High gray whale mortality and low recruitment in 1999: potential causes and implications

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ABSTRACT

This paper documents the high incidence of gray whale deaths in 1999 and presents the hypothesis that some of the whales were starving. Predictions from this hypothesis are tested using data on the frequency and distribution of strandings, the sex and age composition of strandings, estimates of recruitment and physiological condition, and observations of foraging during migration. The data come from multiple sources. The mortality count of 274 gray whales in 1999 was twice as high as in any previous year dating back to 1985. Dead whales were widely distributed along the migratory route, with the majority observed on the northward migration from the Mexican breeding lagoons to Alaska. Most mortalities in Mexico and California were adults and immatures, rather than the usual calves and yearlings. The majority of dead adults in Mexico, California and the Oregon/Washington region were females. Many dead whales were emaciated. Calf production was lower than in the previous six years. Aberrancies in timing and location of migration, as well as foraging on pelagic prey, were observed. These results, and an even higher stranding rate in the Mexican breeding lagoons in 2000, are consistent with the hypothesis that the whales were undernourished. It is argued that the most likely cause of this condition was a decline in the biomass of their principal prey, the benthic amphipods in the Bering and Chukchi Seas over the last decade, due in part to the combined effects of increasing sea surface temperatures and increased predation from the growing population of gray whales themselves. A significant decline in amphipod density could have long-term effects on the future growth and stability of the gray whale population because amphipods recover slowly given their low fecundity and long generation times. Annual monitoring of the status of the amphipods in the Bering and Chukchi Seas, and the effect of *inter alia* sea surface temperature on their biomass, is vital for understanding fluctuations in gray whale mortality and numbers, and the extent to which they are dependent on this food resource.

KEYWORDS: GRAY WHALE; PREDATION; PACIFIC OCEAN; BERING SEA; EL NIÑO; FEEDING GROUNDS; FOOD/PREY; HEALTH; STRANDINGS; NUTRITION; MORTALITY RATE; RECRUITMENT RATE

INTRODUCTION

Numerous gray whales (*Eschrichtius robustus)* from the eastern North Pacific population stranded or were beach-cast in 1999. Reports emanated from the breeding lagoons in Baja California Sur, Mexico, as well as along the migratory route from California, Oregon, Washington, British Columbia and Alaska. Public concern was heightened by extensive newspaper and television coverage of these deaths (e.g. CNN, BBC News, Reuters and Associated Press) that suggested a significant die-off. Speculation on the cause of death was rife, and suggestions included concentrated brine discharges from the salt company in Laguna Ojo de Liebre, poison dye used by drug smugglers, pollution from mining operations and natural causes. Marine mammalogists and administrators at various institutions dealing with marine mammals in Mexico and the United States were flooded with inquiries.

This paper reviews the available information on gray whale strandings from Mexico to Alaska and presents a general hypothesis related to feeding (the 'starvation hypothesis') to explain the high mortality and other unusual aspects of gray whale behaviour and demographics in 1999. The data come from multiple sources: our own, and that of others from stranding networks; preliminary reports; and personal communications. A summary is provided of deaths in and around the breeding lagoons in the winter breeding season from December 1998 to spring (April-May) 1999, and along the migratory route in 1999. Where possible, the spatial distribution, sex and age composition of the dead whales are characterised and compared with previous years. This paper summarises reports on gray whale condition and recruitment, and describes whales seen in unusual places, at unusual times and feeding on uncommon prey. A discussion of the potential causes of the high mortality incidence is provided.

Gray whale migration pattern

Gray whales migrate annually along the west coast of North America (Fig. 1), feeding principally in the Bering, Chukchi and western Beaufort Seas between late May and October and breeding in Baja California, Mexico, between December and March (Swartz, 1986b). In general, gray whales feed in northern waters and then return to southern waters where they fast during the reproductive period while surviving on stored energy reserves (Rice and Wolman, 1971). Whales killed or harvested in the Bering and Chukchi Seas usually have full stomachs (e.g. Bogoslovskaya *et al.*, 1982; Blokhin and Vladimirov, 1983; Blokhin, 1984), while whales landed during migration rarely display evidence of recent feeding (Rice and Wolman, 1971). In addition, stomachs of whales taken from the winter breeding grounds, or those that strand ashore, are usually devoid of food (Scammon, 1874; Sanchez Pacheco, 1998). There are, however, a few reports of whales feeding in the summering lagoons (Villa *et al.*, 1982) and during their northbound migration (Nerini, 1984).

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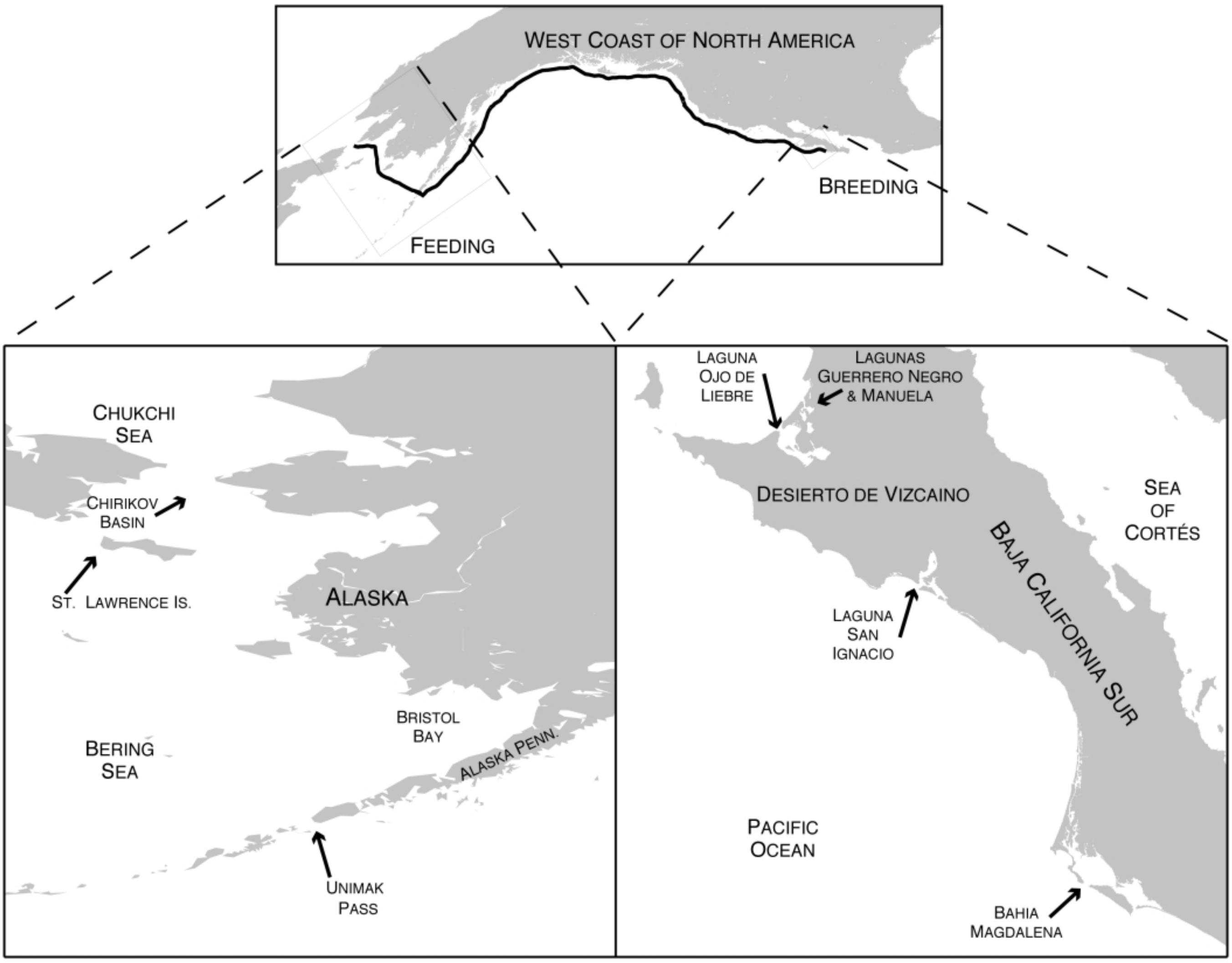

Fig. 1. Migration route of gray whales along the west coast of North America from the summer feeding grounds in the Bering and Chukchi Seas to the winter breeding lagoons in Baja California, Mexico.

Moreover, some whales feed throughout the summer in Canada, Oregon and Washington (Sumich and Gilmore, 1977; Murison *et al.*, 1984; Darling *et al.*, 1998). They have not been seen feeding during the southbound migration from censusing stations in California where most counts during migration have been conducted.

The winter breeding range extends approximately from Point Conception (in southern California) to Cabo San Lucas (Baja California, Mexico), including small numbers in the lower Gulf of California and near Yavaros, a small area off the Mexican mainland (Jones and Swartz, 1984). In February, when occupation of the principal lagoons is beginning to peak, whales can still be observed passing southbound off Monterey, whilst some are already moving north.

Gray whale prey and foraging locations

Gray whales are unique among large cetaceans in that they feed primarily on infaunal benthic organisms, especially gammaridean amphipods, but they also exhibit surface skimming and engulfing behaviour for prey such as ghost shrimp (*Callianassa* sp.), mycid shrimp (*Holmesimysis* sp.) and pelagic crab (*Pleuroncodes* sp.) in the water column (Rice and Wolman, 1971; Darling, 1977; Swartz and Jones, 1981; Murison *et al.*, 1984; Nerini, 1984; Oliver *et al.*, 1984; Würsig *et al.*, 1984; Darling *et al.*, 1998). Whales feeding in southern waters usually feed pelagically while those in the north feed benthically (Nerini, 1984; Darling, *et al.*, 1998).

Their principal prey, amphipods, are sedentary tube-dwelling suspension feeders that live benthically in mud and sand. Gray whales feed on eight species of Ampeliscidae, varying in size from 10-33mm (Coyle and Highsmith, 1994), by scooping up a mouthful of the substrate and straining out the amphipods through the baleen (Oliver *et al.*, 1984; Oliver and Slattery, 1985). The largest and dominant amphipod species in the Bering and Chukchi Seas, *Ampelisca macrocephala*, exceeds 30mm in length and can reach concentrations of over 10,000 individuals per square meter (Feder, 1981). Benthic amphipods are of paramount importance to gray whales, with 1-2 species comprising 90% of their food (e.g. Zenkovich, 1934; 1937; Tomilin, 1957; Nerini, 1984; Highsmith and Coyle, 1992; Coyle and Highsmith, 1994). Gray whales undertake the long migration to feed in locations where these animals are in sufficient abundance to enable approximately an entire year's energy requirement to be harvested in about six months (Highsmith and Coyle, 1992).

Gray whales concentrate much of their feeding in the shallow waters (<50m deep) of the Chirikov Basin (Braham, 1984; see Figs 1 and 2), an area of about $40{,}000\text{km}^2$ that is one of the most productive benthic communities in the world (Grebmeier *et al.*, 1988; Highsmith and Coyle, 1990). *Ampelisca macrocephala* accounts for 70% of the amphipod biomass and production in this area.

BACKGROUND TO THE 'STARVATION HYPOTHESIS'

Starvation hypothesis

The hypothesis considered here is that gray whales were undernourished in 1999. If fewer of their principal prey, the benthic ampeliscid amphipods of the Bering and Chukchi Seas, were available in summer 1998, the whales would have had difficulty acquiring sufficient resources to sustain themselves during the 7,000km southward migration to the breeding lagoons, the winter 1999 breeding season and the return migration to the Bering and Chukchi Seas in spring and summer 1999 (Fig. 1). The hypothesis examined is thus that the whales undertook the long two-way migration (including reproductive activities at the southern end) with insufficient reserves and that inanition and low body reserves were major elements leading to mortalities, decreased reproduction and other observed aberrant behaviour in 1999. Inadequate nutrition and body reserves may be especially problematic for gestating or nursing adult females as they require additional resources (e.g. Rice and Wolman, 1971; Lockyer, 1984; Swartz, 1986b); this would be reflected in increased mortality and reduced calf production (Brambell, 1948; Stein and Susser, 1975). It is one factor being considered in examination of the low reproductive rates of the North Atlantic right whale (IWC, 2000).

Whilst this is clearly not the only possible hypothesis to explain increased mortality, we believe it is one of the most plausible, as explained in the discussion.

Predictions from the starvation hypothesis

If some gray whales were starving, the following predictions should be supported by data collected in 1999:

(1) a higher stranding rate in 1999 relative to previous years;
(2) wide distribution of strandings throughout the range;
(3) more dead adults relative to previous years with a bias in mortality towards adult females;
(4) poor body condition of living and stranded whales;
(5) low calf production relative to previous years (female mammals reduced to a low nutritional plane are likely to abort or fail to wean their calves);
(6) more extensive pelagic feeding during migration than usual; and
(7) aberrant timing or location of whales during migratory movements and during the breeding season, or simply failure to migrate north to Alaska, i.e. over-summering along the migratory route.

Perspective on the study

Population and life history studies of most great whale species are exceedingly difficult because they range widely in the open ocean. The coastal migration pattern of gray whales, throughout which most of them pass within a few kilometres of the coast (Rice and Wolman, 1971; Braham, 1984; Darling, 1984; Herzing and Mate, 1984; Rugh, 1984; Perryman *et al.*, 1998) and where breeding principally occurs in relatively small and accessible lagoons (Swartz, 1986a), differentiates them from other large whales. It is these life history traits that permit the study of changes in mortality and reproduction from year to year. While studies of this kind on gray whales do not approach the level of sophistication of those conducted on many pinnipeds and terrestrial mammals, they offer many advantages over studies of other large whales.

MATERIALS AND METHODS

Observations and strandings in Mexico

This paper summarises the results of periodic searches for dead gray whales by several investigators in and around the lagoons of Baja California Sur, Mexico (Fig. 1), under the aegis of Centro Regional de Investigación Pesquera-La Paz (CRIP-La Paz), del Instituto Nacional de la Pesca (INP) and Universidad Autónoma de Baja California Sur. All searches were conducted during the winter when the whales frequent the area for parturition, nursing and mating. Every accessible carcass was sexed and the total length was measured in a straight line from the tip of the rostrum to the fluke notch. Dead whales were classified according to the stranding condition code of Geraci and Lounsbury (1993) and the total length-age categories of Sanchez Pacheco (1998). Identifying marks were noted or a piece of coloured rope was tied to the animal's left flipper to prevent duplicate counts. The majority of carcasses were not accessible and were simply recorded as dead gray whales. No autopsies for cause of death were conducted.

The perimeter of the breeding lagoons was scanned for dead whales during census surveys conducted from mid-January to April. At Ojo de Liebre lagoon, the beaches were surveyed twice weekly and specific sites were visited after receiving reports of dead whales from salt company workers in Guerrero Negro, from fishermen or from whale watching tour operators (Aarón Eslimán, pers. comm.).

In San Ignacio lagoon, searches for beach-cast whales were made during 28 complete censuses of whale abundance and distribution conducted from 8 February to 28 March, during the years 1996-1999. The surveys followed a basic line-transect design and were conducted by small boat using the geographical lagoon divisions and methodology described by Jones and Swartz (1984) and Urbán *et al.* (1997).

The method at Magdalena Bay involved searching for dead whales during line transect censuses conducted from a 7m boat over 63 days between January and April 1999. Local fishermen and whalewatching boat operators also reported strandings. Seventeen of 18 stranded whales were sexed and measured.

Levels of effort to record dead whales have been variable since such work began in 1978 (e.g. Jones and Swartz, 1984; Sanchez Pacheco, 1998). Search effort in 1999 was probably greater than in previous years due to the increased effort covering the coastline outside the breeding lagoons. Two aerial surveys were conducted outside the lagoons; the first on 26 February covered only the Pacific or western side of the Magdalena Bay area from 25°18'N south to 24°44'N, and the second on 10 March covered most of the Pacific coast of Baja California Sur, from the mouth of Guerrero Negro lagoon (28°07'N', 114°07'W) south to 'El Conejo' (24°04'N, 111°00'W). Reports of dead gray whales from other parts of Mexico were also received.

Observations and strandings from California to Alaska

Reports of dead whales along the migratory route north of Mexico to Alaska covered the period from early January to 15 October 1999. Summaries were obtained of stranded gray whales along the migratory route from regional stranding coordinators in California, Washington and Oregon, British

Columbia, Canada and Alaska. Generally, stranding networks are coordinated as follows. Whale strandings are reported to the strandings network coordinator who notifies a cetologist in the area who visits the site, determines the sex of the animal, takes standard measurements from which age category is determined, describes the moribund animal and possibly takes tissue samples for later analysis. In some cases, an autopsy may be performed. Alternatively, the cetologist may obtain data from the stranded whale first, and then relays this information to the strandings coordinator. In vast, remote areas with few people, such as Alaska, reporting of stranded whales is less thorough than in highly populated areas such as parts of California and Washington. Indeed, most observations in Alaska were opportunistic and associated with aerial surveys flown for reasons other than to count gray whales; under such circumstances it was rarely possible to measure or sex a dead whale.

For animals where a total length was obtained, whales were grouped into the following age categories, based on Rice and Wolman (1971) and Sanchez Pacheco (1998): calves (3.4-8.1m); yearlings (8.2-9.5m); immatures (9.6-11m); and adults (> 11.0m). The calf category encompasses a wider range of lengths than that of Sanchez Pacheco (1998), whose observations in the lagoons were restricted to the winter shortly after the calves were born; in this paper calf deaths are reported along the migratory route until the autumn, by which time their length has increased substantially.

For whales sighted at unusual times and unusual places, personal observations, observations of colleagues, fishermen and others along the migratory corridor were used. Reports from various individuals who responded to a request for information of this kind via the MARMAM (marine mammal) webserver on the internet were also included.

Sea surface temperatures in the Chirikov Basin

High sea surface temperatures (SSTs) affect gray whale foraging by causing a decline in amphipod biomass (Highsmith and Coyle, 1992; Coyle and Highsmith, 1994). Therefore, annual gray whale stranding rates were compared with annual mean SSTs in feeding areas. NOAA Pathfinder satellite measurements of SSTs sampled at three regions in the Chirikov Basin (A. Strong and M. Toscano, pers. comm.) were used to calculate mean SSTs for the years 1985-1999 (Fig. 2). The sample consisted of all SSTs obtained throughout the months of July and August. Sample size varied greatly from year-to-year depending on cloud cover, ranging from a low of six measurements in area three in 1989, to 23 measurements in area three in 1996. SSTs from all three areas were combined to yield mean SSTs per year in the Chirikov Basin ($n = 18$ in 1989, to 78 in 1996).

RESULTS

Number of deaths in 1999 compared to previous years

The total number of gray whales stranded between late December 1998 and 15 September 1999 was 274; this value was higher than any previous year. Fig. 3 provides gray whale stranding data dating back to 1985 for Baja California, Mexico and California, and 1990 for Oregon and Washington. Gray whale strandings peaked in 1999 in all three regions. The increase in strandings in 1999 over previous years was greatest in Mexico. The increase in mortality in 1999, compared with 1998, was also high in British Columbia, increasing from two to eight strandings, and in Alaska from five to 72 strandings. A secondary peak of strandings occurred during the early 1990s in Mexico and the Oregon-Washington region.

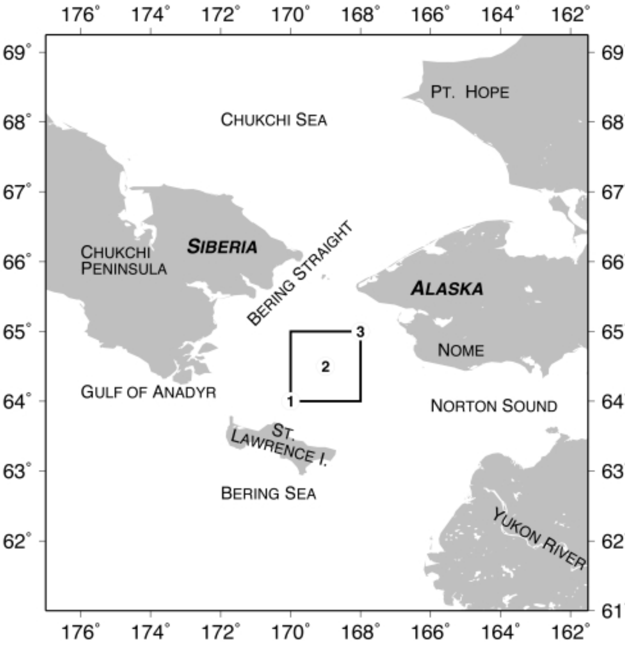

Fig. 2. Map showing sea surface temperature sampling locations in the Chirikov Basin of the Bering Sea.

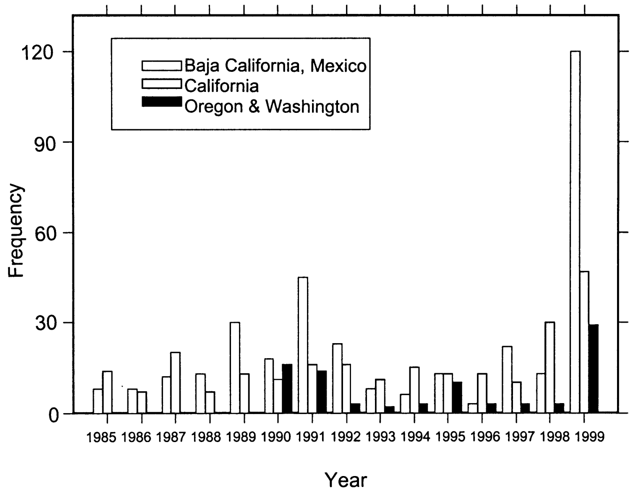

Fig. 3. Gray whale strandings in and around the breeding lagoons of Baja California, Mexico, and the coast of California from 1985-1999, and along the coasts of Oregon and Washington from 1990-1999.

Peak stranding years of gray whales (1991 and 1999), differed from the peak stranding years of other marine mammals from the California region (Fig. 4). Strandings of California sea lions (*Zalophus californianus*), northern elephant seals (*Mirounga angustirostris*) and harbour seals (*Phoca vitulina*), peaked in California in 1992 and 1998.

It is difficult to compare the incidence of whale deaths in Mexico in 1999 to previous years because of annual fluctuations in search effort. However, the relative mortality between years can be estimated by comparing one region for which there are good long-term baseline data. Sanchez Pacheco (1998) monitored stranded gray whales in Ojo de Liebre, Guerrero Negro and Manuela lagoons, as well as offshore of these lagoons, during the winter breeding seasons from 1984-1995. Representatives from the El Vizcaino Biosphere Reserve conducted counts in the same

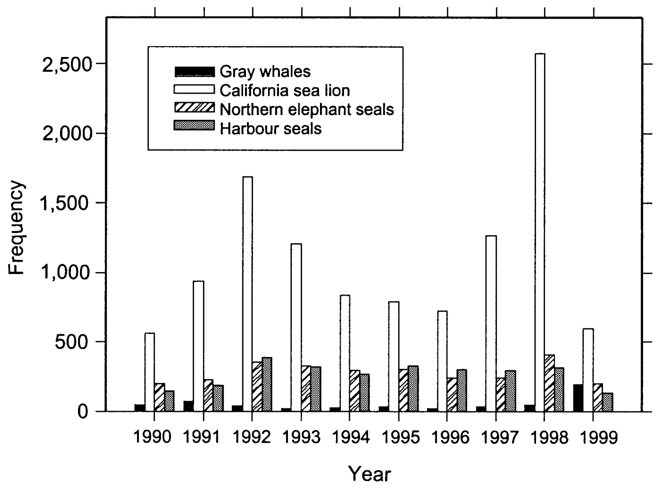

Fig. 4. Gray whale strandings from Mexico to Alaska in relation to strandings of pinniped species (California sea lions, *Zalophus californianus,* northern elephant seals, *Mirounga angustirostris,* and harbour seals, *Phoca vitulina*) along the coast of California during the years 1990-1999.

Table 1

Annual distribution of stranded gray whales in Ojo de Liebre, Guerrero Negro and Manuela lagoons and offshore of these lagoons during 1999 in relation to previous years. Data from 1984-95 are from Sanchez Pacheco (1998). Data from 1997 to 1999 were collected by HP.C. and Aarón Eslimán. na = not available.

Year	Calves (3.4-6.5m)	Yearlings (6.6-9.5m)	2+ years (>9.6m)	Totals
1984	4	3	3	10
1985	4	2	1	7
1986*	3	3	0	6
1987	7	3	1	11
1988	4	6	2	12
1989	7	8	6	21
1990	0	2	14	16
1991	6	2	37	45
1992	7	0	15	22
1993	8	0	0	8
1994*	4	0	1	5
1995	7	4	2	13
1997	na	na	na	14
1998	na	na	na	7
1999	5	10	14	71**

*Incomplete. **Includes 42 unmeasured whales.

area from 1996-1999. This is the most important of the three breeding/calving lagoons for gray whales, in some years accounting for approximately 70% of the calves counted in the Baja California lagoons. There were 71 deaths in this region in 1999 (Table 1). This is more than the number recorded in any other year since 1984, the closest other year being 1991 when 45 were recorded. In both 1991 and 1999, the majority of measured, stranded whales were over 9.6m long, i.e. adults and immatures more than two years old, whereas in most other years the most frequent mortalities were among calves and yearlings.

Spatial and temporal distribution of deaths

The dead whales were distributed throughout the migratory range: 120 in Mexico, 43 in California, 31 in Oregon and Washington, 8 in British Columbia and 72 in Alaska. A total of 44% of the whales were found in Mexico during the breeding season between late December 1998 and late spring 1999. They were widely distributed in all of the breeding lagoons, as well as along the coast of the southern half of the Baja California peninsula, in the Sea of Cortés and along the Sonoran coast (Table 2). As in many previous years, no deaths were recorded in the northern state of Baja California. Only two stranded whales were recorded in this area during the winter in the years 1975-1999 (Pérez-Cortés *et al.*, 1999; Rugh *et al.*, 1999a). The majority of strandings were in the breeding lagoons that accommodate the largest number of whales, such as Ojo de Liebre and its vicinity. Strandings were observed throughout the season (December to early April) and one stranding occurred in May. Peak mortalities (85.8% of the total) occurred during February and March.

A total of 154 dead whales was observed north of Mexico along the migratory route to Alaska between 1 January and 15 September 1999. They were widely distributed along the coasts in each region. For example, in California, strandings were reported from San Diego in the south to near the

Table 2

Gray whale strandings in Baja California, Mexico, in 1999.

	Age composition				Sex			
Location	Adults	Immatures	Calves	Unknown	Males	Females	Unknown	Totals
Vizcaino Bay	9	7	3	9	4	10	14	28
Ojo de Liebre Lagoon	4	4	2	30	4	11	25	40
Guerrero Negro Lagoon	-	-	-	3	-	1	2	3
San Ignacio Lagoon	3	-	2	0	1	4	0	5
San Ignacio Outer Coast	-	-	-	5	-	-	5	5
Magdalena Bay								
Outer coast area	-	-	-	11	-	-	11	11
Almejas Bay	-	-	-	1	-	-	1	1
Magdalena Bay	10	4	1	2	2	14	1	17
López Mateos Lagoon	0	1	1	0	1	1	0	2
Gulf of California								
La Paz Bay	0	1	0	0	0	1	0	1
Sonoran coast[1]	-	-	-	6	-	-	6	6
Banderas Bay	1	0	0	0	0	1	0	1
Totals	27	17	9	67	12	43	65	120
Percent	22.5	14.2	7.5	55.8	10	35.8	54.2	-
Percent (excluding unknowns)	50.9	32.1	17	-	21.8	78.2	-	-

[1] J.P. Gallo, pers. comm.

California-Oregon border. Strandings were most frequent near the largest embayments, San Diego and San Francisco. Similarly, in the Oregon-Washington region, strandings were widespread, but as in most years the majority (90.3%) were along the coast of Washington, particularly in Puget Sound.

The majority of the beach-cast whales in Alaska were on the north and south sides at the base of the Alaska Peninsula and in Bristol Bay (Fig. 1).

Stranding dates reveal that the majority of mortalities in California, Oregon and Washington occurred during the northward migration to Alaska. For the California region, 83.7% of the strandings were between 16 March and 20 September, with peak strandings (46.5%) in April and May. For Oregon and Washington, 93% of the strandings were between 5 April and 4 October, with a peak (54.8%) in April and May. It is not clear whether the few strandings in January and February in this region occurred during the southward or northward migration. All reported deaths in Alaska occurred between 26 May and 25 August; the temporal patterning of strandings in Alaska is a gross estimate because observations were sporadic and opportunistic.

Age and sex composition of stranded whales

Of the 53 stranded whales in Mexico that were measured, 51% were adults (Table 2). Calves made up only 17% of the measured sample. Of 61 carcasses where sex could be determined, the majority (78%) was female. Out of 26 sexed adults, 92% (24) was female.

The majority of the stranded whales in California (51.1%) was composed of adults and immatures over 9.5m long (Table 3). The seven adults for which sex could be determined were females. In Oregon and Washington, 33.3% of the stranded whales were adults and immatures; the majority of strandings (66.7%) were calves and yearlings. Seven of eight adults whose sex was determined were females. All adult strandings occurred between 30 January and 10 May. The majority of the yearling strandings (70.6%) were between 21 May and 26 July. Only one carcass was measured in Alaska, an adult 12m long. Another carcass was estimated at 9-12m long.

Table 3

Sex and age composition of stranded gray whales in 1999 from the California and the Oregon/Washington regions.

Age class	California			Oregon/Washington		
	Number stranded	Sex		Number stranded	Sex	
		Males	Females		Males	Females
Adults	10	0	7	8	1	7
Immatures	10	2	2	1	1	0
Yearlings	5	1	0	9	5	3
Calves	12	5	2	9	3	2
Unknown	6			4		
Totals	43			31		

Body condition

In California, most of the stranded whales in 1999 were reported as undernourished with thin blubber and low levels of oil (J. Cordaro, pers. comm.). Few animals, however, were necropsied or were measured for blubber thickness. F. Gulland (pers. comm.), veterinarian at the Marine Mammal Center, conducted detailed necropsies of two immature males that were stranded in San Francisco Bay. Both whales were described as severely emaciated. Lateral blubber thickness was 7cm in one whale and 8cm in the other, lower than the 8.0-17.0cm range found for northward migrating immature males (Rice and Wolman, 1971). The girth at the axilla of one whale was only 289cm; this measurement was not obtained for the other whale.

Blubber thickness in seven of eight stranded whales sampled in the Oregon/Washington region (B. Norberg, pers. comm.) was in the lower range of samples collected by Rice and Wolman (1971) during the years 1959-1969 (Table 4). For adult females, the largest sampled group ($n = 3$), the mean blubber thickness (9.6cm) was at least 25% below the mean of all previously sampled groups, including immature whales of both sexes. Mean fat content of blubber samples from four whales was extremely low (7.1%), suggesting very low energy reserves (P.S. Ross, pers. comm.).

Aerial photographs of southbound gray whales indicate that the whales were thinner relative to their length in 1999 than in 1997 and 1998 (Perryman *et al.*, 1999).

Four of the dead whales were entangled in fishing nets which may have caused their death. Documented entanglements in Alaska included two whales in 1998 and two whales in 1999.

Calf production

A monitoring programme which began in 1978 recorded the lowest number of mothers with calves in San Ignacio lagoon during winter 1999. Only 45 mothers with calves were counted in early March 1999 (the usual time for the maximum number of mothers with calves). The mean number of mother and calves counted during the period 1978-1982 was 113 (Jones and Swartz, 1984; 1986; Jones *et al.*, 1994). Similarly, the highest single count in mid-February 1999 was of only 17 mothers with calves. In contrast, mothers with calves in mid-February numbered 92 in 1996, 126 in 1997 and 52 in 1998. These low numbers may be due, in part, to a shift in the distribution of whales from the northern lagoons to Magdalena Bay in 1999 (see following section). The maximum number of cows with calves recorded during the 1999 season in the area of Lopez Mateos, the northern sector of Magdalena Bay, was 41, 3.4 times greater than the 12 reported in 1998, but only half the number observed in 1997 (83).

The number of calves counted in the nearshore waters passing Point Vicente, near Los Angeles, California, was the lowest since the 1990/91 season (A. Schulman-Janiger, pers. comm.); counts were significantly lower in 1999 than in the

Table 4

Blubber thickness of gray whales stranded in the Oregon/Washington region in 1999 (B. Nordberg, pers. comm.) compared to the blubber thickness of whales collected in California in 1959-69 by Rice and Wolman (1971).

Age category/ direction	California, 1959-69			Oregon/Washington, 1999		
	No.	Mean (cm)	Range (cm)	No.	Mean (cm)	Range (cm)
Immature males						
Northward	25	12.6	9.5-16.0	1	-	7.5-9.0
Adult males						
Northward	44	12.8	10.5-16.0	1	-	6.5-13.0
Immature females						
Southward	11	14.4	12.5-16.5	1	-	5.2-5.75
Northward	23	12.8	8.0-17.0	1	-	14
Adult females						

[redacted]

two previous years both during the southbound and northbound migrations (Table 5). There was more than an 80% decrease in calves counted both during southbound and northbound migrations. The percentage of calves to total whales migrating in both directions decreased by approximately 75%. The decrease in calves counted in 1999 was more precipitous than the decrease in total whales counted.

In addition, fewer pregnant females, estimated from aerial photographs, were observed in the 1999 aerial survey of southbound whales in California than in 1997 and 1998, suggesting that recruitment was low in 1999 (Perryman *et al.*, 1999).

At Piedras Blancas, California, the estimate of 400 northbound calves in 1999 was the lowest since counts began in 1994 (Perryman *et al.*, 1999). The 1994-98 estimates were 1,000, 601, 1,141, 1,439 and 1,316, respectively. Similarly, the calf production index (calf estimate/population size) of 1.6% in 1999 was the lowest for the last six years.

Aberrant timing, location or feeding of whales during migration and in the lagoons

There were numerous reports of gray whales observed in unusual places at unusual times, often feeding pelagically. This behaviour appeared to be far more common in 1999 than in previous years.

Southward migration

The beginning of the southbound migration past Yaquina Head lighthouse in Oregon was three weeks later in autumn 1998 than during the years 1978-1981 (Mate, 1999). Although the start of the migration was delayed, the peak was only one day later than the latest observed during 1979-1981. Rugh *et al.* (1999b) concluded that there was nothing unusual about the timing of the southbound migration in 1999 based on counts of whales passing near Granite Canyon, a shore station in central California, dating back to 1967.

Winter breeding season in Mexico

There was a more southerly distribution of gray whales during winter than usual in 1999. An unusually high concentration of gray whales was observed off the southern tip of Baja California. Water temperatures throughout Baja California were also lower than usual owing to La Niña conditions. A total of 350-400 gray whales was counted in Bahía Magdalena. This exceeds the total of 68 that was counted in winter 1998, and the average of 150 counted during previous winters. However, the total number of whales in the northern lagoons was lower than usual in 1999. For example, counts in San Ignacio lagoon in 1999 were 30% lower than in 1998, 36% lower than in 1997 and 22% lower than in 1996. The decline in mothers with calves was even greater; in 1999 there was a 67.3% decrease from 1998, an 86.5% decrease from 1997 and an 81.5% decrease from 1996.

On two occasions in winter 1999, one of us (FOU) saw gray whales skim feeding in Magdalena Bay. One whale fed in this way in the same area for three consecutive days. On another occasion, a group of at least 12 whales were observed skim feeding.

From November 1998 to February 1999, 8-12 gray whales were observed in Kino Bay, on the eastern side of the midriff area of the Sea of Cortez (T. Pfister, pers. comm.). In previous years, only one animal per year was seen in this area. The whales were mixed with fin whales (*Balaenoptera physalus*) feeding in shallow cold water (14-16°C) on euphausids. Gray whales were still in the area in mid-April, 1999. J.P. Gallo (pers. comm.) observed three gray whales feeding with fin whales on euphausids close to Guaymas in February 1999.

Northward migration

Typically, most gray whales have migrated north past southern California by May. In July 1999, two gray whales were observed in Bahía San Quintin, Mexico, about 300km south of the United States/Mexico border (G.S. Campbell, pers. comm.); the whales had been present for several weeks. From late April to early May, gray whales were observed lunge feeding at the surface on krill during coastal trips along the north side of the western Santa Barbara Channel in southern California (R. Hart, pers. comm.). Similar behaviour was observed from 18 May-10 June in the presence of humpbacks (*Megaptera novaeangliae*) and blue whales (*Balenoptera musculus*) along the north sides of Santa Rosa and Santa Cruz Islands, the southern side of the western Santa Barbara Channel (R. Hart and F. Benko, pers. comm.). Whale tour operators with 25 years of experience in this area had not previously recorded this type of feeding behaviour.

A gray whale was observed surface skimming off Pillar Point, California, in July 1999 (P. Folkens and T. Pusser, pers. comm.). Some 4-12 gray whales were observed at Point Reyes Headland in central California from May to mid-August; the whales were seen feeding at the mouth of Tomales Bay and in the bay itself (S. Allen, pers. comm.). There were also regular sightings of individuals and small groups in Drakes Bay throughout the summer into mid-August. N. Black (pers. comm.), while studying killer whales (*Orcinus orca*) in Monterey Bay, California, observed gray whales feeding on surface krill during many

Table 5

Total gray whales and calves censused in the nearshore waters of the Palos Verdes Peninsula, 8 miles north of Los Angeles Harbour, in southern California, during the years 1997 to 1999. Census dates for all years are from 1 Dec. - 15 May. Adapted from ACS/LA Point Vicente Gray Whale Census Project reports (A. Schulman-Janiger, project director): *http://www.acs-la.org/GWCensus.htm.*

					Calves					
		Total whales			Southbound			Northbound		
Year	Hours on station	Southbound	Northbound	Turnaround date*	Total	%	Peak no./day	Total	%	Peak no./day
1997	1,804	1,053	1,608	19 Feb.	44	4.2	6	222	13.8	18
1998	1,934	1,230	1,666	12 Feb.	106	8.6	10	174	10.4	17
1999	1,960	6,82	1,383	15 Feb.	15	2.2	2	34	2.5	3

*Date on which northbound whales exceed southbound whales.

days in April, May and June, 1999. She reports not having seen this behaviour occurring with such high frequency in 12 years of working at Monterey Bay.

J. Calambokidis (pers. comm.), who has monitored gray whale occurrence in Washington over several years, observed unusual gray whale feeding in several areas in spring and summer, 1999. Besides the group of seasonal 'resident' gray whales that return annually to Washington waters, he observed a large number of gray whales in several areas of Puget Sound where whales are not usually seen. In addition, a large concentration of over 100 gray whales was observed milling and apparently feeding in one area of the Washington coast in May. V.L. Kirkland (pers. comm.) observed four adult whales along with a mother and calf at the southeast end of Lopez Island in the San Juan Islands of Washington from late April through May 1999; this was the first time that gray whales were seen in this location.

In southeastern and south-central Alaska, there were numerous reports of gray whales appearing in, and remaining at, locations where they had not been seen before. The first gray whale ever seen in Ketchikan was sighted in June 1999; gray whales were also reported off Kodiak Island in late June, and a calf was observed near the Kenai Fjord, off Seward, Alaska, on 25 June (D. Russell, pers. comm.). A gray whale was observed near Sitka, Alaska, throughout April 1999 (*The Daily Sentinel*, April 27 1999), only the second time this has occurred in 15 years. W. Cunningham and S. Stanford (pers. comm.) observed an atypical group of 5-11 gray whales near Goddard Hot Spring, 21km south of Sitka, Alaska, on 23 May 1999; whales were still in the area in mid-September. Although the whales have been seen previously on the outer coast, they have never been seen this close to shore, inside the islands. There was an extensive ice pack in 1999 and the ice break-up was much later than usual for the inshore waters of the Bering Sea. Consequently, there was an unusual gathering of approximately 1,500 gray whales around Hagemeister Island to High Island, Togiak Bay and Nunavachuk Bay in May (J. Browning, pers. comm.). This number of gray whales has not been observed in this area for over five years.

Strandings in relation to SSTs on the foraging grounds and El Niño-Southern Oscillation (ENSO) conditions

Mean SSTs during July and August from three locations in the Chirikov Basin (Fig. 2) are shown for the period 1985-1999 in Fig. 5. Peak SSTs for each region across years are generally similar. Mean SSTs exceeded 6°C for nine of the 10 years between 1990 and 1999. This warm period followed a relatively cool period from 1987-1989, especially for regions two and three. The years 1985 and 1986 were relatively warm, especially in region three. SSTs above 10°C were recorded in six years in region three, being most frequent in 1985 (60% of samples) and 1991 (53% of samples). SSTs above 10°C were only observed in three years in the other two regions: 10% of samples in 1985, 14% in 1991 and 1% in 1998 for region two, and 8% of samples in 1991 and 11% in 1998 for region one.

In Fig. 6, the mean SSTs in July and August from each of the three regions sampled in the Chirikov Basin (Fig. 2) are combined and presented for comparison with the gray whale stranding rate for Mexico, California, Oregon and Washington, and a measure of the strength of ENSO, the Southern Oscillation Index (SOI), which is a standardised measure of the difference in atmospheric pressure between Tahiti in the South Pacific and Darwin in Australia (Trenberth and Hoar, 1996; Konnen *et al.*, 1998; K.T. Richmond, pers. comm.). The 1990s were a relatively long, warm period. Eight years in this decade had a mean SST above the mean (6.43±1.06°C) for the entire 15-year period. The correlation between stranding rate and mean SST in the Chirikov Basin is low (Pearson Product $r = 0.015$, $df = 13$, $P < 0.05$). Moreover, SSTs in the Chirikov Basin are not closely associated with the strength of ENSOs. The high stranding rate in 1991 is associated with a high mean SST in the Chirikov Basin and a strong El Niño. The high stranding rate in 1999 is not linked with an unusually high mean SST in the Chirikov Basin but follows seven years of higher mean SSTs in the Chirikov Basin than usual and lags behind the very strong ENSO of 1997 by two years.

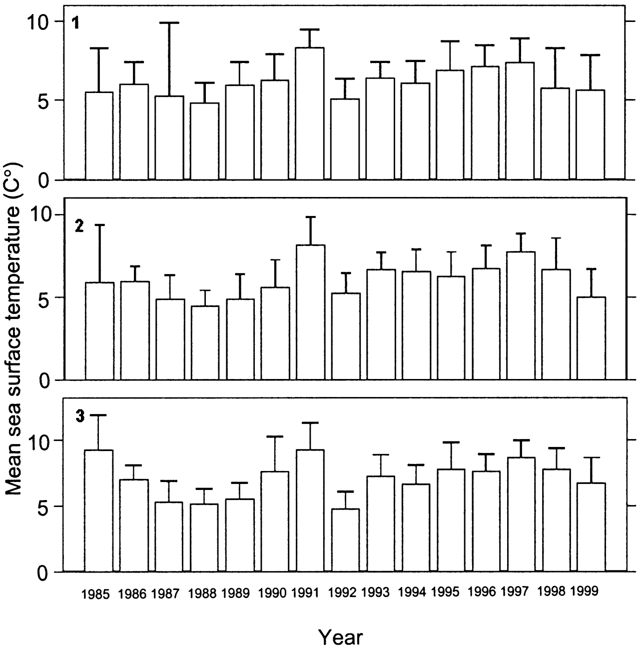

Fig. 5. Mean SST during July and August from three locations in the Chirikov Basin (see Fig. 2) during the period 1985-1999.

DISCUSSION

The results presented above are consistent with the general hypothesis that insufficient body reserves and malnourishment were a major cause of gray whale strandings in 1999. There is stronger support for some predictions than for others.

The number of strandings in 1999 was substantially higher than in previous years dating back to 1985. This was the case in winter in the Mexican breeding lagoons, as well as throughout spring and autumn along the migratory route. Strandings were widespread along the migratory route and a higher number of deaths occurred along the northward leg than in previous years. Whales lose between 11 and 29% of their body weight between the southward and northward migrations (Rice and Wolman, 1971), and thus more whales might be expected to exhaust their limited energy reserves on the return to the foraging grounds.

The sex and age composition of strandings in 1999 differed from previous years in that most of the deaths in the lagoons and in California during the northward migration, were adults and immatures. In the Oregon/Washington region, the proportion of adult deaths was higher than previous years (dating back to 1993). The only other years in which there were such a high number of adult and immature deaths were in the El Niño years, 1990 and 1991. Also in line

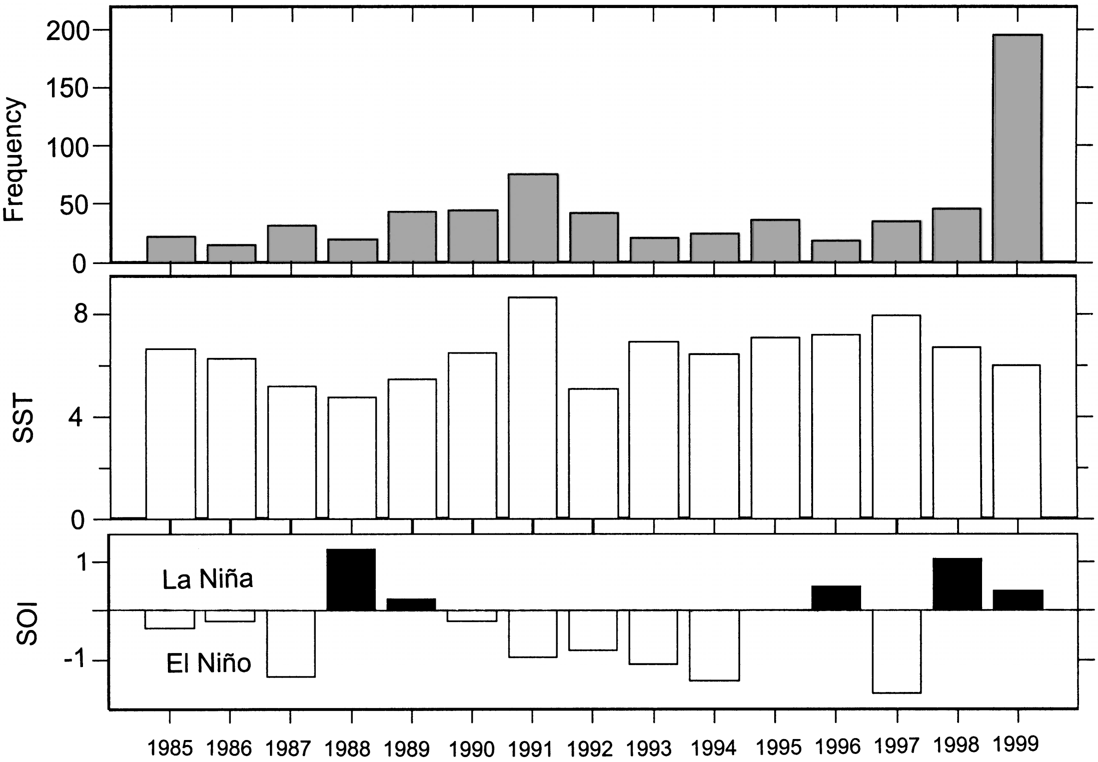

Fig. 6. Gray whale strandings in Mexico, California, Oregon and Washington (top) in relation to mean sea surface temperatures (SST) from all sampling regions in the Chirikov Basin region, combined (middle), and the Southern Oscillation Index (SOI), for the years 1983-1999 (bottom).

with the prediction, adult females stranded more frequently than adult males in 1999 both in the lagoons and along the coasts of California, Oregon and Washington. This contrasts with previous years in which mortality in and around the lagoons was highest among newborn calves, yearlings and juveniles, and adult deaths were rare (Jones and Swartz, 1984; Sanchez Pacheco, 1998). For example, 66 whale deaths in and outside Laguna Guerrero Negro during the winter breeding season of 1980, 1981 and 1982 were distributed as two adults, one yearling and 63 calves (Bryant *et al.*, 1984).

Little systematic data on body condition were obtained in 1999, so the prediction that the stranded whales were in poor body condition could not be thoroughly explored. However, the few observations obtained are consistent with the hypothesis. The thinner size of northbound whales in 1999 compared to the two previous years, as well as an unusually low calf production index (Perryman *et al.*, 1999), suggests poor physical condition. Subjective reports of the stranded whales from California, Oregon and Washington described them as being in poor condition. Estimates of blubber thickness in the Oregon/Washington region revealed less thickness in the animals sampled in 1999 than in a sample obtained during whaling operations in central California from 1959-1969 (Rice and Wolman, 1971). Although blubber thickness is less sensitive than girth as an index of nutritive condition (e.g. Rice and Wolman, 1971; Víkingsson *et al.*, 1988), it has long been used as an indicator of nutritive condition in large whales (Slijper, 1954).

As predicted, calf production was lower in 1999 than in previous years. Fewer calves were counted in the Mexican lagoons. The calf production index (calf estimate/population size) obtained from surveys of northbound calves from Point Piedras Blancas, California, was 1.6% in 1999, far lower than indices ranging from 2.6-6.5% in the previous five years (Perryman *et al.*, 1999). Similarly, from counts of northbound whales at Palos Verdes, California, far fewer calves were born or survived to age six months in 1999 than in the previous two years (A. Schulman-Janiger, pers. comm.). These data suggest that females had difficulty in either giving birth to a viable calf or nourishing the calf sufficiently long enough for it to survive and migrate.

There was moderate support for the predictions that the timing of migration (northbound only) would deviate from previous years, that whales would be observed in unusual locations and that there would be extensive pelagic foraging during migration. Although much of the data presented here are of necessity subjective and anecdotal, emanating from many observers with diverse backgrounds and experience, the most useful information came from observers who had monitored the same area for several years and were in a position to compare observations in 1999 with previous years. The distribution of whales in the lagoons was clearly biased to the southern lagoons in 1999, possibly owing to the colder waters associated with La Niña. Many whales were still migrating north in 1999 long after the northward migration had been completed in most years. In central and southern California, pelagic feeding appeared more prevalent and prolonged than in previous years. This seemed evident despite the fact that some groups of whales do this routinely throughout the year in some areas such as the west coast of Vancouver Island (Darling *et al.*, 1998). Pelagic feeding may have increased due to the abundance of krill in the offshore waters of California in 1999, owing in large part to the cold, productive waters associated with La Niña conditions. It is possible that more whales than usual may have not completed the migration to Alaskan waters in 1999, but rather over-summered along the way; however, there are insufficient data to address this. In summary, the albeit scattered observations are not inconsistent with the hypothesis that the whales were undernourished and took advantage of opportunities to feed on unusual prey species in several areas.

Strandings in 2000

Initial reports reveal that 207 gray whales stranded in the Mexican breeding lagoons and along the Pacific side of Baja California Sur, in the winter of 2000 (Pérez-Cortés M. *et al.*, 2000). This is the same area monitored in 1999 where 113 gray whales stranded, and thus, represents an 83% increase from a record stranding year to the following year. As in 1999, the majority of strandings were inside or near the breeding lagoons with relatively few found along the outer beaches. Once again, the majority (79%) of age-categorised strandings were adults. In contrast to 1999, however, adult male strandings were more frequent (67.5%) than adult female strandings, owing possibly to a rebound effect of the high stranding rate and low pregnancy rate of females in the previous year. Some whales were reported as being skinny and deformed, with a marked concave depression above the neck between the blowhole and the shoulders. These data suggest that the high stranding rate in 1999 was not just an unusual year, a random event, or a direct link to ENSO conditions in 1997-1998, but may be indicative of a continuing trend.

Search effort

One possible explanation for the high stranding rates of gray whales in 1999 and again in 2000 is that it merely reflects increased sightings effort. However, this does not appear likely. For example, search effort along the migratory route in California, Oregon and Washington has not varied systematically over the last decade, yet strandings in 1999 were substantially greater than previous years. Similarly, the search effort in and around Laguna Ojo de Liebre has been consistent since 1984 and yet more stranded whales were observed in 1999 than in previous years (Table 1). By contrast, searching effort for stranded whales was greater in Mexico in 1999 and 2000 than in most previous years, with the additional effort consisting of an aerial survey for stranded whales along the west coast of Baja California Sur between Laguna Ojo de Liebre and the Bahía Magdalena complex (Pérez-Cortés M. *et al.*, 2000). In neither year, however, did the added effort augment the total count significantly; most strandings were found inside and around the breeding lagoons which have been monitored in a similar manner for several years.

Gray whale prey base

The most likely explanation for the 'starvation hypothesis' is a significant decline in the principal prey of gray whales, i.e. the benthic amphipods in the Bering and Chukchi seas. Evidence for this is reviewed below.

Amphipod status and abundance

The abundance and biomass of the amphipod community in the central Chirikov Basin in the Bering Sea decreased by 30% from 1986-1988 (Highsmith and Coyle, 1992). This decline was due mainly to reduced densities of the larger-sized individuals of *A. macrocephala*. Benthic sampling studies southwest of St Lawrence Island and the Chirikov Basin indicate that a significant decline in productivity and a change in the dominant benthic fauna occurred in the 1990s (Grebmeier and Dunton, 2000). These data reveal more than a 50% decrease in benthic biomass from summer 1990 to 1993-1994 (from over 45gC/m^2 to about 20gC/m^2), a decrease that continued through to 1998 and 1999. This suggests that the prime foraging habitat of gray whales was less optimal in the 1990s than in the 1980s. Coincident with this decline in biomass are indications that the benthic community structure has been changing in the region since the late 1980s (Serenko and Koltun, 1992).

Factors controlling the abundance of amphipods

Stoker (1978; 1981) suggested that four factors influence benthic structure and biomass: primary productivity, terrestrial detritus input, current regimes and predation rates. Competition for space between species and reproductive potential will also affect population densities (Coyle and Highsmith, 1994). Food supply is a major regulating factor in benthic biomass in the polar region. This is linked to processes occurring in the overlying water, especially higher primary production and phytoplankton biomass (Grebmeier *et al.*, 1988). The benthic biomass on the shelf of the northern Bering and Chukchi Seas is positively correlated with the quality and quantity of organic carbon reaching the sediments.

By affecting food filtering to amphipods at the ocean bottom, water temperature influences competition between species, predation rates and overall production. Long term increases in sea surface and upper water column temperatures bring about a reduced nutrient supply to the euphotic zone that is associated with a decline in primary productivity, accompanied by decreases in zooplankton, seabirds and kelp production (McGowan *et al.*, 1998). Thus, the structure and dynamics of deep-sea communities is influenced by long-term trends in sea surface temperatures and its effect on particulate organic carbon export from the surface waters to the deep ocean (Smith and Kaufmann, 1999).

Highsmith and Coyle (1991) showed that amphipods exhibit temperature-dependent growth and maturation rates. Warm temperatures result in low age at reproduction, small adult size, small brood size and reduced life span. In contrast, cold temperatures produce long-lived, slow-growing, late-maturing individuals that reach large size and produce large broods. The effect may be due to a decoupling of molting and growth rates, with molting rates being regulated by temperature. At colder temperatures, the amphipods molt less frequently and thus accumulate more mass between molts. Slow maturation results in larger, older adults than one would find in warmer climes. The largest taxa require high organic matter input and low predation rates to mature and reproduce; this allows them to outcompete the smaller taxa for available space. Global warming elevates ampeliscid food requirements favouring higher densities of smaller species such as *A. birulai* over larger species such as *A. macrocephala*, thereby lowering the total biomass (Coyle and Highsmith, 1994; Weisshappel and Svavarsson, 1998). High water temperatures, reductions in organic matter flux and high predation rates favour smaller taxa that can reproduce and colonise quickly (Coyle and Highsmith, 1994).

Threats to amphipods

Declines in amphipod biomass could have been caused by three general factors acting either singly or in concert: (1) increased gray whale predation; (2) long-term physical and biological fluctuations in the Bering Sea ecosystem, including global warming; and (3) higher than usual sea surface temperatures associated with the severe El Niño Southern Oscillation (ENSO) of 1997-1998.

Gray whale population status

Gray whale numbers in the eastern North Pacific, the California-Chukchi population, have been increasing since 1968 (Reilly, 1981) which suggests increasing predation on their principal prey. The population was estimated at 15,647 in 1980 (Reilly, 1984), 18,000 in 1985 (Breiwick and Dahlheim, 1986), 21,113 in 1987/88 (Reilly, 1992), 23,109 in 1994 (Laake *et al.*, 1994) and 22,263 in 1996 (Hobbs *et al.*, 1997). In 1999, the population was estimated at about 26,600 animals (Hobbs and Rugh, 1999), an increase of 19.8% from the 1995-96 surveys. Since 1980, the gray whale population has increased at a rate of 3.29% per year (Perryman *et al.*, 1998). It is generally agreed that the eastern Pacific population has not only recovered from exploitation (Swartz, 1986a) but may even be above its 1846 level, when commercial exploitation began (Reilly, 1992; IWC, 1998). There are signs that the population is approaching carrying capacity, the proportion of harvested females that are pregnant declined steeply from 1987 to 1990 (Reilly, 1992) and decreases in amphipod biomass observed during the 1980s have been linked to increased predator pressure from gray whales (Stoker, 1990; Highsmith and Coyle, 1992).

The estimated annual energetic requirement of gray whales feeding in the Chirikov Basin in the Bering Sea, a prime gray whale feeding area, is near or above the commonly accepted 10% ecological transfer efficiency between trophic levels (Crisp, 1975; Mann, 1982; Parsons *et al.*, 1984; Highsmith and Coyle, 1992). At the current rate of population growth, Highsmith and Coyle (1992) estimate that gray whales will take up to 25% of annual amphipod production in the year 2000. Their modelling studies suggested that these removal rates are not sustainable.

Physical and biological parameters directly influencing benthic populations

Since the mid-1970s, changes in global atmospheric pressure patterns that create persistent blocking ridges over the North Pacific have occurred, leading to decadal and longer shifts in pressure patterns and storm tracks (Francis *et al.*, 1996). These changes or ‘regime shifts’ alter the timing of critical storm events that affect biological productivity (Francis and Hare, 1994; Graham, 1994; Trenberth and Hurrell, 1994). Global warming has been occurring in the Arctic as reflected by recorded warming trends (Martin *et al.*, 1997) and decreasing ice cover over the last three decades (Maslanik *et al.*, 1996; Johannessen *et al.*, 1999; Vinnikov *et al.*, 1999). Concomitant with these physical changes, human exploitation of the ecosystem, especially of whales and fisheries, has increased. During the last three decades, drastic declines in the populations of marine mammals, sea birds and fishes in the Bering Sea have been documented. Tynan and DeMaster (Tynan and DeMaster, 1997) examine potential effects of predicted Arctic climate change on marine mammals, including gray whales, noting the effects of sea ice and the ice edge community in particular. The assemblage of animals in the ecosystem is changing, in particular, the fish assemblage has become pollock-dominated (Francis *et al.*, 1996). Schell (2000) presents evidence that there has been a decline of approximately 30% in primary productivity in the Bering and Chukchi seas since 1966. He recorded changes in carbon isotope ratios in the baleen plates of bowhead whales, *Balaena mysticetus*, collected over the period 1947-1997. These chemical signatures are assumed to reflect food web structure and productivity. Since primary productivity sets the upper limit on biomass yield at all higher trophic levels, and specifically, the benthic amphipods (Grebmeier *et al.*, 1988), this suggests that the carrying capacity of the Bering-Chukchi ecosytem has declined by about 30% in the last 30 years (Springer, 2000). This might, in part, explain observations of low body condition, calf production and survival of walruses in recent years (Lowry, 2000), that also feed on benthic animals.

Polar regions exhibit a strong benthic-pelagic coupling compared with temperate and tropical areas (Stoker, 1981; Grebmeier and McRoy, 1989; Grebmeier, 1993) such that the overlying water column production in the Bering and Chukchi Seas has a direct influence on underlying benthic biomass (Grebmeier *et al.*, 1988; Rowe and Phoel, 1991; Grebmeier, 1993). Thus, the climatic and human-induced changes that affect the ecosystem are expected to have long-term impacts on carbon turnover and on the benthic populations (Francis *et al.*, 1996).

Sea surface temperatures in the Chirikov Basin were higher than usual in 1985-1987 (Fig. 6); a period during which El Niño conditions prevailed (Konnen *et al.*, 1998) and amphipod biomass declined (Highsmith and Coyle, 1992). Similarly, reported decreases in amphipod biomass during the 1990s (Grebmeier and Dunton, 2000) might have been precipitated by high SSTs, when six years were categorised as moderate to strong El Niño years by the Western Regional Climate Center (Trenberth and Hoar, 1996; K. Redmond, pers. comm.). Our analysis (Figs 5 and 6) shows that mean SSTs in the Chirikov Basin in the 1990s were unusually warm, at above 6°C for nine years in the decade.

Increased sea surface temperatures associated with enso 1997-98

High SSTs in the Bering and Chukchi Seas associated with the ENSO cycle may have precipitated a decrease in the biomass of amphipods, exacerbating previous declines due to other causes. Based on temperature anomaly, ENSO 1997-98 was one of the strongest ENSOs of the century (Wolter and Timlin, 1998; McPhaden, 1999). Large-scale oceanic warming in the Tropical Pacific, coupled with a change in atmospheric circulation, affects fisheries and marine life, as well as climatic conditions around the globe (Trillmich and Ono, 1991). Coastal upwelling is depressed in the eastern Pacific because of anomalies between the sea surface and winds that cause a drastic decline in primary (phytoplankton) production, which in turn, adversely affects all creatures at higher trophic levels of the marine food chain. Fish located in nearshore coastal areas migrate to cooler waters farther north or into deeper waters to find food. Many fish that do not migrate die from lack of food or intolerably high temperatures. Increased rainfall increases turbidity and reduces the salinity of coastal waters. Distribution of the prey of many marine mammals changes, making foraging difficult, and leading to high mortality levels (Trillmich and Ono, 1991). In the Bering and Chukchi Seas, other factors associated with the warmer than usual waters may also have been in operation, such as increased predation on amphipods by bottom-feeding fishes and crabs moving into the area with warmer waters (Francis *et al.*, 1996).

The available information indicates that mean SST in the Chirikov Basin in 1998 (Fig. 6) was no higher than the values of the five preceding years, suggesting that ENSO 1997-98 alone, did not provide sufficient warming to account for a significant drop in amphipod biomass, and possibly, explain the high gray whale stranding rates in 1999 and 2000. Rather, SSTs in the Chirikov Basin were unusually high during most of our sampling period, suggesting that if the prey base of whales was reduced by climate warming, it was due to an increase over several years rather than to a single hot year.

Moreover, gray whale strandings were not highly correlated with summer SSTs in the Chirikov Basin over the last 15 years. Fedorov and Philander (2000), analysing SST in the Eastern Pacific dating back to the 1890s, report that the properties of the Southern Oscillation changed to higher than normal temperatures during the 1980s and 1990s; La Niña episodes were very weak or absent while El Niño reached record amplitudes in 1982 and 1997 and was unusually prolonged in 1992. Peak gray whale strandings in 1991 were associated with a high mean SST in the Chirikov Basin but the high stranding rate in 1999 was two years later than the high SST in 1997.

In summary, although there have been no direct studies to investigate links between the high stranding rate of gray whales and putative low energy reserves due to inadequate foraging on amphipods in Alaskan waters, indirect and circumstantial evidence strongly implies such an association. If a decline in amphipod biomass provided insufficient forage for gray whales thereby weakening their physiological condition and accounting for the high stranding rates in 1999 and 2000, it would appear to have been due to a combination of factors. Such factors include increased predation on the amphipods by the increasing number of whales and the depressing effect on amphipod biomass of a progressive warming trend over the last several years. If gray whales have become food-limited, a high stranding rate and lowered reproduction would be expected to continue until an equilibrium is reached. Highsmith and Coyle (1992) point out that any perturbation causing extensive mortality in a high latitude ampeliscid population with low fecundity and long generation times is expected to result in a marked decrease in secondary production rate and the population would take a long time to recover, possibly tens to hundreds of years. If this scenario is correct, the gray whale population could level off or even decline in the next decade or so. Alternatively, gray whales may begin feeding increasingly in other areas and on different prey such as krill at the surface. Determining whether the whales were food-limited in 1999 and 2000 may depend on trends in gray whale abundance, as well as their distribution, mortality rate and birth rates in the next few years or decades.

Climate conditions at feeding grounds can have profound effects on the population dynamics of a species (e.g. Den Held, 1981). Stillett *et al.* (2000) showed that the demographics of a migrant bird, the black-throated blue warbler, may be strongly influenced by large-scale climate changes affecting not only survival in southern wintering grounds but also reproductive performance in northern breeding areas. Fecundity rate was lower under El Niño conditions than in La Niña years, an effect attributed to the body mass of the fledglings. Under El Niño conditions, there was a reduction in the biomass of lepidopteran larvae, the favourite food of the warbler. As a consequence, El Niño (with a low SOI value) resulted in a decrease in the number of new yearlings entering the population the following year.

Prey reduction followed by increased mortality from starvation is well documented in sea otters, *Enhydra lutris*. Numerous studies (e.g. Riedman and Estes, 1990) show that they can exert a profound limiting influence on their invertebrate prey populations such as sea urchins (*Strongylocentrotus purpuratus*), Pismo clams (*Tivela stultorum*), abalone (*Haliotis* spp.), Dungeness crabs (*Cancer magister*) and mussels (*Mytilus californianus* and *M. edulis*). Kenyon (1969) showed that as the sea otter population at Amchitka Island, Alaska, grew towards food limitation, starvation-related mortality increased significantly. Otters became limited in their search for fish and octopus to a narrow belt of water surrounding the island, less than 30m deep. Bottom-dwelling prey species in this zone were reduced. Large juveniles and aging adults could not obtain a sufficient quantity of high calorie food and were forced to forage on hard-shelled, low-calorie invertebrates that eroded their teeth to the gumline. They were forced to seek food during sustained periods of rough seas, which exhausted their body reserves and led to the development of enteritis, a symptom of starvation and stress. Adults weighed less than otters from less crowded populations. The gastrointestinal tract of otters that died on beaches was either empty or contained only hard-shelled organisms. Ralls and Siniff (1988) found that juvenile females in the central part of the range in California spent more time foraging and experienced higher mortality than other age and sex classes. Because these juveniles of high reproductive value were at a competitive disadvantage, they reasoned that food availability limited further population growth.

In conclusion, the high mortality rate of gray whales in 1999, the low calf production, as well as the unusual sex and age distribution of dead whales and apparent aberrancies in timing, location and behaviour during migration and the reproductive season, are consistent with the hypothesis that the animals had low body reserves and suffered inanition. The information presented here suggests that this may be due to a decrease in their principal prey on the summer feeding grounds brought about by increased predation and the depressing effect of increasing water temperature over the last decade on amphipod biomass. This has important implications for the growth and stability of the gray whale population. The health of amphipod communities in gray whale feeding areas, particularly the Chirikov Basin in the Bering Sea has important implications for higher trophic levels and should be monitored regularly, especially with respect to fluctuations in ambient water temperature. In addition, research priority should be given to studies to further test the hypothesis presented here, including (1) assessing body condition of whales at the time of stranding; and (2) continuing to monitor population status, strandings and reproduction.

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