

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.

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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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S.E. Moore.¹ National Oceanic and Atmospheric Administration, Alaska Fisheries Science Center, National Marine Mammal Laboratory, 7600 Sand Point Way N.E., Seattle, WA 98115, U.S.A.

J.M. Grebmeier. Department of Ecology and Evolutionary Biology, University of Tennessee, 569 Dabney Hall, Knoxville, TN 37996, U.S.A.

J.R. Davies. National Oceanic and Atmospheric Administration, Northwest Fisheries Science Center, Conservation Biology Division, 2725 Montlake Boulevard E., Seattle, WA 98112, U.S.A.

¹Corresponding author (e-mail: Sue.Moore@noaa.gov).

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).

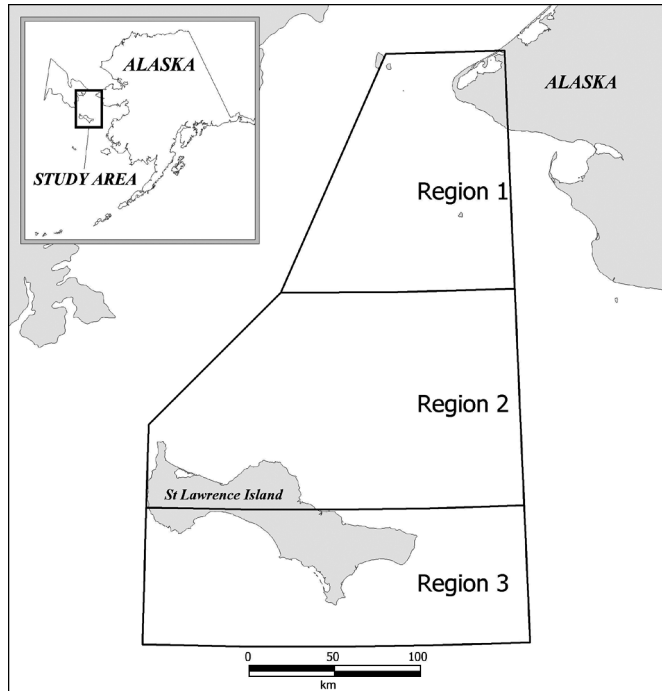
The survey area was post stratified to three regions (Fig. 1), focused on the Chirikov Basin (regions 1 and 2) and waters south and east of St. Lawrence Island (region 3). Whale distribution was plotted and an index of relative abundance calculated as the number of whales seen per survey kilometre. This 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 m² 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			Grand total
	1	2	3	
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/m² and numerous stations showing 20–30 g C/m² (>10 000 individuals/m²). Conversely, biomass at most stations in regions 2 and 3 ranged from 10 to 20 g C/m², with the highest measure at 20–30 g C/m².

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						Total	
	1		2		3		Number	Sighting rate
	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/m² 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/m²) 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.

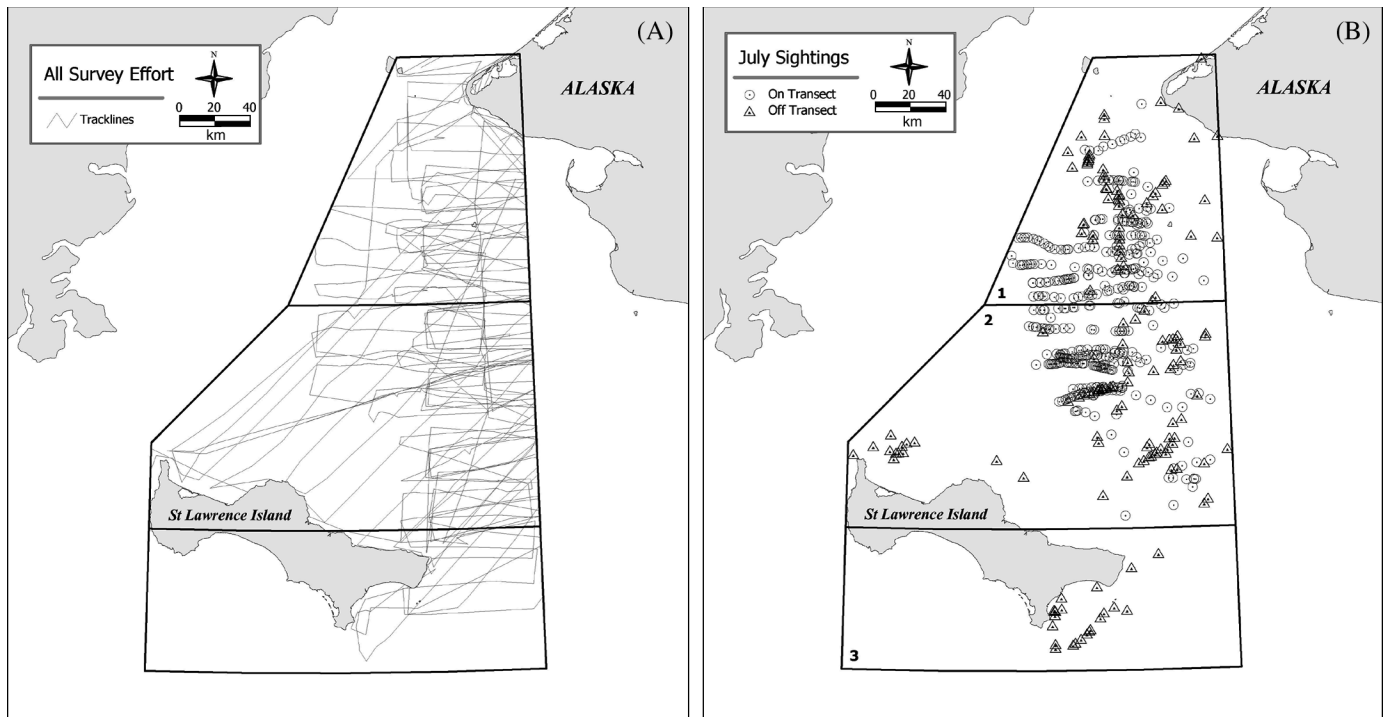
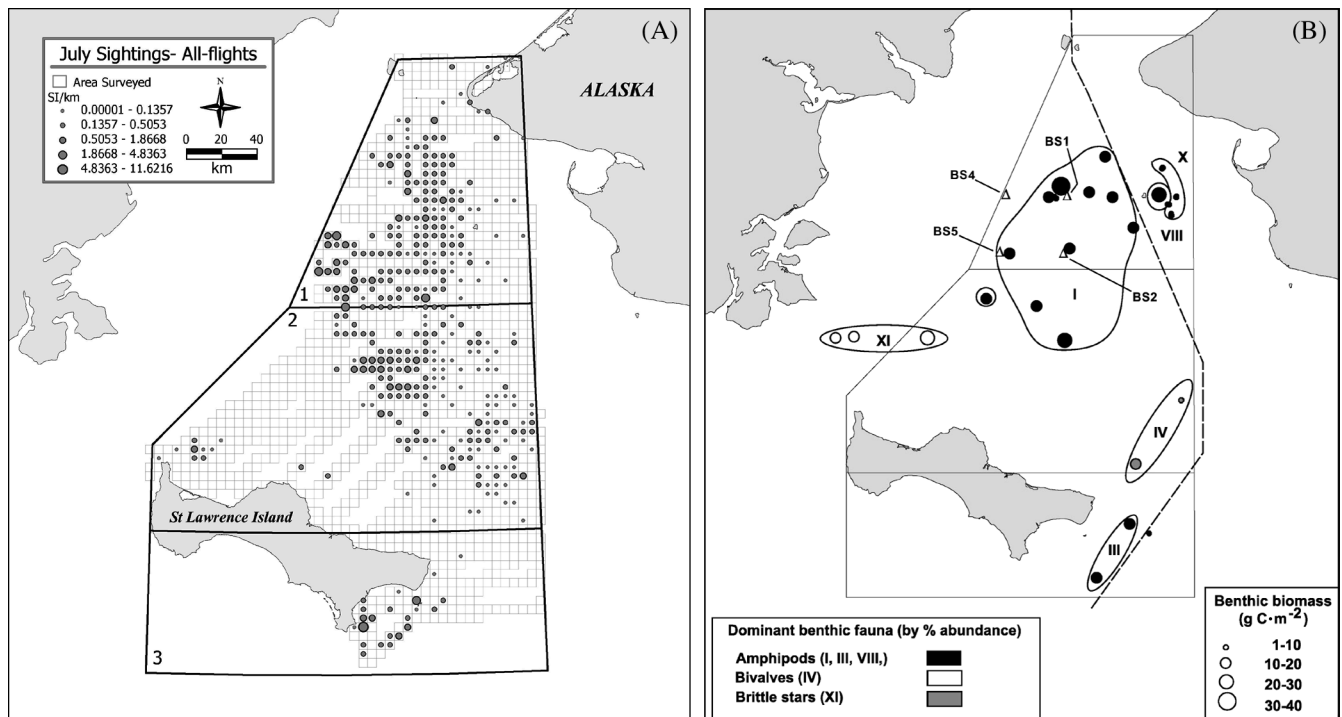


Fig. 3. Sighting rates (no. of whales/km) for gray whales, in 5-km blocks, for July 1981–1985 (A) and the distribution of benthic faunal communities in 1984–1986 (B); modified from Grebmeier et al. (1989). In B, note locations of the benthic stations (BS1, BS2, BS4, BS5), for which time series are shown in Fig. 4.



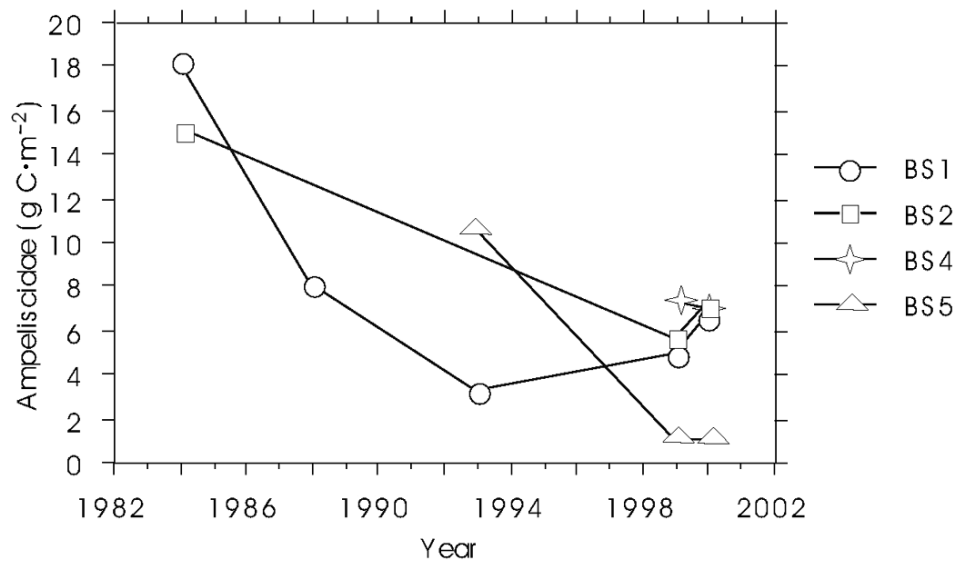
habitat (i.e., the 1980s) with a time when this habitat may be less than optimal. Regional indices of relative abundance show that gray whales were dynamic in their movements through the Chirikov Basin from May through November. In some years, the highest regional indices occurred in autumn,

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).

Benthic faunal group	Water type	Mean abundance (no./m ²)	Ampeliscidae (%)	Mean biomass (g C/m ²)	Sediment composition (%) ^a					
					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	—	—	—	—	—	—

^aSC, 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 sen-

sitive 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.

Period	Region		
	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.

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