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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

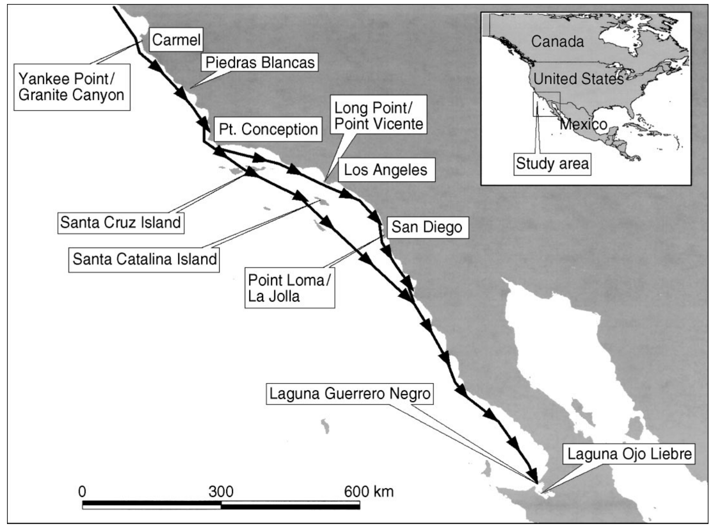

FIG. 1. Map of gray whale census sites located along the California, USA, coast and place names mentioned in the text. Arrows indicate the migration path of southbound whales.

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

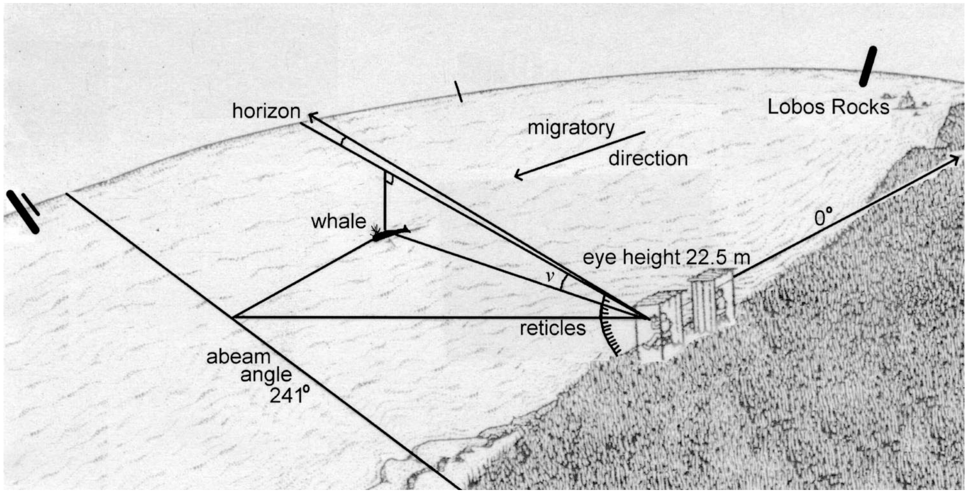

FIG. 2. Diagram of observer field of view at the Granite Canyon station near Carmel, California, where paired observers independently record whale sightings. Vertical angle to a sighting (v) is established relative to the horizon by using reticles in the binoculars (the horizon is 0.15° below true horizontal). 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-

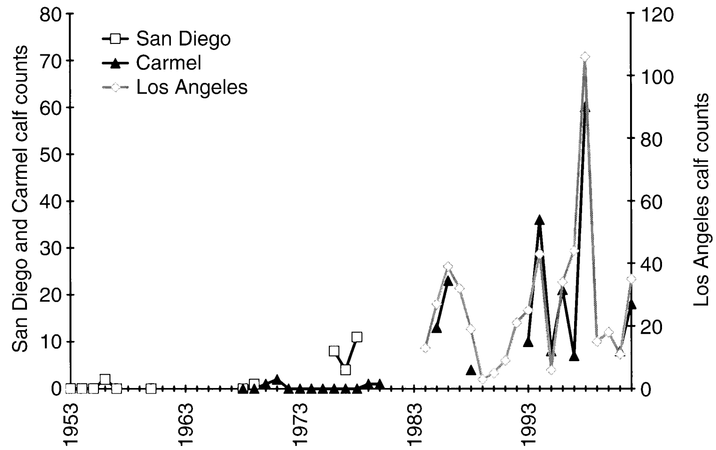

FIG. 4. Counts of gray whale calves observed during the southbound migration at counting stations near San Diego, Los Angeles, and Carmel, California.

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

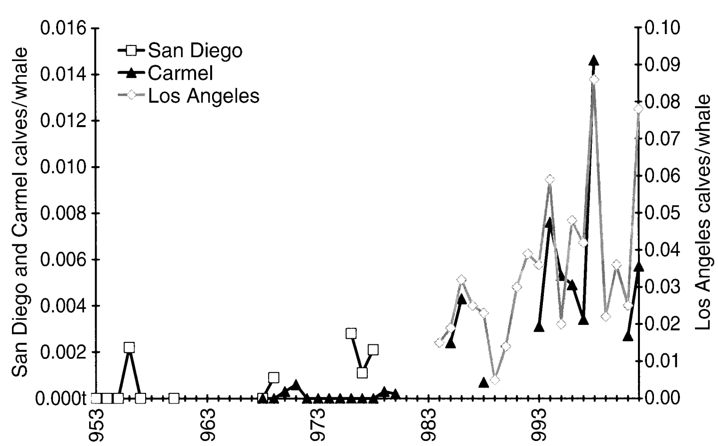

FIG. 5. Proportion of gray whale calves (calves/whale) observed during the southbound migration at counting stations near San Diego, Los Angeles (ACS), and Carmel, California.

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

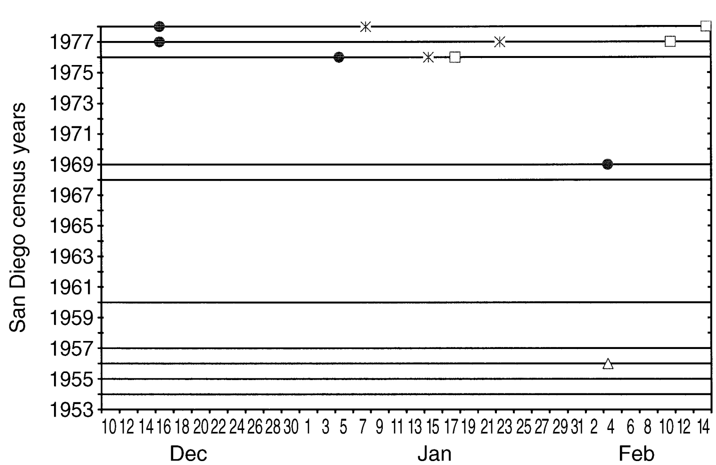

FIG. 6. Seasonal distribution of gray whale calf sightings at the southernmost counting stations near San Diego, California. Solid circles indicate first sighting of the season, stars (⁎) indicate median date, and open squares indicate last sighting. The open triangle in February 1956 represents two calf sightings for which observation dates were not provided (see Gilmore 1960).

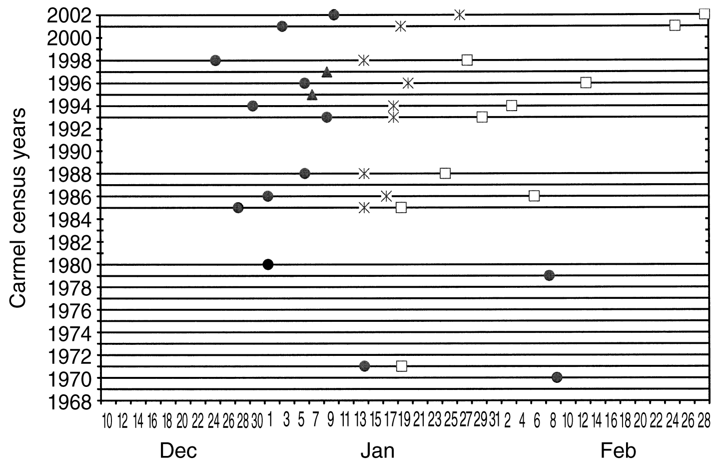

FIG. 7. Seasonal distribution of gray whale calf sightings at the northernmost counting stations near Carmel, California. Solid circles indicate first sighting of the season, stars (⚹) indicate median date, and open squares indicate last sighting. Solid triangles in 1995 and 1997 indicate first sighting 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

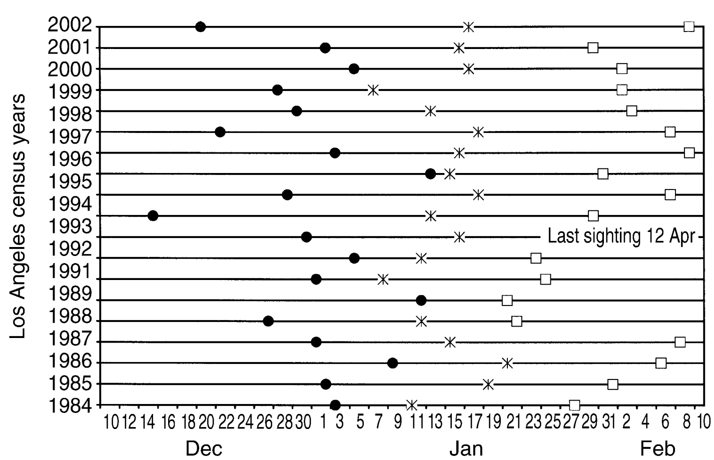

FIG. 8. Seasonal distribution of calf sightings at the ACS counting stations near Los Angeles, California. Solid circles indicate first sightng of the season, stars (⚹) indicate median date, and open squares indicate last sighting.

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

[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.

Distance	Aerial survey†		Shore-based standard watch‡	
	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.

Date	Location	Disposition	Distance from Mexico lagoons km	Distance from Mexico lagoons 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 km	d	Source
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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Literature Cited

Baird, R. W., P. J. Stacey, D. A. Duffus, and K. M. Langelier. 2002. An evaluation of gray whale (*Eschrichtius robustus*) mortality incidental to fishing operations in British Columbia, Canada. Journal of Cetacean Research and Management **4**(3):289–296.

Bodkin, J. L., and R. J. Jameson. 1991. Patterns of seabird and marine mammal carcass deposition along the central California coast, 1980–1986. Canadian Journal of Zoology **69**:1149–1155.

Buckland, S. T., and J. M. Breiwick. 2002. Estimated trends in abundance of eastern Pacific gray whales from shore counts (1967/68 to 1995/96). Journal of Cetacean Research and Management **4**(1):41–48.

Coyle, K. O., and R. C. Highsmith. 1994. Benthic amphipod communities in the northern Bering Sea: analysis of potential structuring mechanisms. Marine Ecology Progress Series **107**:233–244.

Dohl, T. P., R. C. Guess, M. L. Duman, and R. C. Helm. 1983. Cetaceans of central and northern California, 1980–1983: status, abundance, and distribution. Outer Continental shelf (OCS) Study MMS 84–0045. Minerals Management Service, Los Angeles, California, USA.

Dohl, T. P., K. S. Norris, R. C. Guess, J. D. Bryantand, and M. W. Honing. 1981. Summary of marine mammal and seabird surveys of the Southern California Bight area, 1975–78. Volume III. Investigators' Report, Part II, Cetacea of the Southern California Bight.

Dunham, J. S., and S. A. Duffus. 2001. Foraging patterns of gray whales in central Clayoquot Sound, British Columbia, Canada. Marine Ecology Progress Series **223**:299–310.

Findlay, L. T., and O. Vidal. 2002. Gray whale (*Eschrichtius robustus*) at calving sites in the Gulf of California, Mexico. Journal of Cetacean Research and Management **4**(1):27–40.

Fleischer, L. A., and T. Schweder. 2002. Gray whales on their winter grounds in Baja California Sur, Mexico (1980–1998). Paper SC/54/BRG11 presented to the IWC Scientific Committee, April 2002. International Whaling Commission, Impington, Cambridge, UK.

Fuchs, A. R., and M. J. Fields. 1999. Parturition, nonhuman mammals. Pages 69–82 *in* E. Knobil and J. D. Neill, editors. Encyclopedia of reproduction. Volume 3. Academic Press, San Diego, California, USA.

Gardner, S. C., and S. Chávez-Rosales. 2000. Changes in the relative abundance and distribution of gray whales (*Eschrichtius robustus*) in Magdalena Bay, Mexico during an El Niño event. Marine Mammal Science **16**(4):728–738.

Gilmore, R. M. 1955. Census of the California gray whale: winter 1954–55. U.S. Department of the Interior, U.S. Fish and Wildlife Service. National Marine Mammal Laboratory, National Marine Fisheries Service (NMFS), National Oceanic and Atmospheric Administration (NOAA), Seattle, Washington, USA.

Gilmore, R. M. 1960. A census of the California gray whale. U.S. Fish and Wildlife Service Special Scientific Report (Fisheries) **342**:1–30.

Hare, S. R., and N. J. Mantua. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. Progress in oceanography **47**(2–4):103–145.

Henderson, D. A. 1972. Men and whales at Scammon's Lagoon. Dawson's Book Shop, Los Angeles, California, USA.

Henderson, D. A. 1984. Nineteenth century gray whaling: grounds, catches and kills, practices and depletion of the whale population. Pages 159–186 *in* M. L. Jones, S. L. Swartz, and S. Leatherwood, editors. The gray whale, *Eschrichtius robustus*. Academic Press, Orlando, Florida, USA.

Heyning, J. E., and M. E. Dahlheim. 1990. Strandings and incidental takes of gray whales. Paper SC/A90/G2 presented to the IWC Scientific Committee Special Meeting on the Assessment of Gray Whales, Seattle, April 1990. International Whaling Commission, Impington, Cambridge, UK.

Heyning, J. E., and T. D. Lewis. 1990. Entanglements of baleen whales in fishing gear off southern California. Report of the International Whaling Commission **40**:427–31.

Highsmith, R. C., and K. O. Coyle. 1992. Productivity of arctic amphipods relative to gray whale energy requirements. Marine Ecology Progress Series **83**:141–150.

Hobbs, R. C., and D. J. Rugh. 1999. The abundance of gray whales in the 1997/98 southbound migration in the eastern North Pacific. Paper SC/51/AS10 presented to the IWC Scientific Committee, May 1999. International Whaling Commission, Impington, Cambridge, UK.

Hubbs, C. L. 1959. Natural history of the gray whale. Pages 313–316 *in* H. R. Hewer and N. D. Riley, editors. Proceedings of the XVth International Congress of Zoology, 16–23 July 1958. William Cowles, London, UK.

Hubbs, C. L. 1960. The marine vertebrates of the outer coast. Symposium: the biogeography of Baja California and adjacent seas. Part II. Marine biotas. Systematic Zoology **9**: 134–147.

Jones, M. L., and S. L. Swartz. 1987*a*. Radio-telemetric study and aerial census of gray whales during their southward migration in the Channel Islands National Marine Sanctuary, January 1986. Contract number 50-ABNF-6-00067, U.S. Department of Commerce, NOAA, Sanctuary Programs Division, Washington, D.C., USA.

Jones, M. L., and S. L. Swartz. 1987*b*. Distribution, numbers, and behavior of gray whales in the Channel Islands National Marine Sanctuary during the southward migration, January 1987. Prepared for U.S. Department of Commerce, NOAA, Sanctuary Programs Division, Washington, D.C., USA.

Jones, M. L., and S. L. Swartz. 1990. Abundance and distribution of gray whales in the Channel Islands National Marine Sanctuary during the southward migration in January 1986 and 1987. Paper SC/A90/G17 presented to the IWC Scientific Committee Special Meeting on the Assessment of Gray Whales, Seattle, April 1990. International Whaling Commission, Impington, Cambridge, UK.

Laake, J. L., D. J. Rugh, J. A. Lerczak, and S. T. Buckland. 1994. Preliminary estimates of population size of gray whales from 1992/93 and 1993/94 shore-based surveys. Paper SC/46/AS7 presented to the IWC Scientific Committee, May 1994. International Whaling Commission, Impington, Cambridge, UK.

Leatherwood, S., and D. W. Beach. 1975. A California gray whale calf (*Eschrichtius robustus*) born outside the calving lagoons. Southern California Academy of Sciences Bulletin **74**(1):45–46.

Le Boeuf, B. J., M. H. Pérez-Cortés, R. J. Urbán, B. R. Mate, and U. F. Ollervides. 2000. High gray whale mortality and low recruitment in 1999: potential causes and implications. Journal of Cetacean Research and Management **2**(2):85–99.

Lerczak, J. A., and R. C. Hobbs. 1998. Calculating sighting distances from angular readings during shipboard, aerial, and shore-based marine mammal surveys. Marine Mammal Science **14**(3):590–599.

Malme, C. I., P. R. Miles, C. W. Clark, P. Tyack, and J. E. Bird. 1984. Investigations of the potential effects of underwater noise from petroleum industry activities on migrating gray whale behavior. Phase II: January 1984 migration. Report No. 5586, Contract number 14-12-0001-29033. U.S. Department of Interior, Minerals Management Service, Anchorage, Alaska, by Bolt Beranek and Newman, Incorporated, Cambridge, Massachusetts, USA.

Miller, A. J., D. R. Cayan, T. P. Barnett, N. E. Graham, and J. M. Oberhuber. 1994. Interdecadal variability of the Pacific Ocean: model response to observed heat flux and wind stress anomalies. Climate Dynamic **9**:287–302.

Miller, R. V., J. H. Johnson, and N. V. Doroshenko. 1985. Gray whales (*Eschrichtius robustus*) in the western Chukchi and East Siberian Seas. Arctic **38**(1):58–60.

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.

Moore, S. E., R. J. Urbán, W. L. Perryman, F. Gulland, M. H. Perez-Cortes, P. R. Wade, L. Rojas-Bracho, and T. Rowles. 2001. Are gray whales hitting 'K' hard? Marine Mammal Science **17**(4):954–958.

Nerini, M. 1984. A review of gray whale feeding ecology. Pages 423–450 *in* M. L. Jones, S. L. Swartz, and S. Leatherwood, editors. The gray whale, *Eschrichtius robustus*. Academic Press, Orlando, Florida, USA.

Niebauer, H. J. 1998. Variability in Bering Sea ice cover as affected by a ''regime shift'' in the north Pacific in the period 1947–96. Journal of Geophysical Research **103**(C12):27, 717–27, 737.

Niebauer, H. J. 1999. The 1997–98 El Niño in the Bering Sea as compared with previous ENSO events and the ''regime shift'' of the late 1970s. Proceedings of the 1998 Science Board Symposium on the Impacts of the 1997/98 El Niño Event on the North Pacific Ocean and its Marginal Seas. North Pacific Marine Science Organization (PICES) Scientific Report No. 10:87–89.

Norman, S. A., M. M. Muto, D. J. Rugh, and S. E. Moore. 2000. Gray whale strandings in 1999 and a review of stranding records in 1995–1998. Paper SC/52/AS5 submitted to the IWC Scientific Committee, June 2000. International Whaling Commission, Impington, Cambridge, UK.

Norris, K. S., R. M. Goodman, B. Villa-Ramirez, and L. J. Hobbs. 1977. Behavior of the California gray whale (*Eschrichtius robustus*) in southern Baja California, Mexico. Fishery Bulletin (U.S.) **75**(1):159–172.

Perryman, W. L., M. A. Donahue, P. C. Perkins, and S. B. Reilly. 2002. Gray whale calf production 1994–2000: Are observed fluctuations related to changes in seasonal ice cover? Marine Mammal Science **18**(1):121–144.

Perryman, W. L., and M. S. Lynn. 2002. Evaluation of nutritive condition and reproductive status of migrating gray whales (*Eschrichtius robustus*) based on analysis of photogrammetric data. Journal of Cetacean Research and Management **4**(2):155–164.

Reilly, S. B. 1984. Assessing gray whale abundance: a review. Pages 203–223 *in* M. L. Jones, S. L. Swartz, and S. Leatherwood, editors. The gray whale, *Eschrichtius robustus*. Academic Press, Orlando, Florida, USA.

Reilly, S. B., D. W. Rice, and A. A. Wolman. 1983. Population assessment of the gray whale, *Eschrichtius robustus*, from California shore censuses, 1967–80. Fishery Bulletin (U.S.) **81**(2):267–281.

Rice, D. W. 1965. Offshore southward migration of gray whales off southern California. Journal of Mammalogy **46**(3):500–501.

Rice, D. W. 1981. Status of the eastern Pacific (California) stock of the gray whale. Pages 181–187 *in* FAO Advisory Committee on Marine Mammal Research Working Party on Marine Mammals. FAO Fisheries Series (5). Volume III. Mammals in the Seas. General papers and large cetaceans. Rome, Italy.

Rice, D. W., and A. A. Wolman. 1971. The life history and ecology of the gray whale (*Eschrichtius robustus*). American Society of Mammalogists Special Publication Number **3**:viii–142.

Rice, D. W., A. A. Wolman, and H. W. Braham. 1984. The gray whale, *Eschrichtius robustus*. Marine Fisheries Review **46**(4):7–14.

Rice, D. W., A. A. Wolman, D. E. Withrow, and L. A. Fleischer. 1981. Gray whales on the winter grounds in Baja California. Report of the International Whaling Commission **31**:477–493.

Rugh, D. J., J. M. Breiwick, M. E. Dahlheim, and G. C. Boucher. 1993. A comparison of independent, concurrent sighting records from a shore-based count of gray whales. Wildlife Society Bulletin **21**(4):427–437.

Rugh, D. J., J. M. Breiwick, R. C. Hobbs, and J. A. Lerczak. 2002. A preliminary estimate of abundance of the eastern North Pacific stock of gray whales in 2001 and 2002. Paper SC/54/BRG6 presented to the IWC Scientific Committee, April 2002. International Whaling Commission, Impington, Cambridge, UK.

Rugh, D., R. Ferrero, and M. Dahlheim. 1990. Inter-observer count discrepancies in a shore-based census of gray whales (*Eschrichtius robustus*). Marine Mammal Science **6**(2): 109–120.

Rugh, D., and M. A. Fraker. 1981. Gray whale (*Eschrichtius robustus*) sightings in the eastern Beaufort Sea. Arctic **34**: 186–187.

Rugh, D. J., J. A. Lerczak, R. C. Hobbs, J. M. Waite, and J. L. Laake. 2002. Evaluation of high-powered binoculars to detect inter-year changes in offshore distribution of gray whales. Journal of Cetacean Research and Management **4**(1):57–61.

Rugh, D. J., K. E. W. Shelden, and A. Schulman-Janiger. 2001. Timing of the southbound migration of gray whales. Journal of Cetacean Research and Management **3**(1):31–39.

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.

Scammon, C. M. 1874. The marine mammals of the northwestern coast of North America, described and illustrated: together with an account of the American whale-fishery. John H. Carmany, San Francisco, California, USA. [Reprinted in 1968 by Dover Publications, New York, New York, USA.]

Shelden, K. E. W., and J. L. Laake. 2002. Comparison of the offshore distribution of southbound migrating gray whales from aerial survey data collected off Granite Canyon, California, 1979–96. Journal of Cetacean Research and Management **4**(1):53–56.

Shelden, K. E. W., D. J. Rugh, J. L. Laake, J. M. Waite, P. J. Gearin, and T. R. Wahl. 2000. Winter observations of cetaceans off the northern Washington coast. Northwestern Naturalist **81**:54–59.

Stoker, S. W. 1990. Distribution and carrying capacity of gray whale food resources in the northern Bering and Chukchi Seas. Paper SC/A90/G13 presented to the IWC Scientific

Committee, April 1990. International Whaling Commission, Impington, Cambridge, UK.

Sumich, J. L. 1983. Swimming velocities, breathing patterns, and estimated costs of locomotion in migrating gray whales, *Eschrichtius robustus*. Canadian Journal of Zoology **61**(3):647–652.

Sumich, J. L., and J. T. Harvey. 1986. Juvenile mortality in gray whales (*Eschrichtius robustus*). Journal of Mammalogy **67**(1):179–182.

Sund, P. N. 1975. Evidence of feeding during migration and of an early birth of the California gray whale (*Eschrichtius robustus*). Journal of Mammalogy **56**(1):265–266.

Sund, P. N., and J. L. O'Connor. 1974. Aerial observations of gray whales during 1973. Marine Fisheries Review **36**(4):51–52.

Swan, J. G. 1870. The Indians of Cape Flattery, at the entrance to the Strait of Fuca, Washington Territory. Smithsonian Contributions to Knowledge **16**:1–108.

Swartz, S. L. 1986. Gray whale migratory, social and breeding behavior. Report of the International Whaling Commission, Special Issue **8**:207–229.

Swartz, S. L., and M. L. Jones. 1983. Gray whale (*Eschrichtius robustus*) calf production and mortality in the winter range. Report of the International Whaling Commission **33**: 503–507.

Swartz, S. L., M. L. Jones, J. Goodyear, D. E. Withrow, and R. V. Miller. 1987. Radio-telemetric studies of gray whale migration along the California coast: a preliminary comparison of day and night migration rates. Report of the International Whaling Commission **37**:295–299.

Urbán, R., J., A. Gómez-Gallardo, U.,and S. Ludwig. 2003*a*. Abundance and mortality of gray whales at Laguna San Ignacio, Mexico, during the 1997–98 El Nino and the 1998–99 La Nina. Geofisica International **42**(3):439–446.

Urbán, R., J., L. Rojas-Bracho, H. Pérez-Cortés, A. Gómez-Gallardo, S. L. Swartz, S. Ludwig, and R. L. Brownell, Jr. 2003*b*. A review of gray whales (*Eschrichtius robustus*) on their winter grounds in Mexican waters. Journal of Cetacean Research and Management **5**(3):281–295.

Wade, P. R. 2002. A Bayesian stock assessment of the eastern Pacific gray whale using abundance and harvest data from 1967–1996. Journal of Cetacean Research and Management **4**(1):85–98.

Withrow, D. E. 1990. Aerial surveys of gray whales off the central California coast during the 1987/88 southbound migration. Paper SC/A90/G3 presented to the IWC Scientific Committee Special Meeting on the Assessment of Gray Whales, Seattle, April 1990. International Whaling Commission, Impington, Cambridge, UK.

Withrow, D. E., R. C. Hobbs, and K. E. W. Shelden. 1993. Offshore distribution of gray whales along the central California coast during the 1992–93 southbound migration. Paper SC/45/AS3 submitted to the IWC scientific committee, April 1993. International Whaling Commission, Impington, Cambridge, UK.

Withrow, D. E., J. L. Laake, and K. E. W. Shelden. 1994. Offshore distribution of gray whales along the central California coast during the 1993–94 southbound migration. Paper SC/46/AS8 submitted to the IWC scientific committee, May 1994. International Whaling Commission, Impington, Cambridge, UK.