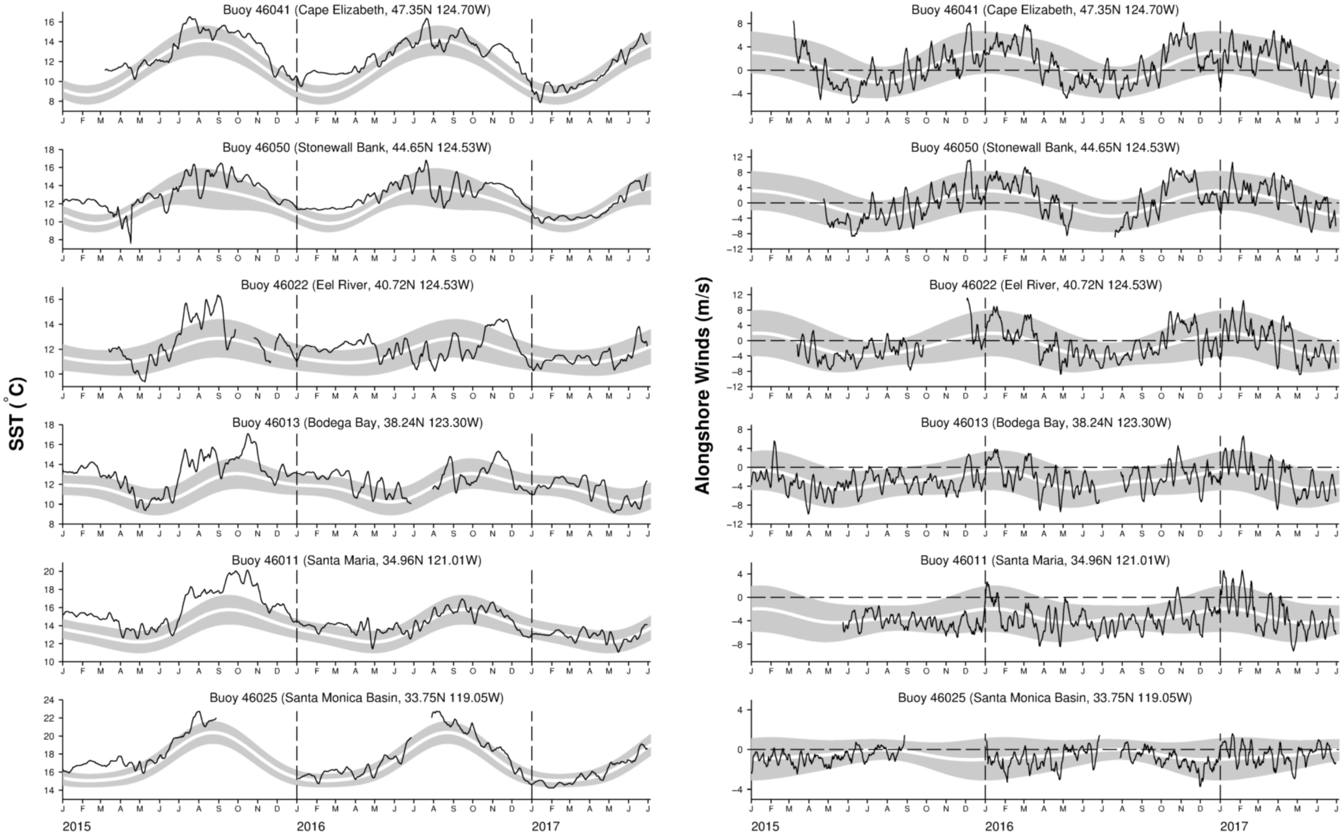

Figure 7. Time series of daily sea surface temperatures (left) and alongshore winds (right) from various National Data Buoy Center (NDBC) coastal buoys along the CCS for January 2015 to June 2017. The wide white line is the biharmonic annual climatological cycle at each buoy. Shaded areas are the standard errors for each Julian day. Series have been smoothed with a 7-day running mean. Data provided by NOAA NDBC. Additional buoy information can be found at http://www.ndbc.noaa.gov/.

especially evident in the southern bight and latitudes south of 39°N during the summer of 2015 and winter of 2015–16. In fact, for the line at 33°N the subsurface temperatures were anomalously high for the whole water column from spring of 2014 to the winter of 2016. During the winter and early spring of 2017, near-surface temperatures (0–50 m) for all the lines were slightly above average, turning below average by the late spring for depths between the surface and 150 m.

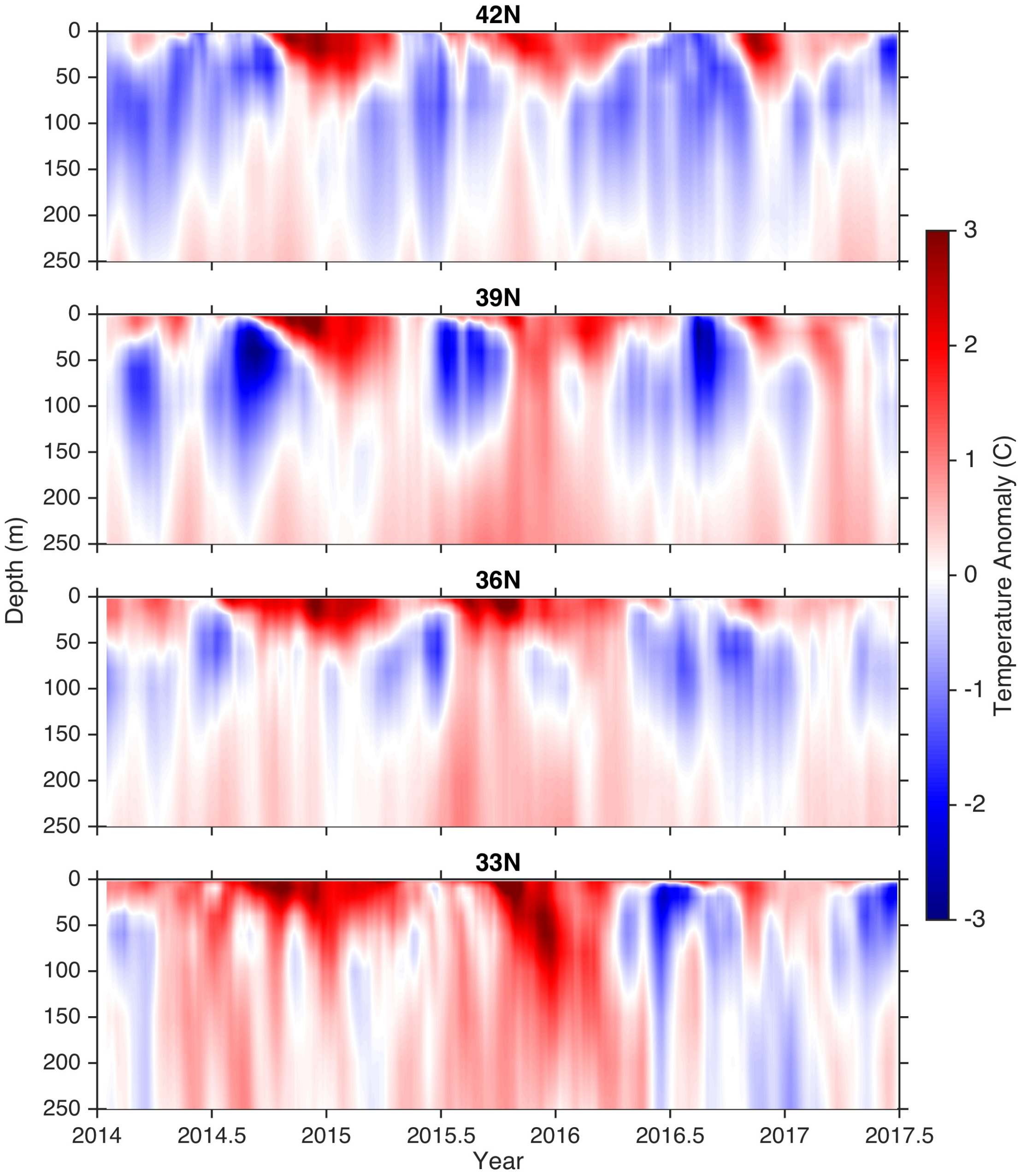

Figure 8. Temperature anomalies relative to the 1999–2011 climatology, derived from a data assimilative ocean reanalysis of the California Current System (http://oceanmodeling.ucsc.edu/ccsnrt/), are shown at four latitudes off the US West Coast. Temperatures are averaged from the coast to 100 km offshore and smoothed with a 30-day running mean.

Primary Production in the California Current System

Anomalously high chlorophyll during the spring occurred along Central California in 2014 and along the whole coast from northern Washington to Point Conception in 2015, which likely represents, to a degree, *Pseudo-nitzschia* (see McClatchie et al. 2016 for more complete description) (fig. 9)[4]. However, during these two years chlorophyll levels were below average off southern California. Spring chlorophyll levels in 2016 were below average for the whole coast except for a few localized increases along Washington and central California coasts (McClatchie et al. 2016). Spring 2017 chlorophyll values were lower than average for the majority of the CCS but showed increases in central California and around the Channel Islands. The elevated chlorophyll in spring 2017 for the Channel Islands corresponded to significant toxin event caused by *Pseudo-nitzschia* (modeled data shown in lower panels of fig. 9).

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[4] https://www.nwfsc.noaa.gov/research/divisions/efs/microbes/hab/habs_toxins/hab_species/pn/index.cfm

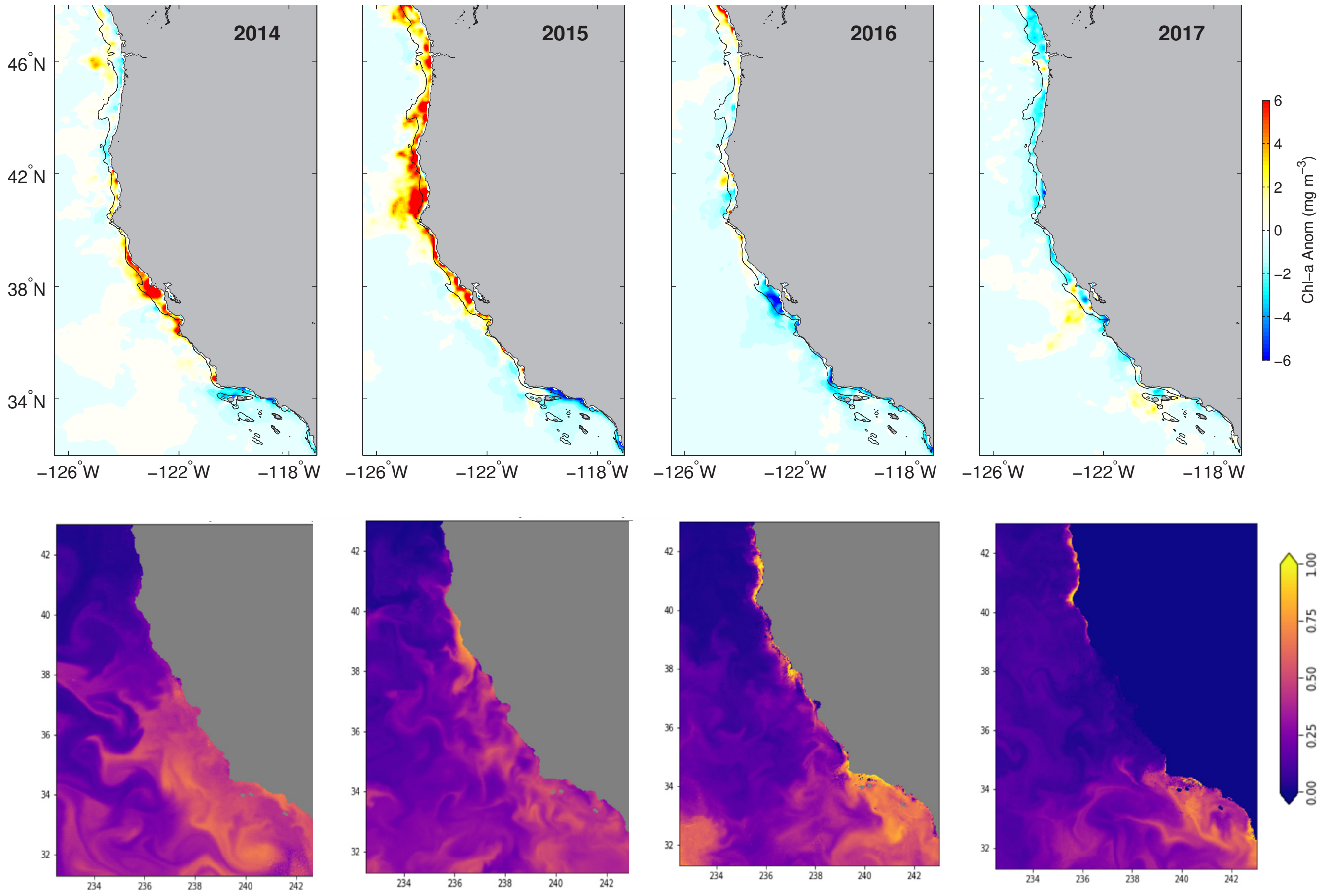

Figure 9. Top) Chlorophyll *a* anomalies from Aqua MODIS for: spring (March–May) of 2014–2017. Monthly anomalies were averaged onto a 0.1° x 0.1° grid and the climatology was based on the time period from 2002–17. The data were obtained from http://coastwatch.pfel.noaa.gov/. Bottom) predicted probability of domoic acid > 500 nanograms/L, during the same times periods as the top pane from http://www.cencoos.org/data/models/habs/previous.

REGIONAL OBSERVATIONS OF ENVIRONMENT AND LOWER TROPHIC LEVELS

Northern California Current: Oregon (Newport Hydrographic Line)

The warm anomalies that intruded onto the Oregon shelf surface waters in September 2014 remained throughout 2015, 2016, and continued into 2017, dominating the local hydrography and impacting pelagic communities. The upwelling season (spring transition) began early on 27 March 2016 and ended on 29 September 2016 (fig. 4), resulting in an upwelling season that was eight days longer than the 40-year climatology. Upwelling in 2016 cooled the warm temperatures that began during the winter of 2015–16 and continued into spring of 2016, resulting in neutral sea surface and deeper water temperatures on the shelf from June through September (figs. 7, 10). During this upwelling period, shelf waters were slightly saltier while deep waters on the slope were mostly neutral throughout 2016 and into 2017. Despite above average upwelling (fig. 4), nitrogen concentrations remained below average throughout 2016 and into 2017 (fig. 10). Following the upwelling season in 2016, the shelf waters returned to anomalously warm and fresh conditions, which were similar to the previous two years.

The zooplankton community remained in a lipid-depleted state throughout 2016 and into 2017. The zooplankton community was dominated by lipid-poor tropical and subtropical copepods and gelatinous zooplankton that generally indicate poor feeding conditions for small fishes. Pyrosomes (*Pyrosoma atlanticum*), a tropical species, were first observed in the fall of 2016 and their biomass increased greatly in the spring of 2017. With the exception of the upwelling months in 2016, the biomass of lipid-rich northern ("cold water") copepods was the lowest observed in the 21-year time series (fig. 10). During June through September, the biomass anomalies of the northern copepods were reduced slightly in response to upwelling, however the anomalies still remained strongly negative. The biomass of southern ("warm water") copepods fluctuated greatly, with

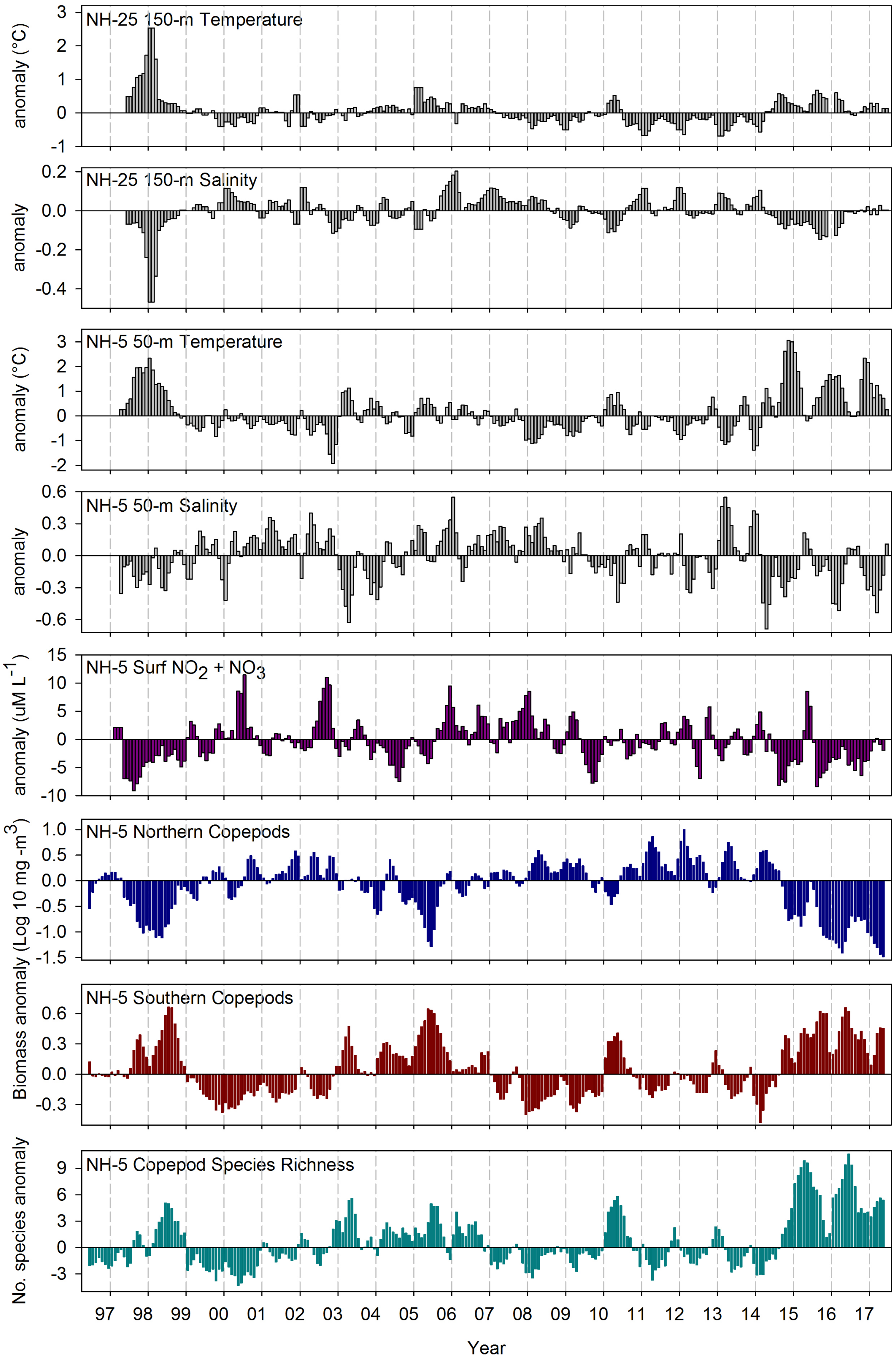

Figure 10. Time series plots of local physical and biological anomalies (monthly climatology removed) from 1997–2017 at NH-25 (Latitude: 44.6517 N Longitude: 124.65 W; top two panels) NH-5 (Latitude: 44.6517 N Longitude: 124.1770 W; lower six panels) along the Newport Hydrographic Line. Temperature and salinity from 150 m and 50 at NH-25 and NH-5 respectively, NO2 + NO3 from the surface, and copepod biomass and species richness anomalies are integrated over the upper 60 m. All data were smoothed with a 3-month running mean to remove high frequency variability.

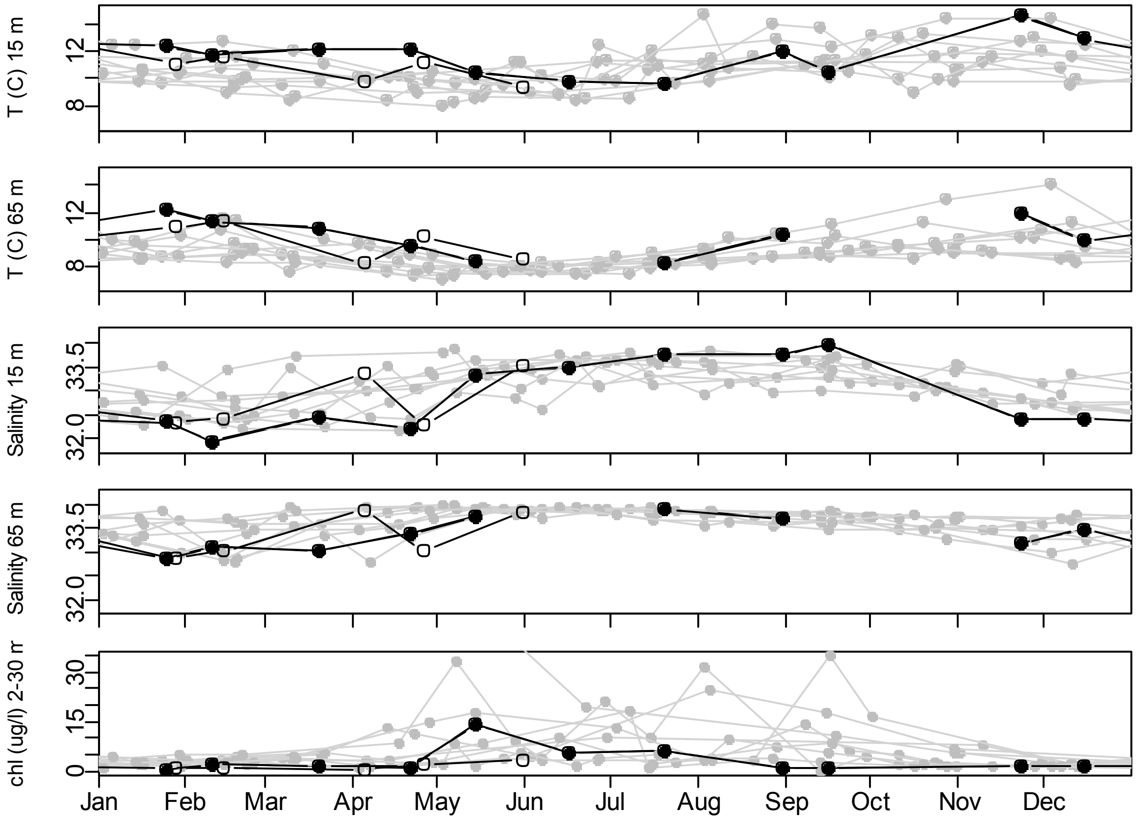

Figure 11. Hydrographic observations along the Trinidad Head (TH) Line at station TH02. Panels from top to bottom show temperature at 15 m, temperature at 65 m (near the sea floor), salinity at 15 m, salinity at 65 m, and mean (uncalibrated) chlorophyll *a* concentration from 2–30 m. Closed black circles represent 2016, open circles represent 2017, and grey time series represent previous years.

the highest biomass anomalies occurring during the upwelling months and lower anomalies during the winter (fig. 10). In 2015 and in 2016, the seasonal shift from a winter copepod community to a cold summer community that results from the Davidson Current in winter and its disappearance in spring did not happen (data not shown). This transition in the copepod community also did not occur during 1998, however it is unusual to remain in a warm-water copepod community for two consecutive years. This last occurred in 2003, 2004, and 2005 (fig. 10).

Copepod species richness was the highest in the time series during the summer of 2016[5]. Many of the rare species observed during this period had Transition Zone and North Pacific Gyre affinities and many of the species have never (or rarely) been observed off Newport since sampling began in 1969 (Peterson et al. 2017). The presence of these species greatly increased the species richness, which exceeded the number of species observed during the strong El Niño in 1998 (fig. 10). Like cold-water copepods, euphausiid biomass during 2016 was among the lowest in 21 years and the coastal euphausiid, *Thysanoessa spinifiera*, was largely absent (data not shown; Peterson et al. 2017).

Northern California Current: Northern California (Trinidad Head Line)

Coastal waters off northern California were warmer and fresher than usual during early 2016, but cooled in response to strong upwelling during summer. Warmer, fresher water was again observed over the shelf following relaxation from upwelling in early fall 2016. Coastal waters were slightly cooler in early 2017 relative to early 2016 (figs. 8, 11), yet remained higher than most previous observations in the record, which is consistent with larger scale patterns in the CCS (figs. 3, 8). These patterns manifested throughout the water column over the inner to midshelf (fig. 11), and extended to surface waters offshore, but did not have a strong signal at depth over the outer shelf (fig. 8). Upwelling in spring 2016 led to a phytoplankton bloom that peaked in late spring and persisted through the summer (figs. 9, 11). *Pseudo-nitzschia* were a major component of this bloom, leading to low to moderately high concentrations of particulate domoic acid (the neurotoxin produced by

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[5] Copepod data were based on samples collected with a 0.5 m diameter ring net of 202 μm mesh, hauled from near the bottom to the sea surface. A TSK flowmeter was used to estimate volume of water sampled.

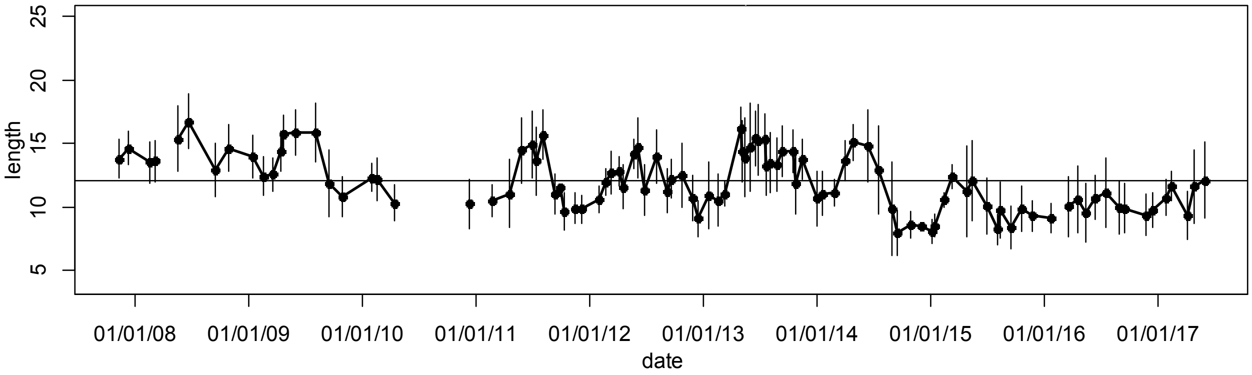

Figure 12. Density-weighted mean (points) and standard deviation (whiskers) of rostral-dorsal length of adult *Euphausia pacifica* collected along the Trinidad Head Line (aggregated over stations TH01 to TH05). Horizontal line indicates mean length taken over entire time series. Samples are collected by fishing bongo nets (505 µm mesh) obliquely from a maximum depth of 100 m (or within a few meters of the sea floor in shallower areas) to the surface.

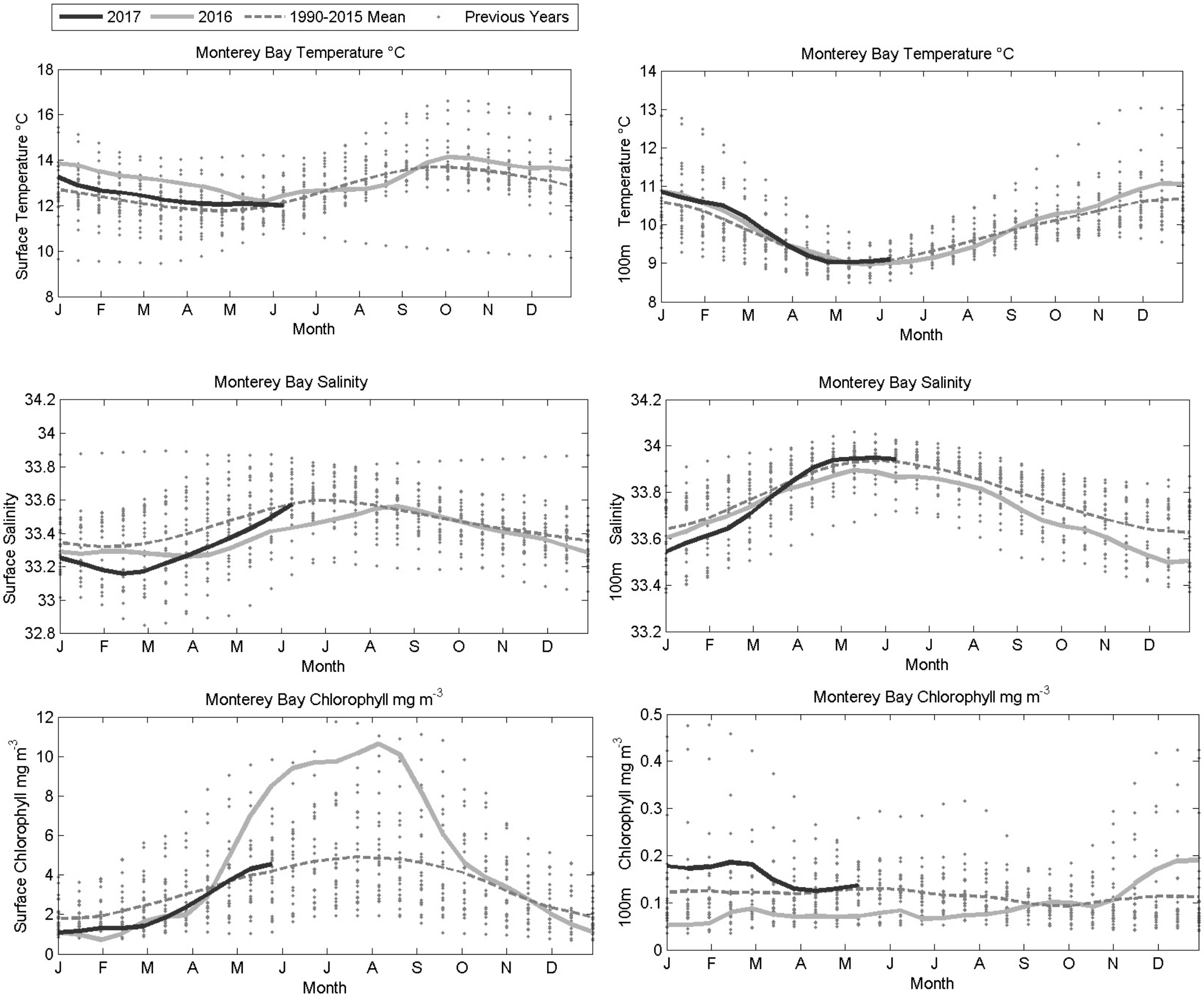

Figure 13. Temperature (top panels), salinity (middle panels) and chlorophyll *a* concentration (bottom panels) at the surface (left-hand column) and at 100 m (right hand column) observed at the M1 mooring in Monterey Bay, CA.

Pseudo-nitzschia; 0 to > 16,000 ng l^{-1}) in June 2016 that declined over the course of the summer. Chlorophyll concentrations have remained low through spring 2017 (figs. 9, 11). No hypoxic events were observed during 2016 and early 2017.

Zooplankton population and community data reflected the ongoing biological response to the persistence of warmer-than-usual water masses off northern California. For example, mean length of adult *Euphausia pacifica* collected along the Trinidad Head Line has remained consistently smaller than usual (fig. 12). Larger individuals were captured during periods of upwelling-driven cooling, and have been more consistently encountered during 2016 and early 2017, but the population continues to be dominated by smaller adults. The warm-water euphausiids *Euphausia recurva* and *Nyctiphanes simplex* were captured during winter and early spring 2016. Both species also occurred in winter samples from 2016–17, suggesting that warm-water zooplankton communities remained in the region but were displaced from coastal waters during periods of sustained upwelling. Copepod community data have not been updated through this period, but cursory inspection of samples and anecdotal observations made during analysis of krill samples suggest that cold-water copepods remain relatively rare or absent. Pyrosomes were present at unusually high densities throughout 2016 and early 2017, with the greatest abundance occurring during spring 2017. Large pyrosomes (i.e., individuals too large to be retained in preserved samples) were much more frequently and consistently encountered during 2016 and early 2017 than in previous years. Salps were abundant for a brief time during summer and fall 2016.

Central California Current: Monterey Bay

Temperatures at the surface and 100 m recorded at M1 (36°45'0" N 122°1'48" W) mooring in Monterey Bay were near average in 2017 and similar to the values from 2016. Surface salinities were also near the climatological average during this time period, although in early 2017 surface waters were somewhat fresher (fig. 13). Chlorophyll at the surface was low during winter 2016 but increased concomitantly with increased upwelling during summer and stayed elevated until October when upwelling weakened (fig. 4). Chlorophyll remained slightly below average until May 2017. At 100 m, chlorophyll remained below average during 2016 through November, at which point, it was near average until April 2017. Generally, aside from extremely elevated surface chlorophyll during June–September 2016 associated with anomalously strong upwelling (fig. 4), conditions at M1 were typical. In contrast to other regions, there were no significant toxic blooms in Central California, but there were a series of "red tide" events in the nearshore caused by the dinoflagellate *Akashiwo sanguinea*.

Southern California Current: CalCOFI Survey[6]

Over the last 12 months, mixed layer temperature anomalies remained above the long-term average (fig. 14) but were 1 to 1.5°C cooler than those observed during the marine heatwave in 2014–15. The cooling of surface waters since 2015–16 is clearly shown in the Hovmoeller plots of 10 m temperatures along CalCOFI line 90, and temperatures at 100 m depth had returned to the long-term average (figs. 8, 15).

Over the last three years water column stratification in the upper 100 m was primarily driven by high surface ocean temperatures (McClatchie et al. 2016), and this trend continued over the last year (fig. 14). Mixed layer salinity was slightly below long-term averages for the last three years (fig. 14). Temperature-salinity distributions for the offshore, California Current, upwelling, and Southern California Bight areas were not dramatically different from previous years, and neither region showed the pronounced warming of the surface layer seen in 2015–16.

The depth of the σ_t 26.4 isopycnal (fig. 16), which can indicate nutrient availability and transport, was close to its long-term average over the last 12 months, contrasting with high (deep) values observed during the previous two years. Bjorkstedt et al. (2012) speculated that concentrations of oxygen at depth had been declining since the year 2000 to values not observed previously. It appears that this trend has ended (fig. 16). Indeed, one could argue that there is no trend in the O_2 time series at σ_t 26.4 from 2003 until the present (fig. 16). The same is true for the nitrate time series (fig. 16). Changes in N*, which is a biogeochemical indicator which reflects the deficit of nitrate in a system relative to concentrations of phosphate, over the last year have also been small (fig. 16).

Mixed layer concentrations of chlorophyll were extremely low during the marine heat wave and the 2015–16 El Niño. Chlorophyll concentrations returned

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[6] These results are based on four seasonal CalCOFI cruises (Ohman and Venrick 2003) in July and November of 2016 and January and April of 2017. The sampling domain encompasses the southern California Current, the Southern California Bight, the coastal upwelling region at and north of Pt. Conception and an offshore area at the edge of the North Pacific Gyre.

Results are presented as time series of averages over all 66 standard CalCOFI stations covered during a cruise or as anomalies of such values with respect to the 1984–2012 time period. When appropriate, averages from selected regions are used based on a subset of the 66 standard CalCOFI stations. The buoyancy frequency was calculated for all depths and averaged for the upper 100 m of the water column. The nitracline depth is defined as the depth where concentrations of nitrate reach values of 1 µM, calculated from measurements at discrete depths using linear interpolation. Mesozooplankton displacement volumes for the last 12 months are not yet available. Methods used to collect and analyze samples are described in detail at www.CalCOFI.org/methods. At each station a CTD cast and various net tows were carried out. This report focuses on the hydrographic, chemical and biological data derived from ~20 depths between the surface and ~515 m, bottom depth permitting.

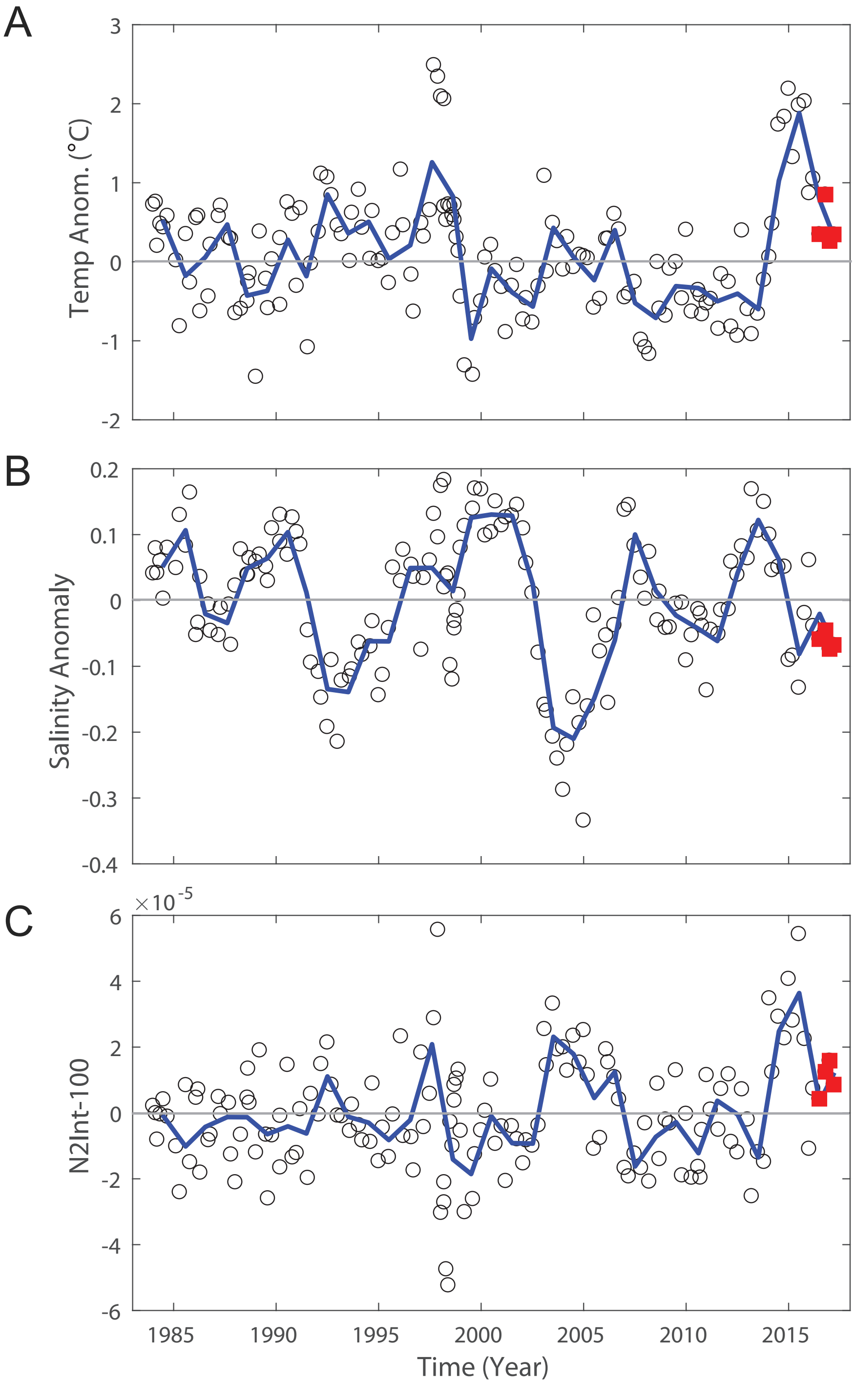

Figure 14. Cruise averages of property anomalies for the mixed layer (ML) of the 66 standard CalCOFI stations (Figure 1) for 1984 to the spring of 2017. A) ML temperature, B) ML salinity. C) buoyancy frequency squared (N2) in the upper 100 m. Data from individual CalCOFI cruises are plotted as open circles; data from the four most recent cruises, 201607 to 201704, are plotted as solid red symbols. Blue solid lines represent annual averages, grey horizontal lines the climatological mean, which is zero in the case of anomalies. Anomalies are based on the 1984 to 2012 time period.

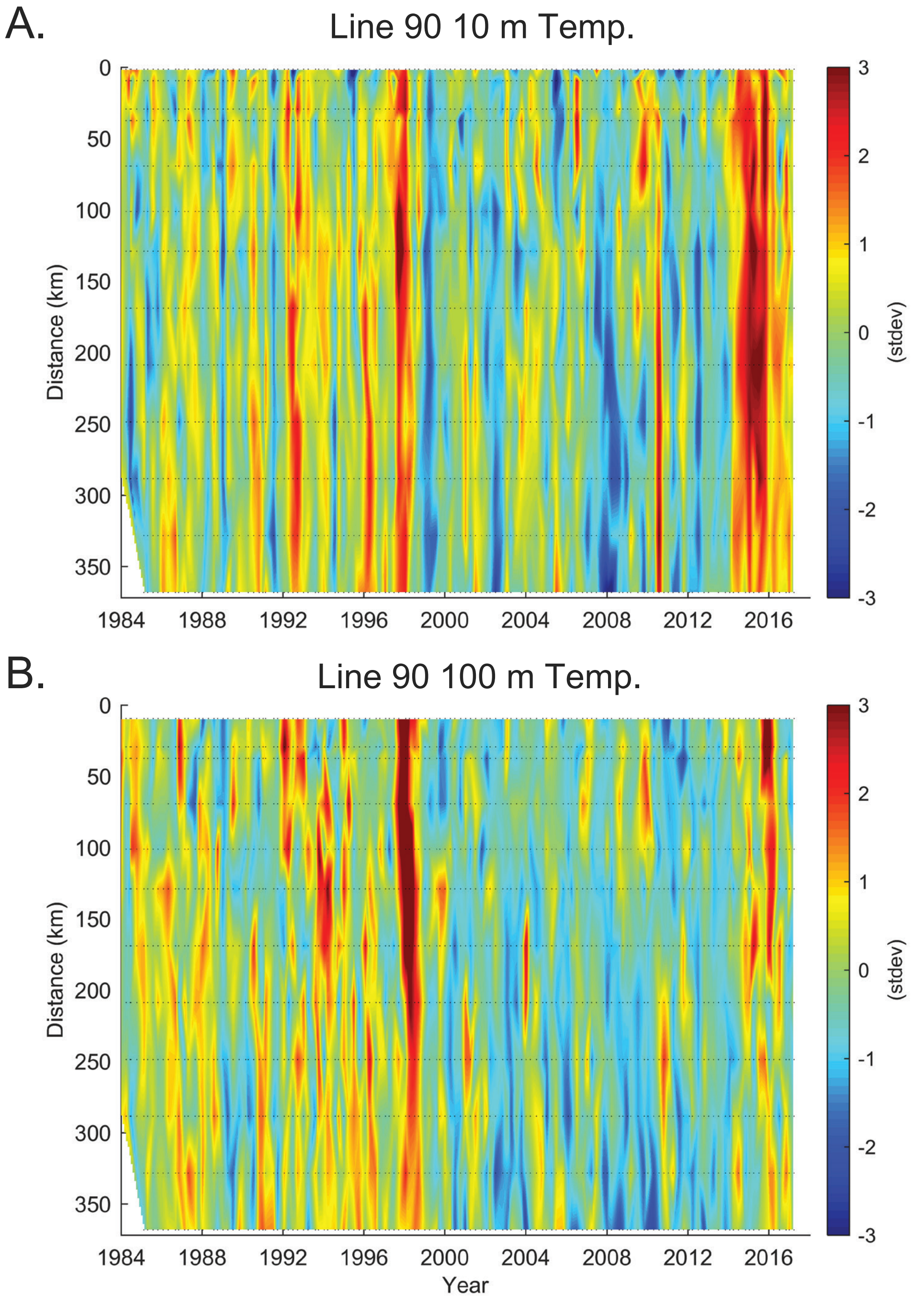

Figure 15. Standardized temperature anomalies for CalCOFI line 90 plotted against time and distance from shore for a depth of 10 m (A) and 100 m (B). Plotted data are deviations from expected values in terms of standard deviations in order to illustrate the strength of the relative changes at different depths.

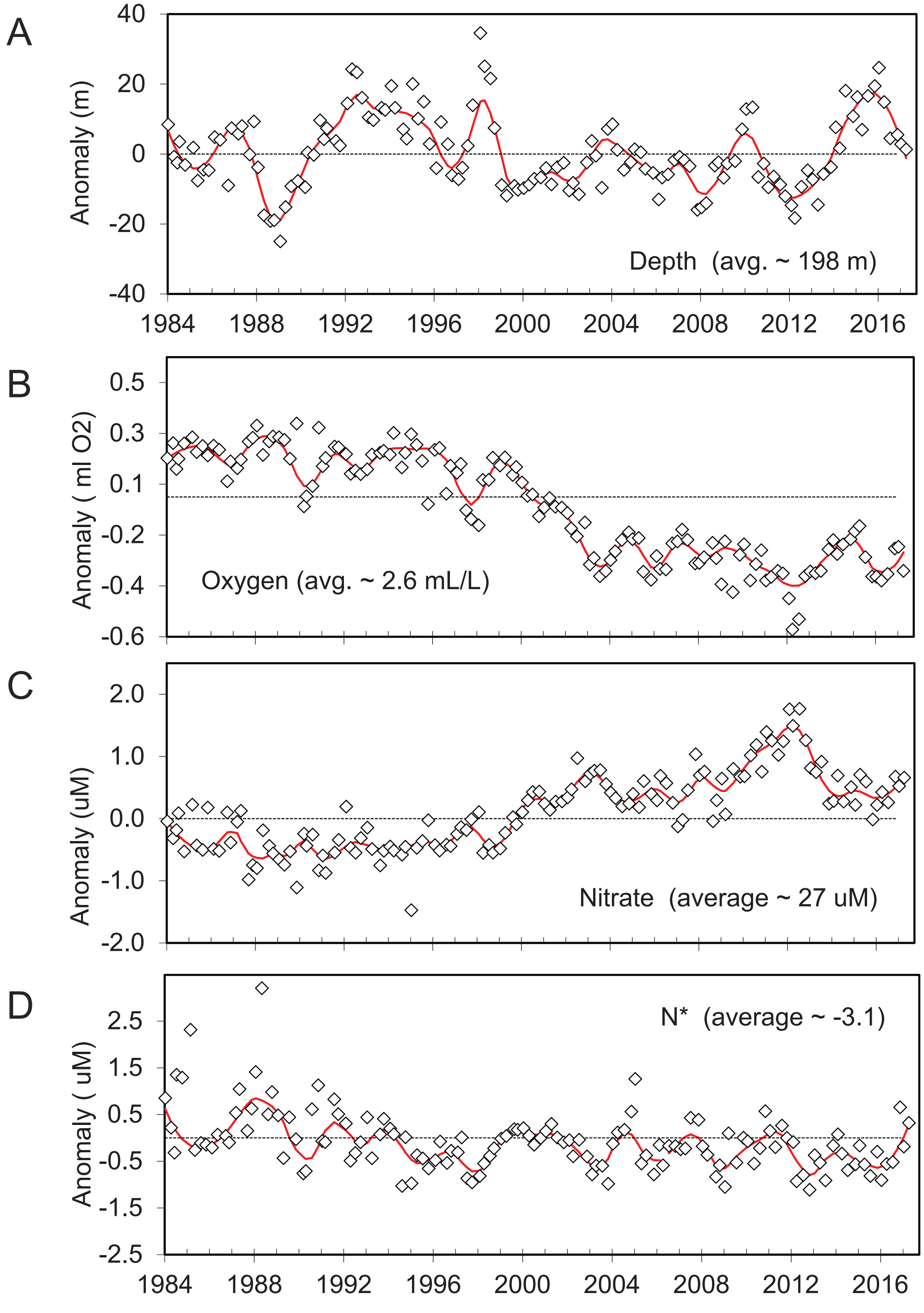

Figure 16. Anomalies of hydrographic properties at the σt 26.4 isopycnal (open diamonds) averaged over the 66 standard CalCOFI stations. Shown are anomalies of isopycnal depth, oxygen, nitrate, and N*, which is a biogeochemical indicator which reflects the deficit of nitrate in a system relative to concentrations of phosphate (Gruber & Sarmiento 1997). The solid red line represents a LOESS fit to the data; average values for the properties are listed. Anomalies are based on the 1984 to 2012 time period.

to the long-term average over the last 12 months (fig. 17). Values of mixed layer nitrate concentrations and nitracline depth (fig. 17) were also close to their long-term average, consistent with the hypothesis that phytoplankton biomass in the CalCOFI study area is primarily controlled by the availability of inorganic nutrients such as nitrate, which in turn is controlled by stratification. The depth distributions of chlorophyll in the offshore, California Current, and upwelling areas were similar to those observed between 1984 and 1997 (http://calcofi.

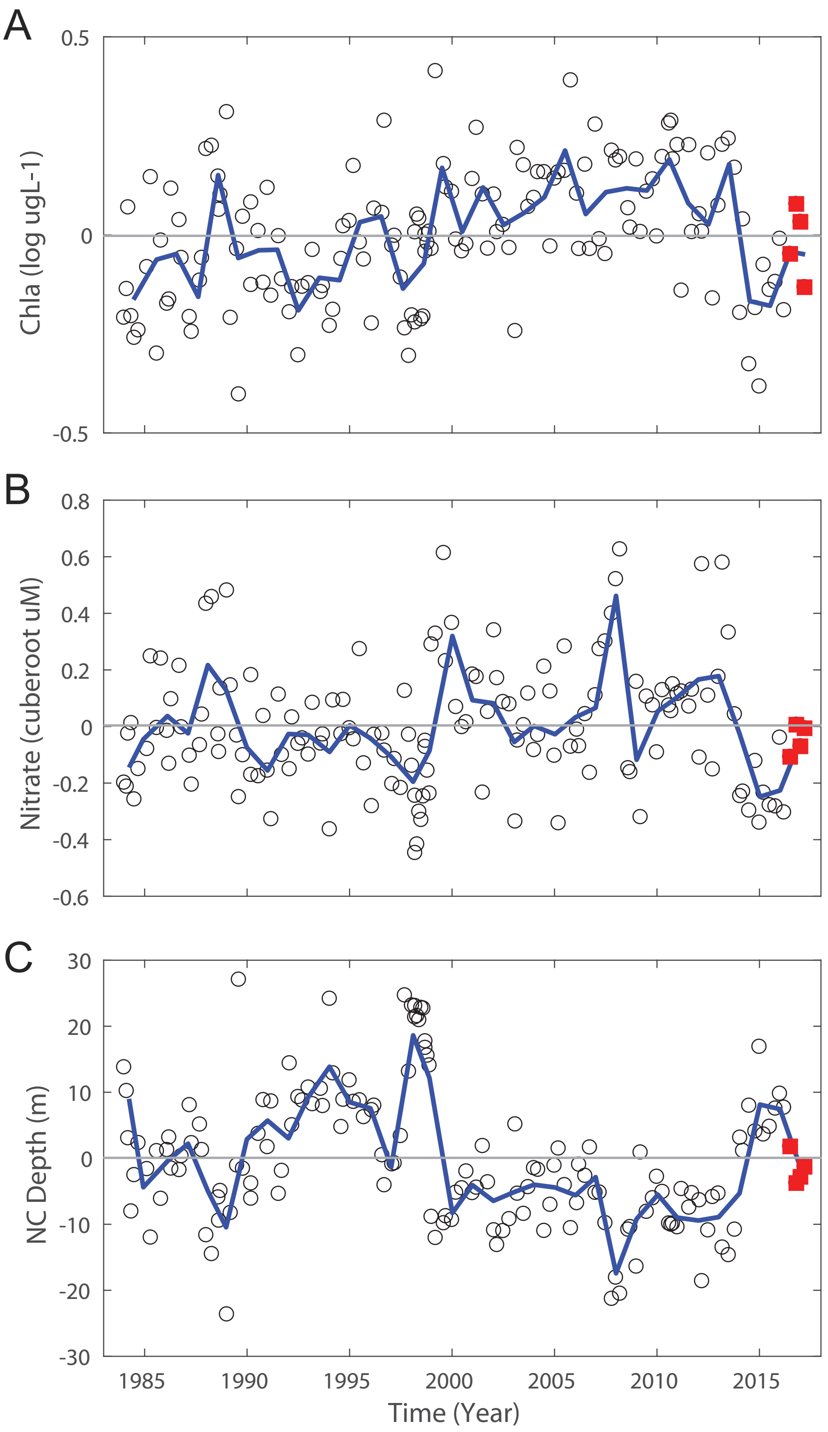

Figure 17. Cruise averages of properties for a depth of 10 m for the CalCOFI standard grid plotted as anomalies relative to the mean of the time series. A) The log10 of chlorophyll *a*, B) the cube root of nitrate, and C) nitracline depth.

org/cruises.html). The chlorophyll maximum in the offshore and California Current region was 10 to 20 m deeper than during the last decade. In the Southern California Bight the chlorophyll maximum was substantially stronger than maxima observed over the last 15 years but the mechanism driving these changes is unknown.

Southern California Current: Harmful Algal Blooms (HAB)

As part of the 2016 CalCOFI surveys, near-surface samples were collected for domoic acid to see if there would be an HAB response to the El Niño conditions. Toxin concentrations were negligible during 2016. In

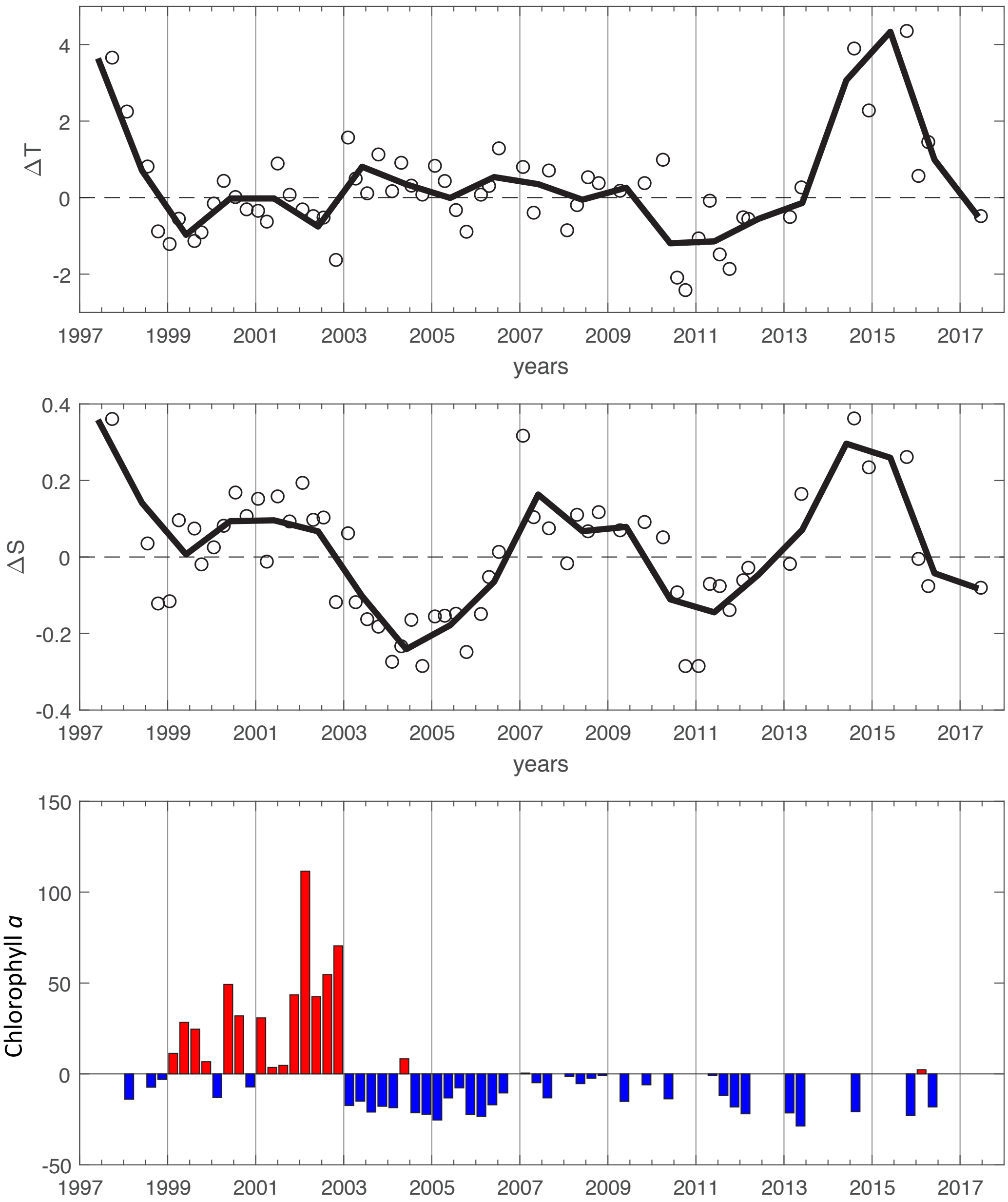

Figure 18. Interannual variability of the mixed layer temperature anomalies (°C) and salinity anomalies in the IMECOCAL region for the period 1997–2017 (white circles) and the mean of each year (thick line). Depth-integrated (0–100 m) chlorophyll *a* anomalies (mg m^{-2}) in the IMECOCAL region.

contrast, a significant bloom developed in April–May 2017, with numerous bird mortalities and marine mammal strandings. The bloom was localized to the Southern California Bight region, but achieved very high particulate domoic acid concentrations (exceeding 50,000 ng/L). This caused an unusual mortality event for multiple marine bird species, dominated by loons (*Gavia* spp., 75% of strandings). Sixteen loons were sampled for toxins, and all were positive for domoic acid. One loon had a sardine in its gullet at the time of death, which contained 681 ppm domoic acid. Concentrations in the loons (liver, kidney, bile) tested as high as 88 ppm (the regulatory limit for human consumption of fish and shellfish is 20 ppm). The bloom region corresponded to the elevated chlorophyll in Figure 9.

Southern California Current: Baja California (IMECOCAL)[7]

Similar to other areas in the California Current, the magnitude of anomalously warm conditions of 2014–

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[7] The IMECOCAL program conducts quarterly cruises off the Baja California peninsula since 1997–98 El Niño. However, during 2012–17 the sampling frequency has been more sporadic and the last two years the surveys have been carried out exclusively off north Baja California.

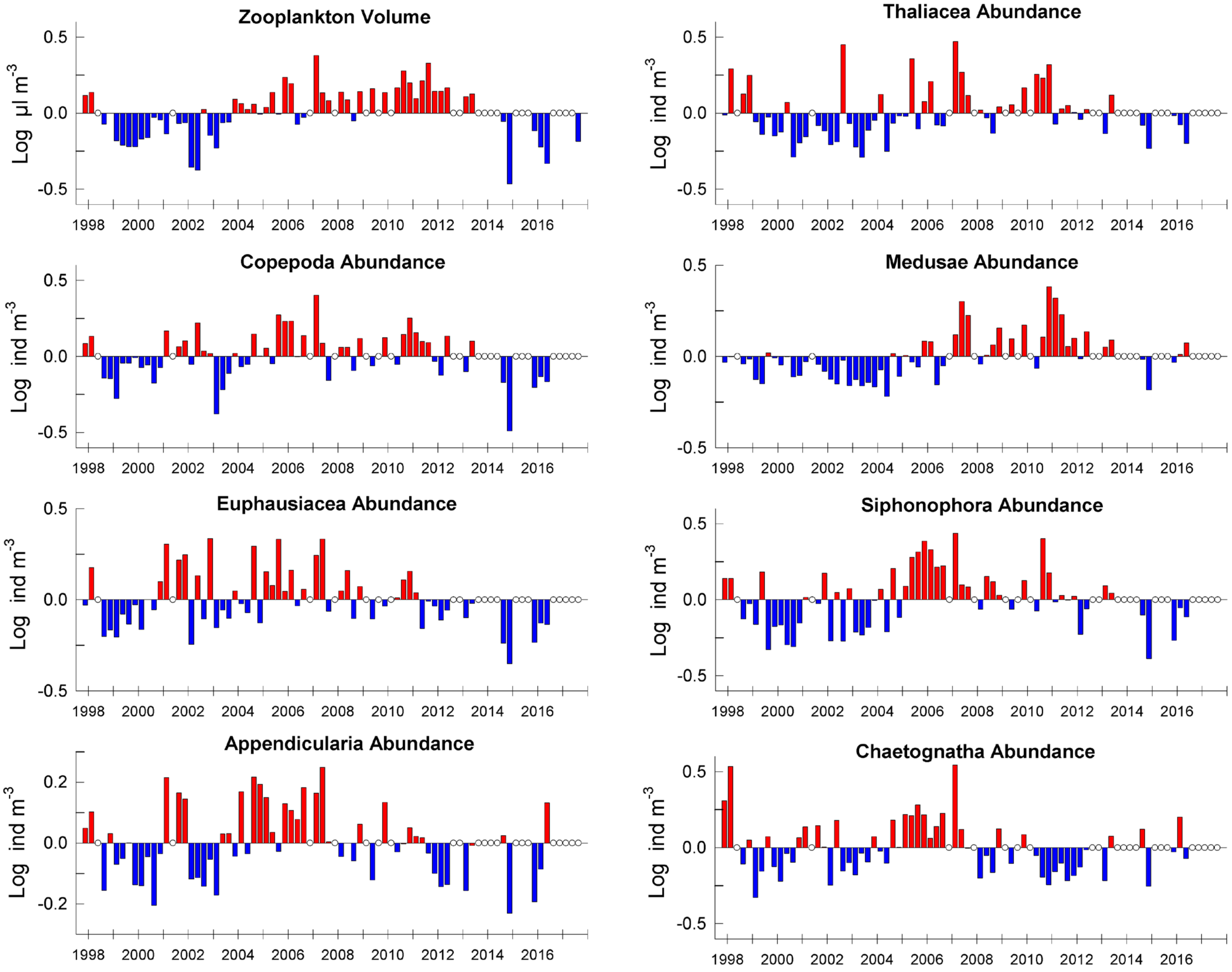

Figure 19. Zooplankton volume anomalies and abundance anomalies of zooplankton groups for the Baja California Peninsula (IMECOCAL) region. Each bar represents a single cruise and open circles represent cruises that did not take place or were omitted due to limited sampling. Data were converted to logarithms.

15 was reduced in 2016 off Baja California (fig. 18)[8]. By June 2017, surface waters transitioned to slightly cooler than average. The last result should be taken with caution because the cruise was carried out in early summer during overcast conditions. Similar to temperature, salinity anomalies of the mixed layer in April 2016 shifted from more saline waters associated with 2014–15 to fresher than average water, and remained this way into 2017 (fig. 18).

Chlorophyll from 2003-2016 remained anomalously low (fig. 18)[9]. However, there were data missing for the most productive season (spring) in recent years 2015–17. It is worth noting that anomalies presented in this updated figure differ from the figure reported in McClatchie et al. (2016) for the time interval 2008–16. This is due to a methodological error found and the application of a correction factor to values collected after 2008.

Zooplankton biomass anomalies have only recently tracked chlorophyll anomalies in this region (fig. 19)[10].

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[8] The hydrographic data were collected using seabird sensors factory calibrated prior to each cruise. CTD data were computed by Seasoft based on EOS-80. After that, the thermodynamic variables were processed using Matlab functions from SEA-MAT. The mixed layer depth was estimated following the methodology by Jeronimo and Gomez-Valdes (2010) for the IMECOCAL grid. Harmonics were computed for mixed layer properties for all stations for which sufficient data exists. Our approach to obtain the long-term variability follows that of Bograd and Lynn (2003).

[9] Phytoplankton chlorophyll-*a* data were analyzed from water collected at discrete depths in the upper 100 m, filtering water onto Whatman GF/F filters, following the fluorometric method. Integrated chlorophyll anomalies were estimated removing seasonal means. Chlorophyll was not measured in the cruise performed in 2017.

[10] Zooplankton was sampled with oblique tows of a bongo net (500 µm of mesh width) from 210 m to the surface. Displacement volume was measured in all samples and zooplankton taxa were counted in nighttime samples only. For more reference about water samples collections and zooplankton techniques visit the IMECOCAL Web page: http://imecocal.cicese.mx.

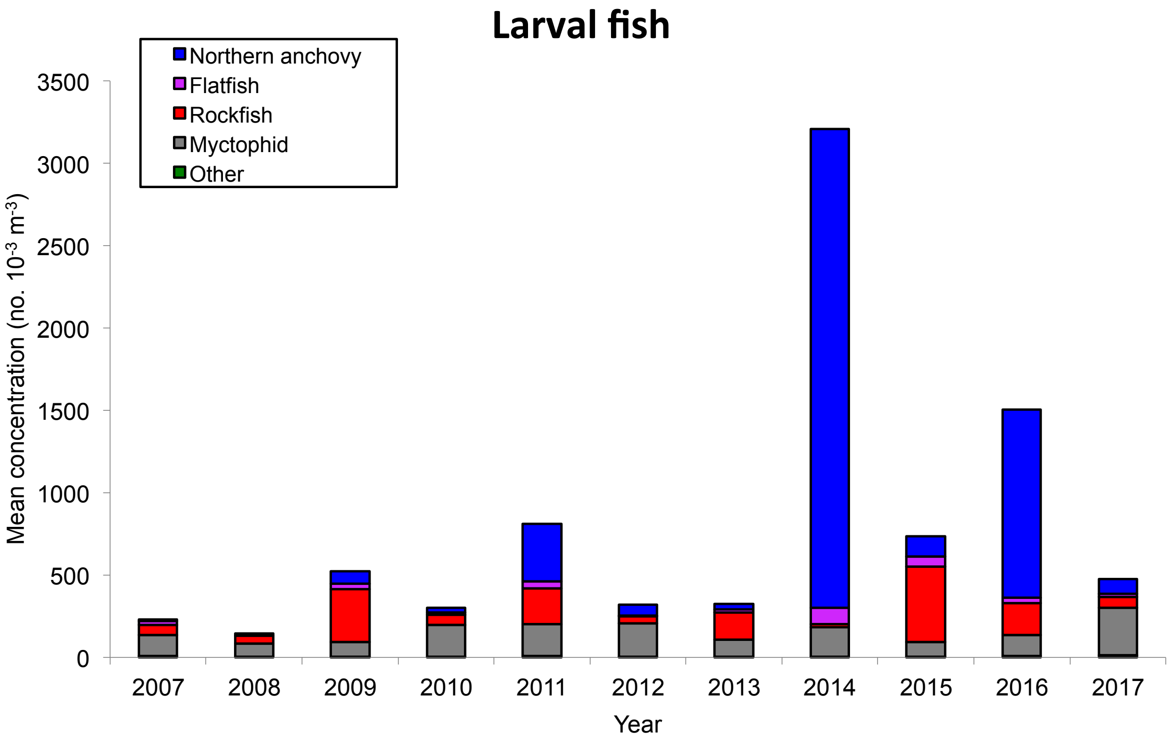

Figure. 20. Mean concentrations (no. 10^{-3} m^{-3}) of the dominant larval fish taxa collected during June–July in 2007–17 along the Newport Hydrographic (NH; 44.65°N, 124.35–125.12°W) and Columbia River (CR; 46.16°N, 124.22–125.18°W) lines off the coast of Oregon.

During 2014–16, an anomalously low biomass of zooplankton coincided with low chlorophyll concentrations. Prior to this (2003–13), zooplankton biomass tended be greater than average despite the anomalously low concentration of chlorophyll over this same period. In June 2017, zooplankton biomass remained anomalously low despite cooling water temperatures. The main crustacean grazers (copepods and euphausiids) as well as gelatinous groups (tunicates, siphonophores, and medusae) may have contributed to the extremely low biomass of zooplankton observed (fig. 19). The negative anomalies of zooplankton biomass and abundances of functional groups during El Niño 2015–16 are in contrasts with El Niño 1997–98 when positive anomalies of copepods, euphuausiids, tunicates, and siphonophoes were observed. The unique coincidence between zooplankton in the two periods were positive anomalies of chaetognaths abundance during both the 2015–16 and the 1997–98 El Niño.

It is difficult to distinguish the contribution of the marine heat wave or El Niño on the low abundance of zooplankton in the Baja California. An increase in temperature could be the result of either, producing a similar effect on subtropical species, which usually are dominant in the region (Jiménez-Pérez and Lavaniegos 2004; Lavaniegos and Ambriz-Arreola 2012). Also, negative anomalies in some groups, such as euphausiids, appendicularians, and chaetognaths, occurred since 2011, previous to the marine heat wave event.

REGIONAL EPIPELAGIC MICRONEKTON AND SALMON OBSERVATIONS

Northern California Current: Washington and Oregon

Newport Hydrographic Line and Pre-recruit Survey The larval epipelagic micronekton community along the central-northern coast of Oregon in June 2017 was similar to the average community structure found in the same area and season during the previous ten years in terms of composition and relative concentrations of the dominant taxa (fig. 20)[11]. The exception was unusually

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[11] Micronekton samples were collected from 3–4 stations representing coastal (<100 m in depth), shelf (100–1000 m), and offshore (>1000 m) regions along both the Newport Hydrographic (NH; 44.65°N, 124.35–125.12°W) and Columbia River (CR; 46.16°N, 124.22–125.18°W) lines off the coast of Oregon during June–July in 2007–17 (See Auth 2011 for complete sampling methods). In addition, post-larval (i.e., juvenile and adult) fish were collected using a modified-Cobb midwater trawl (MWT) with a 26 m headrope and a 9.5 mm codend liner fished for 15 min at a headrope depth of 30 m and ship speed of ~2 kt. MWT collections were made at 4–6 evenly-spaced, cross-shelf stations representing coastal, shelf, and offshore regions along nine (five in 2017) half-degree latitudinal transects between 42.0 and 46.0°N latitude in the northern California Current region during June–July in 2011–17 (although no sampling was conducted in 2012). Sampled volume was assumed to be uniform for all hauls. All fish collected were counted and identified to the lowest taxonomic level possible onboard, although pre-recruit rockfish were frozen and taken back to the lab for identification using precise meristic and pigmentation metrics.

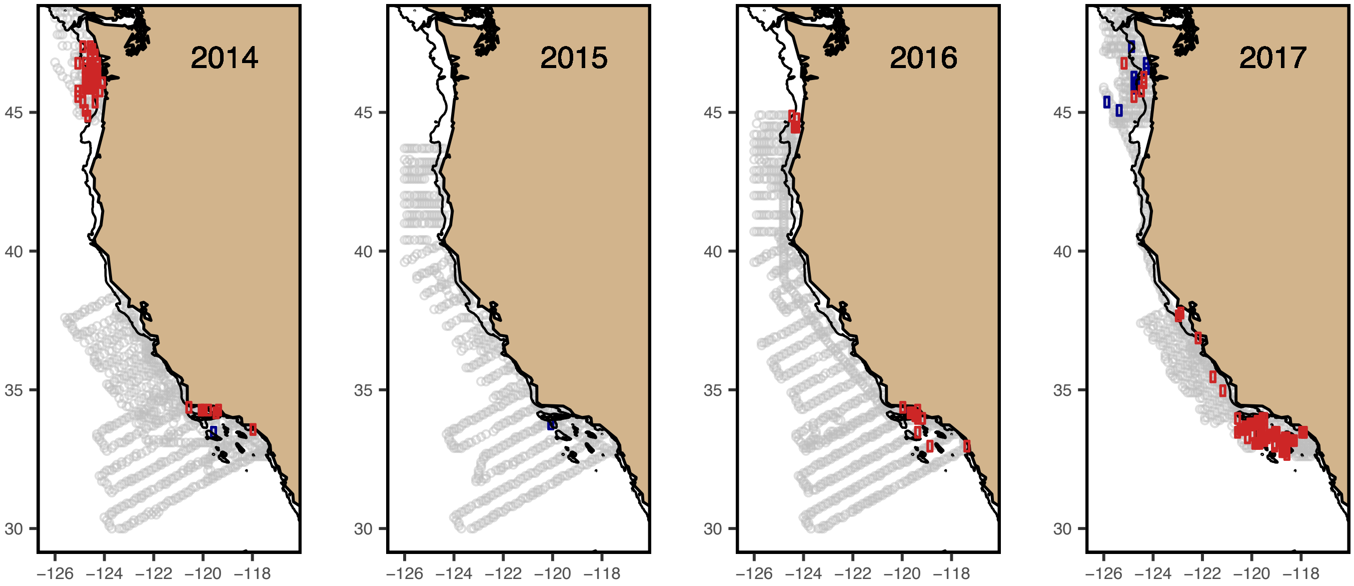

Figure 21. Northern anchovy egg density anomalies from continuous underway fish egg sampler (CUFES) surveys March–July 2014–17. Anomalies are shown for values greater than 2 eggs/m^3 (red, Observation – Mean) or less than –2 eggs/m^3 (blue) based on 0.1˚ bin spatial averages. North of 44˚N there were only 12 years of data: 2003, 2004, 2006, 2007, 2008, 2010, 2011, 2012, 2013, 2014, 2016, and 2017. Note that central California southward has been surveyed since 1997.

high concentrations of larval northern anchovy (*Engraulis mordax*) in 2014 and 2016 resulting from anomalously high spawning activity in the region (fig. 21)[12]. Total mean larval concentration was near average based on the 11-year time series. Larval myctophids in 2017 were found in the highest concentration since sampling began in 2007 as were "other" taxa, although other taxa still only accounted for <3% of the total mean larval concentration.

The post-larval fish community in the northern California Current in June 2017 was similar to the community structure found in the same area and season during the previous two years primarily due to the continued dominance of Pacific hake (*Merluccius productus*), which comprised 83% of the mean abundance of "other" taxa and ~ 60% of the total mean abundance of all post-larval fish (fig. 22). The abundance of smelt in 2017 was tied with that in 2016 for the lowest of the six-year time series, while the abundance of clupeiformes in 2017 was tied with that in 2016 for the highest, primarily due to the high concentration of northern anchovy collected just off the mouth of the Columbia River. Rockfish abundance in 2017 was the second highest of the time series, with the dominant species consisting of shortbelly (*S. jordani*; 50% of total rockfish), blue (*S. mystinus*), darkblotch (*S. crameri*), and widow (*Sebastes entomelas*). In addition, medusafish (*Icichthys lockingtoni*) were collected in far higher numbers than ever before in the six-year time series, probably due to their affinity for pyrosomes which were present in unprecedented numbers throughout the sampling area.

Columbia River plume region: Juvenile Salmon and Ocean Ecosystem Survey The June fish and invertebrate assemblage in the northern California Current during 2017 was unusual and dominated by species that normally occur in warmer ocean waters to the south of the study area[13]. A nonmetric multidimensional scaling (NMDS) ordination clearly showed that the 2015–17 assemblages were outliers, distinct not only from the 1999 La Niña assemblages, but also from the assemblage sampled during the 2005 warm event in the northern California Current (fig. 23).

The fish and invertebrate community in 2017 was similar to the past two warm years of 2015 and 2016 (fig. 23). Taxa indicative of 2017 included the pyrosome, Pacific pompano (*Peprilus simillimus*), Pacific chub mackerel (*Scomber japonicus*), and jack mackerel (*Trachurus symmetricus*). Pyrosomes are tunicates that are normally

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[12] Egg data is from continuous underway fish egg sampler (CUFES). While the southern/central region has been surveyed since 1997, the survey expanded north of 44˚N only in 12 years: 2003, 2004, 2006, 2007, 2008, 2010, 2011, 2012, 2013, 2014, 2016, and 2017. Spatial anomalies are estimated on 0.1˚ bins.

[13] Pelagic fish and invertebrate catch data were collected by the Juvenile Salmon and Ocean Ecosystem Survey (JSOES, NWFSC NOAA/Bonneville Power Administration) surveys using surface trawls on standard stations along transects between northern Washington and Newport, OR, in June from 1999 to 2016. All tows were made during the day at predetermined locations along transects extending off the coast to the shelf break (Brodeur et al. 2005). We restricted the data set to stations that were sampled consistently over the sampling time period (>9 y). Numbers of individuals were recorded for each species caught in each haul and were standardized by the horizontal distance sampled by the towed net as CPUE (number/km towed). A log(x+1) transformation was applied to the species at each station and then averaged by year for each species. The species data matrix included the 27 most abundant species captured over the 18 years sampled years (27 species x 18 years). A nonmetric multidimensional scaling (NMDS) ordination was used to describe the similarity of each year's community in species space.

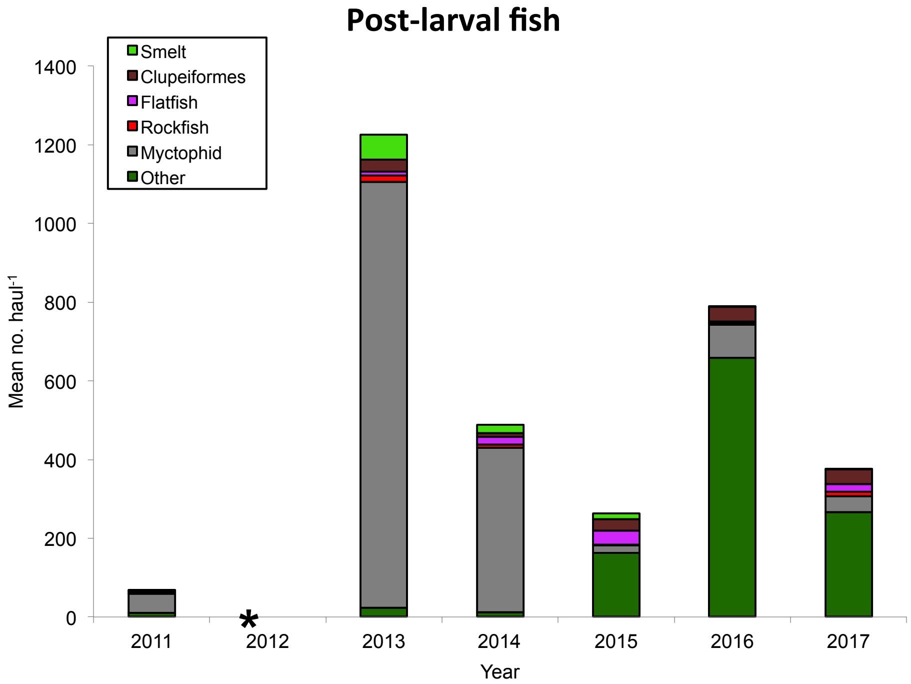

Figure 22. Mean catches (no. haul^{-1}) of the dominant post-larval fish taxa collected during June–July in 2011–17 along nine half-degree latitudinal transects between 42.0° and 46.0°N latitude in the northern California Current region. * = no samples were collected in 2012.

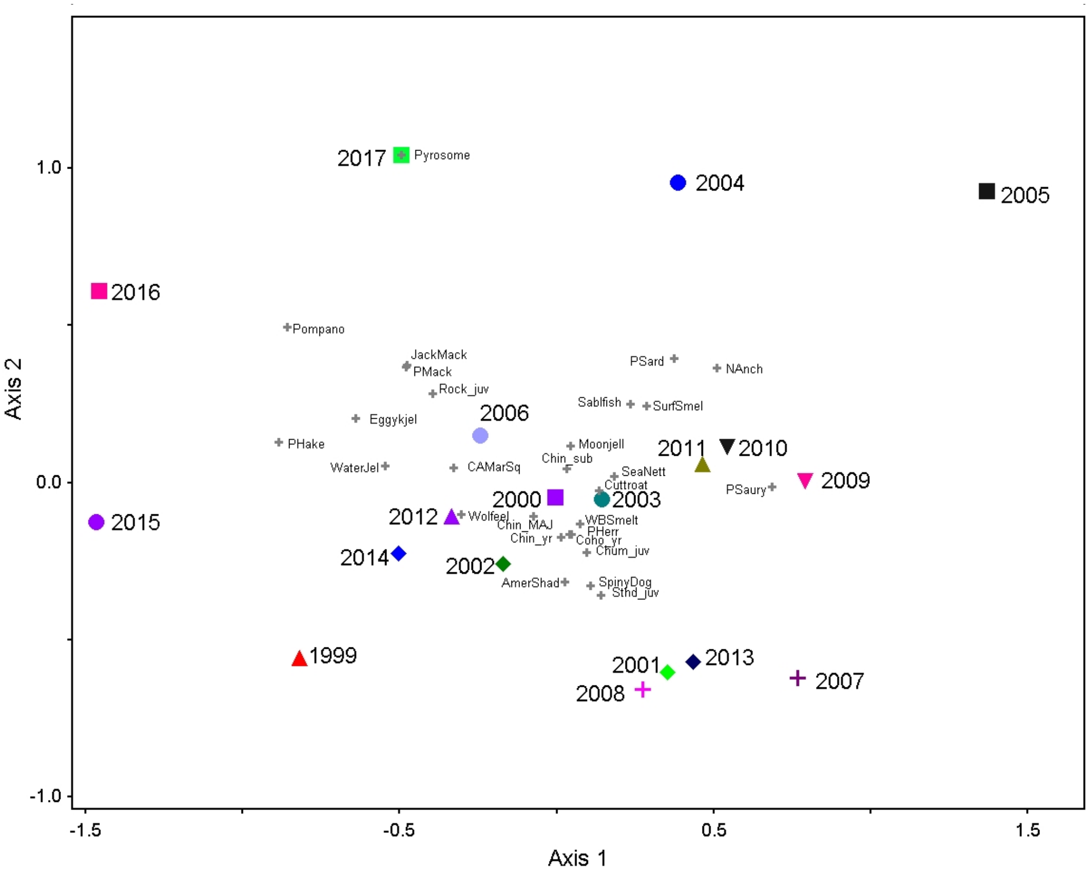

Figure 23. NMDS ordination of northern California Current pelagic assemblages. The NMS ordination explained 80.8% of the total variability in the first two dimensions. Pelagic fish and invertebrate catch data were collected by the NWFSC NOAA/Bonneville Power Administration surveys using surface trawls on standard stations along transects between northern Washington and Newport, OR, in June from 1999 to 2016. All tows were made during the day at predetermined locations along transects extending off the coast to the shelf break (Brodeur et al. 2005).

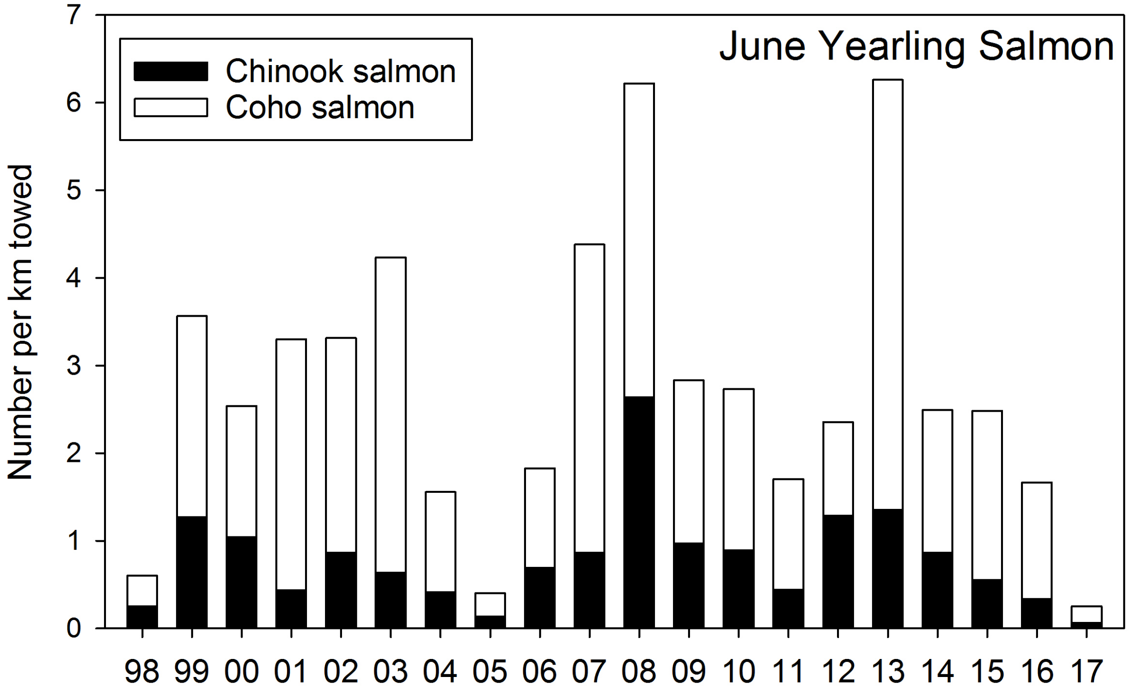

Figure 24. Catches of juvenile coho (black bars) and Chinook (white bars) salmon off the coast of Oregon and Washington in June from 1998–present.

found in the tropics, and have never been captured on the continental shelf during this survey or any previous surveys off central Oregon to northern Washington to our knowledge, although in recent years it has been found increasingly farther north off the shelf in other surveys[14]. But during June 2017 pyrosomes were present in 37% of the hauls, sometimes exceeding hundreds of individuals.

The jellyfish community off Washington and Oregon was also quite different than previous years. The usual numerically dominant large jellyfish is a cool-water associated scyphozoan species, sea nettle (*Chrysaora fuscescens*). However, during the warm ocean years of 2015 and 2016, the more offshore taxa of Hydromedusae, the water jelly (*Aequorea* spp.) was much more abundant and densities of *Chrysaora* were low. In June 2017 both *Chrysaora* and *Aequorea* were caught in average densities.

Salmon and salmon forage indicators in northern California Current Catches of yearling salmon off Washington and Oregon in June may be a good indicator of early ocean survival of yearling Chinook (*Oncorhynchus tshawytscha*) and coho salmon (*O. kisutch*). The abundance of yearling Chinook salmon during June is positively related to spring Chinook jack and adult salmon counts at the Bonneville Dam (with 1 and 2 year lags, respectively), as does the abundance of yearling coho salmon to subsequent coho smolt to adult survival[15] (Morgan et al. 2017). Catch per unit effort (number per km trawled) of both yearling Chinook and coho salmon during the June 2017 survey was the lowest of the 20-year time series from 1998 to 2017 (fig. 24). This suggests that adult returns of both spring Chinook in 2019 and coho salmon in 2018 will be significantly lower than average.

The biomass of fish larvae in late winter from the Newport Hydrographic Line provides an index of fish that are the common prey of juvenile salmon when they enter the ocean in spring and summer, and correlates with juvenile salmon survival and return as adults (Daly et al. 2013, 2017)[16]. The food biomass for out-migrating juvenile salmon in winter (January–March) 2017 was the highest in the 20-year time series (fig. 25), largely attributable to presence of young-of-the-year (YOY) rockfishes.

In addition to the increased biomass of fish prey potentially available to out-migrating juvenile salmon, the type of fish prey (assemblage) that are available for salmon also influences salmon survival. Importantly, the overall community composition of winter ichthyoplankton in 2017 was similar to 2015 and 2016 and predicted a poor food community for the salmon (fig. 26).

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[14] http://news.nationalgeographic.com/2017/06/pyrosome-fire-body-bloom-eastern-pacific-warm-water

[15] https://www.nwfsc.noaa.gov/oceanconditions/Juvenile Salmon Catch

[16] Ichthyoplankton samples were collected from 5 stations spaced ~9 km apart along the NH line. Sampling was conducted approximately every 2 wk between January and March. Only samples from January–March were used, assuming that larvae collected during these months would have had sufficient time to grow to the average size of prey eaten by juvenile salmon in late spring and early summer.

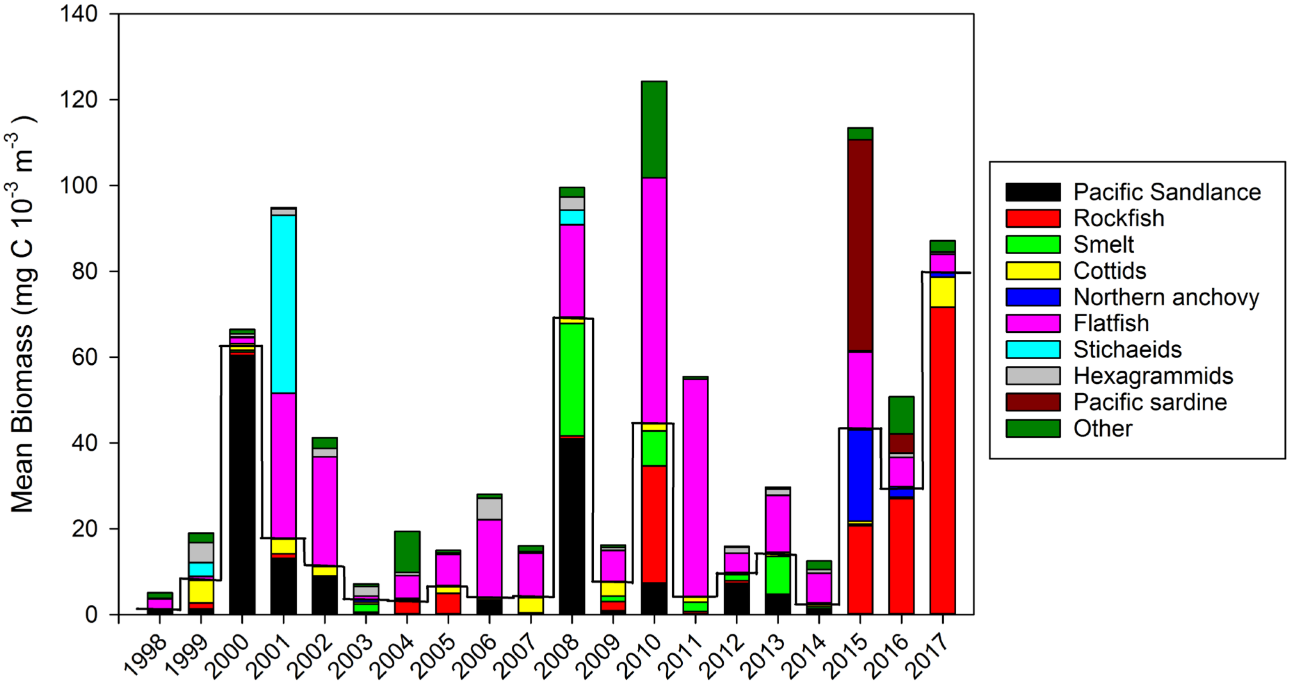

Figure 25. Annual mean biomass (mg C 10^{-3} m^{-3}) of the five important salmon prey taxa (below solid line) and five other dominant larval fish taxa (above solid line) collected during winter (January–March) in 1998–2017 along the Newport Hydrographic line off the coast of Oregon (44.65°N, 124.18–124.65°W). Figure expanded from one presented in Daly et al. (2013).

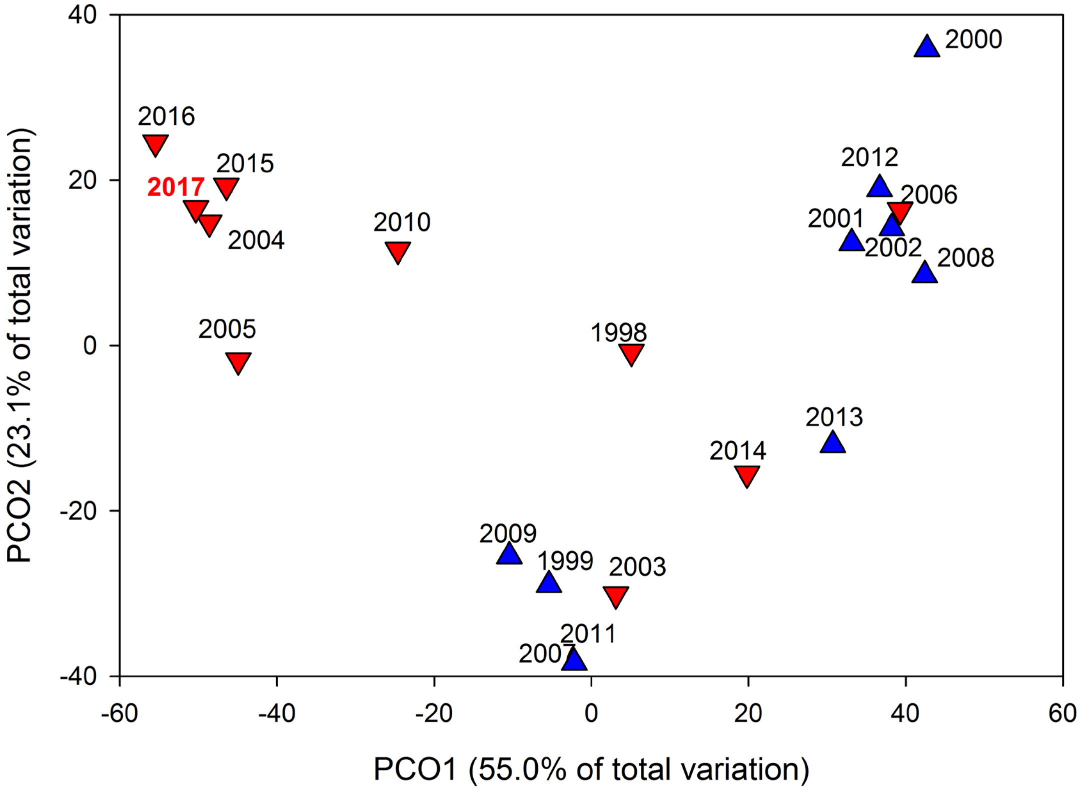

Figure 26. Principal coordinate analysis of the prey composition of winter ichthyoplankton that are important prey for out-migrating juvenile salmon (Pacific sand lance, osmerids, cottids, northern anchovy, and rockfishes). Red symbols indicate positive winter PDO (warm ocean temperatures) and blue indicates negative winter PDO (cold ocean temperatures). The larvae were collected during winter (January–March) in 1998–2017 along the Newport Hydrographic line off the coast of Oregon (44.65°N, 124.18–124.65°W). Figure expanded from one presented in Daly et al. (2017).

Based on axis 1 values (55% variance explained along this axis) from principal coordinate analysis of the prey composition of winter ichthyoplankton, the index of the 2017 prey composition predicts poor prey conditions for currently out-migrating juvenile salmon. In 2017, 90% of the winter ichthyoplankton composition was warm ocean condition taxa consisting of rockfishes and northern anchovy larvae. The relationship between the principle component 1 (PC1) axis values (prey composition) with spring Chinook salmon adult returns to Bonneville Dam two years later is: $P = 0.003$; $R^2 = 48.0\%$ (1998–2014; 1999 outlier year excluded). The biomass of ichthyoplankton in winter predicts returns of spring Chinook salmon to Bonneville Dam in 2019 to be just below ~230,000, and the prey composition prediction is one of the lowest of the time series at ~74,000.

Higher than average ichthyoplankton biomass but poor ichthyoplankton composition occurred in the warm ocean years 2015–17. Of particular note during January–March 2017, southern California winter-spawned larvae were present for the third winter in a row (e.g., Pacific hake and Pacific sardine [*Sardinops sagax*]; Auth et al. 2017). Sardine larvae were present in winter 2017, but not in high amounts, and were located at inshore stations (NH 1 and 10) and some were >10 mm long (Auth unpublished data). Of note, juvenile sardine were eaten for the first time in the time series by coho and Chinook salmon in May and June 2016 (Daly and Brodeur unpublished data), indicating that sardine are a new prey resource for the salmon in warm ocean conditions.

Summary of epipelagic micronekton and salmon in northern CCS Taken as a whole, the micronekton community and juvenile salmon abundance during winter to June 2017 off Washington and Oregon indicate continued perturbation from "normal" conditions. The abundance of pyrosomes may have indicated abnormal water transport in 2017. It is not yet clear whether the findings of 2017 are a result of the marine heat wave combined with the 2015–16 El Niño or whether ocean processes unique to 2017 combined with the previous warm years resulted in the altered community structure.

Central California[17]

Above average catches of YOY rockfishes were observed off central California in late spring 2017, although these catches were lower than the high catches observed in 2015 and 2016 (fig. 27). Catches in the southern region increased from below average values in 2016 to the greatest values in the (shorter) 13-year record in that region in 2017. Catches of YOY rockfish in north-central California were below average, such that there was a gradient in relative catch rates from record highs in the Southern California Bight to below average (but above historic low levels) in northern California.

In the Southern California Bight during 2017, catches of adult northern anchovy were comparable to past (2004) high levels, while catches continued to be very sparse in other regions of the California Current sampled by this survey (fig. 27). The survey also samples YOY northern anchovy and YOY Pacific sardine, for which catches of both increased during the 2015–16 warm event, and, in 2017, stayed above previous low levels in northern and central areas while continuing to increase to very high levels in the Southern California Bight (data not shown, but see Sakuma et al. 2016). Although the sparse catches for adult Pacific sardine and adult northern anchovy north of Southern California Bight indicate that the biomass of each may be too low to be meaningfully indexed by the survey, the increase in catches of YOY northern anchovy, in particular, are consistent with an increase in that population which is likely more concentrated in nearshore habitats not sampled by the survey. An increase in adult northern anchovy nearshore is also consistent with the egg enumeration data in 2017 (fig. 21) and seabird diets (presented below), both of which indicated above average adult northern anchovy abundance in the region. The abundance of both krill and market squid (*Doryteuthis opalescens*), increased significantly in all regions in 2017, both ranked at the third highest value since 1990 in the core region (fig. 27).

Thetys as well as other salps were less abundant than recent years in all but the southern region, where other salps increased relative to 2016 (fig. 28). Pyrosomes continue to be caught in very large numbers across all regions (fig. 28), with particularly high catches (of primarily very small pyrosomes) in the southern region. Catches of scyphozoan jellyfish (primarily *Aurelia* spp. and *Chrysaora* spp.) continued to be unusually low in 2017, a pattern that emerged in 2015 (fig. 28). The high numbers of pelagic red crabs (*Pleuroncodes planipes*) and California lizardfish observed in 2015 and 2016 (Leising et al. 2015; McClatchie et al. 2016) were not observed in 2017 possibly indicating cooler water regionally.

There are sharp differences in principal component (PC) loadings between coastal pelagic (Pacific sardine, northern anchovy) and mesopelagic species (myctophids) relative to most of the YOY groundfish, krill, and cephalopods. The two leading PCs for the assemblage are shown in a phase plot (fig. 29). The dramatic separation of the 2013–16 period was apparent as those years were

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[17] Epipelagic micronekton samples were collected during May and June by the Southwest Fisheries Science Center Rockfish Recruitment and Ecosystem Assessment Survey and the Northwest Fisheries Science Center Pre-recruit Groundfish Survey, covering a geographic range from the US/Mexico border (32.5°N) to southern Washington (46.5°N). A modified midwater Cobb trawl (10–30 m headrope depth) was used to sample pelagic species along the CCE in the mixed layer where juvenile salmon are typically found. Methods were standardized between regions beginning in 2011 (Sakuma et al. 2016).

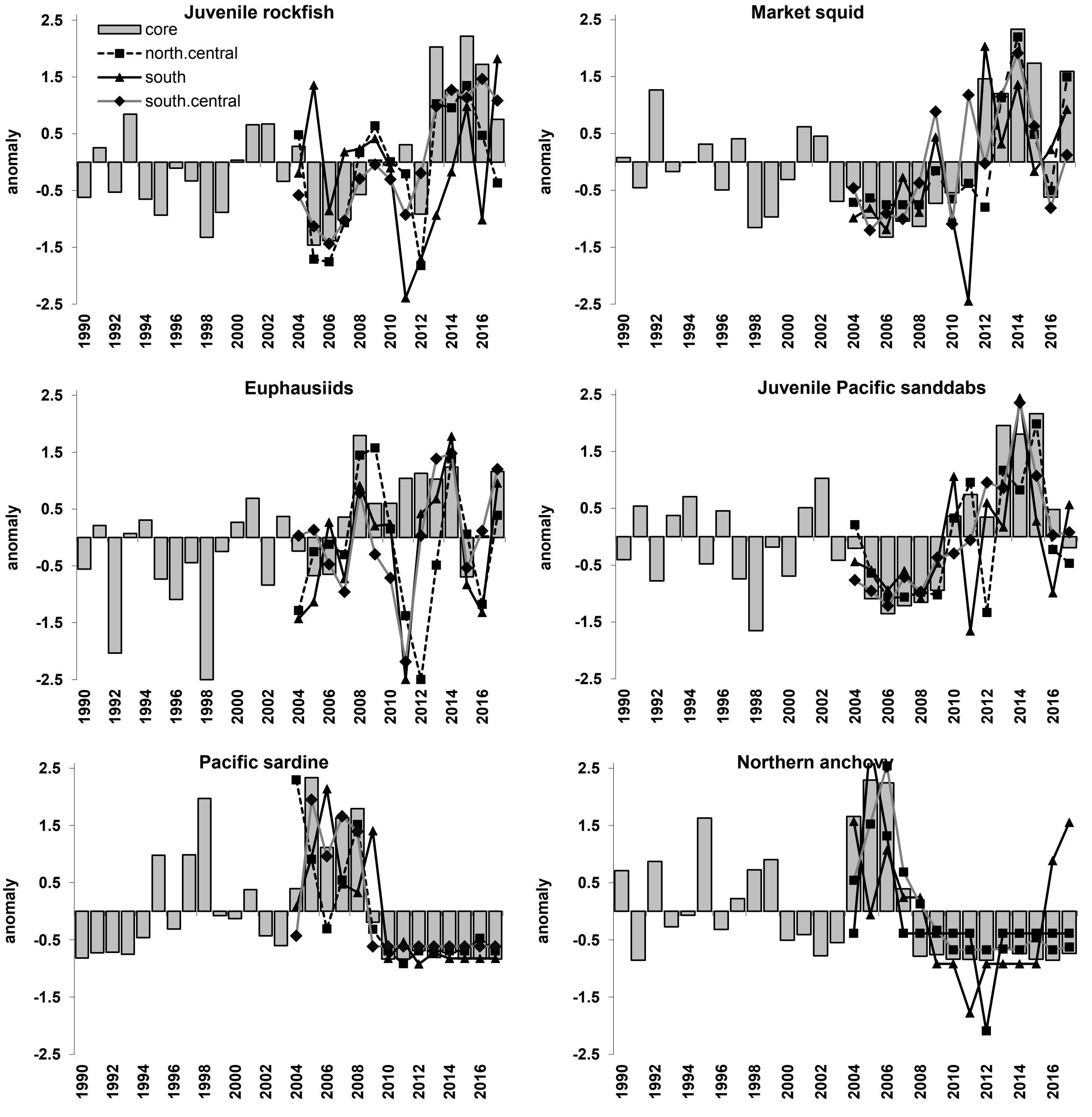

Figure 27. Long-term standardized anomalies of several of the most frequently encountered pelagic forage species from rockfish recruitment survey in the core (central California) region (1990–2017) and the southern, south-central and north-central survey areas (2004–17). Forage groups are YOY rockfish, market squid, krill (primarily *Euphausia pacifica* and *Thysanoessa spinifera*), YOY Pacific sanddab, Pacific sardine and northern anchovy.

extremely orthogonal to the low productivity years of 1998, 2005, and 2006. However, in 2017 the observed community switched to what might be considered a "normal" state, centrally located among the years 1990–2016. The switch in the forage base has important implications for seabirds, marine mammals, salmon and adult groundfish that forage primarily, or exclusively, on one or another component of the forage assemblage.

Southern California Current: CalCOFI region

The spring coastal pelagic fish survey in 2017 on NOAA ship *Reuben Lasker* was focused on northern anchovy rather than Pacific sardine and consequently the offshore extent of transects was reduced. No trawling was conducted offshore and unlike 2015 and 2016, no sampling was conducted north of San Francisco in 2017. The spring CalCOFI cruise on NOAA ship

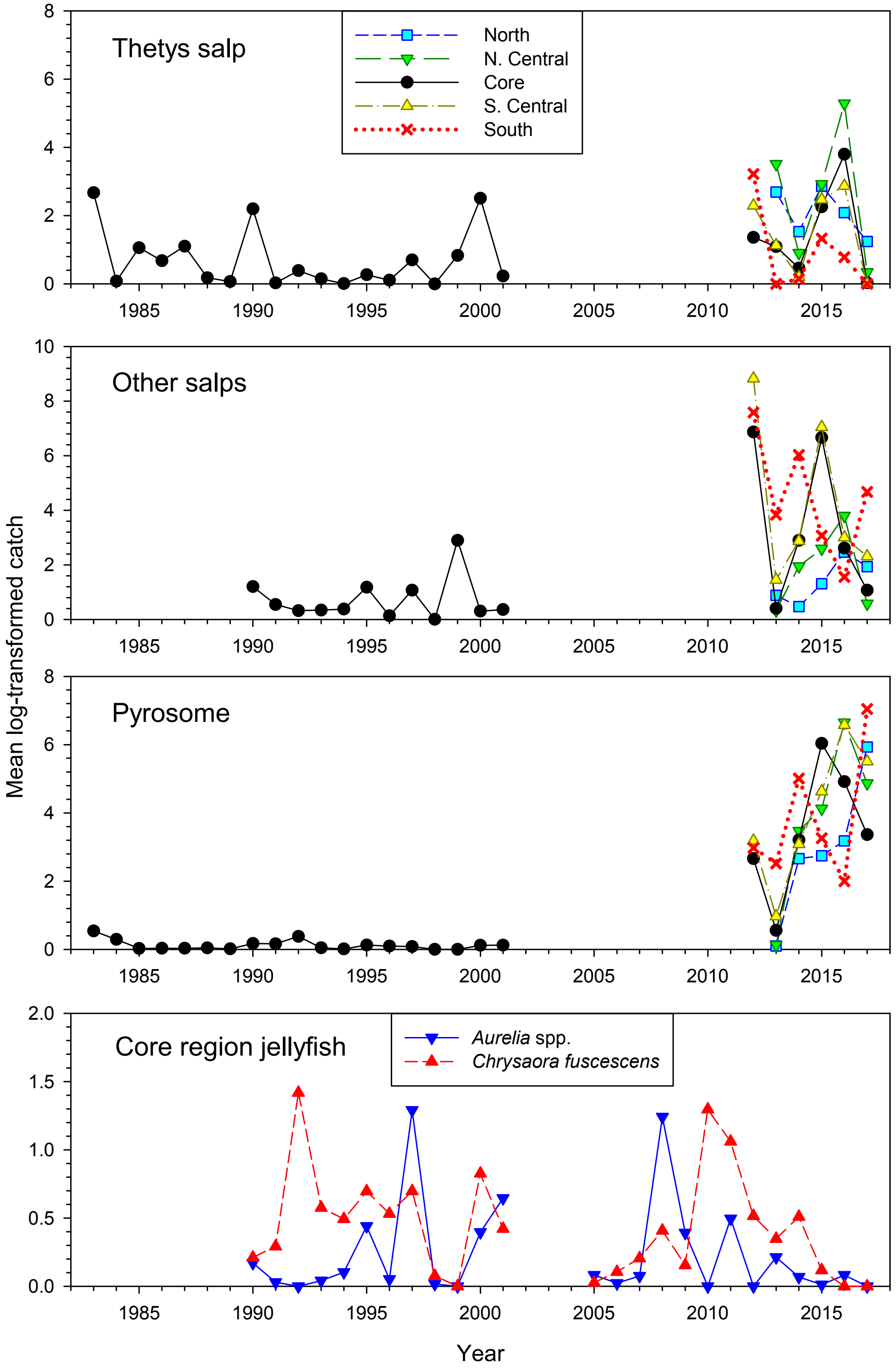

Figure 28. Standardized catches of jellyfish (*Aurelia* and *Chrysaora* spp.) and pelagic tunicates in the core and expanded survey areas.

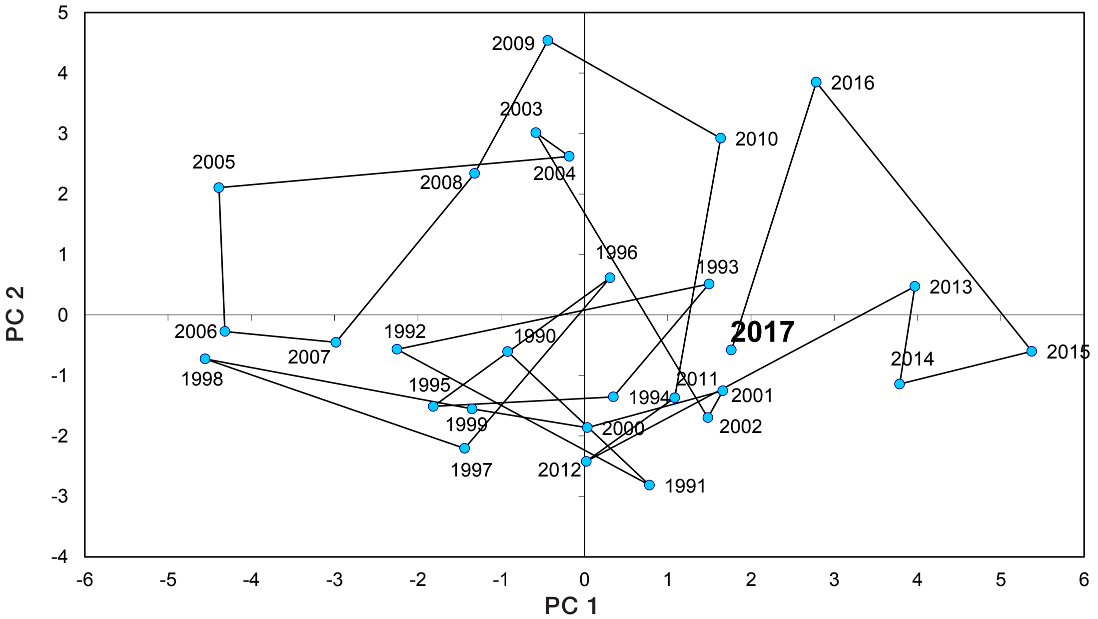

Figure 29. Principal component scores plotted in a phase graph for the nine key taxonomic groups of forage species sampled in the central California core area in the 1990–2017 period.

Bell M. Shimada sampled the usual 113-station winter and spring pattern (San Diego to San Francisco) (fig. 30).

Anchovy eggs in spring 2017 were notably more abundant than in 2016 (fig. 31). Anchovy eggs were also an order of magnitude more abundant in spring 2016 compared to 2015, but the increase was spatially restricted to small areas off Ventura, California and Newport, Oregon. By contrast, in spring 2017 anchovy eggs were widespread in the Southern California Bight, indicating that eggs were both more widely distributed and present at higher density than in 2016. It is notable that the highest egg count was very localized (again, off Ventura, California) and was associated with an extreme trawl catch of more than 600 kg of almost pure anchovy. This single catch was an order of magnitude larger than all of the other forage fish trawl catches on the entire cruise, and presumably represented a large school of northern anchovy.

In 2017, few anchovy eggs, and no adults, were collected north of Point Conception (fig. 30) although other continuous underway fish egg sampler surveys demonstrate concentrations of northern anchovy eggs off the Columbia River (fig. 21). Peak northern anchovy spawning off California generally occurs during March, so spawning patterns detected by the spring cruise may not be representative of the full northern anchovy spawning season.

Sardine and jack mackerel eggs were found at very low concentrations in the spring of 2017, consistent with the long-term trend. Sardine eggs were most abundant off the central California coast, south of Monterey, California (fig. 30). In 2016 the spawning distribution of sardine eggs was centered farther north (43˚–44.5˚N, off Oregon) than in spring 2015 (41˚–43˚N, California-Oregon border), but we are unsure if there was significant sardine spawning off Oregon in 2017 (fig. 31).

Whereas the ichthyoplankton assemblage (larval; an earlier stage than represented in fig. 27) in 2014–16 (based on spring samples from lines 80 and 90) was characterized by high abundances of southern, offshore mesopelagic fishes such as *Ceratoscopelus townsendi*, Gonostomatidae (mostly in the genus *Cyclothone*), *Triphoturus mexicanus*, and *Vinciguerria* spp. (mostly *V. lucetia*; these taxa are colored red on fig. 32), the 2017 assemblage was more "normal" (fig. 32). In multivariate space based on NMDS, NMDS 1 largely separated years when southern species (red font, fig. 32) were predominant (high NMDS 1) from years with primarily northern species (low NMDS 1; blue font on fig. 32), and NMDS 2 distinguished years with high Pacific sardine (high NMDS 2) and high northern anchovy (low NMDS 2). The 2017 assemblage fell in the middle of both NMDS axes 1 and 2, indicating that the assemblage was characterized by species with cosmopolitan distributions (colored green in fig. 32) and unexceptional abundances of both Pacific sardine and northern anchovy across the sampled region.

Evaluation of common mesopelagic taxa indicated that warm-water taxa generally declined between 2016 and 2017 while abundances of cool-water taxa were similar between these years. The southern warm-water taxa *Vinciguerria* spp. and *C. townsendi* fell to relatively low abundances in the spring of 2017 (fig. 33). The southern myctophid *T. mexicanus* declined dramatically from 2016

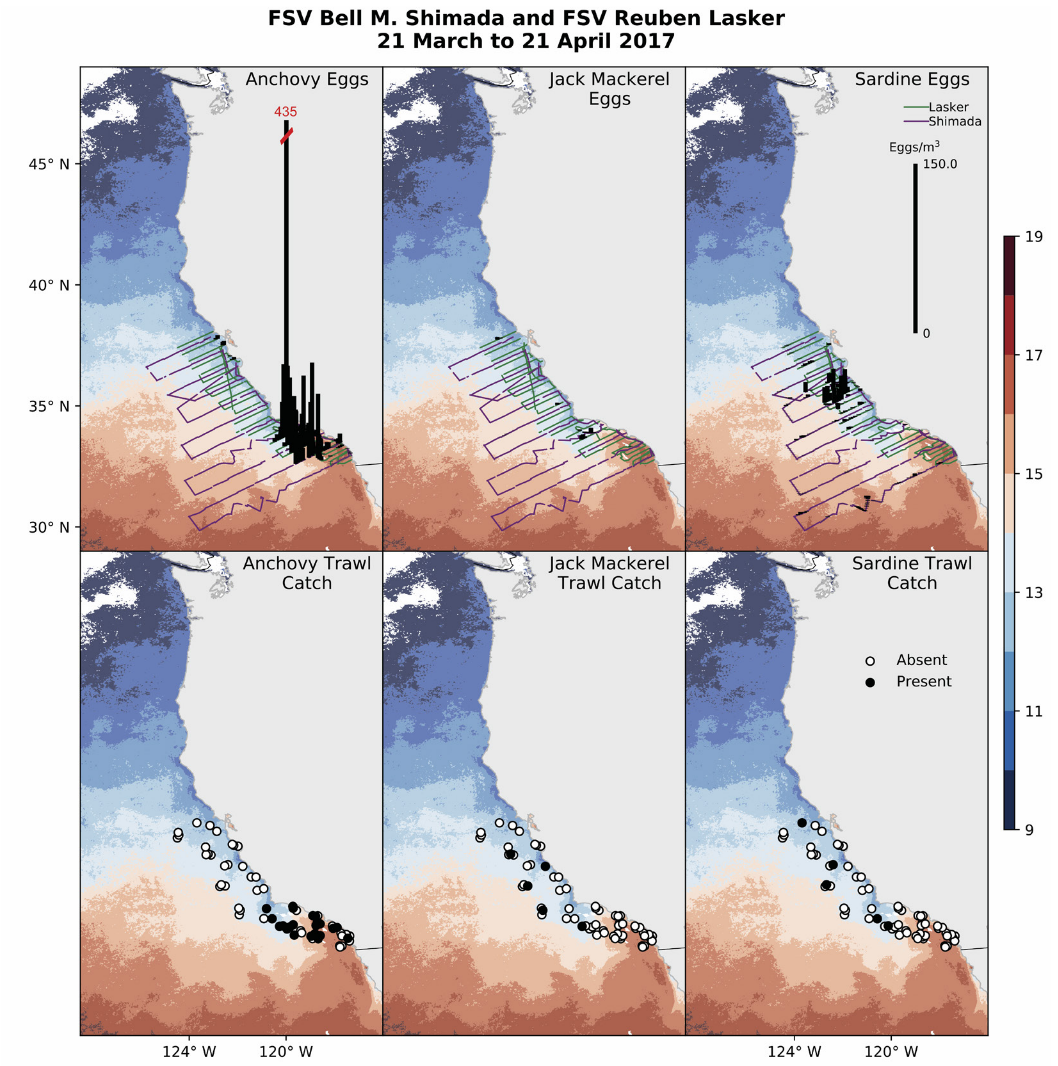

Figure 30. Density of eggs of northern anchovy, jack mackerel, and sardine collected with the continuous underway fish egg sampler (CUFES) during the spring 2017 CalCOFI and coastal pelagic fish cruises overlaid on satellite sea surface temperatures (˚C). Lower panels represent trawls in which anchovy, jack mackerel, and sardine where absent or present.

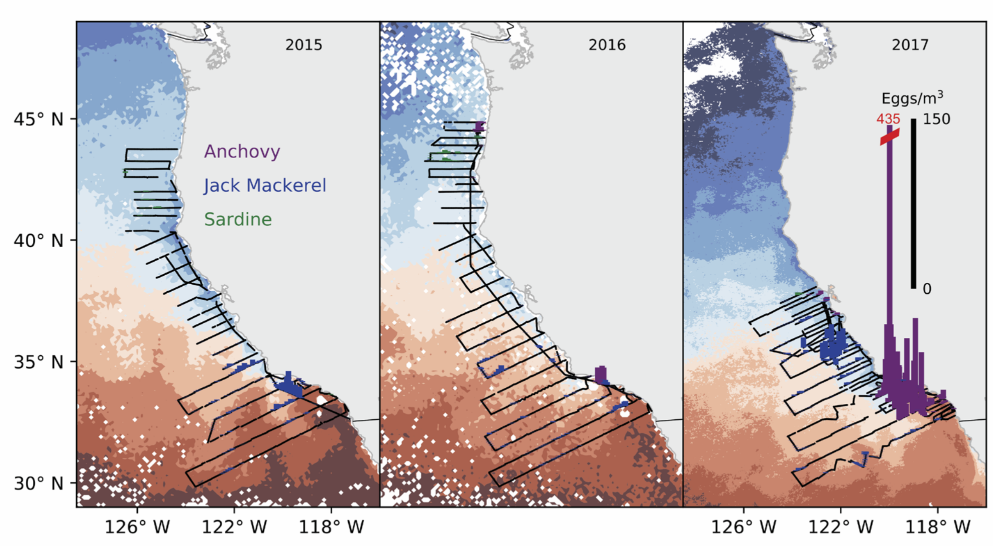

Figure 31. Density of eggs of northern anchovy, jack mackerel, and sardine collected with the continuous underway fish egg sampler (CUFES) during the spring 2015–17 CalCOFI and coastal pelagic fish cruises overlaid on satellite sea surface temperatures (˚C; scale bar is shown in Figure 30).

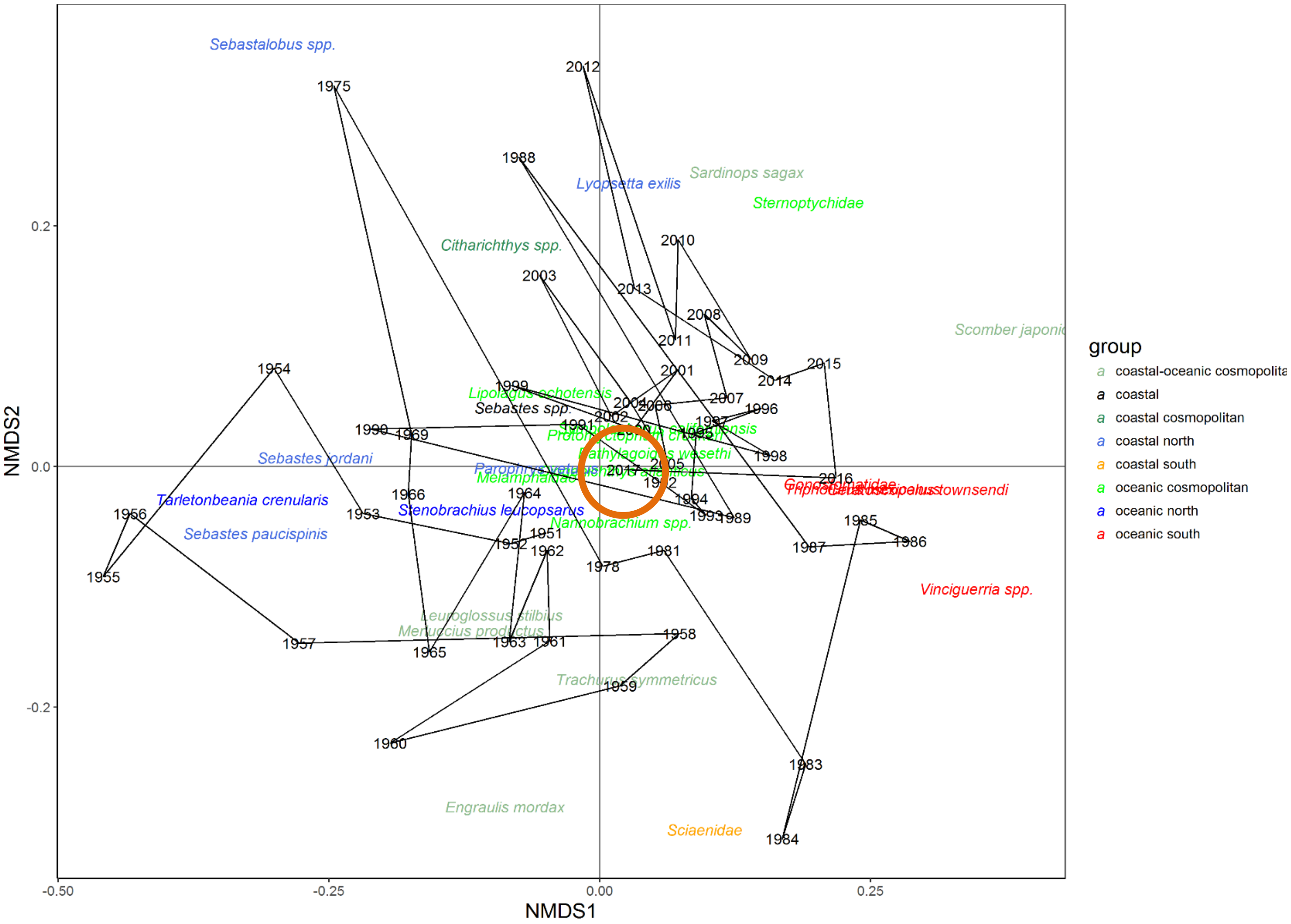

Figure 32. NMDS analysis depicting the composition of forage assemblage from lines 80 and 90 during the spring among years. The color of the species names characterizes their habitat affiliation and biogeographic range. Species in red or orange font are southern California Current, blue font are northern California Current, and green font are cosmopolitan. Open orange circle denotes the location of 2017.

but was still high relative to most years, while Gonostomatidae declined in 2017 to approximately average abundances (fig. 33). The northern cool-water myctophid *Stenobrachius leucopsarus* increased a bit relative to 2015–16 to near average levels (fig. 33), while another northern myctophid, *Tarletonbeania crenularis*, remained low (fig. 33).

For coastal pelagic species that are fished to varying degrees, northern anchovy abundance in spring was very similar to 2016 (fig. 34). Northern anchovy abundance from spring samples has been low since the early 1990s (with the exception of 2005), and 2017 had the third highest abundance of this species since 1994 (fig. 34). Abundance of northern anchovy in 2017, however, was still low relative to peaks between the 1950s and 1994. Pacific sardine, jack mackerel, and Pacific chub mackerel abundances were low in 2017 (fig. 34).

Shannon-Weaver diversity was almost exactly at a median level in spring of 2017 (fig. 35). This index tends to be low when coastal pelagic species are very abundant (e.g., correlation r = –.70 between Shannon-Weaver and northern anchovy) and high when southern mesopelagics are relatively abundant (e.g., r = .35 between Shannon-Weaver and *T. mexicanus*). The median diversity reflects results of the multivariate analysis on individual taxa suggesting that 2017 was characterized by having unexceptional abundances of both the southern mesopelagic taxa and northern anchovy. Overall species richness based on an estimated asymptote from bootstrap species accumulation curves was at the upper 75th quantile in 2017 and increased by approximately 8 species in comparison with 2016. Species richness also correlates positively with abundances of southern offshore species (e.g., r = .53 between Gonostomatidae and richness). Although the southern offshore species were down from 2015–16, some taxa (e.g., *T. mexicanus*, Gonostomatidae) were still relatively abundant (fig. 34). In addition, while a few commonly found taxa such as *Citharichthys* spp., shortbelly rockfish, and *Sebastes*

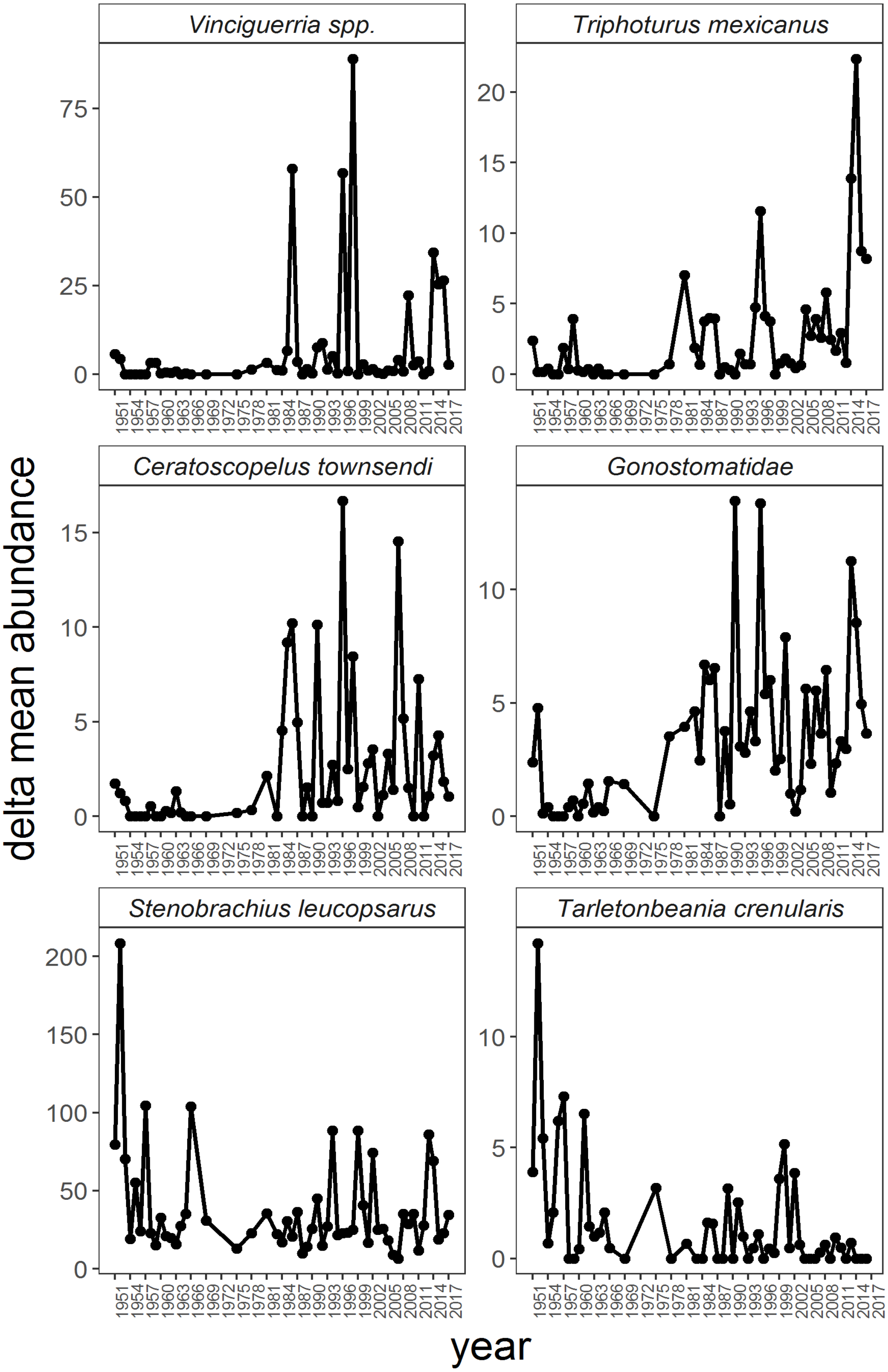

Figure 33. Delta-mean abundances of common mesopelagic taxa in spring between 1951 and 2017. Delta-mean calculations are used to estimate mean values from data with high numbers of samples that contain zero values (Pennington 1996). The four taxa in the top panels (*Vinciguerria* spp., *Triphoturus mexicanus*, *Ceratoscopelus townsendi*, and Gonostomatidae) have southern distributions relative to southern California and the two in the bottom panels (*Stenobrachius leucopsarus* and *Tarletonbeania crenularis*) are more broadly distributed to the north.

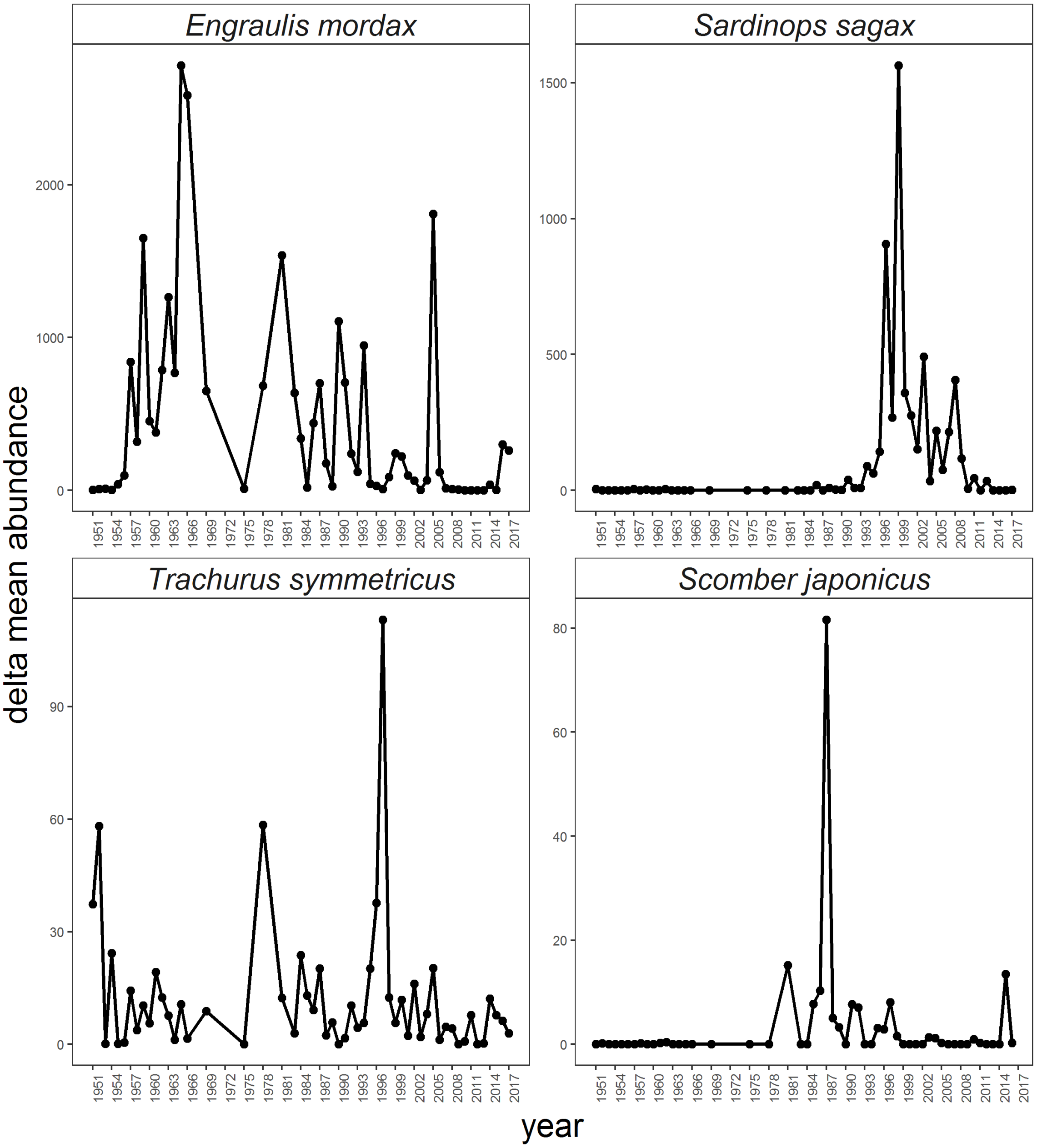

Figure 34. Delta-mean abundances of the most common coastal pelagic species that are to some extent commercially fished. Delta-mean calculations are used to estimate mean values from data with high numbers of samples that contain zero values.

paucispinis were completely absent in 2016, these taxa were again present in 2017.

REGIONAL PATTERNS IN BIRDS AND MARINE MAMMALS

Northern California Current: Yaquina Head, Oregon

Common murres (*Uria aalge*) at Yaquina Head experienced reproductive failure in 2016, as they had in 2015. Most (97%) murre eggs laid (n = 183) were not incubated long enough to hatch chicks. This was the second consecutive year of almost complete reproductive failure, and the only times this occurred during the 15 years of data collection. Murres at Yaquina Head exhibited a 6-year run (2011–16) of low reproductive success that is approximately a quarter the success of the first 9 years of our study (1998–2002, 2007–10, fig. 36). Murre reproductive success during the 2014–16 are the lowest on record. As in previous years, the reproductive failure is a combination of top-down predation and bottom-up food limitation. While the top-

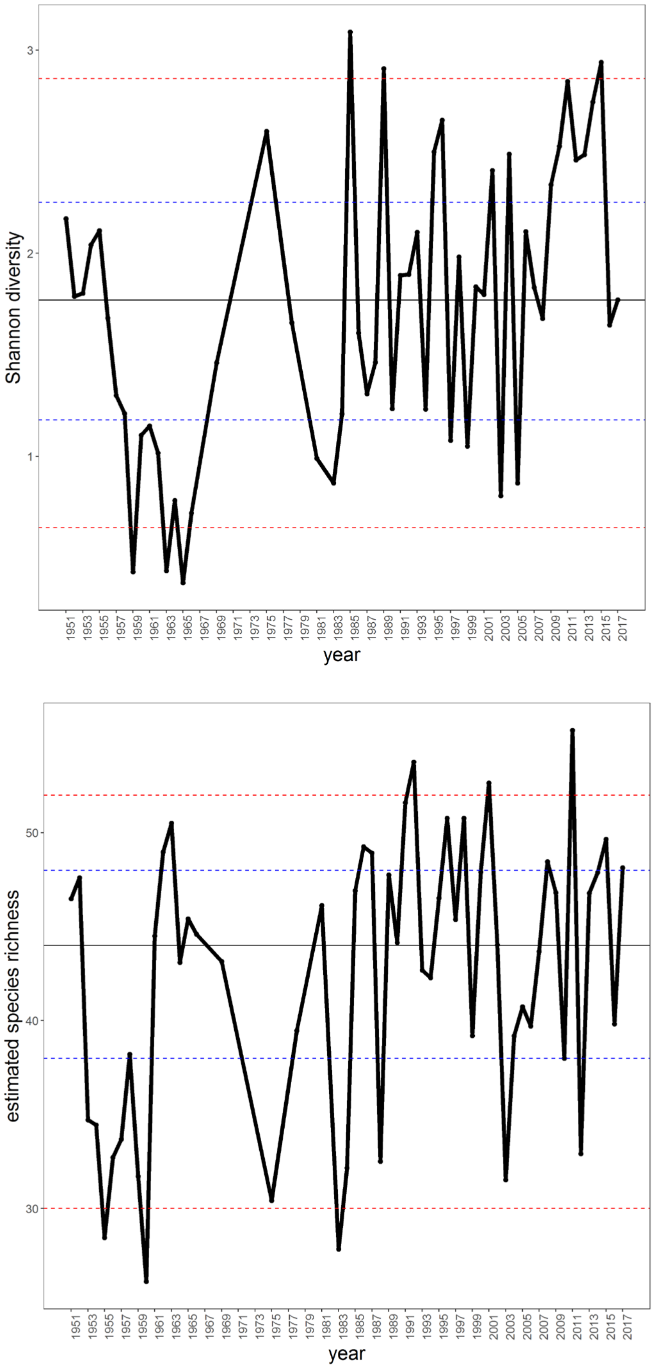

Figure 35. Shannon-Weaver diversity and estimated taxa richness of the larval assemblage. Dashed, horizontal blue lines depict 25th and 75th quantiles, dashed red lines 5th and 95th quantiles, and solid, horizontal black lines the median values.

down signal is most prominent, the bottom-up signal is evident. For example, the only location where a few murre chicks fledged in 2015 and 2016 was a small rock near sea level, not used for rearing chicks in previous years, and generally out of the way of predators. Even at this mostly predator-free site where a new study plot was added in 2016, the murre reproductive success was only 0.21 fledglings/pair, which is among the lowest recorded for the whole colony in our time series and similar to reproductive success during the 1998 El Niño (Gladics et al. 2015).

Since 2011 much of the reproductive loss for murres has been due to egg and chick predators (Horton 2014), however, 2016 had the highest rate of murre egg and adult loss, with 4.21 eggs destroyed and 0.28 adult murre fatalities per hour of observation (n = 243 hours). As in 2015, the disturbance by primarily bald eagles (95%; *Haliaeetus leucocephalus*) in 2016 was so intense early in the breeding season that most eggs were not incubated long enough to hatch chicks. Persistent eagle disturbance early season is also in part responsible for the later chick hatching dates of murres.

Brandt's (*Phalacrocorax penicillatus*) and pelagic (*P. pelagicus*) cormorant were both successful at rearing young. Brandt's cormorants reproductive success (0.87 fledglings/nest) was lower than 2015 (1.70 fledglings/nest), but greater than 2014 (0.72 fledglings/nest) and overall slightly above the long-term mean (fig. 37). Median hatch date (June 27th) was among the earliest recorded in our time series (fig. 37). Average brood size (1.65 chicks) was close to the long-term average (fig. 37).

Pelagic cormorants had their second highest reproductive success (1.37 fledglings/nest), only surpassed by 2013 (2.13 fledglings/nest; fig. 36). There were 30 nests visible from observation platforms, also second only to 2013 (34 nests) and more than double 2015 (11 nests). Pelagic cormorant reproductive success has been highly variable during our time series. Median hatch date (July 13th) was close to the long-term average (fig. 37).

The three main forage fish species fed to murre chicks in the Yaquina Head region have been smelt (Osmeridae), Pacific herring or sardine (Clupeidae), and Pacific sand lance (*Ammodytes hexapterus*). The relative proportion of the three species can be similar or one species may be numerically dominant in a given year. The failure of most of the colony prior to chick rearing provided an added challenge for diet data collection in 2015 and 2016. We were able to collect diet data, however, very few of these samples were likely fed to chicks, but instead simply adults flying into the colony with fish. Diets in 2016 were again dominated by smelt (82%), continuing a trend of smelt-dominated diets for six of the past seven years (since 2010; fig. 38). Murre diets in 2016 had the highest proportion of smelt (82%) recorded in a single year, with sand lance a distant second (16%). Pacific sand lance continues to be minimal in diets since 2010. The dominance of smelt, and lack of herring and sand lance is even notably different than diets during the 1998 El Niño (fig. 38). Sand lance are generally more prom-

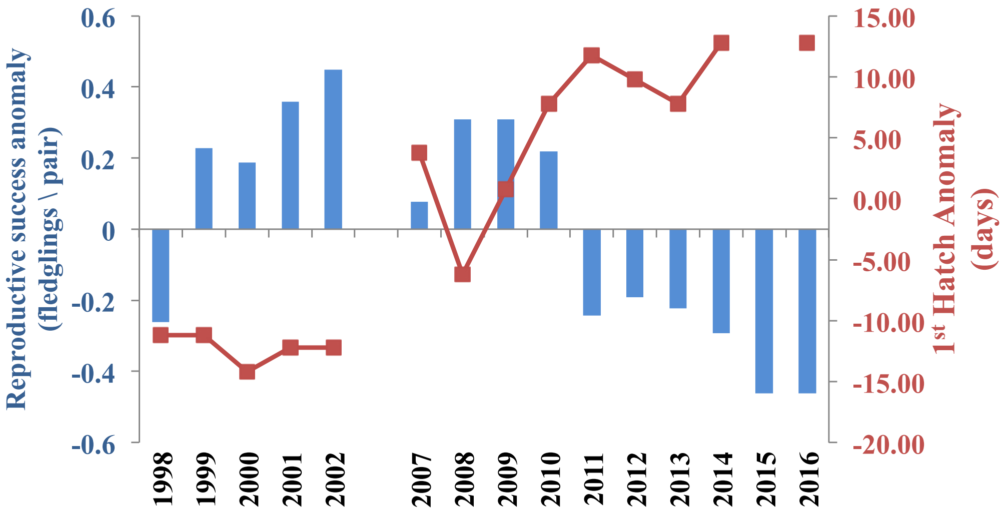

Figure 36. Anomalies of first chick hatch date and reproductive success for common murres nesting at Yaquina Head, Oregon, 1998–2016. 2016 was the second year that the colony failed to produce chicks from all but one small area where <10 chicks fledged each year.

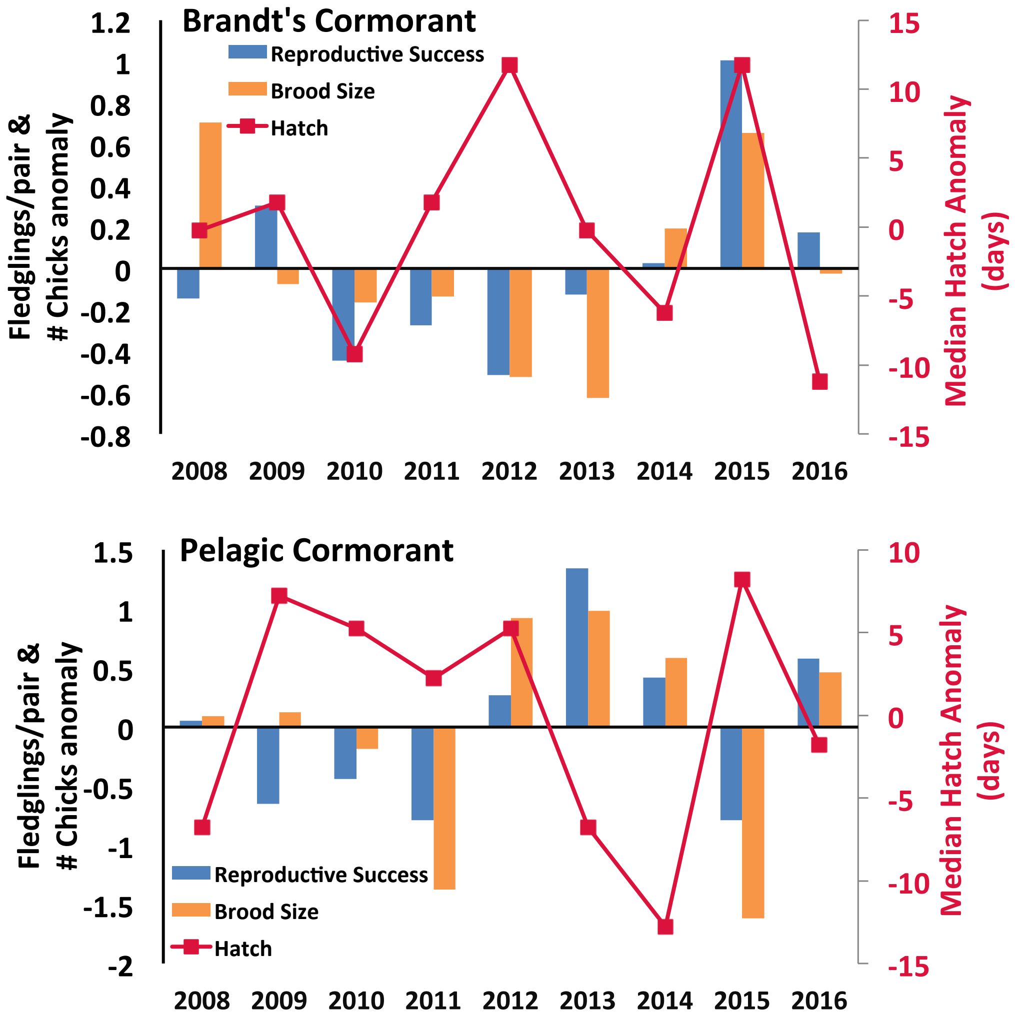

Figure 37. Anomalies of reproductive success and brood size for cormorants nesting at Yaquina Head, Oregon, 2008–16. Cormorants had average to above average reproductive success and brood size. Red lines indicate hatch date anomalies for cormorants.

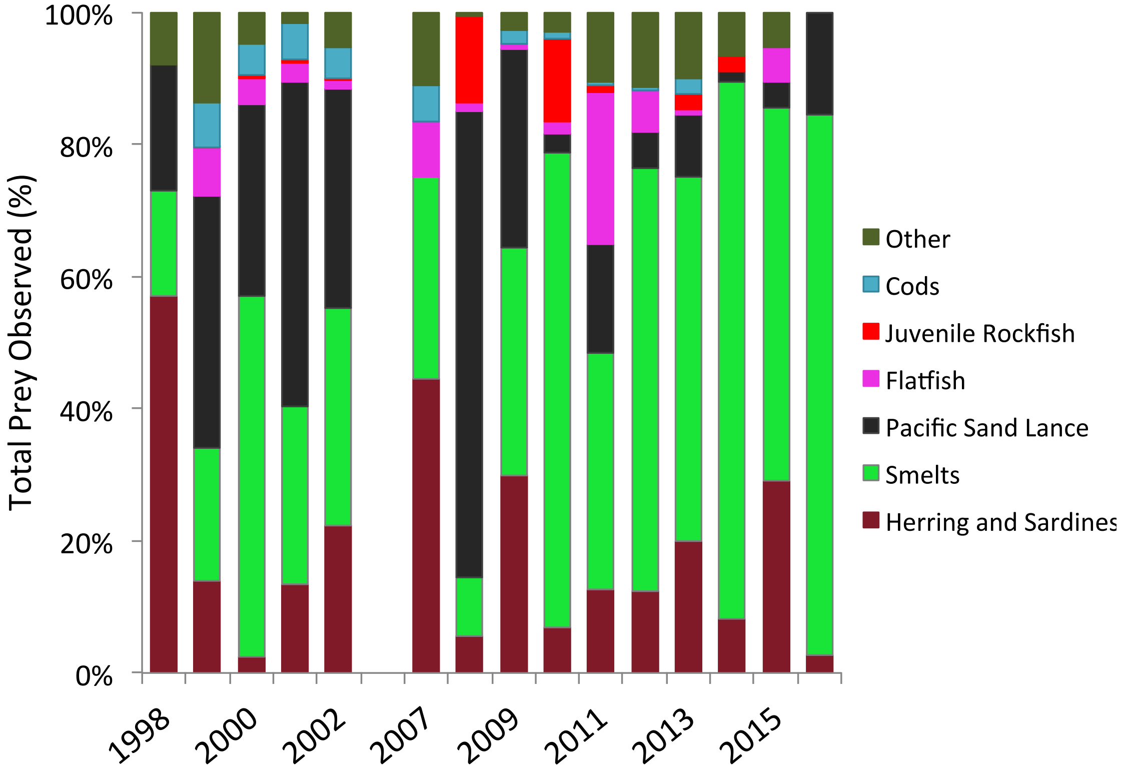

Figure 38. Prey fed to common murres chicks (% occurrence) at Yaquina Head Oregon, 1998–2016.

inent in murre diets during cold water years (Gladics et al. 2014, 2015), as highlighted by their prevalence in 2008 (fig. 38). Clupeids (primarily Pacific herring, *Clupea pallasii*), are generally associated with warmer water and positive PDO (Gladics et al. 2015), although their occurrence in recent warm water years has been lower than expected.

Northern California Current: Cape Flattery, Washington to Newport, Oregon

Notably, mean bird densities at sea for the 2017 strip transect surveys between Cape Flattery and Newport were the lowest observed during the 13-year data set and may indicate continued poor reproductive performance of resident breeders in 2017 (i.e., common murre)[18]. There was an apparent downward trend in common murre abundance at sea since 2015, with the third lowest mean density value on the record (9.27 birds per km^2) occurring in 2017 (fig. 39). This species was also aggregated near the Columbia River mouth, with 70.5% of all individuals observed on the three transects closest to the Columbia River (Willapa Bay, WA and Columbia River/Cape Mears, OR). Common murres are usually the most numerous breeding species found in the California Current during the upwelling season. Murres may have been affected by low forage fish availability beyond the Columbia River plume. The region near the Columbia River mouth where common murres were observed was also the area where northern anchovy were collected in surveys, including the same survey as the bird observations, and where above-average egg densities were observed with continuous underway fish egg sampler (fig. 21).

Sooty shearwater (*Ardenna grisea*) abundance in 2017, although very similar to that in 2011, was the lowest value yet observed in all 2003–17 June surveys (8.96 birds per km2) (fig. 39). Sooty shearwaters were highly aggregated in their distribution, with almost all (85.8%) individuals observed during the survey found on two transect lines immediately north of the Columbia River mouth (Grays Harbor and Willapa Bay, WA) where adult northern anchovy were observed during the same period. Given that sooty shearwaters are the most numerous non-breeding piscivorous species found in the California Current during upwelling season (May–September), their absence may reflect a lack of available prey in the offshore oceanic and Oregon waters found on the shelf in 2017, an hypothesis supported by the unusual micronekton assemblage observed in the same survey (fig. 23).

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[18] Seabird observations from an annual June survey encompassing 8 cross-shelf transects (extending ~30–50 km offshore) between Cape Flattery, WA and Newport, OR provide information on density patterns for the northern domain of the California Current.

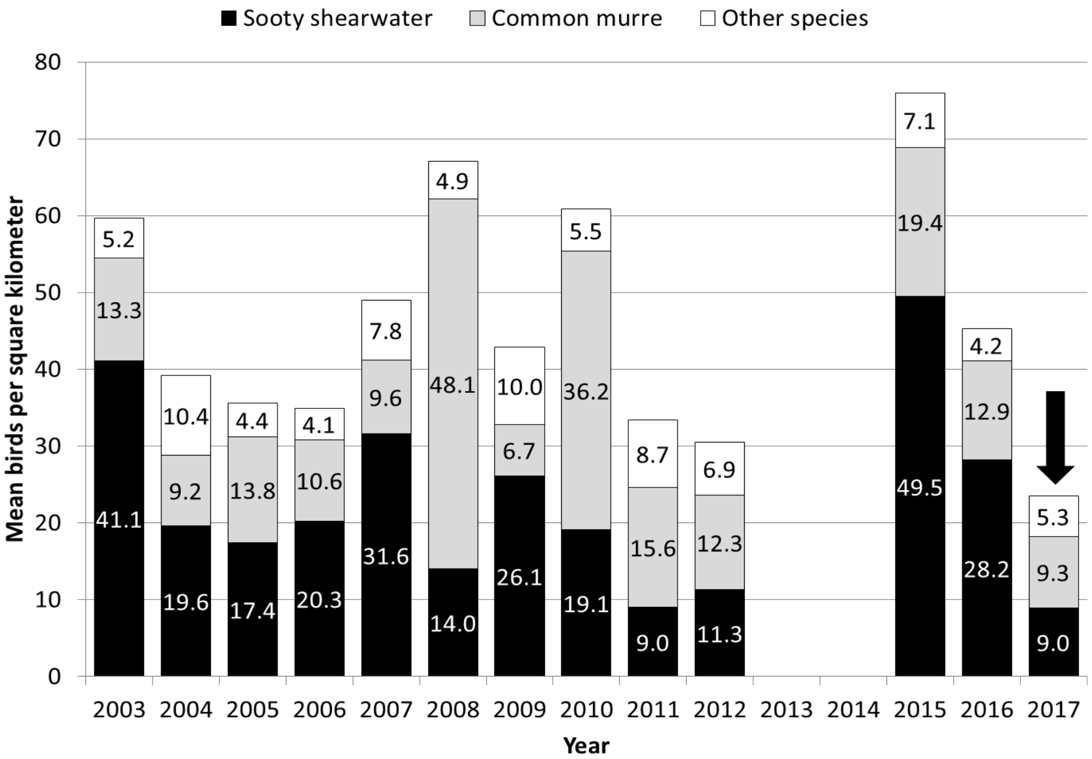

Figure 39. Seabird observations from an annual June survey encompassing 8 cross-shelf transects (extending ~30–50 km offshore) between Cape Flattery, WA and Newport, OR provide information on density patterns for the northern domain of the California Current.

Northern California Current: Castle Rock National Wildlife Refuge[19]

Common Murre are the most abundant surface-nesting seabird at Castle Rock and their reproductive success, nesting phenology, and chick diet have been studied since 2007. The percent of nesting pairs that successfully fledged young in 2016 was based on 93 breeding pairs monitored every other day for the duration of nesting. During 2016, murres only produced 0.16 fledglings per pair, which was 78% lower than the long-term average for this colony and the poorest year observed during the 10-year time-series (fig. 40). Although many murres hatched eggs (63%), chick starvation was frequent and 74% of chicks died prior to fledging. While the bottom-up food limitation was the primary cause of mortality, this food limitation caused murres to frequently leave chicks alone at the colony in search of prey, and these unprotected chicks were sometimes predated opportunistically by western gulls (*Larus occidentallis*) also nesting at the island. Reproductive failure of common murres at Castle Rock is consequential for the overall population of murres nesting in the California Current as this island is one of the most populous colonies south of Alaska (Carter et al. 2001).

In 2016, the average nest initiation date was 19 May, which was 10 days later than the long-term average at this colony (fig. 40) likely due to the later onset of upwelling-favorable winds (fig. 4) and weaker NPH and preconditioning (Schroeder et al. 2009, fig. 6). Although the timing of nesting by murres is not a direct response to the onset of upwelling, the increased availability of food associated with upwelling improves the body condition of egg-laying females and thereby influences the timing of nesting (Reed et al. 2006; Schroeder et al. 2009).

In 2016, the diversity of prey fed to chicks was lower than usual, (11 of 21 prey types observed), and no new prey types were observed[20]. Proportion of northern anchovy was 23x greater than the long-term average in 2016. Despite this increased prevalence of anchovy, smelt remained the predominant prey fed to chicks (fig. 40). Notably, the total number of prey observed at the colony was much less than usual because most chicks starved

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[19] In recent times, Castle Rock National Wildlife Refuge (hereafter Castle Rock) has frequently been the most populous single-island seabird breeding colony in California (Carter et al. 2001). This island is located off the coast of Crescent City, just south of Point St. George, in the northern California Current System. To facilitate long-term monitoring of seabirds nesting at this colony, a remotely-controlled video monitoring system was installed at this island in 2006. For purposes of assessing the state of the California Current, the reproductive performance of common murre and Brandt's cormorants is provided. For common murre, nesting phenology and chick diet between 2007 and 2016 is also provided.

[20] To determine prey composition fed to common murre chicks, 2-hour diet surveys were conducted 6 days per week during the murre chick-rearing period (approximately 23 hours surveyed in 2016).

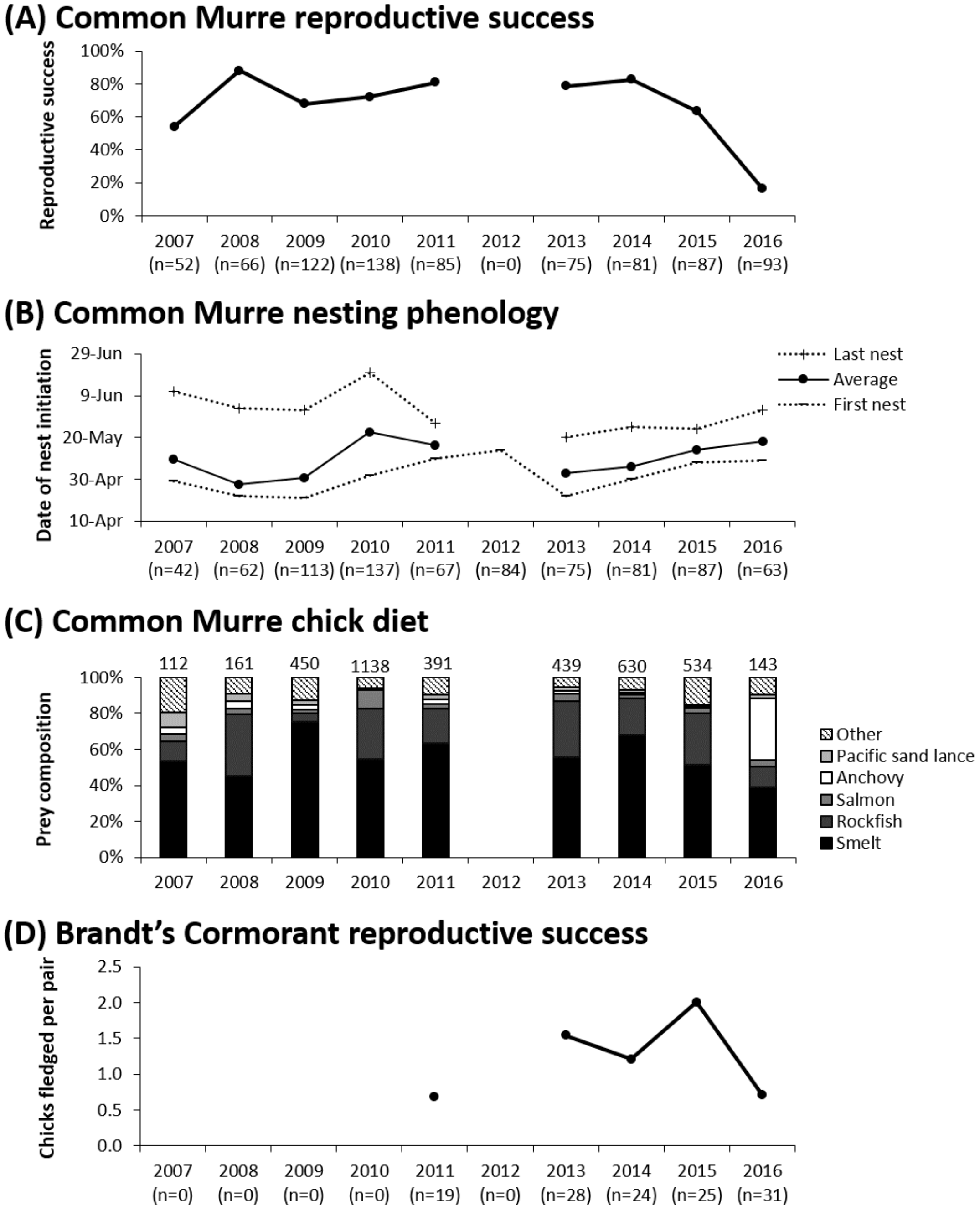

Figure 40. Reproductive data for seabirds nesting at Castle Rock National Wildlife Refuge (hereafter Castle Rock), Del Norte County, CA between 2007 and 2016; (A) Percent of common murre nesting pairs that successfully fledged young. The sample size (n) represents the total number of nesting pairs observed per year, and this figure does not include the success of replacement clutches. (B) First, average, and last dates for nests initiated by common murres. The date of nest initiation was the defined as the day that an egg was laid at a nest-site. The sample size (n) represents the total number of nests observed each year where nest initiation dates were accurate to ±3.5 days. (C) Composition of prey delivered to chicks by common murre. Numbers above each bar indicate the total number of prey identified each year. (D) Chicks fledged per nesting pair of Brandt's cormorant. The sample size (n) represents the total number of nesting pairs observed per year, and this figure does not include the success of replacement clutches. For each section, data from 2012 is lacking due to premature failure of the video monitoring system.

before they reached fledging age. Interestingly, murre diet data from Castle Rock and Yaquina Head continued to show northerly shifts in the forage fish community during 2016. Specifically, murres at Castle Rock had a dramatic increase in northern anchovy (more typical of central California colonies to the south) and Yaquina Head remain dominated by smelt (more typical of Castle Rock to the south).

Brandt's cormorant are the second-most abundant surface-nesting seabird at Castle Rock and their reproductive success has been studied since 2011. Based on 31 nests observed every three days throughout the 2016

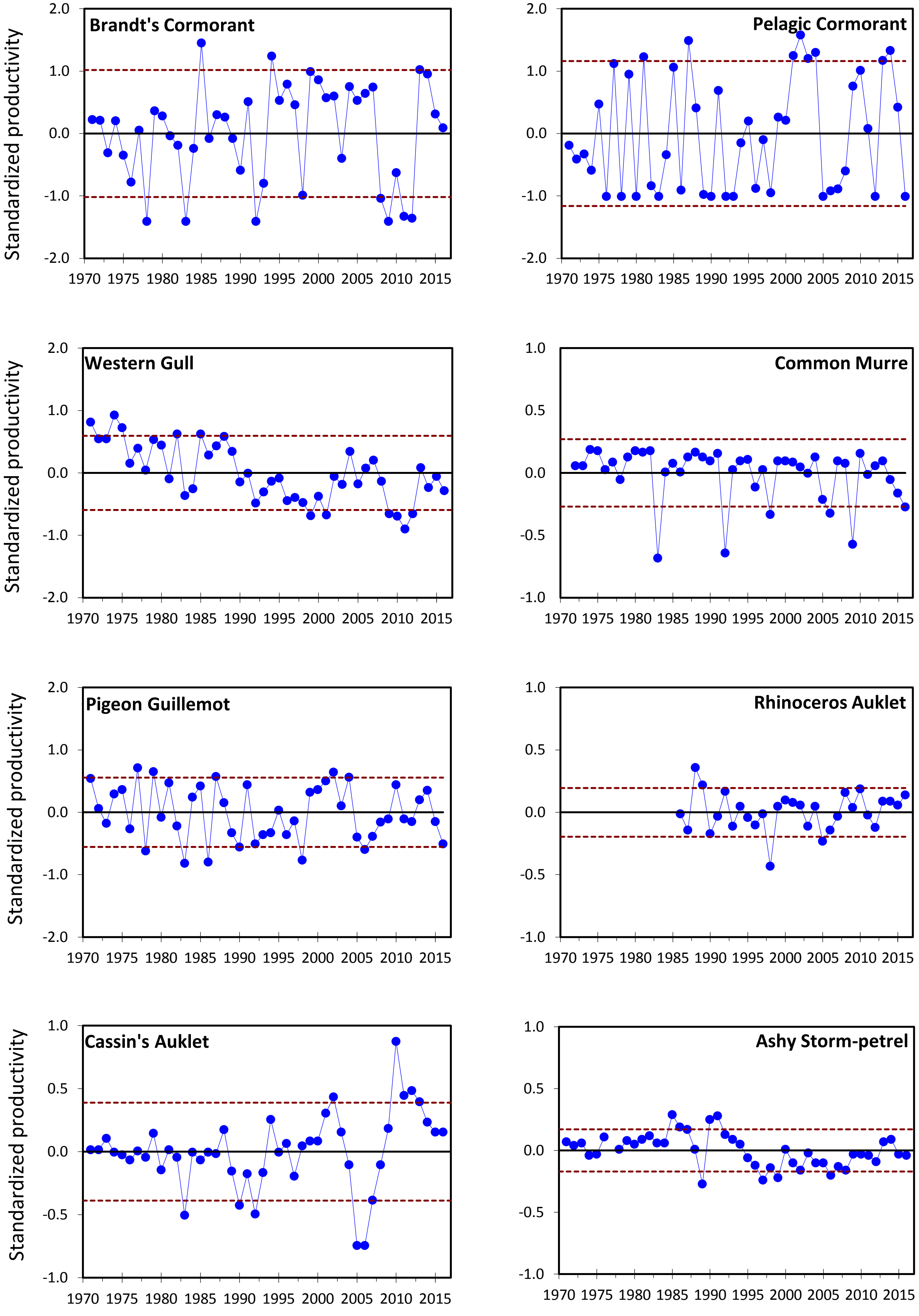

Figure 41. Standardized productivity anomalies (annual productivity minus 1971–2017 mean productivity) for 8 species of seabirds on Southeast Farallon Island.

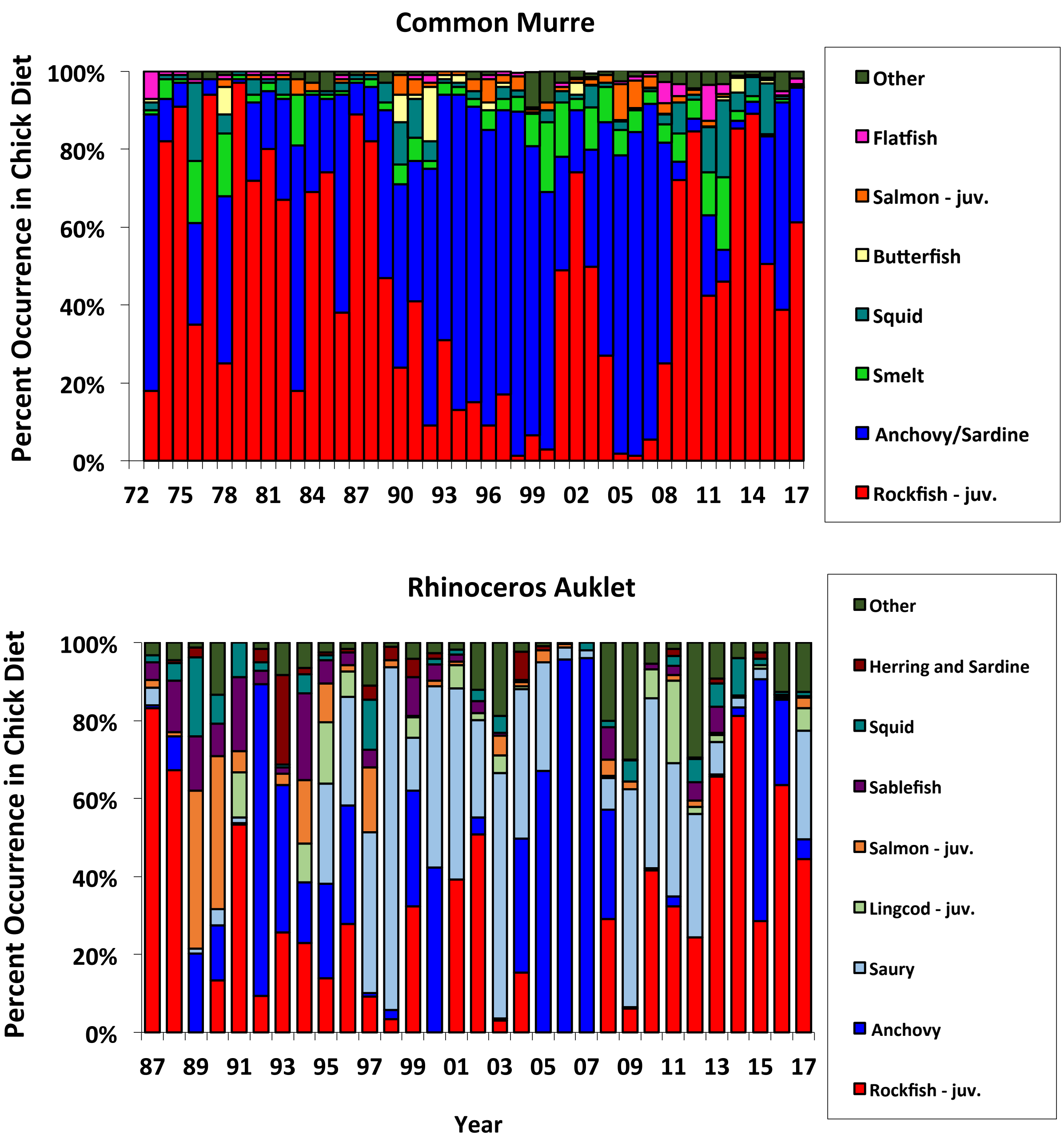

Figure 42. Diets of common murre and rhinoceros auklets returning to feed chicks 1987–2017. Note bar color differences between panels.

season, breeding pairs produced 0.71 chicks on average which was 1.9x lower than the long-term average at this colony and the second lowest observation since monitoring began (fig. 40). This reduction in success between 2015 and 2016 mirrored observations at Yaquina Head.

Central California: Southeast Farallon Island

Warm water conditions, such as those observed during the recent El Niño, typically lead to very low breeding success and even breeding failure for seabirds (fig. 41). This generally proved to be true in 2016 with reduced breeding populations and reproductive success for most species. However, the availability of common forage taxa such as rockfishes and krill muted the response relative to previous El Niño events such as 1998 during which these forage taxa were well below average (fig. 27). Overall breeding success of seabirds during the 2016 breeding season at Southeast Farallon Island can best be classified as a below average year for most species. Reproductive success was lower for most species when compared to 2015, including complete breeding failure for pelagic cormorants and the lowest success for pigeon guillemots (*Cepphus columba*) in 10 years. Common murres, Brandt's cormorant, and west-

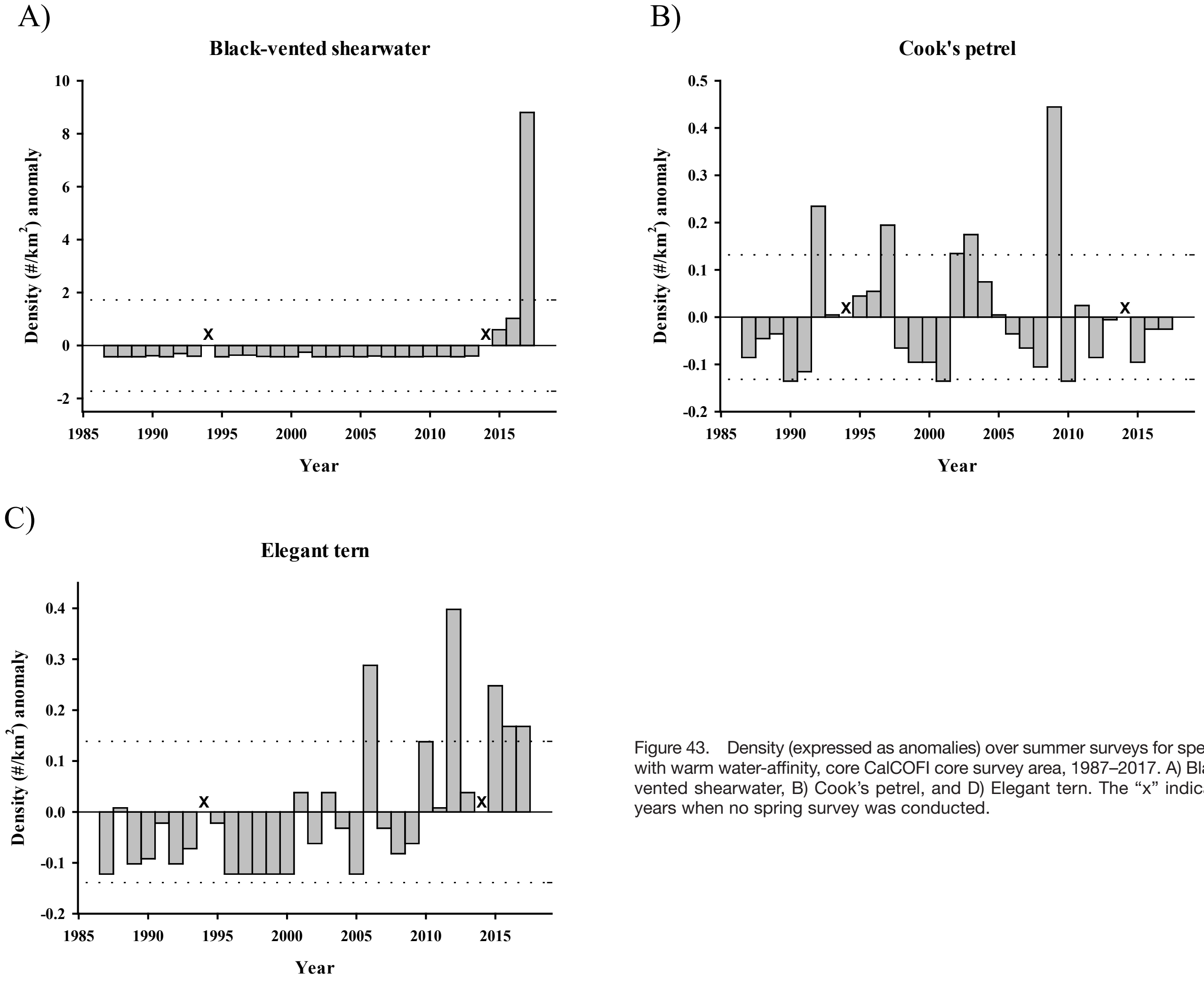

Figure 43. Density (expressed as anomalies) over summer surveys for species with warm water-affinity, core CalCOFI core survey area, 1987–2017. A) Black-vented shearwater, B) Cook's petrel, and D) Elegant tern. The "x" indicates years when no spring survey was conducted.

ern gull likewise suffered lower than average breeding success. Cassin's auklets (*Ptychoramphus aleuticus*) and rhinoceros auklets (*Cerorhinca monocerata*) were the only species to have higher than average breeding success. Cassin's auklets attempted few second broods but did manage to successfully fledge chicks from two of them, typically a sign of productive ocean conditions. Though the second broods did not significantly contribute to overall productivity this season, a high success rate for first broods resulted in an overall productive season.

Effects on breeding populations were mixed. Brandt's cormorants, Cassin's auklets, pigeon guillemots and western gulls all decreased whereas pelagic cormorants, double-crested cormorants (*Phalacrocorax auritus*) and tufted puffins (*Fratercula cirrhata*) increased. The western gull breeding population estimate was the lowest observed during our 46 years of monitoring while pigeon guillemots, Brandt's cormorants and Cassin's auklets were the lowest they have been in the last five years.

Following the strong upwelling periods in late March and April 2016 (fig. 4), zooplankton abundance (primarily krill) was average (fig. 27). Although diet analysis has not been completed, preliminary visual inspection of Cassin's diet samples indicated that krill remained the dominant item in auklet prey. This likely allowed for the higher than expected breeding in 2016 for Cassin's auklets. Similarly, the diets of common murre and rhinoceros auklet can be indicative of the current-year preyscape and resultant foraging behavior (Wells et al. 2017) and, ultimately, the reproductive success (Wells et al. 2008). Juvenile rockfish, a preferred prey, remained a significant portion of the diet fed to chicks in 2016 and 2017 (fig. 42) suggesting that significant reproductive failure is unlikely in 2017.

In general, although the 2015–16 El Niño may not have had as great an impact as previous events, the number of birds attempting to breed and their breeding success were both reduced during 2016. Chicks generally took longer to grow and fledged at lower weights

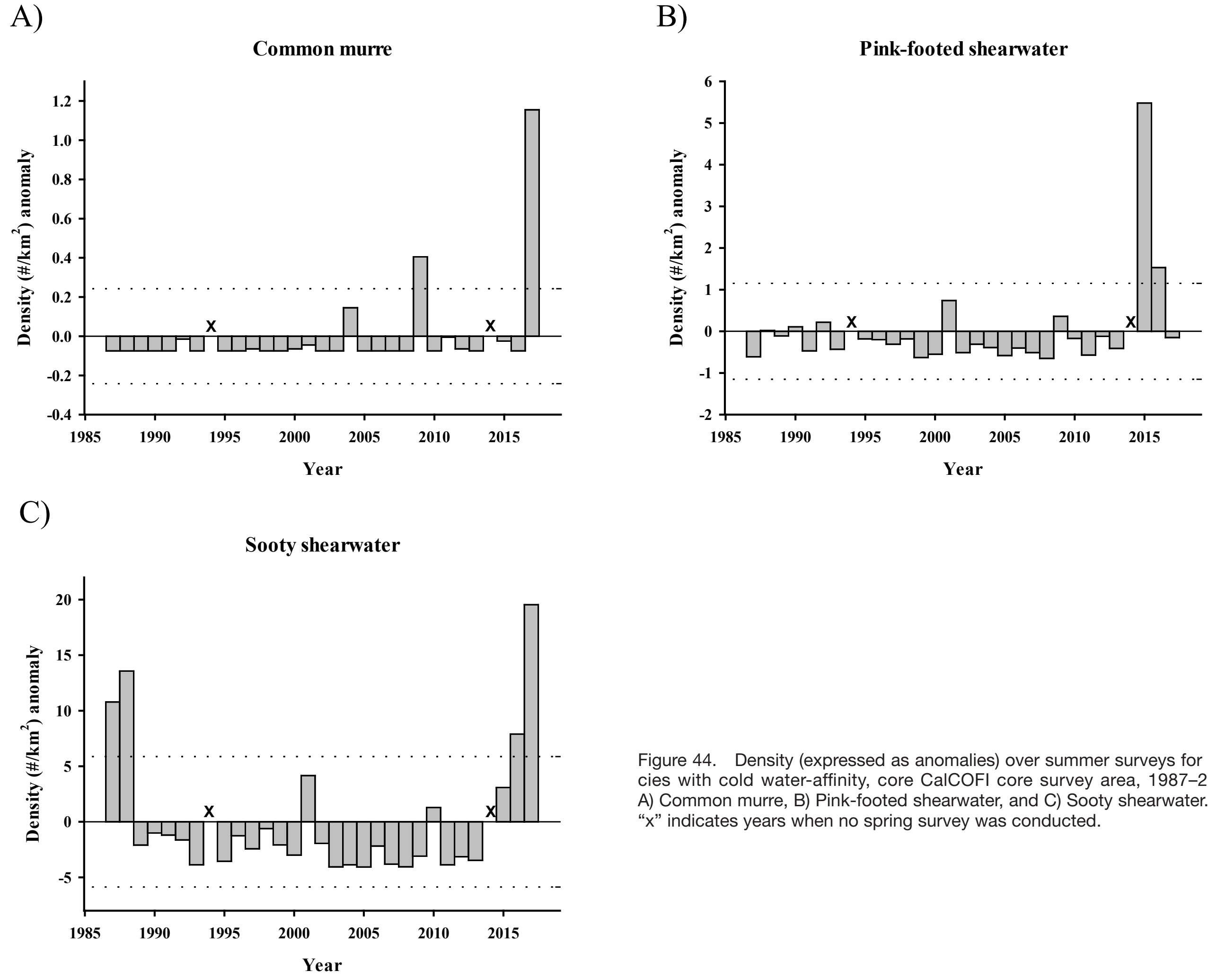

Figure 44. Density (expressed as anomalies) over summer surveys for species with cold water-affinity, core CalCOFI core survey area, 1987–2017. A) Common murre, B) Pink-footed shearwater, and C) Sooty shearwater. The "x" indicates years when no spring survey was conducted.

than in the past few seasons. Warm water continued to bring unusual species into the region. These included record numbers of brown boobies (*Sula leucogaster*), a few persistent blue-footed boobies (*Sula nebouxii*) and the first island record for least storm-petrel (*Oceanodroma microsoma*), all species that are normally found in more tropical regions.

Southern California Current: CalCOFI

Seabird distribution and abundance was surveyed during the 2017 summer CalCOFI cruise and seabird densities are presented here for the core survey area (defined here as the six CalCOFI lines, 77–93), 1987–2017. Anomalies of seabird species density in summer are indicative of species with affinities for warm and cold-water conditions (Hyrenbach and Veit 2003; Sydeman et al. 2009; Santora and Sydeman 2015). For summer, species with warm water-affinity include black-vented shearwater (*Puffinus opisthomelas*), Cook's petrel (*Pterodroma cookii*), and elegant tern (*Sterna elegans*) (fig. 43[21]). Cold water-affinity species include common murre, pink-footed shearwater (*Ardenna creatopus*), and sooty shearwater (fig. 44). Notable results from the 2017 summer survey indicate higher than average density of the warm-water species black-vented shearwater (highest density since 1992) and elegant tern. Interestingly, two of the three cool water-affinity species' (sooty shearwater and common murre) densities are well above any observed summer values since 1987. This is in stark contrast to results from northern California Current surveys that observed record low densities and may reflect superior foraging conditions within the core survey region during the 2017 spring CalCOFI cruise.

Sea Lions: San Miguel Island

California sea lions (*Zalophus californianus*) are permanent residents of the CCS, breeding in the California Channel Islands and feeding throughout the CCS

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[21] https://static1.squarespace.com/static/56a6b01dd8af105db2511b83/t/5931b5aa59cc68dd30ae919b/1496429995317/FI_Report_CAC_2017_summer.pdf

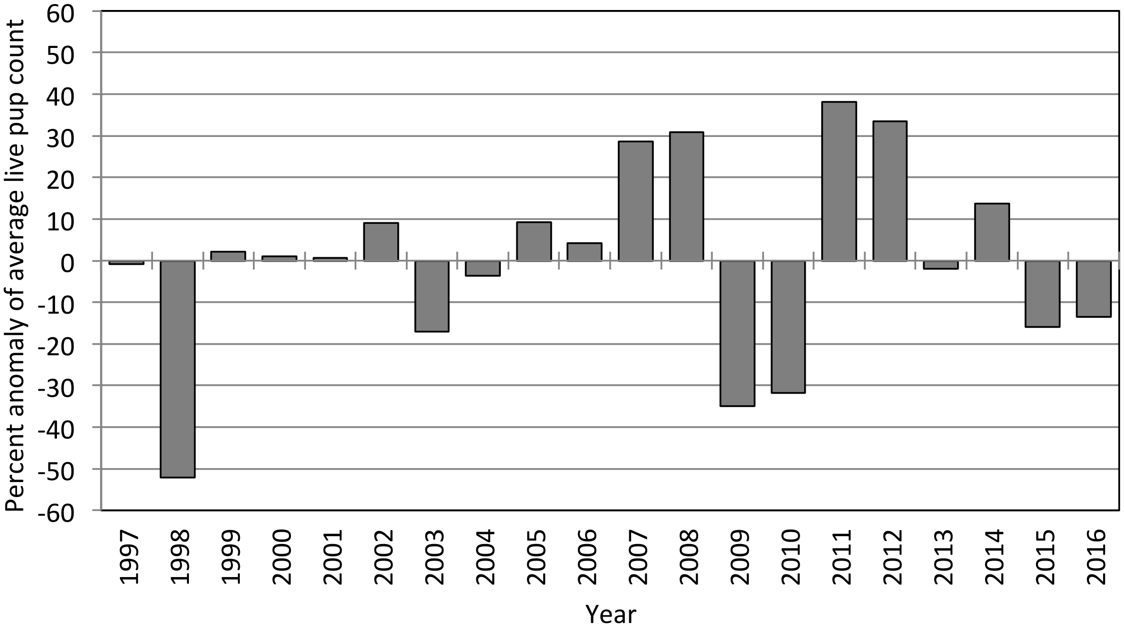

Figure 45. The percent anomaly of live California sea lion pup counts at San Miguel Island, California, based on a long-term average of live pup counts between 1997–2016 in late July when surviving pups were about 6 weeks old.

in coastal and offshore habitats[22]. They are also sensitive to changes in the CCS on different temporal and spatial scales and so provide a good indicator species for the status of the CCS at the upper trophic level (Melin et al. 2012). Two indices are particularly sensitive measures of prey availability to California sea lions: pup production and pup growth during the period of maternal nutritional dependence[23]. Pup production is a result of successful pregnancies and is an indicator of prey availability to and nutritional status of nursing females from October to the following June. Pup growth from birth to 7 months of age is an index of the transfer of energy from the mother to the pup through lactation between June and the following February which is related to prey availability to nursing females during that time[24].

In 2016, California sea lion pup births at San Miguel Island were 14% below the long-term average between 1997 and 2016 but showed a slight improvement from 2015 (16% below) (fig. 45)[25]. Pup condition and pup growth for the 2016 cohort increased from the record lows for the 2015 cohort. The average weights of three-month-old pups were 1.7 kg and 2.0 kg higher than the long-term average for female and male pups, respectively (fig. 46), representing a 10% increase in pup condition in 2016 compared to 2015. After two years of extremely low growth rates in 2014 and 2015, pup growth rates from three to seven months of age for female and male pups were similar to the 20-year average in 2016, marking a significant improvement in growth rates (fig. 47).

Since 2009, the California sea lion population has experienced low pup survival, low pup births, or both (Melin et al. 2012; McClatchie et al. 2016; DeLong et al. 2017). In March 2013, an unusual mortality event was declared for California sea lions in southern California in response to unusually high numbers of young pups from the 2012, 2014, and 2015 cohorts stranding along the coast and at San Miguel Island and other rookeries (Wells et al. 2013; Leising et al. 2014; Leising et al. 2015; McClatchie et al. 2016)[26]. The unusual mortality event was associated with poor foraging conditions for

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[22] San Miguel Island, California (34.03°N, 120.4°W) is one of the largest colonies of California sea lions, representing about 45% of the US breeding population. As such, it is a useful colony to measure trends and population responses to changes in the marine environment.

[23] We used the number of pups alive at the time of the live pup census conducted in late July and the average weights of pups at 4 months and 7 months of age between 1997 and 2016 as indices of the population response to annual conditions in the CCS. The number of live pups in late July represents the number of pups that survived from birth to about 6 weeks of age. Live pups were counted after all pups were born (between 20–30 July) each year. A mean of the number of live pups was calculated from the total number of live pups counted by each observer. A long-term average live pup count based on counts between 1997 and 2016 was used to create annual anomaly percentages from the long-term average.

[24] Each year, between 200 and 500 pups were weighed when about 4 months old. Pups were sexed, weighed, tagged, branded, and released. Up to 60 pups were captured in February and weighed and measured at 7 months of age. Of the 60 pups captured in February, up to 30 pups were branded and provided a longitudinal dataset for estimating a daily growth rate between 4 months and 7 months old.

[25] We used a linear mixed-effects model fit by REML in R to predict average weights on 1 October and 1 February in each year because the weighing dates were not the same among years. The model contained random effects with a sex and days interaction (days = the number of days between weighing and 1 October and 1 February) which allowed the growth rate to vary by sex and year, and a full interaction fixed effects of sex and days. The average weights between 1997 and 2016 were compared to the long-term average for the average pup weights between 1975 and 2016.

[26]http://www.nmfs.noaa.gov/pr/health/mmume/californiasealions2013.htm

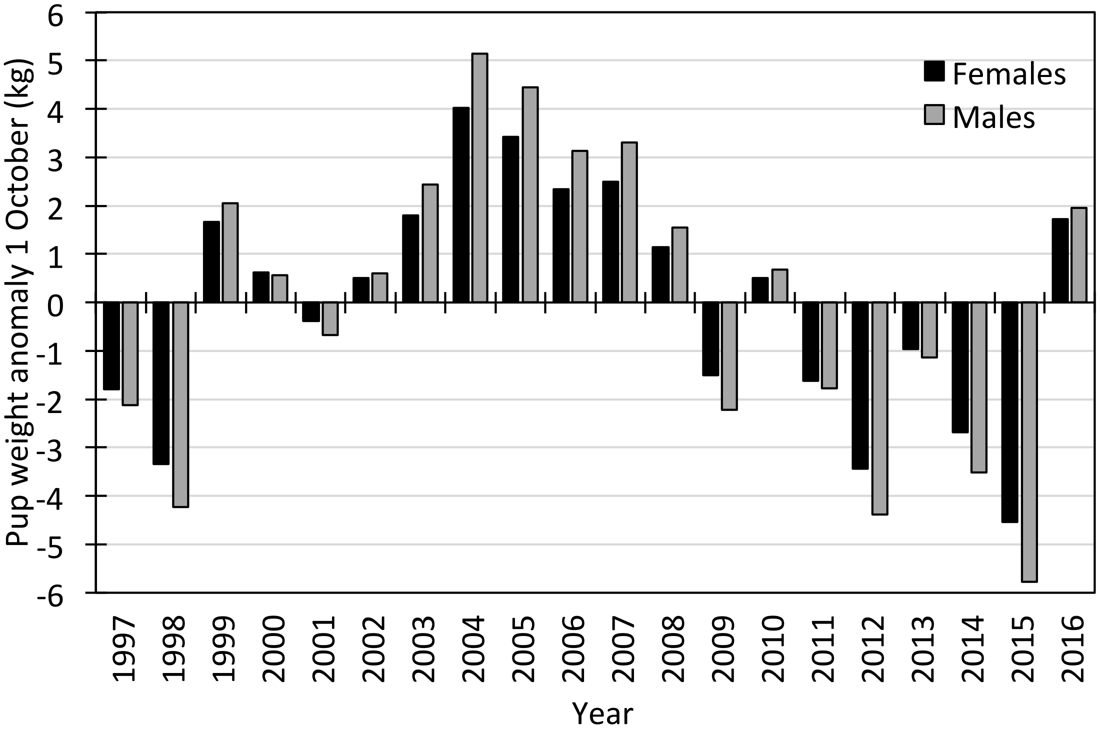

Figure 46. Average pup weight anomaly (kg) from predicted average weights of 3-month-old female and male California sea lion pups at San Miguel Island, California, from the long-term average between 1997 and 2016.

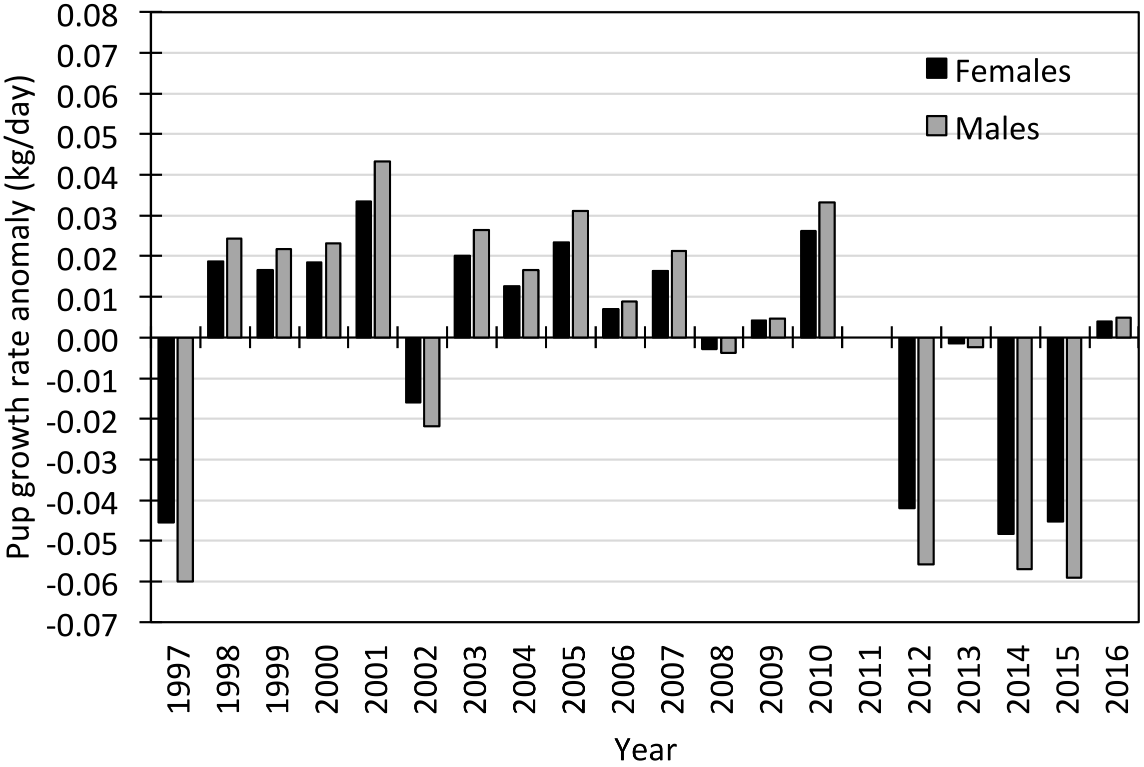

Figure 47. Average daily growth rate anomaly of female and male California sea lion pups between 3 and 7 months old at San Miguel Island, California, from the long-term average between 1997 and 2016.

nursing females due to shifts in the availability of prey and prey community composition in the central and southern CCS during the period of pup nutritional dependence. The low numbers of births in 2016 reflect the effects of low numbers of births and poor pup and juvenile survival since 2009 that have reduced the number of reproductive females in the population. However, the improved condition of pups in 2016 indicates that nursing females experienced better foraging conditions during the 2016–17 nursing period and were able to support the nutritional demands of their pups. The improved condition of pups in 2016 coincided with the return to a nursing female diet with high frequencies of northern anchovy (92%) and Pacific hake (63%) compared to a diet rich in juvenile rockfish and market squid that dominated the food habits during the unusual mortality event.

Marine Mammal Surveys: CalCOFI Surveys

On-effort visual detections of baleen whales for 2014–17 are shown in fig. 48[27]. During winter and spring cruises, most baleen whale sightings occurred within 200 nm of the shoreline. A nearshore shift in distribution of humpback whales (*Megaptera novaeangliae*) was seen during the spring in the 2016 and 2017 cruises. During summer, there were more baleen whale sightings along the continental slope and in offshore waters. During fall cruises in 2015 and 2016 baleen whale sighting were concentrated in the Channel Islands region.

Odontocete detections for 2014–17 are shown in Figure 49. In general, short-beaked common dolphins (*Delphinus delphis*) were detected offshore more frequently than inshore. In 2015, short-beaked common dolphins were not observed in the offshore areas, but they were present in the offshore areas during the summer and fall of 2016.

DISCUSSION

In this paper, we have not attempted to develop a quantitative model integrating all these data series. However, when we examine them in total, bolstered by current literature, we can make assertions about the temporal and spatial evolution of the California Current ecosystem encompassing the majority of links between environmental influences, population productivity, reproductive and foraging dynamics of top-predators, and the overall trophic structure. We finish with a comment regarding unanticipated ecosystem interactions resulting from recent anomalous ocean conditions and the realized and potential impact they have on coastal communities.

A weak La Niña in 2016, and stormy winter and sluggish upwelling in 2017

From spring 2016–spring 2017, the NPGO was at near-average values and the PDO remained positive, with values lower than the exceptionally high values of 2014–16. A weak tropical La Niña event was marked by modest negative ONI values from summer 2016–winter 2017. Together, these indices suggest that basin-scale patterns did not likely favor strong coast-wide productivity anomalies from spring 2016 to spring 2017. Above average upwelling north of 36˚N persisted from the spring to the fall of 2016 (March–September). By January and February 2017, stronger-than-average downwelling winds occurred in northern California Current (fig. 4) related to a continued weak NPH (fig. 6). As upwelling began in March and April 2017 it was weaker than typical north of 36˚N. Ultimately, chlorophyll during the March–May of 2017 was below average throughout much of the CCS with localized areas with positive chlorophyll anomalies in central California and the Channel Islands (fig. 9). The positive chlorophyll anomalies in central California may have been associated with strongly positive upwelling anomalies that began in May (fig. 4). As late-winter and spring conditions influence productivity of the forage base across the CCS (Logerwell et al. 2003; Schroeder et al. 2009, 2014) and structuring of the ecosystem (Wells et al. 2016, 2017), the observed weak upwelling conditions north of 36˚N during March–April 2017 could negatively affect the availability of forage to predators through 2017.

Dissimilar conditions emerged in the south and the north

Regional surveys during the 2016 El Niño found that surface waters were anomalously warm across the CCS and were also anomalously warm at depth south of Cape Mendocino (figs. 4, 7, 8). Through 2016, northern CCS copepod communities had an anomalously high abundance of subtropical species (fig. 10). Chlorophyll concentrations were low across the California Current in 2016. At Trinidad Head there was a *Pseudo-nitzschia* bloom in spring that abated by June. In the central and southern CCS domoic acid concentrations were negligible during 2016 (fig. 9).

Early in 2017 physical and biological conditions were dissimilar between the northern, central, and southern CCS. Surface conditions north of Cape Mendocino remained anomalously warm (fig. 4), chlorophyll was very low (fig. 9), and copepod species richness patterns

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[27] Marine mammal surveys were initiated as part of the CalCOFI cruises in 2004. Visual monitoring incorporates standard line-transect survey protocol which includes two experienced observers scanning for marine mammals during transits between CalCOFI stations. Information on all cetacean sightings was logged systematically, including species, group size, reticle of cetacean position relative to the horizon, relative angle from the bow, latitude, longitude, ship's heading, behavior, environmental data and comments.

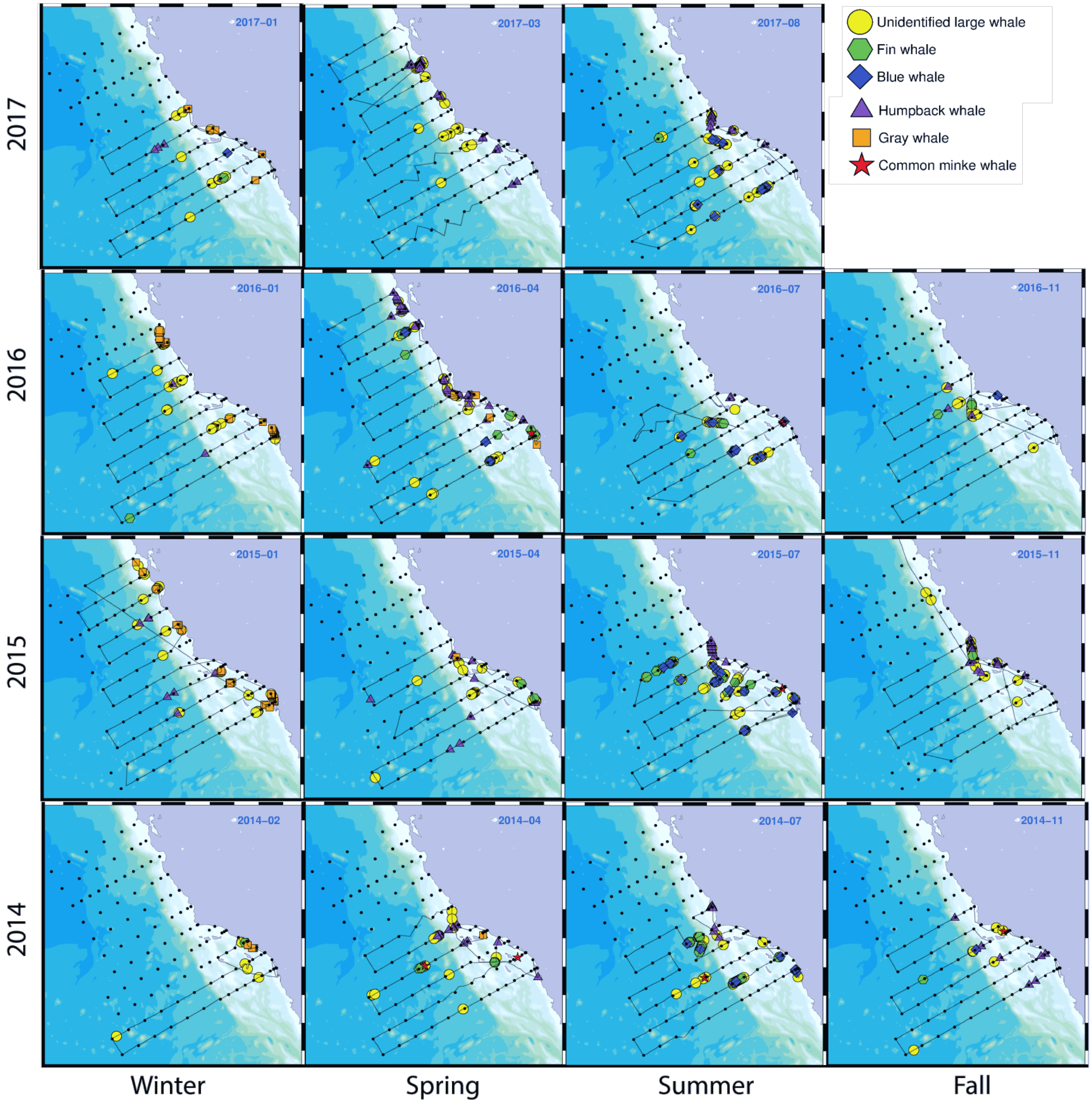

Figure 48. On-effort baleen whale sightings during CalCOFI cruises 2014–17. CalCOFI stations are represented by black dots and the ship's trackline is represented as a solid black line between stations. Symbol shapes and colors denote different species, as per legend.

were representative of southern assemblages in 2017 (table 1, fig. 10). Further, in January–April 2017 downwelling anomalies were evident along the West Coast from Monterey Bay to Vancouver Island, which were associated with increased storm events especially in California (figs. 3, 4). Southern and central regional surveys indicated that environmental conditions were typical for the longer time series, which suggests that central and southern regions may be returning to "normal." However, atypically, the increased chlorophyll in spring 2017 around the Channel Islands during April–May corresponded with a significant toxic event linked to increased estimates of *Pseudo-nitzschia* abundance (fig. 9). The event was responsible for an unusual mortality event for a number of seabirds and exceeded the regulatory limit for human consumption of fish and shellfish.

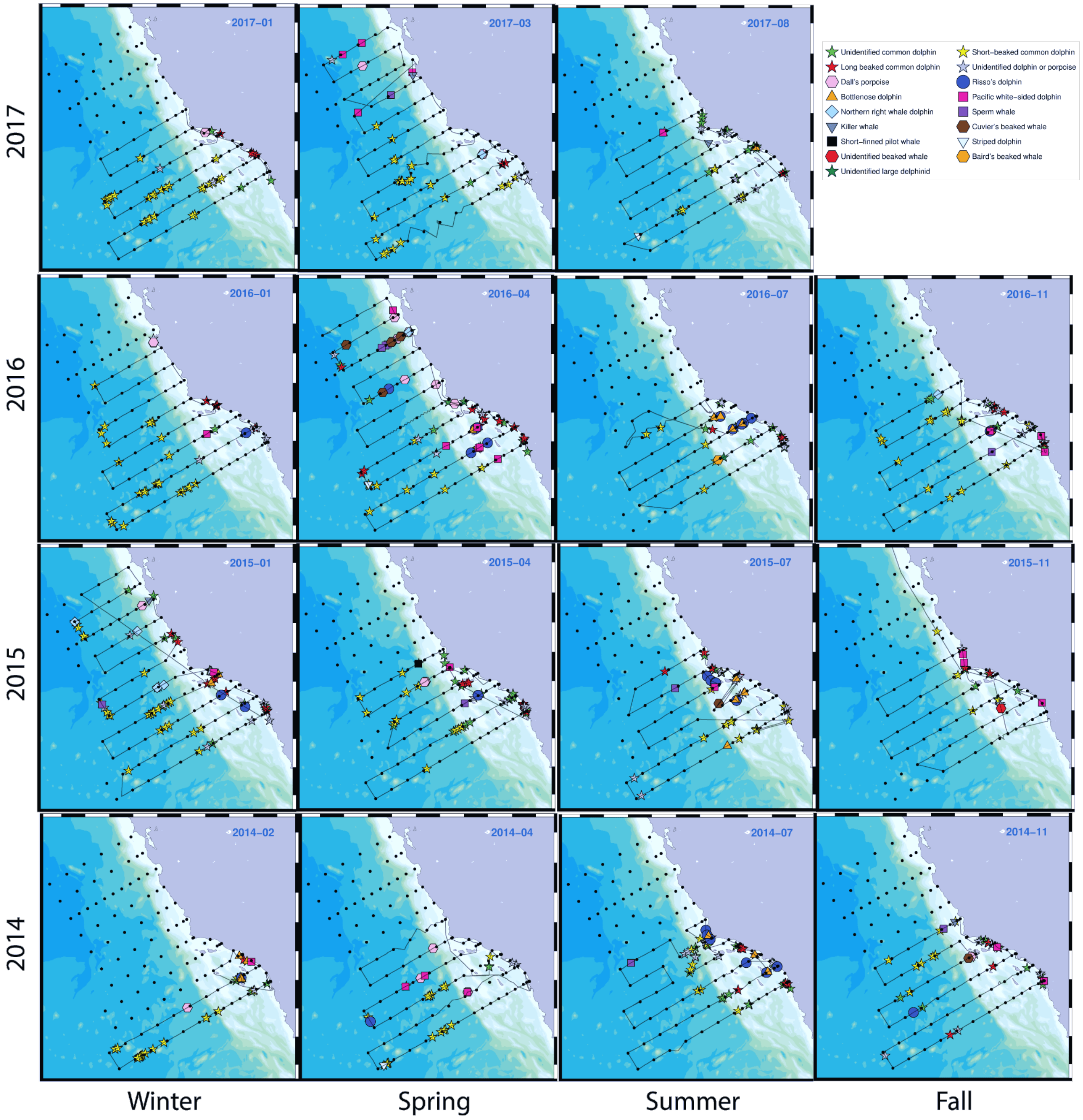

Figure 49. On-effort odontocete sightings during CalCOFI cruises 2014–17. CalCOFI stations are represented by black dots and the ship's trackline is represented as a solid black line between stations. Symbol shapes and colors denote different species, as per legend.

Micronekton communities responded to regional conditions and northern anchovy had notable spawning events

Micronekton abundance, distribution, and community structure reflect the larger patterns in environmental and zooplankton variability observed throughout the CCS. Namely, while conditions south of Cape Mendocino were typical of the longer times series, the northern regions did not return to a "normal" state following the end of the 2014–16 marine heatwave (Auth et al. 2017; Peterson et al. 2017). Specifically, the northern CCS was anomalously warm at the surface and the micronekton community was dominated by taxa originating from the south and off the shelf (e.g., pompano, myctophids, YOY Pacific hake, and YOY rockfishes) (Auth et al. 2017). In 2017 the dominant signal of warm-water taxa on the shelf included the extreme abundance of pyrosomes, which have been found with increasing frequency since 2014 in the northern California Current, but never in the extreme densities on the shelf region as observed this year (Brodeur, unpub.). The anomalously strong northward winds and the associated downwelling that occurred in the northern CCS in January–February 2017 (figs. 3, 4, 7) may have led to poor preconditioning of coastal waters (Hickey et al 2006; Logerwell et al. 2003) and directly contributed to the presence of offshore and southern taxa on the shelf in winter and spring. There may also be a biological reason for the reduction in typical fish taxa. Specifically, many of these fishes are short-lived and are regional residents. It is not unreasonable to expect that the preceding three years of poor productivity (due to the marine heat wave and El Niño) may have simply reduced their spawning stock biomass.

It is also notable that a greater than average abundance of northern anchovy has been observed in the northern CCS since 2014. As well, egg enumeration data indicates their spawning activity has been high (fig. 21). Interestingly, the most anomalous event in the southern CCS was the increased spawning activity of northern anchovy (fig. 31). While the greatest spawning activity was in the Southern California Bight and Columbia River shelf regions, greater than average spawning activity was also observed at a few isolated locations nearshore in central California (fig. 21). The mechanisms driving these dense spawning aggregations largely in the northern and southern parts of the CCS are to yet be determined, but they are consistent with the predictions of the Basin Model (MacCall 1990), which states that as the overall population abundance is reduced, as has been observed in recent years[28], dense spawning aggregations may be concentrated in areas of particularly suitable habitat. In the case of northern anchovy, they would be impinged along the remaining good habitats nearshore and expand to less optimal habitat as the population increases; such expansion may now be occurring in the core anchovy habitat within Southern California Bight.

Salmon habitat and observations

Recent climate extremes contributed to sharp downturns in the abundance (catch + escapement) of many West Coast Chinook and coho salmon populations. Historically poor freshwater conditions were caused by California's extreme "hot drought" from 2012–15. A broader "western snow drought" in 2015 related to a combination of precipitation and record high surface air temperatures contributed to extreme high freshwater temperature in many western rivers in 2015 that will impact catches and escapement during 2017–20. Record high coastal ocean temperature from 2014–16 and the associated ecosystem impacts that included shifts to more subtropical forage communities and shifting predator distributions likely contributed to sharp declines in survival rates for many US West Coast salmon populations. Fishery impacts included sharply reduced Chinook salmon landings in West Coast commercial fisheries and very low escapements in California's Klamath and Sacramento Rivers in 2016 (PFMC 2017a). The Klamath River fall Chinook ocean abundance forecast was the lowest on record (since 1985). This low abundance forecast and conservation concerns for other weak stocks led to heavily constrained or closed commercial, recreational, and tribal fisheries in California and Oregon (PFMC 2017b).

Results from northern surveys indicate that 2017 likely had anomalously high early-marine mortality for Columbia Basin origin coho and Chinook salmon. Specifically, 2017 had the lowest catch for juvenile Chinook and coho salmon in coastal surveys in the 20-year times series (1998–2017; fig. 24). The record-low catch is likely related to the forage composition (fig. 26) for out-migrants soon after they entered marine waters (Daly et al. 2017) rather than river conditions as the springtime stream flow was about average as the majority of smolts out-migrated in 2017. Early marine survival for 2017 out-migrants will influence the bulk of the adult coho salmon returns in 2018 and the bulk of the Columbia River Chinook salmon returns in 2019.

For the central CCS, environmental conditions in freshwater, estuaries and the coastal ocean from spring 2016 to summer 2017 were notably different than those during the 2012–15 hot drought and 2014–15 marine heat wave and 2016 El Niño. Out-migration flows in the Sacramento River were exceptionally low in spring 2014, 2015, and 2016. They were so low that emergency measures were taken that included trucking hatchery juveniles to the Bay-Delta for release[29,30]. By contrast, flows were high in spring 2017. Sacramento River stream temperature in 2014–15 was exceptionally high and contributed to record-low egg-to-fry survival for Central Valley winter-run Chinook salmon (Martin et al. 2016), while from spring 2016–summer 2017 stream temperatures were much more favorable for salmon. The improved freshwater conditions in 2016–17 likely resulted in improved salmon growth and condition at the time of out-migration to sea, thus improving their likelihood of survival (Woodson et al. 2013). Unfortunately,

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[28] http://usa.oceana.org/sites/default/files/maccall_et_al_anch_biomass_remains_low_2012-2015.pdf

[29] https://www.fws.gov/sfbaydelta/fisheries/salmon_trucking_and_release.htm

[30] https://www.fws.gov/sfbaydelta/documents/2015_coleman_salmon_trucking_nr.pdf

at-sea observations of juvenile salmon from California are unavailable. However, ocean ecosystem indicators of early salmon survival have been developed for central California (Wells et al. 2016, 2017). For both spring 2016 and spring 2017 conditions in the Gulf of the Farallons were near normal. Likewise, the forage community supporting central California salmon in spring 2016 and 2017 was not significantly below average. Similarly, seabird diets on the Farallon Islands in springs 2016 and 2017, which have been linked to early salmon survival (fig. 42; Wells et al. 2017), were typical (i.e., largely rockfishes and northern anchovy) and did not demonstrate a significant increase in predation on juvenile salmon. Considering this suite of indicators based on ecosystem conditions related to key freshwater and marine salmon life stages, a Central Valley fall-run Chinook salmon fishery impact like that observed in 2007–08 (or 2016–17) appears to be unlikely for 2018–19.

Seabird reproductive success and foraging behavior reflect forage communities regionally

The reproductive success of seabirds in 2016 (the most current year available) was negatively related to latitude. In addition, there existed a northward shift in the prey field. In the northern California Current, at Yaquina Head and Castle Rock breeding colonies, some of the lowest reproductive success rates on record were observed. Nest failures were attributed to a combination of bottom-up and top-down forces. At Castle Rock, most chicks died of starvation, whereas at Yaquina Head, most nests failed due to predation by bald eagles seeking alternate prey. At-sea surveys of distribution and abundance of seabirds in northern California Current indicate that the reproductive success in 2017 may also be catastrophic. Namely, extremely low abundances were observed for migrant and central-place feeders. The few occurrences of common murre and sooty shearwaters observed at sea in 2017 in the north were at the locations where rare concentrations of forage (i.e., northern anchovy) were also observed, indicating close coupling of available forage patches and seabird aggregations. Preliminary observations at Castle Rock and Yaquina Head in 2017 also corroborate this speculation of catastrophic reproductive failure; fledging success of murres was 0%, with most chicks starving in the first few days, and it is likely Brandt's cormorants at Castle Rock also failed to produce young.

South of Cape Mendocino seabird reproductive success was generally below average. However, the significant decreases noted in the north were unapparent. Examination of the prey field (fig. 27) and the diets (fig. 42) indicate that the availability of primary forage taxa to seabirds remained average although the overall community was diverse (Santora et al. 2017a) and, in 2016, atypical (fig. 29) likely resulting from the inclusion of offshore forage taxa on the shelf during the El Niño event.

In 2017 the divergent characteristics of the environment, forage assemblages, and seabird abundances were apparent. For example, in southern California where forage communities were typical and the surface waters only slightly warmer than typical, the abundance of sooty shearwater was far above average. Yet, in the northern CCS abundance of sooty shearwater was the lowest in the observed record; observations also confirm lower abundance in central California (but within 1 SD of mean)[31]. As sooty shearwater migrate northward along the California Current, it is possible that they stopped their migration in southern California to benefit from persistent trophic hot spots there (Santora et al. 2017b) rather than continue to the northern California Current to lower quality forage assemblages. In addition, forage may have been reduced on their main foraging grounds in the Alaskan Bering-Sea Aleutian Islands ecosystem. Although unconfirmed, the seabirds in the south may be responding to the increased abundance of northern anchovy in the Southern California Bight (figs. 21, 27, 31); in the northern surveys the increased density of anchovy was isolated to the region of Columbia River mouth where the few seabirds were observed (fig. 21).

California sea lions show signs of recovery since the unusual mortality event

Increases in the abundance of northern anchovy coincided with improved condition of pups in 2016. Namely, lipid-rich northern anchovy and Pacific hake occurred in greater frequencies in the nursing female diet compared to the diet during the unusual mortality event that was dominated by juvenile rockfishes and market squid, which have low caloric value. The superior diet of nursing females translated into better condition of their dependent pups. If foraging conditions continue to improve, pup condition and survival should also improve. However, pup production will likely remain suppressed for several more years because the smaller cohorts produced from the unusual mortality event will comprise a greater proportion of the breeding population.

Whales shifting to nearshore habitats

There was a shoreward shift in the distribution of baleen whales. This distributional shift is quite apparent in central and southern California where there has been a recent, dramatic increase in whale entanglements with fixed fishing gears[32]. Humpback whales likely forag-

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[31] https://static1.squarespace.com/static/56a6b01dd8af105db2511b83/t/59cd54e09f7456363177e20d/1506628834109/FI_Report_NMFS_JRES_2017.pdf

[32] http://www.westcoast.fisheries.noaa.gov/mediacenter/WCR%202016%20Whale%20Entanglements_3-26-17_Final.pdf

ing on the increased nearshore abundances of northern anchovy are the most at risk[33]. However, gray (*Eschrichtius robustus*) and blue (*Balaenoptera musculus*) whales have also been increasingly encountering gear. While yet to be determined, there are several potential causes for the increased interactions such as increased population abundance and increased predation on anchovy as an alternative prey. For example, humpback whales shift their foraging patterns between nearshore and offshore prey communities (Ainley and Hyrenbach 2010), focusing their foraging effort on krill during cool, productive years and on northern anchovy more inshore during years of delayed upwelling or lower productivity (Fleming et al. 2016).

Human dimensions

The ecosystem conditions observed during the last few years demonstrate the impacts that ocean variability and unanticipated environmental-food web-fishery interactions can have on coastal communities. For example, the marine heat wave was associated with coast-wide blooms of *Pseudo-nitzschia australis* that resulted in fishery season delays and closures (e.g., Dungeness crab, razor clams, rock crab) (Leising et al. 2015, McClatchie et al. 2016, McCabe et al. 2016). Further, due to increased SST, adult northern anchovy and associated spawning aggregations nearshore became more common in the northern CCS. Presumably, while foraging on the nearshore schools of northern anchovy, a dramatic increase of human-predator interactions occurred, including whale entanglements with fixed fishing gears that were deployed in greater density during the condensed and delayed Dungeness crab season of 2016. The risk for these interactions may increase if northern anchovy, a nearshore resident, continues to increase in abundance, or if there are further delays (or increased late-season effort) in Dungeness crab and other fixed-gear fisheries. Beyond fishery impacts, there could also be a need for alteration of coastal shipping lanes in trophic hot spots to reduce ship strikes on whales (Redfern et al. 2013, Santora et al 2017b).

The low catches of juvenile salmon in the northern CCS survey may indicate a significant impact on the fisheries and dependent communities. Salmon represent an example of how unanticipated, negative synergistic interactions can emerge. Salmon recruitment is reliant on ocean and river conditions the salmon experience early in life. In 2007–08, Central Valley Chinook salmon fishery collapsed requiring a Congressional appropriation of $170,000,000 from disaster relief (Lindley et al. 2009). The proximate cause of that collapse was poor ocean conditions in central California during 2005–06 (Lindley et al. 2009). Specifically, the anomalous ocean conditions and low productivity reduced forage availability that motivated a switch by predators, such as common murre, from preferred prey to adult northern anchovy nearshore. This switch in foraging behavior led to increased incidental predation on juvenile salmon as they outmigrated to sea. This interaction between ocean environment whereby bottom-up influences in the ocean environment led to top-down impacts on salmon was largely responsible for the extreme mortality of juvenile salmon and the subsequent collapse of the fishery (Wells et al. 2017). Similar mechanisms have been argued for salmon in the northern California Current (Pearcy 1992; Emmett et al. 2006; Phillips et al. 2017) and could be a contributor to the low juvenile salmon numbers observed in the northern survey during 2017. As predator populations increase, especially for potential salmon predators such as common murre (Wells et al. 2017) and humpback whales (Chenoweth et al. 2017), the impacts of poor ocean conditions on salmon may be magnified. One potential mitigation effort is to improve freshwater conditions such that more, larger, and an increased portfolio of salmon life histories contribute to increased diversity in the smolt out-migration to sea (e.g., more diversity in ocean-entry timing, smolt size, or migration routes) (Carlson and Satterthwaite 2011; Woodson et al. 2013). However, improvements to inland habitat would not be disconnected from interactions with agriculture, hydropower, and flood control. Regardless, the ocean is not always the primary determinant of recruitment. The "hot drought" affecting California from 2012–15 is considered a dominant driver of the lowest escapement to Central Valley since the collapse of the fishery a decade ago (PFMC 2017a). In such cases, recruitment of salmon to the fishery may rely on mitigation of mortality in freshwater by exceptional ocean ecosystem productivity where smaller (Woodson et al. 2013) and ill-timed (Satterthwaite et al. 2014) out-migrants have a better opportunity of survival.

Ultimately, given the highly variable CCS ecosystem and its variety of interacting components, management actions aimed at sustainability in living marine resources and resource systems will require an ecosystem-based fishery management approach. Efforts to better understand ecosystem interactions and the cascading consequences of anomalous ocean conditions will be critical to the ability of managers to respond effectively to variable ocean conditions while avoiding undesirable impacts to fisheries, protected resources and coastal communities.

Extending the empirical results of these and similar integrative programs to quantitative models capable of evaluating competing management scenarios may be a key aspect of affective management in a variable environment.

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[33] http://www.sfchronicle.com/bayarea/article/Why-eye-popping-whale-shows-off-the-California-12172489.php

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