Timing of the gray whale southbound migration

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ABSTRACT

The southbound migration of the eastern North Pacific stock of gray whales (*Eschrichtius robustus*) has been documented by the National Marine Fisheries Service most seasons since 1967 at or near Granite Canyon, in central California, and by the American Cetacean Society's Los Angeles Chapter every season since 1985 at Point Vicente, southern California. This has provided a rare opportunity to examine cetacean migratory timing data over a relatively long time series. In 1998/99, anecdotal reports indicated a major change had occurred in the timing of the migration, which prompted this study to compare the observed timing relative to expected dates. Although no observers were at Granite Canyon in 1998/99, data collected from this site indicated that prior to 1980, annual median sighting dates ranged from 4-13 January (overall median = 8 January; CI = 1.3), but since then there has been a one-week (6.8 day; CI = 2.0) delay, with median dates now ranging from 12-18 January (overall median = 15 January; CI = 1.7). This delay in timing is better represented as a shift in dates than as a trend, and it occurred shortly after a major oceanographic regime shift in the North Pacific Ocean. The shift in whale sighting dates occurred equally in the onset of the migrations (when the first 10% of the whales passed a site), the median (50%) and end (when 90% of the whales passed). At Granite Canyon, there were no significant trends in these dates prior to 1980 or in dates following the shift. In mid-February (median = 15 February, CI = 1.9, at Point Vicente), few gray whales are still going south and some are already migrating north. Most of the migration (the period between the 10% and 90% sighting dates) occurs across a period of 34 days (CI = 2.0), but the entire southbound migration may take >70 days to pass a location in any given year. It takes a whale approximately 54 days to migrate from the north central Bering Sea to the lagoons in Baja California (8,000km), but some whales may travel as far as 10,000km. Based on available observations and calculations using a travel rate of 147km/day, current median (peak) sighting dates of the southbound migration should be: 1 December in the north central Bering Sea (here considered the theoretical starting point for the migration); 12 December at Unimak Pass, Alaska; 18 December for Kodiak Island, Alaska; 5 January for Washington State; 7 January for Oregon; 15 January for central California; 18 January in southern California; and 24 January at the northern lagoons in Baja California (considered here to be the terminus of the migration). Although no observations were made at Granite Canyon in 1998/99, sightings made at Yaquina Head, Oregon (median sighting date = 7 January) and at Point Vicente (median = 20 January) indicate that the timing of that migration was consistent with previous years.

KEYWORDS: GRAY WHALES; MIGRATION; MONITORING; LONG-TERM CHANGE; TRENDS; ARCTIC; NORTHERN HEMISPHERE; PACIFIC OCEAN; SURVEY–SHORE-BASED; NORTH PACIFIC

INTRODUCTION

The National Marine Fisheries Service (NMFS) initiated several research projects in the winter of 1998/99 to better understand the migration of gray whales (*Eschrichtius robustus*) through Washington State, an adjunct of Makah whalers' interest in avoiding local whales (Shelden *et al.*, 1999). The research was designed to document the progress of the southbound migration and to describe the whales' distribution relative to shore. These projects included: (1) aerial surveys off the west coast of Washington (Shelden *et al.*, 2000); (2) watches from a lighthouse on Tatoosh Island, west of Cape Flattery, Washington State (Jones, 1999); and (3) observations from a lighthouse at Yaquina Head, near Newport, Oregon (Mate and Poff, 1999) - a site used for similar counts in 1978-81 (Herzing and Mate, 1984; Fig. 1). Although the NMFS has conducted a full census of the southbound migration at Granite Canyon (or Yankee Point) near Carmel, California, 20 times since 1967, there were no observations there in 1998/99. Therefore, to compare the timing of the 1998/99 migration to other years, we relied primarily on data from the annual counts conducted since 1985 by the American Cetacean Society's Los Angeles Chapter (ACS/LA) at Point Vicente, near Los Angeles, California.

Based on a few anecdotal accounts and premature reports, the 1998/99 southbound migration initially appeared to be very late. This received considerable media attention (e.g. Anonymous, 1998a; b; Mapes, 1998; Shukovsky, 1998; Hamilton, 1999; Schneider, 1999). Accordingly, there was a need to collect all available evidence to assess the temporal nature of this migration. The following report synthesises information obtained from all shore-based observation sites where systematic counts of gray whales have been made (Fig. 1). The objective was to provide a retrospective timetable for the southbound migration past shore stations where gray whale sightings have been tallied systematically during one or more seasons in the past, including a comparison of this timetable to available records for the migration in 1998/99.

METHODS

Defining the peak of the migration

The peak of the southbound migration is defined here as the date when 50% of the whale sightings had been recorded at a research site (i.e. the median date), or (if data were not available for calculating the median) the date corresponding with the apex of a unimodal sighting curve (e.g. Fig. 2). Peak dates used here are based on locations where sufficient numbers of sightings were made to be considered representative of whale occurrence throughout most or all of a migration, generally with >2hr/day for >38days of watch effort per season (e.g. Mate and Poff, 1999). Whenever the literature indicated peaks as medians (e.g. Buckland and Breiwick, 2001) or maximum sighting dates (e.g. Jones and Swartz, 1984) or peaks in sightings (e.g. Braham, 1984; Herzing and Mate, 1984), the respective term was also used here. The median dates reported from Granite Canyon (50th

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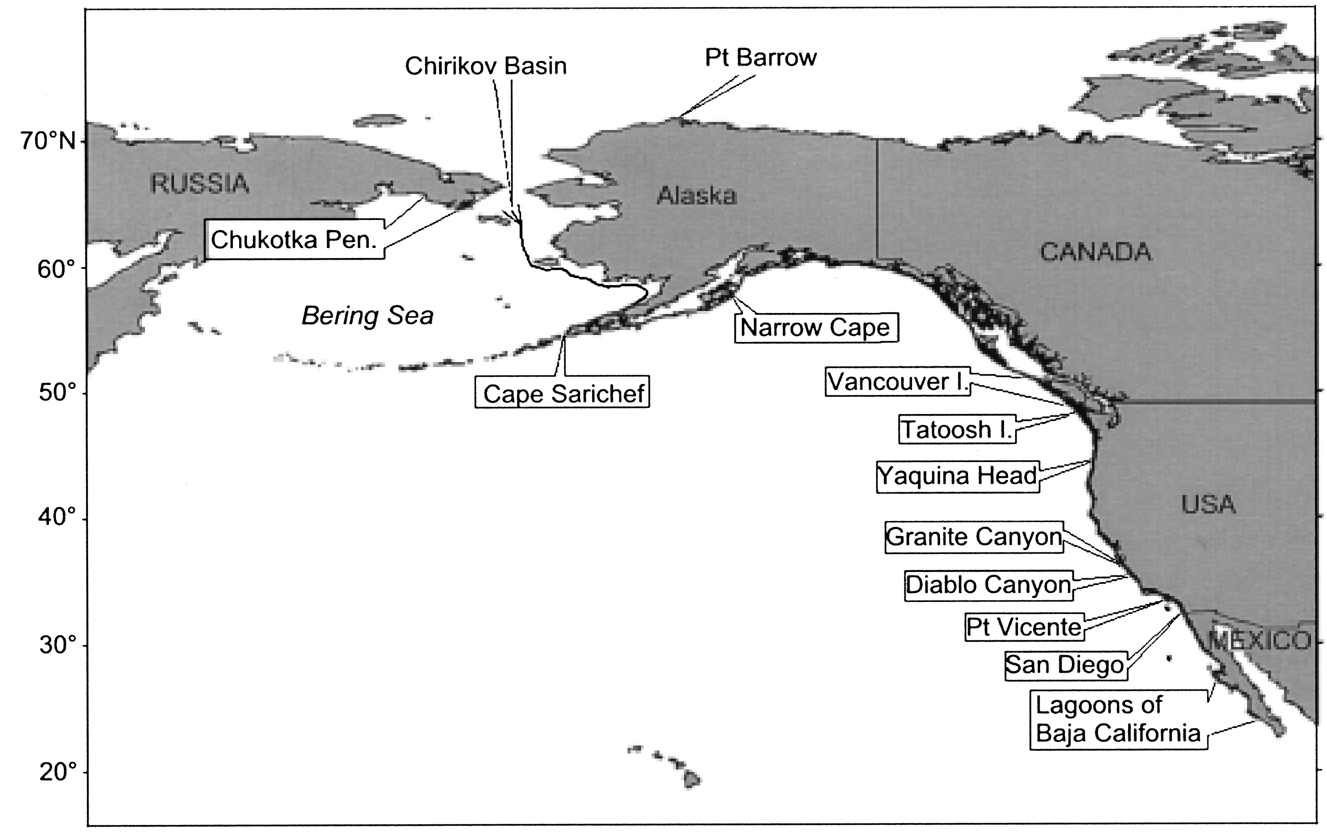

Fig. 1. Boxed entries indicate shore-based sites sometimes used to observe migrating gray whales. The whales' migratory route, shown here (as per Braham, 1984), generally parallels the shore within the 30-50m depth contour.

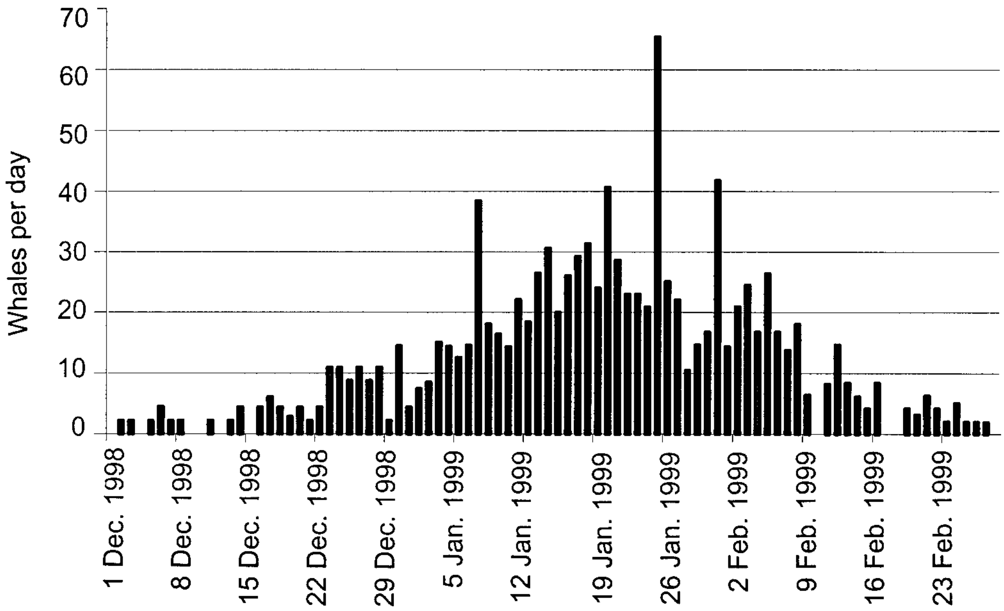

Fig. 2. Gray whale sighting data from the southbound migration in 1998/99 at Point Vicente, California. The first 10% of the migration had passed the station by 28 December; 50% had passed by 20 January (the median, or peak date); 90% had passed by 8 February.

percentiles, shown in Table 1), as well as the 10th and 90th percentile dates, are based on the Hermite polynomial fit to the temporal distribution of sightings of whale groups for the respective year (1967/68 to 1987/88 in Buckland and Breiwick, 2001; 1992/93 and 1993/94 in Laake *et al.*, 1994; 1995/96 in Hobbs *et al.*, 2001 and 1997/98 in Hobbs and Rugh, 1999). The data from Granite Canyon form the primary measure for establishing the timing of the migration, with dates from other sites compared to these.

Migratory travel rate

During their southbound migration, the median speed for gray whales is 6.13km/hr (=147km/day), according to results from nine whales monitored by radio tags for <1 day each near the Granite Canyon census station in California (Swartz *et al.*, 1987). There is no evident diel variation in swimming speed (Perryman *et al.*, 1999), so this speed can be used to represent day and night travel. Because this precisely calculated rate for short time periods does not

Table 1

Observed and expected migratory dates at Granite Canyon, California, the site of the NMFS shore-based counts of gray whales. Columns A-C show number of days since the start of January for the respective year. Column A shows the observed median date for sightings on the respective year. Dates in column B are based on 10 January as the typical median date prior to 1980 and a one day per three year delay following 1980 (Buckland and Breiwick, 2001). Column C dates are based on one median date prior to 1980 (8 January) and one after 1980 (15 January) as used in the current study.

Median dates				
Observed (A)		Expected (B)	Expected (C)	Data source
8 Jan. 1968	= 8.5	10	8	Buckland and Breiwick, 2001
8 Jan. 1969	= 8.2	10	8	Buckland and Breiwick, 2001
5 Jan. 1970	= 5.9	10	8	Buckland and Breiwick, 2001
8 Jan. 1971	= 8.1	10	8	Buckland and Breiwick, 2001
9 Jan. 1972	= 9.5	10	8	Buckland and Breiwick, 2001
13 Jan. 1973	= 13.8	10	8	Buckland and Breiwick, 2001
9 Jan. 1974	= 9.4	10	8	Buckland and Breiwick, 2001
7 Jan. 1975	= 7.4	10	8	Buckland and Breiwick, 2001
4 Jan. 1976	= 4.5	10	8	Buckland and Breiwick, 2001
8 Jan. 1977	= 8.7	10	8	Buckland and Breiwick, 2001
6 Jan. 1978	= 6.6	10	8	Buckland and Breiwick, 2001
7 Jan. 1979	= 7.2	10	8	Buckland and Breiwick, 2001
10 Jan. 1980	= 10.7	10	8	Buckland and Breiwick, 2001
14 Jan. 1985	= 14.7	11.3	15	Buckland and Breiwick, 2001
14 Jan. 1986	= 14.9	12	15	Buckland and Breiwick, 2001
12 Jan. 1988	= 12.5	12.7	15	Buckland and Breiwick, 2001
13 Jan. 1993	= 13.9	14.3	15	Laake *et al.*, 1994
18 Jan. 1994	= 18.6	14.7	15	Laake *et al.,* 1994
16 Jan. 1996	= 16.6	15.3	15	Hobbs *et al.,* 2001
18 Jan. 1998	= 18.4	16	15	Hobbs and Rugh, 1999

include potential deviations in migratory travel expected over long distances, long distance travel speeds were calculated by comparing sighting rates at widely separated shore-based stations where full-season counts were conducted in the same year (and see Swartz, 1986). A peak in sightings observed on 2 December 1978 at Cape Sarichef on the westernmost tip of the Alaska Peninsula/Unimak Island (Rugh, 1984) and on 28 December 1978 at Yaquina Head (Herzing and Mate, 1984) indicates a travel time of 26 days. Almost the same travel time, 27 days, was observed on the following year: 10 December 1979 at Cape Sarichef (Rugh, 1984) and 6 January 1980 at Yaquina Head (Herzing and Mate, 1984). Swimming for approximately 3,900km[1] in 26 or 27 days results in migratory travel rates of 150 or 144km/day, respectively. Comparable results were made by matching sighting peaks at Cape Sarichef (Rugh, 1984) with those recorded at Granite Canyon (Buckland and Breiwick, 2001): whales took 37 and 32 days to cover the distance of nearly 5,000km in 1978 and 1979, indicating travel rates of 135 and 156km/day, respectively. The median of these four long-distance calculations (147km/day) is the same as the median reported by Swartz *et al.* (1987); therefore, this travel speed (147km/day; CI = 10.0) is considered representative for gray whales throughout their southbound migration.

Precision of the timing estimates

Dates presented in the following analysis are considered approximations because: (1) only a single travel rate (147km/day) was used rather than a range (CI = 137-157km/day); (2) data for each tagged whale were collected over time intervals of only 6-19 hours (Swartz *et al.*, 1987); (3) estimated distances have inherent, unknown errors depending on whether whales travel more directly between headlands or travel closer to coastlines than was approximated here; and (4) median dates are not consistent for every migration. However, the range in calculated speeds amounts to only ±6 days even at the extremes of the migratory distances used in this study, and the travel speed from tagged whales was corroborated by comparing respective migratory dates between pairs of distant counting stations; in addition, calculated and observed dates were nearly identical for each of the counting stations where data were available (Table 2). For the 20 years of data collected at Granite Canyon, annual dates ranged only –4 to +6 days relative to the overall median dates (CI = 1.0), and at Point Vicente, the 14 annual median dates ranged from only –3 to +12 days (CI = 2.4). The sum of these approximations and ranges means that the timing of the southbound migration generally may be estimated to within a few days of the expected date for the respective site.

Analytical methods

Nonparametric tests were used in most of the statistical analyses performed here to avoid underlying assumptions of distribution – as noted by Hollander and Wolfe (1973, p.1) such procedures are only 'slightly less efficient' if the underlying distribution is, in fact, normal and even 'wildly more efficient' if the distribution is not normal. In particular, the Theil Test was applied for regression analysis, and the Wilcoxon Rank Sum Test was used for tests of differences in medians between two-sample populations (Hollander and Wolfe, 1973). All confidence intervals (CI) are based on 95% probability.

RESULTS AND DISCUSSION

Locations with sighting dates

The following locations are all of the known shore-based sites where there has been at least some systematic documentation of the timing of the southbound migration of gray whales (Fig. 1).

[1] Travel distances were measured on maps scaled 1:2,500,000, generally following the 30-50m depth contour (as used by Gilmore, 1960), while minimising distances between headlands, roughly depicted in Fig. 1. This coastal route was first described by Pike (1962), and gray whale sighting locations along the route were confirmed by Braham (1984).

Table 2

Migratory timing of gray whales during their southbound migration. Shore stations are selected sites where counts of gray whales have been made during the southbound migration. Distances are the approximated number of kilometres the average whale might travel from the previous shore station. Expected (A) dates are based on travel time relative to Granite Canyon with its known date of 15 January. Column B dates are observed local averages from seasons prior to 1998/99.

Shore station	Distances	Travel time (147km/day)	Median dates		
			Expected (A)	Observed (B)	Observed date in 1998/99
Cape Sarichef, Unimak Pass	-	-	12 Dec.	12 Dec.[1]	Not seen
Narrow Cape, Kodiak Island	975km	6.6 days	18 Dec.	-	Not seen
Tatoosh Island, Washington	2,525km	17.2 days	5 Jan.	-	Not seen
Yaquina Head, Oregon	432km	2.9 days	7 Jan.	8 Jan.[1]	7 Jan.
Granite Canyon, California	1,052km	7.2 days	15 Jan.	15 Jan.	Not seen
Point Vicente, California	485km	3.3 days	18 Jan.	18 Jan.	20 Jan.
Laguna Guerrero Negro, Mexico	790km	5.4 days	23 Jan.	Early Feb.	Not seen
Laguna Ojo de Liebre, Mexico	30km	0.2 days	24 Jan.	25-29 Jan.[1]	Not seen
Laguna San Ignacio, Mexico	350km	2.4 days	26 Jan.	9 Feb. (or later)	Not seen

[1]Published dates prior to 1980 are adjusted for the 7 day shift in medians that occurred since 1980.

Chukotka Peninsula (roughly 64-67°N and 170°-176°W)
Melnikov *et al.* (1997) reported results from 30 observers at 15 sites around the Chukotka Peninsula (not shown in Fig. 1) where whale sightings were recorded from shore or from whaleboats, mostly in 1994 and 1995. Most whale sightings were within 5km of shore. Gray whales began leaving the northwestern coast of Chukotka in early September (1994) or the second half of October (1995), years with late and early ice arrival, respectively. The last whales in this area were seen in late September (1994) or late October (1995). The last sightings in the Bering Strait region were in early October to late November, and the last whales near the coast of the northern Bering Sea were seen in late October to late November. Yablokov and Bogoslovskaya (1984) provided a review of Russian studies of gray whales and concluded that this stock departs from northern seas beginning in the middle of October or November, depending on the year, and some whales are still in the area (the southern tip of the Chukotka Peninsula) as late as mid-November or mid-December.

Cape Sarichef, Alaska (54°36'N 164°56'W)
Cape Sarichef, overlooking Unimak Pass, is on the western edge of the longest obstruction in the gray whale's migration - the nearly contiguous Unimak Island and Alaska Peninsula - which protrudes over 1,300km from the Alaskan mainland, lying between the Bering Sea and the Pacific Ocean. Shore-based surveys of the southbound migration were conducted at Cape Sarichef during November/December 1977-79 (Rugh, 1984). Peak sighting dates were recorded on 23 November 1977 (high count), 3 December 1978 (median) and 7 December 1979 (median). The timing in 1977 is not used in the following analysis because it was a season with only 17 days of sampling. Using the average of the other two years (5 December) and allowing for a 7-day shift in the migration (see 'Peak dates' below), the peak should now occur on 12 December (Table 2). This is exactly the same date back-calculated from Granite Canyon 5,000km away (34 travel days) where the peak of the migration occurs on 15 January (Table 2). There were no observational records collected at Unimak Pass in 1998/99, so the timing in this season cannot be confirmed.

Narrow Cape, Kodiak Island, Alaska (57°25'N 152°20'W)
No regular counts of gray whales have been conducted at Kodiak Island, but observations have been made by local biologists as opportunity allowed. On 27 December 1998, hundreds of gray whales were seen at Narrow Cape during a one-day bird survey (R. MacIntosh, NMFS, pers. comm.). These were the highest counts ever in 43 years, according to Al Cratty Jr., a fisherman passing through the area at that time (pers. comm., op. cit.). Many gray whales were also seen at Narrow Cape on 30 December, but far fewer were seen a few days later (K. Wynne, University of Alaska, pers. comm.). These sightings were 9-12 days later than expected for this site (Table 2), but the observations were from only a few days and do not provide a portrayal of the passing of the migration.

Vancouver Island, British Columbia (50°40'N 128°30'W to 48°30'N 124°30'W)
Pike (1962) described the peak of the southbound migration through British Columbia and Washington as being in late December based on opportunistic sightings from lighthouses in December and January 1953-60. No median date was given for the southbound migration past Vancouver Island in 1972-77, but observations there indicate that maximum counts occurred during the latter half of December (Darling, 1984).

Tatoosh Island, Washington (48°23'N 124°44'W)
No regular shore-based counts of gray whales have been conducted in Washington because the widely spread offshore distribution makes it impractical to count most of the whales migrating through the area (Green *et al*., 1995; Shelden *et al*., 2000). Aerial surveys in Washington from November 1998 to January 1999 (Shelden *et al*., 2000) and the watch from the Tatoosh Island lighthouse 30 November to 16 December 1998 (Jones, 1999) resulted in very few gray whale sightings, making it difficult to determine when most whales passed through this area. Although the peak date of the migration should have been on 5 January 1999 (Table 2), only three gray whales (two groups) were seen on an aerial survey conducted on that date between the shore and seaward as far as 56km to the west, and no gray whales were seen on a vessel-based search in that area on the same date (Shelden *et al*., 2000). The peak of the migration may have been missed because of limitations in field of view, lulls in the migration or because whales were travelling beyond the seaward limit of the tracklines (Shelden *et al*., 1999).

Yaquina Head, Oregon (44°41'N 124°05'W)
In 1978/79-1980/81, and again in 1998/99, systematic observations were conducted from a lighthouse on Yaquina Head, near Newport, Oregon. Peak sighting dates for the southbound migration were 28 December 1978, 6 January 1980, 1 January 1981 (Herzing and Mate, 1984) and 7

January 1999 (Mate and Poff, 1999). Using 1 January as the average date for 1978-81, and allowing for the 7-day shift in median dates (see 'Peak dates'), the peak of the 1998/99 migration should have passed Yaquina Head on 8 January 1999. This was virtually the same date (7 January) that the migration was expected to pass here based on the timing at Granite Canyon and travel distance between the two sites (Table 2). On the other hand, if the 7-day shift is applied only to dates prior to 1980, then the 1978-81 migratory dates would average out to be 4 January. The observed peak in sightings on 7 January 1999 (Mate and Poff, 1999) indicates that the timing of the migration in 1998/99 was either as predicted in Table 2, or it was three days late.

Granite Canyon, California (36°26'N 121°55'W)
The most often used observation site for southbound gray whales has been at Granite Canyon, near Carmel, California. NMFS conducted full-season surveys of the southbound migration past this site (or nearby at Yankee Point) annually from 1967/68 through 1979/80 and during seven of the subsequent 19 years (Table 1, Fig. 3). Timings of the onset, peak and end of the migration are explained below. The median date for the southbound migration is currently expected to be on or about 15 January (Table 2), but no systematic observations were made during 1998/99 to confirm the timing.

Diablo Canyon, California (35°15'N 120°0'W)
Counts of gray whales were conducted at Diablo Canyon by TENERA Environmental Services each year from 1981-94 (Stephens *et al.*, 1994). On average, there was a peak in sighting rates centred around 7 January, but the mid-point between dates of first sightings of southbound whales each year ($\bar{x}$ = 28 December) and the last southbound sightings ($\bar{x}$ = 13 February) was 20 January. Because counts were conducted for only 3 hrs/day and 3 days/wk ($\bar{x}$ = 33 days/yr) at Diablo Canyon, compared to 9 or 11hr/day and 7 days/wk at Granite Canyon and Point Vicente, the latter sites are used for more precise estimates of migratory timing.

Point Vicente, California (33°44'N 118°24'W)
The American Cetacean Society's Los Angeles Chapter (ACS/LA) has conducted full-season counts of gray whales at or near Point Vicente (near Los Angeles, California) annually since 1985. This includes counts throughout most daylight hours from 1 December until mid-May. The median dates for each of the southbound migrations over 13 years (1985/86 to 1997/98) has ranged from 15 to 30 January (Schulman-Janiger, 1999), with an overall median of 18 January (CI = 2.4). The difference between this median date and the one observed at Granite Canyon (3.4 days), agrees with the calculated time it would take the whales to swim the 485km from Granite Canyon to Point Vicente at 147km/day (3.3 days). In the winter of 1998/99, the median date for gray whale sightings was 20 January (Fig. 2), only two days after the expected date of 18 January (Table 2). Therefore, the southbound migration in 1998/99 was within the range of error for dates predicted from other seasons (16-21 January).

In most years, there is an overlap between the southbound and northbound migrations in southern California. Off Point Vicente, the turnaround period (when most whales have stopped going south and the migration north has not yet begun) generally lasts for several days. During this period, sighting rates are reduced, and whales are seen travelling in both directions. However, in 1999 this turnaround period lasted two weeks, resulting in a pronounced hiatus between migrations. The mid-point between the end of the southbound migration and start of the northbound migration was 15 February 1999, which is about the same as the average turnaround date (15 February; CI = 1.9) from previous seasons.

San Diego (32°45'N 117°16'W)
Observations of gray whales were conducted at Point Loma and/or La Jolla, near San Diego, most winters between 1946/47 and 1977/78 (listed in Reilly, 1984). Gilmore (1960) found that southbound gray whales were usually seen

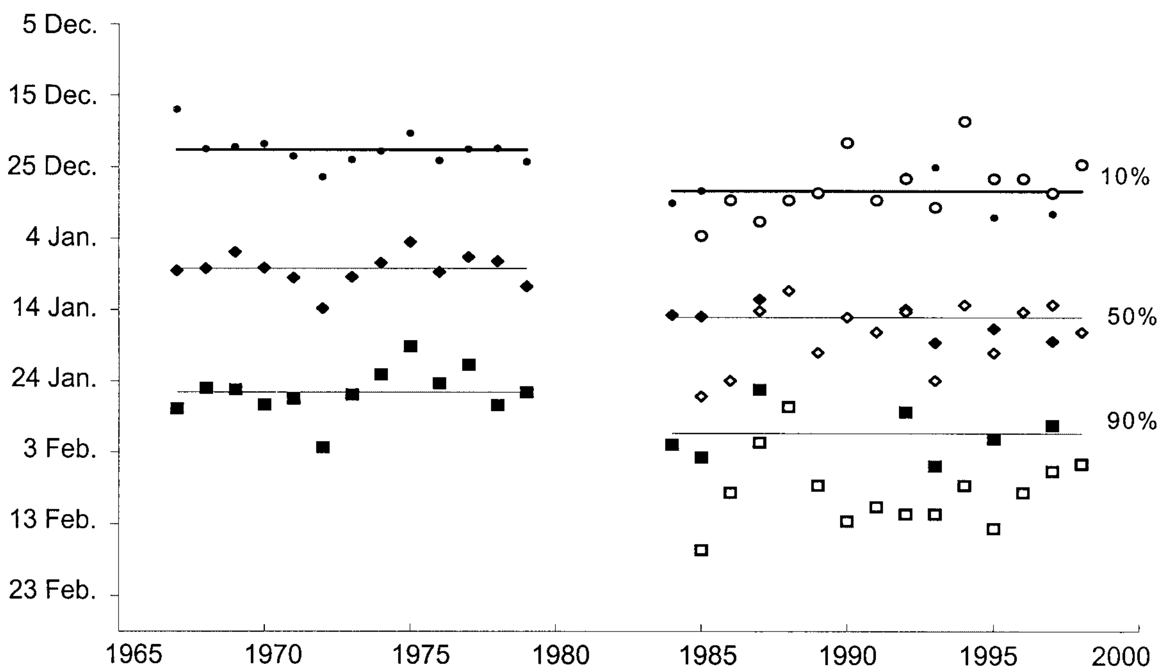

Fig. 3. Dates of gray whale sightings during their southbound migrations as they passed shore-based observers in California at Granite Canyon (black symbols) and Point Vicente (open symbols). The Point Vicente sightings have been adjusted by 3.3 days for whale travel time between Granite Canyon and Point Vicente. Circles indicate when 10% of the sightings passed the respective station; diamonds indicate the median (50%) dates; squares indicate when 90% passed. The lines represent median dates at Granite Canyon.

during the latter half of November, though not commonly until after the middle of December. The peak occurred during the middle two weeks of January. Based on the published data for 1956/57 at this site (Gilmore, 1960), the median date was 12 January. Adding seven days for the shift in migratory dates observed since the 1970s (see 'Peak dates') would mean that the peak is currently expected to pass on 19 January. This is the same date calculated from travel distance (~160km) and speed (147km/day) of the peak passing Point Vicente (on 18 January). By mid-February, the southbound migration was virtually over and the northbound migration begun (Gilmore, 1960). These sighting records agree well with the recent records from Point Vicente.

Lagoons in Baja California Sur (approx. 24°-27°N and 112°-113°W)

Gray whales arrive in Baja California in late December or early January and apparently move from lagoon to lagoon until almost all have left the area 9-11 weeks later in March (Jones and Swartz, 1984). Because the lagoons of Baja California are the terminus of the southbound migration, it is difficult to get an accurate assessment of the timing of the peak of the migration there. If the migration continued south at a constant 147km/day as far as Laguna Guerrero Negro (the northernmost lagoon), maximum counts would be expected there on 23 January (Table 2). Instead, in a study conducted in 1980-82 (Bryant *et al*., 1984), maximum counts were observed in early February. Laguna Ojo de Liebre is 30km south of Laguna Guerrero Negro, but maximum counts (in 1979 and 1980) were much earlier, on 19-23 January (Withrow, 1983), a time when the migration may be expected to arrive based on calculations in Table 2. Perhaps, then, the majority of whales migrate down the coast as far as Laguna Ojo de Liebre before moving north and/or south to the other lagoons. Jones and Swartz (1984) conducted an intense study further south in Laguna San Ignacio in 1978-82 and reported maximum counts of single whales on 9 February (Table 2) and maximum counts of cow/calf pairs in late March or early April. The other lagoons had similar dates for single whales (1-10 February), but counts of cow/calf pairs were highest between 4 and 12 February (instead of March or April), depending on the lagoon (see also Withrow, 1983; Bryant *et al*., 1984; Swartz, 1986). These dates did not seem to change significantly from year to year through the study period (Jones and Swartz, 1984). In 1925 and 1926, the peak sighting date in Magdalena Bay was on 22 January (Risting, 1928); more recently (1982-1985), Swartz (1986) reported peak counts between 7-10 February for northern Magdalena Bay. A recent study (11 February to 29 March 1997) found maximum counts of gray whales in Laguna San Ignacio occurred during the last week of February (Urbán-R *et al*., 1998), which compares favourably with the combined dates for single and cow/calf pairs observed by Jones and Swartz (1984). This indicates that the migratory timing in this area may not have changed significantly since the 1970s.

Migratory timetable

A timetable (Table 2), based on observed and calculated dates, was established to provide an estimation of whale passage dates at specific locations along the route used by gray whales during their southbound migration from Alaska to Mexico. To project the calculated timetable to the theoretical start of the migration, a median location for the population was used, such as in the Chirikov Basin, half-way between the Bering Strait and St Lawrence Island (Braham, 1984; Moore and Ljungblad, 1984). There are nearly 1,700km from this location to Unimak Pass, based on migrating whales travelling straight south to Nunivak Island and then roughly parallel to the shoreline south of Nunivak (Fig. 1). Assuming a travel rate of 147km/day, a whale could cover this distance in about 12 days. Since the median migration date at Unimak Pass is 12 December (Table 2), the median departure date from the Chirikov Basin would be about 1 December. Therefore, to get from the centre of the summer grounds in the Chirikov Basin to their wintering area in Laguna Ojo de Liebre on 24 January (Table 2), the average whale migrates approximately 8,000km (an estimate similar to the 7,602km calculated by Swartz, 1986) in roughly 54 days (assuming it maintains a constant travel rate throughout the migration). Whales that spend the summer at the extremes of the distribution, such as in the Canadian Beaufort Sea (Rugh and Fraker, 1981) or Siberian Sea (Miller *et al*., 1985), might migrate over 10,000km to get to Baja California.

Onset of the migration

The timing of the start of the southbound migration is difficult to define. Some whales are southbound near Point Barrow as early as mid-August (Maher, 1960; DR, pers. obs.) and begin leaving the western Chukchi Sea between early September and the second half of October (Melnikov *et al*., 1997). The last of the whales go through the Bering Strait sometime between early October and late November (Melnikov *et al*., 1997). Generally, then, most gray whales are migrating out of northern seas sometime between mid-October and November, but some have been seen near the Chukotka Peninsula as late as mid-December (reviewed in Yablokov and Bogoslovskaya, 1984). These dates, mostly prior to the 1 December median date calculated here for the Chirikov Basin, may indicate an initial displacement that occurs before whales reach the travel speed typical of the southbound migration, perhaps the effect of *Zugunruhe*, or restlessness, when the urge to migrate gradually prevails over the urge to continue feeding. On the other end of the migration route, southbound gray whales have been seen in Oregon and northern California as early as September (Gilmore, 1960) and October (Scammon, 1874). At Granite Canyon, there are usually one or more whales seen per day at the start of each study in mid-December. Observations at Point Vicente have begun on 1 December each year since 1984, and usually gray whales are reported within the first five days or at least by 11 December. Because many whales spend summers well south of Alaska (Pike, 1962; Rice and Wolman, 1971; Darling, 1984; Gosho *et al*., 1999), it is impractical to designate a date for the first whale in a migration.

The date when 10% of the annual sightings have passed a station (i.e. the onset of the migration; see Fig. 2) currently occurs on 30 December at Granite Canyon (16 days before the median date) and 1 January at Point Vicente (17 days before the median date). Since 1980, there has been a 6.8-day delay in the arrival of the first 10% of the migration (Fig. 3; $p << 0.01$ comparing dates before and after 1980; combining 1968-88 data from Buckland and Breiwick, 2001 with unpublished NMFS data and 1986-99 data from Schulman-Janiger, 1999). This parallels the 6.8-day shift observed in median dates (see 'Peak dates' below). There was no significant trend in dates prior to 1980 ($p = 0.11$); since 1980 there appears to be a trend towards earlier arrivals ($p = 0.02$) at a rate of –0.3 days per year (CI = 0.5) when data from Granite Canyon and Point Vicente were combined ($n = 15$). However, there was no apparent trend in data from

Granite Canyon alone ($p = 0.33$; $n = 7$), so the appearance of a trend in the combined data may be an artefact of sighting effort in the beginning of the first few seasons at Point Vicente when volunteers had not yet fully developed their search images for whales early in the migration.

Peak dates

Table 1 and Fig. 3 present median (peak) dates from Granite Canyon between 1967/68 and 1997/98, and Table 2 applies observed and calculated dates to the primary observation stations along the gray whale's migratory route. There has been a change in the median dates that the migration passes Granite Canyon: prior to 1980, median sighting dates ranged from 4 to 13 January, and after 1985, median dates ranged from 12 to 18 January (Table 1; $p < 0.001$). This change occurred in spite of the consistency in survey protocol and analytical methods (see 'Methods' above). Census start dates have ranged from 8-18 December ($\bar{x}$ = 12 December prior to 1980 and 11 December after 1985); end dates have ranged from 2-23 February ($\bar{x}$ = 7 February prior to 1980 and 14 February after 1985). These start and end periods have so few sightings that any differences in effort between years will have only a minimal affect on the modelled distribution.

There are various approaches that could be used for describing the change in median dates across this period. Because there was a hiatus in counts between 1980 and 1985, it is convenient to compare the data from either side of this break. There were no significant trends prior to 1980 ($p = 0.36$) nor after 1980 ($p = 0.46$). Buckland and Breiwick (2001) used 10 January as the typical passage date prior to 1980 with an average change of approximately one day every three years since then (using available data through 1987/88); however, from the data presented in their table 4, it appears that prior to 1980 the typical date was actually 8 January (median = 8.2; mean = 8.4; CI = 1.3) rather than 10 January. When including data since 1987/88, there is an apparent shift in dates rather than a trend (Fig. 3), such that the median migration date is now about one week (6.8 days; CI = 2.0) later than prior to 1980, i.e. it now occurs on 15 January (median = 15.0; mean = 16.8; CI = 1.7). A Wilcoxon Rank Sum Test shows that the 1day/3yr calculation does not explain the observed data ($p < 0.01$; i.e., reject H_0: $\Delta = 0$) as well as does the shift in the timing ($p = 0.30$; i.e. there is no significant difference between the observed data and the two respective median dates). Accordingly, a median date of 8 January has been used for the estimated peak of southbound migrations at Granite Canyon prior to 1980, and a median of 15 January has been used for years following 1980. This shift in migratory dates follows a climatic 'regime shift' in the North Pacific Ocean in the mid or late 1970s (Francis *et al.*, 1998; Niebauer, 1998) and may be somehow related.

Instead of using the obvious break in the data between 1980 and 1985, dates may be selected where there is an apparent trend. For instance, from 1975-1984 there is a distinct linear regression ($p = 0.028$). This does lend itself more closely to the dates of the climatic regime shift, but the undulating nature of the data makes this selection of dates somewhat arbitrary, so the analysis here will treat 1980 as the approximate time of the change in migratory timings. If there were data for the years between 1980 and 1985, this change might appear as a trend instead of a shift. It is assumed that if whale travel speeds do not change significantly between years and that the onset of the migration is always at about the same time (cued, perhaps, by something as regular as photoperiod), then the apparent changes in median sighting dates (Fig. 3) may be due in part to differences in the median locations of whales prior to the start of their migration.

Duration of the migration

Most of the southbound migration occurs within approximately two months, much shorter than the three-month long northbound migration (Pike, 1962). The latest full study at Granite Canyon, from 13 December 1997 to 24 February 1998 (Hobbs and Rugh, 1999), covered 74 days during which whales were passing on virtually every day. At Point Vicente, there was an average of 73 days (ranging 62-81 days) between the first and last southbound sighting (ACS/LA, unpublished data). At Granite Canyon, there was an average of 33.5 days (CI = 2.0) during which 80% of the sightings occurred (using the difference between dates when 10% and 90% of the annual sightings were recorded). At Point Vicente, 80% of the sightings occurred across a period of 42.6 days (CI = 3.5). The date when 90% of the annual sightings were recorded currently occurs on 1 February at Granite Canyon (CI = 2.8; 17 days after the median date) and on 12 February at Point Vicente (CI = 2.7; 25 days after the median date)[2].

End of the migration

Annual dates on which 90% of the whales passed Granite Canyon are now 6.5 days later than they were prior to 1980 (Fig. 3; data from Buckland and Breiwick, 2001; NMFS, unpublished data; $p = 0.01$, comparing dates before and after 1980). Data from Granite Canyon show no apparent trends prior to 1980 ($p = 0.14$) or after 1980 ($p = 0.50$), nor was there a trend in dates at Point Vicente from 1986-99 ($p = 0.48$; data from Schulman-Janiger, 1999)[2].

The date that marks the transition between the southbound and northbound migrations, referred to as the turnaround date, has not changed since 1985 ($p = 0.40$; ACS/LA, unpublished data). Not only through the years, but at every location where data have been collected, there has been a phenomenal consistency in turnaround dates. In Laguna San Ignacio - at the terminus of the migration for many whales - mean maximum counts of whales was on 15 February (CI = 21 days; Jones and Swartz, 1984). Data collected in the 1950s near San Diego showed that the end of the southbound migration and beginning of the northbound migration occurred in mid-February (Gilmore, 1960). All turnaround dates at Point Vicente have occurred between 8-21 February, averaging 15 February (CI = 1.9; data from Schulman-Janiger, 1999). At Granite Canyon, observations generally continued only until counts were very low, which usually meant there was no record of the start of the northbound migration; however, in years when sightings continued until late February, the turnaround date appeared to be in mid-February (e.g. Rugh *et al.*, 1999). In Oregon, during 1979-81, the last southbound migrants were seen 1, 4 and 9 February and the first northbound migrants were seen 27, 21 and 22 February, respectively (Herzing and Mate, 1984); the average mid-point between these dates was 14 February. Of course, not all whales start or end their migration on the same date, but it does appear that for most whales the urge to migrate south has dissolved by mid-February. The consistency of these turnaround dates (all in mid-February) across the past 30 or more years and at all

[2] Data for the end of season cannot be combined between these sites because at Granite Canyon counts were terminated in mid-February or whenever the southbound migration seemed to be complete, while at Point Vicente counts continued through both the southbound and northbound migrations.

locations is suggestive of a very regular migratory cue - such as a change in photoperiod (day lengths) - which would end one migration and begin the next wherever the whales might be, even if they had not completed the migration south.

Climatic regime shift and migratory timing

Although the initiation and termination of the gray whale southbound migration may be triggered by photoperiod, the shift in migration dates after 1980 indicates there could be some other environmental factors that affect migratory timing. Perhaps the oceanographic regime shift in the late 1970s (Francis *et al*., 1998; Niebauer, 1998) influenced availability of food resources and resulted in a redistribution of whales on the feeding ground, which then effected a delay of one week in median migration dates. This would suggest a shift in location of about 1,000km (6.8 days $\times$ 147km/day), equivalent to a displacement from the southern Bering Sea to the Chirikov Basin. Such a shift in distribution is not readily visible in the available data: although in 1958-81 there were large groups of gray whales seen in the central and southern Bering Sea (between St Matthew and Nunivak Islands and along the north coast of the Alaskan Peninsula), large groups were also seen in the Chukchi Sea during this period (Braham, 1984). The change in migratory dates may have resulted from a northward relocation of the population partly through greater dispersion of whales, some being found far to the northwest in the Siberian Sea (e.g. Miller *et al*., 1985) or to the northeast in the Canadian Beaufort Sea (e.g. Rugh and Fraker, 1981; Richardson, 1999). As the population increases in abundance, increased competition for food resources is expected. This may lead to a wider distribution of whales as their search for food covers increasingly greater areas (Yablokov and Bogoslovskaya, 1984; Stoker, 2001), and they subsequently would have farther to travel when migrating south. There appears to be a significant decrease in available biomass, perhaps because this population of gray whales is approaching carrying capacity (Highsmith and Coyle, 1992; Coyle and Highsmith, 1994; Stoker, 2001). However, in spite of their need to rebuild fat reserves and in spite of the vagaries of arctic weather and sea ice, gray whales continue to migrate south each year with remarkable regularity.

ACKNOWLEDGEMENTS

Members of the Scientific Committee of the IWC expressed particular interest in having this study completed following the considerable media attention that came from sketchy reports of an anomalous migration in the winter of 1998/99. Accordingly, the National Marine Mammal Laboratory (NMML) of the Alaska Fisheries Science Center, NMFS, NOAA, provided support for this study. Because NMML did not conduct a census of the southbound migration in the winter of 1998/99, we relied heavily on results from the American Cetacean Society's Los Angeles Chapter (ACS/LA) census at Point Vicente. ACS/LA directed teams of volunteers doing systematic searches throughout all daylight hours for the entire duration of the southbound and northbound migrations, as they have been doing for many years. Technical edits were provided by James Lee and Gary Duker of the Alaska Fisheries Science Center, NMFS, NOAA. Reviews of this document were made by David Withrow and Marilyn Dahlheim, both biologists at NMML, and Douglas DeMaster, Director of NMML. Sue Moore, Leader of the Cetacean Assessment and Ecology Program at NMML, made extensive revisions and helped streamline this document. Wayne Perryman, of the Southwest Fisheries Science Center, NMFS, NOAA, and an anonymous reviewer provided helpful directions for strengthening this manuscript.

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