Evaluation of nutritive condition and reproductive status of migrating gray whales (*Eschrichtius robustus*) based on analysis of photogrammetric data

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ABSTRACT

Vertical aerial photographs were collected of gray whales migrating along the California Coast between 1994 and 1998 to readdress some published findings on the biology and life history of this population based on examination of specimens. For each whale, an attempt was made to measure standard total length, the width of the whale at its widest point, the distance from the tip of the rostrum to the widest point, and the width of the flukes. For southbound gray whales, early migrants were longer on average and more likely to be parturient than those migrating later. Near-term pregnant females were wider relative to their length than other southbound gray whales. This difference was easily detected by visual inspection of the images and through statistical evaluation of length and width data. There was 100% agreement between identification of parturient females based on linear regression analysis of length and width and discriminate analysis of all measurements. Based on the proportion of parturient females to those with calves during sampling of southbound whales, the median calving date was estimated to be 13 January. Southbound calves averaged 4.6m in length; those photographed northbound in late April, at an age of about three months, averaged 7.1m. Average length for yearlings, based on combined southbound and northbound data, was 8.5m. Residuals from a regression of width on length were compared, and significant changes in the relationship were detected which were consistent with changes in nutritive condition or fatness described from examination of whales taken along the California Coast between 1959 and 1969 (Rice and Wolman, 1971). Parturient females were the widest relative to their length and northbound cows with calves were the narrowest in the sample. The relationship between length and width for migrating gray whales that were not parturient or associated with a calf, showed that southbound gray whales were significantly wider than northbound whales photographed approximately 60 days later. These results indicate that the predictable but relatively small changes in condition or fatness of gray whales associated with fasting during their winter migration can be reliably detected in measurements from vertical aerial photographs.

KEYWORDS: GRAY WHALE; PHOTOGRAMMETRY; MORPHOMETRICS; PREGNANCY; GROWTH; CONDITION

INTRODUCTION

As with most species of large cetaceans, our understanding of the basic biology and life history of the eastern Pacific population of gray whales (*Eschrichtius robustus*) is derived mainly from the examination of animals killed in fisheries. For this population, most specimens have come from the Chukotkan native fishery, which has taken gray whales in the Bering and Chukchi Seas since the mid-1930s and those animals taken under special research permits along the California coast between 1959 and 1969. Examinations of whales from the Chukotkan fishery have provided much of the basic knowledge on the growth, physiology, reproduction and food habits for this population (Zimushko and Ivashin, 1980; Bogoslovskaya *et al.*, 1981; Blokhin, 1984; Yablokov and Bogoslovskaya, 1984; Blokhin and Tiupeleev, 1987). Recently, most of the whales from this fishery have been taken from nearshore waters, and the non-random distribution of whales on the feeding grounds has biased this sample towards immature specimens and females.

In addition, 316 gray whales were taken under seven scientific research permits issued to the US Bureau of Commercial Fisheries (now the National Marine Fisheries Service) under Article 8 of the Convention of the International Whaling Commission between 1959 and 1969. Land-based catcher boats were used to capture whales which were brought to the Richmond Shore Stations (inside San Francisco Bay) in California, where external measurements and biological samples were collected. These takes were conducted to provide representative samples from both the southbound and northbound migrations. The monograph by Rice and Wolman (1971) presenting the results of this study remains the most comprehensive review of the biology and ecology of this population. Among the many findings on basic anatomy, growth and reproduction that complement the Russian studies, these authors reported partial temporal segregation by age, sex and reproductive status in migrating gray whales. They also found that gray whales experience a weight loss of between 11-25% during approximately 60 days of fasting between their southbound and northbound migrations past central California. They reported that changes in girth were better indicators of this change in condition than measurements of blubber thickness. Although they planned to sample all segments of the population, no northbound cows with calves were taken. In addition, the authors recognised that their analyses were based on data from one source, with some known biases (i.e. selection of larger whales by gunners) and they recommended that their findings be re-examined through other approaches with different biases (Rice and Wolman, 1971; Rice, 1990).

The data available from the Russian and scientific catch are supplemented by information from stranded gray whales, a few that have been captured live, as well as a small set of body measurements made from photographs. Although most of these samples support the findings from the studies involving direct takes, there are some notable exceptions. For instance, size at birth estimated from stranded calves, with the exception of a very recent sample (Pacheco, 1998), is generally smaller than that taken from near-term foetuses or calves captured live (Norris and Gentry, 1974; Bryant *et al.*, 1984; Jones and Swartz, 1984; Sumich, 1986). In addition, growth rates for young gray whales based on stranded and captive whales indicate that growth is much slower than that projected from fishery data (Sumich, 1986). The reason for this apparent difference in estimated growth

remains unresolved, although it may be related to the possibility that weaker, slower growing calves are more prone to stranding.

This paper presents the results of an aerial photogrammetric sampling programme that was modelled after the effort conducted more than 25 years ago by Rice and Wolman (1971). Migrating gray whales were photographed as they passed along the California coast and the field effort was scheduled in an attempt to collect representative samples of the southbound and northbound migrations. The field season was extended into April and May to include the northbound gray whale cows with calves. Measurements from vertical photographs of gray whales were examined for evidence of temporal segregation during the migrations, for indications of reproductive status, and for changes in shape that may reflect reduction in nutritive condition during the winter migration. The goals of the study were to determine whether data from high resolution aerial photographs could be used to detect changes in nutritive and reproductive condition in gray whales, and to review other findings based on examination of fishery and stranded specimens.

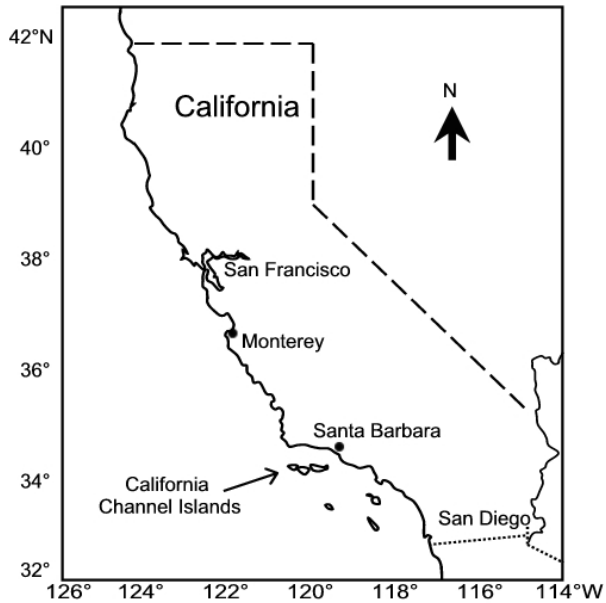


Fig. 1. Aerial photographs of gray whales were taken around the California Channel Islands and along the central California coast between Santa Barbara and Monterey.

MATERIALS AND METHODS

The measurements presented in this paper were made on vertical aerial photographs of gray whales taken near the coast between Monterey, California and the California Channel Islands (Fig. 1). Photographing of gray whale cows and calves began during the northbound migration in 1994 and continued each spring through 1998. In 1996, sampling of northbound gray whales was expanded to include the adults and juveniles that comprise the first phase of this migration; this photographic sampling continued in 1997 and 1998. In the winters of 1997 and 1998, gray whales were also photographed during the southbound migration. Since migrating gray whales reportedly segregate by age, sex and reproductive condition during the southbound and the first phase of the northbound migrations (Rice and Wolman, 1971; Poole, 1984), the field effort was scheduled to span the peaks of these migrations (Table 1). Although the southbound migration is characterised by a steep and predictable peak in migration rates (Rugh *et al.*, 2001), the northbound migration is much more diffused and selection of a peak date can be somewhat arbitrary (Pike, 1962; Herzing and Mate, 1984; Poole, 1984). The northbound peak date for this study was selected as 14 March based on the studies cited above and the observations of gray whale migration rates within the Southern California Bight.

Aerial photographs were taken with a 126mm format KA76 military reconnaissance camera (image size 114mm × 114mm) that was mounted vertically over a hatch in the deck of a *Partenavia* aircraft. A bubble level was attached to the top of the camera and the orientation of the camera was adjusted during each pass to ensure that the photographs were collected vertically. When the camera fired, a data acquisition system recorded an altitude reading from a *Sperry* 300 series twin transducer radar altimeter, and a position from a GPS unit. Gray whales were photographed from altitudes between 135 and 245m. The majority of the photographs (about 98%) were taken with *Kodak* Aerecon Plus-X aerial film. Two colour transparency films, *Kodak* MS 2448 and *Kodak* HS SO359, were tested early in the experiment and the resolution of the black and white negatives was consistently superior to the colour transparencies.

Table 1

Dates of aerial photographic missions to sample southbound and the first phase of the northbound migrations of gray whales. This sampling was conducted around the California Channel Islands.

Migration	Sampling periods		
	Early	Peak	Late
Southbound migration	6, 7 Jan. 1997 30,31 Dec. 1997	17, 18 Jan. 1997 17 Jan. 1998	29, 30 Jan. 1997 23, 24 Jan. 1998
Northbound migration (Phase 1)	11 Mar. 1998	14, 15 Mar. 1996	25, 26, 27 Mar. 1996 18, 19 Mar. 1997 20 Mar. 1998

Measurements from photographs

The black and white negatives were reviewed on a light table and the whales selected for measurement were those clearly visible and swimming near the surface. If acceptable photographs were available from more than one pass over a pod of whales, natural marks were used to identify individuals and thus avoid inclusion of duplicate measurements from the same whale. A high resolution digital camera (*Diagnostic Instruments* SPOT) mounted above the light table was used to capture images of individual whales which were then transferred to a computer. The whales were measured with either *Image*, a software package developed by the *National Institutes of Health*, or *Image Pro Plus*, produced by *Media Cybernetics*. The distances measured on the computer screen were multiplied by the scale of the photograph (scale = altitude/lens focal length) to convert them to true or ground distances. Because data from radar altimeters are generally precise but may be biased, calibration experiments were conducted each season to determine the sign and magnitude of any bias in the recorded altitude readings. In these experiments, several photographic passes were made over pipes of known length that were towed offshore. These experiments were conducted over water to avoid the small positive bias that has been reported from calibration experiments conducted over targets on land (Koski *et al.*, 1992). Correction factors were then developed for recorded

altitudes based on linear regression of recorded altitude and altitude calculated from target measurements, as shown in Fig. 2 (Perryman and Lynn, 1993; Gilpatrick, 1996; Perryman and Westlake, 1998).

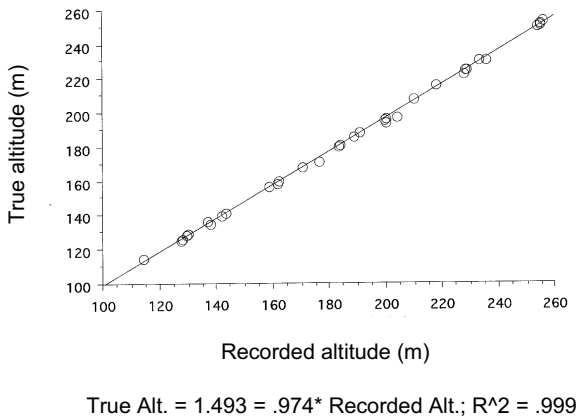


Fig. 2. The altimeter calibration equation calculated for altimeter readings recorded during photographic missions flown in 1997. True altitudes were determined by measurements of targets of known length.

For each whale, an attempt was made to measure total length (L_t); the width of the whale at the widest point (W_m); the distance from the tip of the rostrum to the widest point (RW_m); and fluke width (F_w) as shown in Fig. 3. After making several photographic passes over a whale, many excellent images were often achieved in which these characters could be accurately measured. The following criteria were used for selecting the best measurements. Because the normal movements associated with swimming can make L_t, RW_m, and F_w appear smaller when seen from above, the largest measurement was selected when more than one measurement was obtained from the photographs. Measurements of W_m can be either positively or negatively biased as the whale bends its body to begin a dive or from distortion caused by waves created as a whale slides along the surface. For this feature, the measurement was selected from the photograph in which the body of the whale was not flexed and both sides of the whale were most distinct.

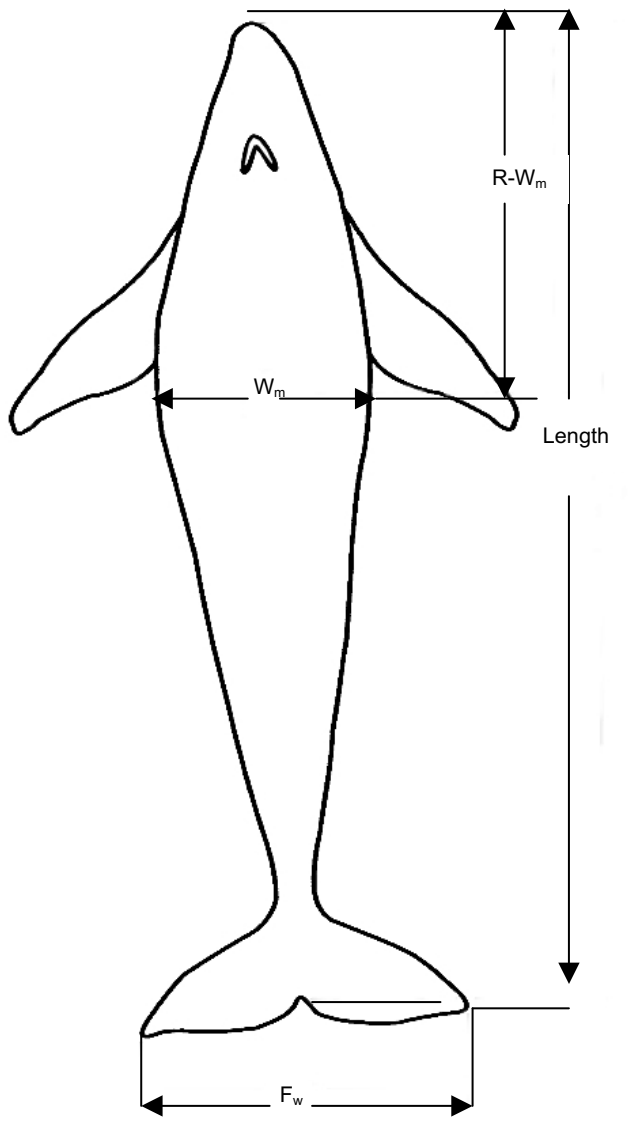


Fig. 3. Features measured on vertical photographs of migrating gray whales.

Accuracy and precision

A common concern in any study based on measurements of continuous variables is whether the measurements are accurate (reflective of the true distance measured) and precise (differences between repeated measures of the same feature on the same individual are small). To test the accuracy of the measurements, two 7.6cm diameter sections of plastic pipe were towed offshore and photographed from the range of altitudes used while photographing gray whales. The lengths of the two pipes were approximately that of a cow (12.02m) and a calf (6.02m). The pipes were measured with the same image capture and measurement system used for measuring whales. All measurements of these targets were performed by individuals who did not know the true lengths of the targets. The average lengths from the target photographs were 12.04m ($n = 41$; $s = 0.169$) and 6.04m ($n = 41$; $s = 0.093$). Measurement accuracy in the test was within 1% for each pipe and coefficients of variation (CV) for the two sets of measurements were 0.014 and 0.015 for the longer and shorter pipes respectively.

Although the target measurements indicate that lengths of semi-rigid objects floating at or near the surface can be determined within an acceptable degree of accuracy and precision, these data do not replicate the additional variance found in repeated measures of mammals that flex their bodies as they swim. To test the precision of the measurements of whales, the coefficients of variation (CV) were calculated for a series of whales that had been photographed several times. CVs were only calculated for whales that were measured on at least three photographs. For L_t, W_m and F_w, the averages of the CVs were 0.020, 0.035 and 0.030 respectively. The level of sampling precision and tendency for measurement error to represent a larger proportion of shorter measurements are consistent with other photogrammetric studies on large cetaceans (Best and Rüther, 1992; Koski *et al.*, 1992; Angliss *et al.*, 1995).

Analyses

The measurements of adult and juvenile gray whales were divided into strata based on whether they were photographed before, during, or after the peak of the migrations (Table 1). The means of the lengths of whales from these strata were then compared to look for evidence of the partial temporal segregation in migrating whales reported by Rice and Wolman (1971). For instance, asymptotic length for female gray whales is larger than for males, and the average length

for a sample of whales that included a disproportionate number of adult females would likely be longer than the average of a sample composed of mostly adult males or a combination of males and older juveniles. In tests of the hypothesis of homogeneity in length between strata, observations were truncated at 10m to eliminate the few very small juveniles that were found in some strata. Tukey/Kramer tests were used for post hoc comparisons, because the power of this test remains high when sample sizes are unequal (Day and Quinn, 1989).

The following assumptions were made about the age, sex and reproductive condition of individual whales based on their size, association with a smaller whale or their shape. It was assumed that all whales < 8m in length and swimming in close association with a large whale (> 11m) were calves. The larger whale swimming in close association with a calf was identified as the mother of that calf, and is referred to as a cow or an adult female. Some whales were also classified as parturient or near-term pregnant females based on the relationship between their length and width. These animals are referred to as 'parturient females' in the text to distinguish them from other females that may have recently become pregnant.

It was noted that the ratio of parturient to post-partum female gray whales changed as the southbound migration progressed. A logistic model was fitted to the proportion of those female gray whales identified as reproductive (cows with calves and parturient females) that were post-partum for missions flown on 30-31 December, 6-7 January, 17-18 January and after January 22nd. From this, the median birth date for this population was estimated. The confidence intervals for this estimate were estimated by anchoring the model at 100% for the last point, bootstrapping each of the other points and refitting the model 999 times. This estimate of median birth date is dependent upon the assumption that calving is dependent upon the duration of the pregnancy, not the geographic location of the near-term pregnant female. This assumption is supported by recent findings suggesting a relationship between the shift towards later migrations in recent years and an increase in sightings of calves along the California coast (Shelden *et al.*, 1997; Rugh *et al.*, 2001; Buckland and Breiwick, 2002).

The measurements included data that reflect whale size (L_t) and shape (W_m, RW_m). In order to compare sets of shape measures between groups of whales that differ in size, it was first necessary to remove the effect of size on shape. A least squares regression technique was selected that has been shown to be very effective in removing the effect of size in morphometric studies (Atchley *et al.*, 1976; Reist, 1985) and in evaluation of condition indices for harbour porpoise (Read, 1990). A linear regression of each shape parameter was performed on length and the resulting residuals from these regressions were used as size-free variates for normal hypothesis testing. Tests were conducted between groups of whales that were identified based on their direction of migration or reproductive condition (cows and parturient females).

The main reason for comparing measures of shape was to determine whether documented seasonal changes in gray whale nutritive condition could be detected in measurements from photographs. Gray whales rely on the oxidation of stored fats to support their metabolic needs during the migration, and thus are thinner when they return to their feeding grounds in the Arctic than when they departed (Rice and Wolman, 1971; Blokhin, 1984). Rice and Wolman (1971) reported that the changes in condition from fatter southbound to thinner northbound gray whales were best reflected in changes in girth. W_m was used as the proxy for girth and an investigation of whether changes in condition were reflected in changes in the relationship between length and width was calculated. The location of the point of maximum width (RW_m) was also compared to determine whether this measure varies with reproductive or nutritive condition.

Several multivariate techniques were used during the exploratory phase of the analyses, but only the results of one discriminant analysis are reported in this paper. Multivariate analyses were performed in *MiniTab* (release 10) and all other analyses were done in *Statview* (version 5). Differences were considered statistically significant if $P < 0.05$.

RESULTS

Southbound gray whales

The lengths of 303 southbound gray whales were measured from the photographs collected in 1997 and 1998. The measurements were divided into three strata based on the timing of the photographic missions relative to the peak of the southbound migration (Fig. 4). Calves of the year were found in all three strata and represented about 5% of the total length sample. These data probably overestimate the proportion of calves in the southbound migration because cows with calves spend more time at the surface and were thus more easily detected from the air. Average length for the southbound calves was 4.6m ($n = 15$; range 4.3-4.9m), and average length for the accompanying cows was 12.2m ($n = 15$; range 11.4-13.0m). No significant correlation was found between the length of a cow and her calf ($r = 0.261$; $P = 0.35$). Unlike calves, the very small juvenile gray whales which averaged 8.5m ($n = 5$; range 8.1-8.8m) were all photographed late in the migration. The length samples in the three strata were truncated at 10m; the null hypothesis that the means of the three strata did not differ was tested and rejected ($F = 9.948$, $P < 0.001$). *Post hoc* tests found that whales photographed prior to the peak of the migration were longer on average than those from the peak or post-peak strata (Table 2).

While reviewing the photographs of southbound gray whales, it was noted that some of the longer whales (> 11m) were exceptionally wide relative to their length (Fig. 5). These wide-bodied whales were most common early in the southbound migration (Fig. 6) and were suspected by the authors to be near-term pregnant females. A technique commonly used to identify outliers in regression analysis was selected to separate these parturient females from the remainder of the sample.

L_t and W_m measurements for whales photographed late in the migration (when no exceptionally wide whales were detected) and those < 11m in length were used to build a linear model for the length and width relationship for whales that fall within the main cluster of points (i.e. not exceptionally wide) shown in Fig. 6. Measurements of whales swimming with a calf were excluded from this exercise. The standard deviation of the residuals for this regression of L_t (x) and W_m (y) was calculated and then the relationship between width and length was compared for the southbound whales not used to construct the model. It was assumed that any whale whose L_t and W_m measurements produced a residual that was greater than 1.99 ($t_{(0.05)(85)}$) standard deviations from the above regression was an outlier (parturient). A total of 34 southbound gray whales were classified as parturient females based on their large positive

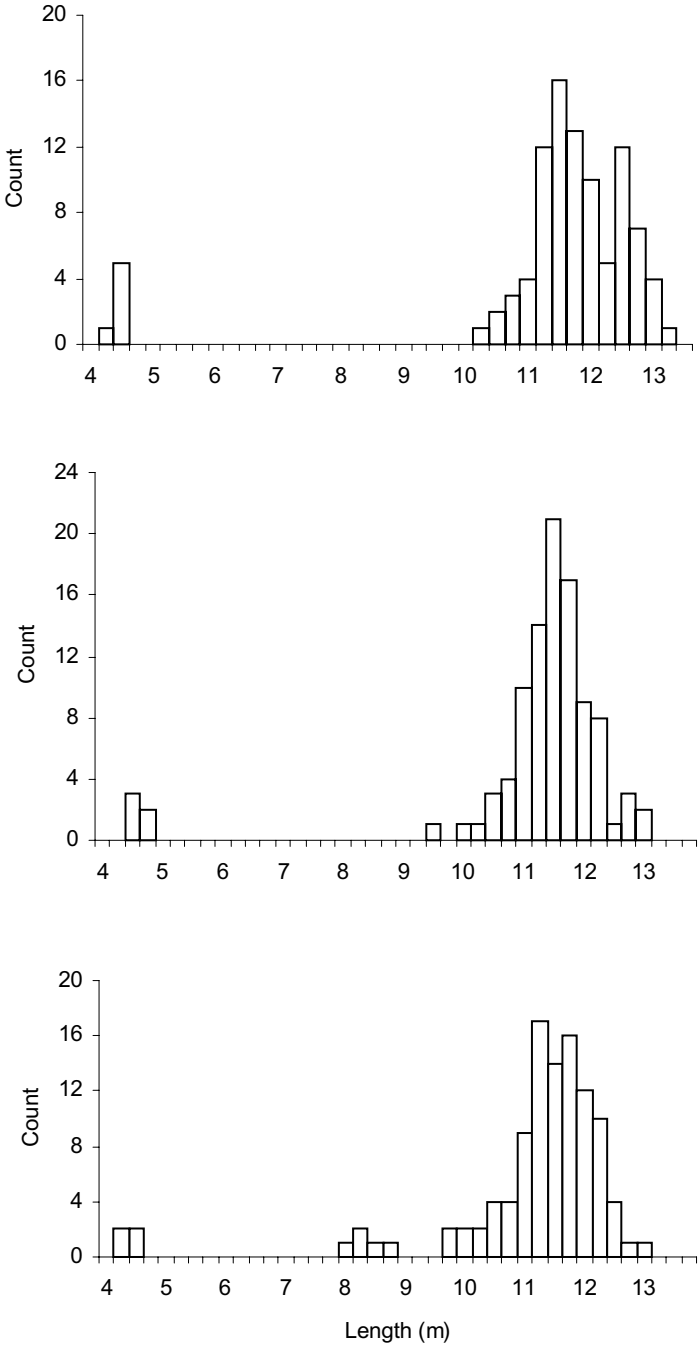


Fig. 4. Histograms of lengths for whales photographed early (12/30-1/7), near the peak (1/17-1/18), and late (1/23-1/30) in southbound migrations of 1997 and 1998.

Table 2

Results of Tukey/Kramer *post hoc* comparisons between means of lengths for gray whales >10m photographed early, near the peak and late in the southbound migration.

	Sample size	Mean (m)	Comparisons	Differences	Critical difference	P<0.05
Early	90	11.95	Early *vs* peak	0.296	0.260	Yes
Peak	95	11.65	Early *vs* late	0.479	0.255	Yes
Late	103	11.47	Peak *vs* late	0.183	0.251	No

residuals. For both the parturient and the remaining southbound gray whales sampled, there was a positive linear relationship between length and width (parturient females $F = 10.95$, $P < 0.01$; remaining southbound $F = 115.09$, $P < 0.01$) (Fig. 7).

Inconsistencies in the classification of parturient females based on L_t and W_m were investigated by performing a discriminant analysis on the full set of measurements (L_t, W_m, RW_m and F_w) for all southbound whales > 10m. A cross-validation technique was used in the analysis to reduce the probability of overly optimistic matches with the original classifications. There was 100% agreement between classifications based on the regression technique and discriminant analysis.

In late December, about 47% of the southbound gray whales photographed were either 'parturient' or accompanied by a calf. By the end of January, parturient females and females with a calf decreased to 2% of the photographic sample. While the number of parturient females and cows decreased, the proportion post-partum (cows with calves/parturient females + cows with calves) increased steadily as the migration progressed. The data were divided into four samples (30-31 December, 6-7 January, 17-18 January and after 22 January) and the proportion post-partum was calculated for each. A logistic model was fit to these four points (Fig. 8) and it was estimated that the median birth date for parturient gray whales passing through the Channel Islands was 13 January (95% confidence intervals 12-15 January).

Northbound gray whales

Phase 1- adults and juveniles

Nine missions were flown to sample the adult/juvenile phase of the northbound migration; 273 whales were measured from the photographs. The data were divided into three strata based on the dates of the photographic mission relative to an estimated migration peak of 14 March (Fig. 9). Length strata were truncated, at 10m and the null hypothesis that the means of the samples were equal was tested. Tests revealed no difference in average length for whales photographed before, during, or after the peak of the northbound migration ($F = 0.108$, $P = 0.898$). The relationship between length and width was consistent across strata. The six small juveniles, mean length 8.5m (range 8.29-8.93m) photographed (including one from Phase 2) were found near the peak or late in the migration. No cow-calf pairs were found in this phase of the migration.

Phase 2 —cows and calves

Northbound gray whale cows and calves were photographed between mid-April and early May each year from 1994-1998 (Figs 10a and 10b). Calves averaged 7.10m in length ($n = 112$) and ranged from 5.5-8.1m. Cows averaged 12.4m ($n = 98$) and ranged from 11.2-13.9m. A significant positive linear relationship ($b = 0.245$, $p = 0.002$) was found between the length of a cow and the associated calf (Fig. 11). Thus, longer cows were associated with longer calves.

Adult females

Due to their shape (southbound whales only) or association with a calf, 49 southbound and 98 northbound gray whales were classified as adult females. Southbound adult females were somewhat shorter on average (12.1m) than those photographed northbound (12.4m) (t-test, $P = 0.012$).

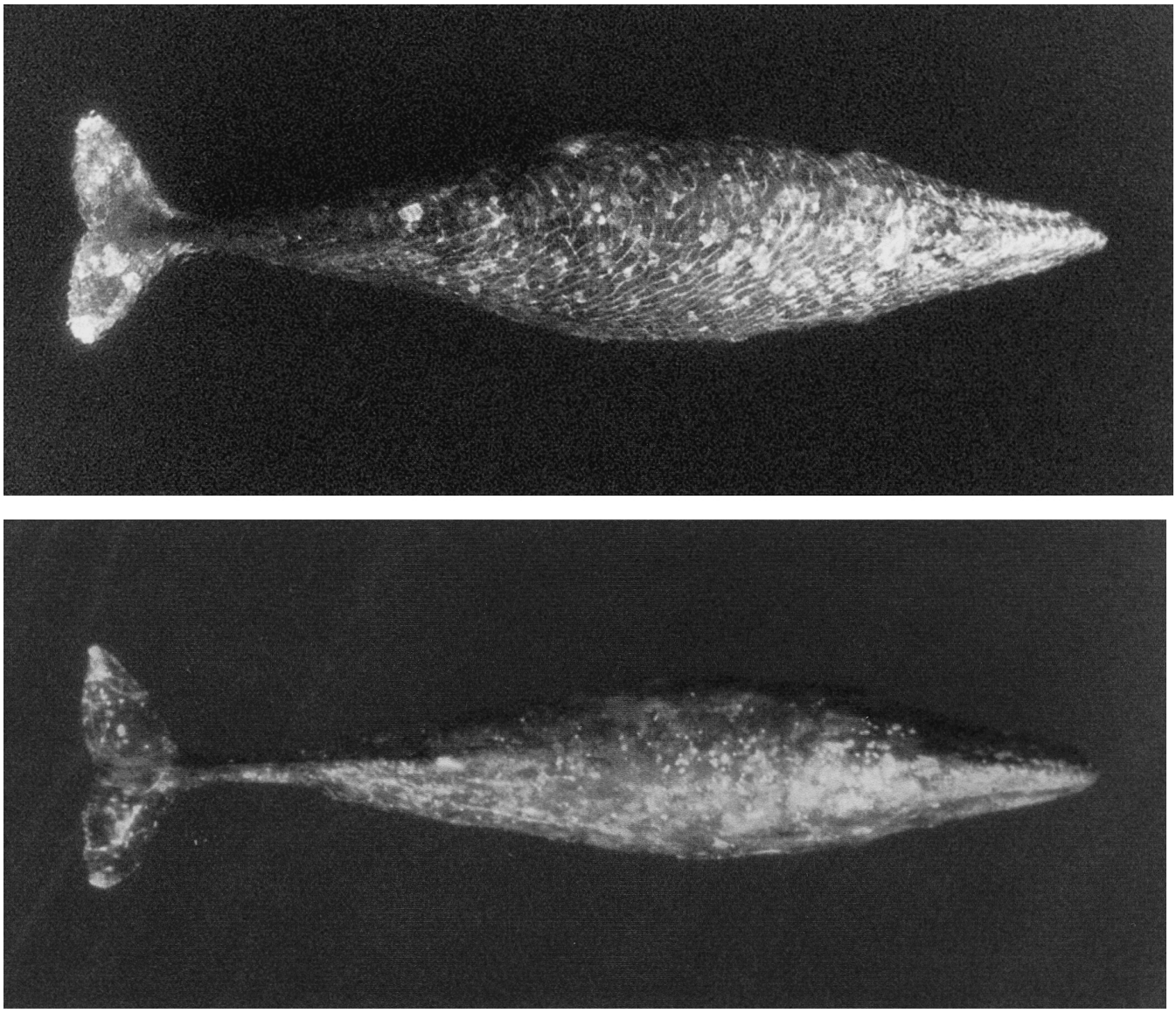


Fig. 5. Vertical photographs of two southbound gray whales illustrating the difference in shape between very wide whales and those more fusiform in shape.

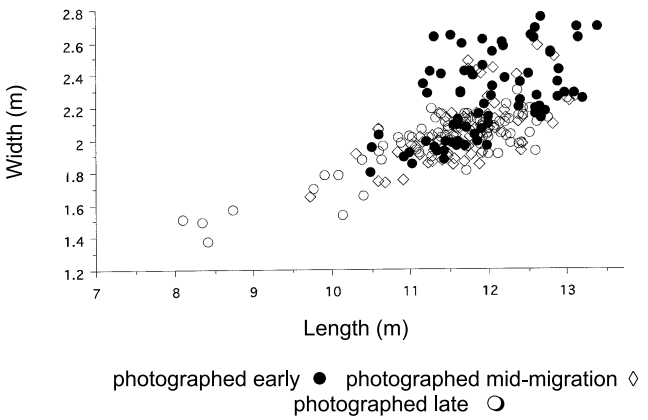


Fig. 6. Plot of length and width of southbound whales photographed early (●), near the peak (◇) and late (○) in the southbound migrations of 1997 and 1998.

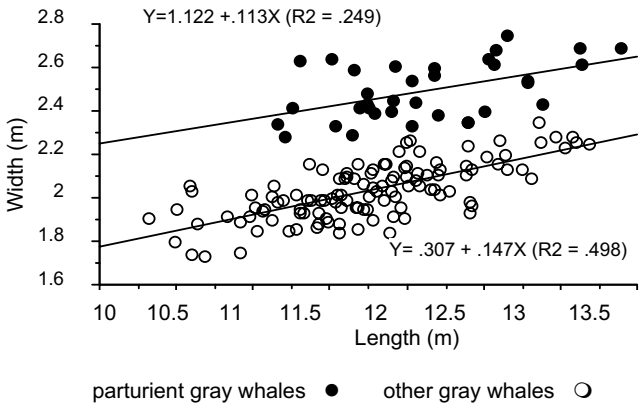


Fig. 7. Plot of length and width measurements for parturient (●) and other southbound gray whales (○). Measurements of southbound gray whales accompanied by calves were excluded from this dataset. Lines represent least squares linear regression fits to each dataset.

Possibly younger, shorter females that were parturient or had given birth during the southbound migration are more likely to lose their calf and thus were not classified as cows in the northbound sample.

Length at one year

Length distributions from measurements of south and northbound gray whales (Fig. 12) included a group of very small juvenile whales that were separate from the main

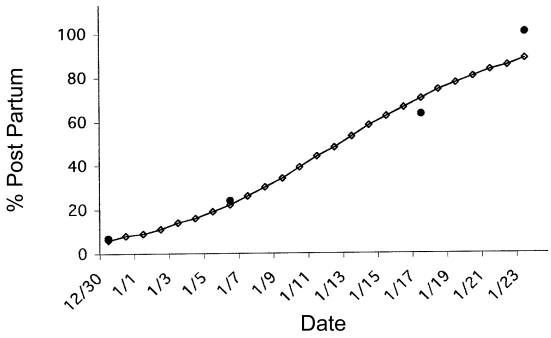
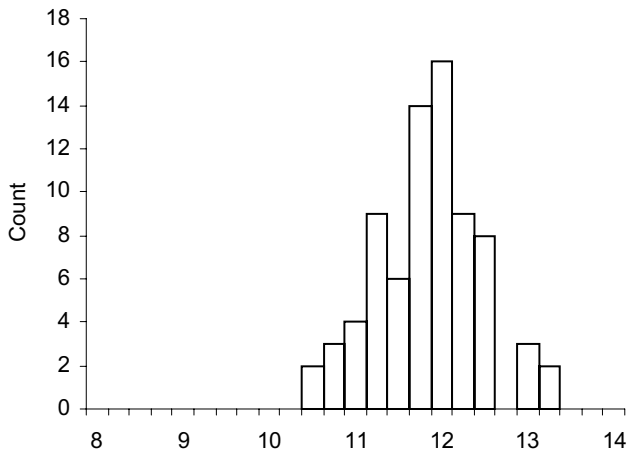
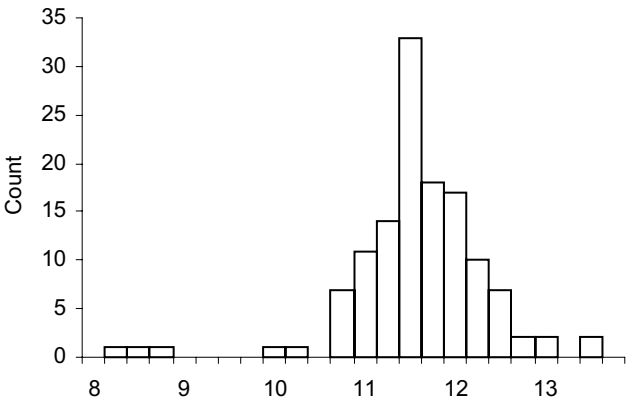
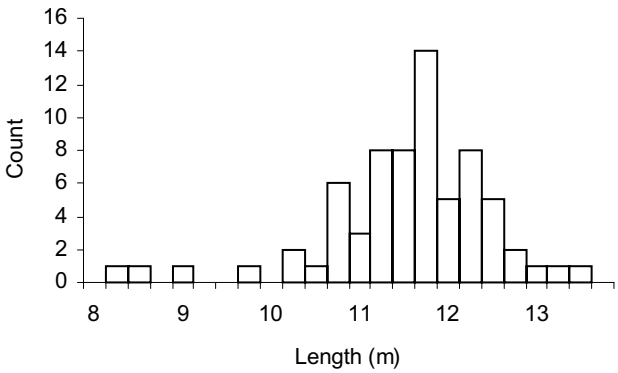


Fig. 8. Fit of a logistic model to the fraction of reproductive female gray whales (parturient and cows with calves) that were post-partum for the four sampling periods in 1997 and 1998.

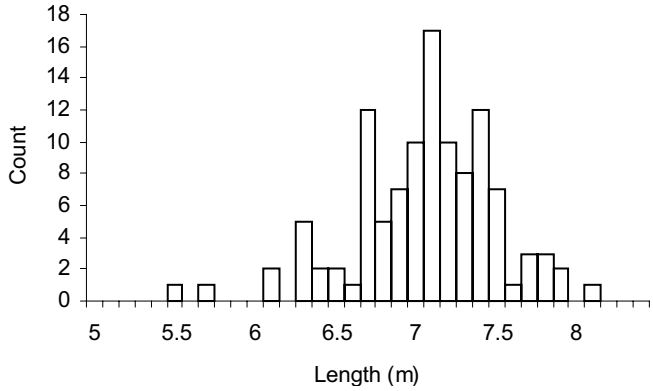






early = 3/11 peak = 3/14-3/18 late = 3/20-3/25

Fig. 9. Histograms of lengths for whales photographed early (3/11), near the peak (3/14-3/18), or late (3/20-3/25) in northbound migrations of 1996-1998.



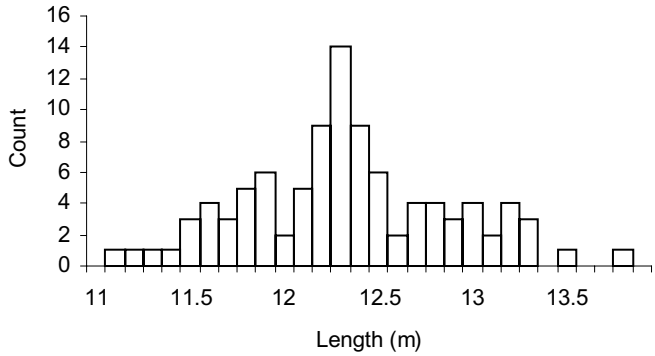


Fig. 10a and b. Histograms of lengths of calves (a) and cows (b) photographed migrating northbound along the central California coast between 1994 and 1998.

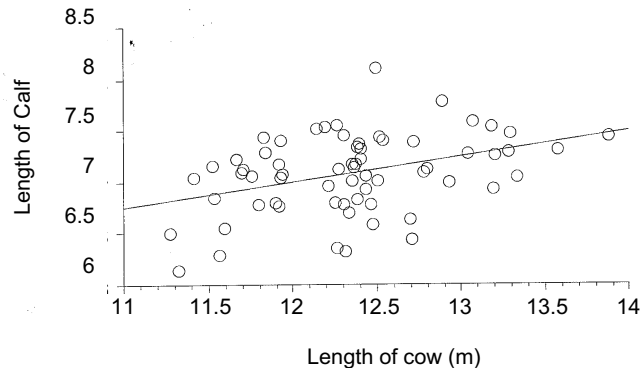


Fig. 11. Relationship between length of northbound cows and their associated calves measured from vertical aerial photographs. Line in the figure is the least squares linear regression fit to these data.

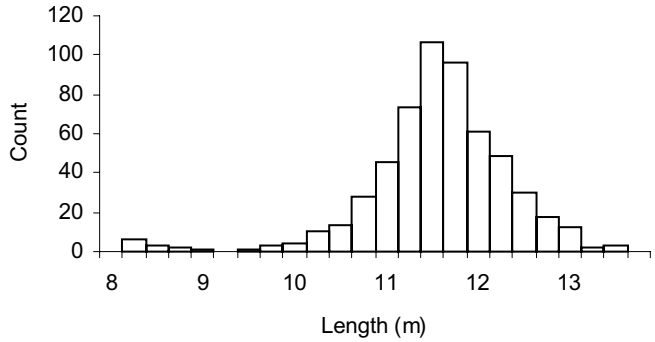


Fig. 12. Lengths of all southbound and northbound gray whales, with the exception of calves of the year, measured from vertical aerial photographs.

distributions. These small juveniles represented about 2% of the total dataset, and were probably yearling gray whales. The average length for each sample, and thus the combined sample, was 8.5m ($n = 11$; range 8.1-8.9). The categorisation of these yearlings was based on the assumption that the hiatus in length distribution represents the difference in length between one- and two-year-old gray whales. The sample probably underestimates the proportion of one-year-olds in the migration because these whales were small, difficult to detect from the air, and were generally found swimming alone.

Nutritive condition-fatness

For all whales (except calves), a linear regression was fitted to the length and width measurements and the residuals of this least squares fit were saved as derived shape variables. The means of the residuals (ANOVA) for parturient females, southbound cows, southbound adults and juveniles, northbound adults and juveniles, and northbound cows were compared and the null hypothesis that they were the same was rejected ($F = 317.8$, $P < 0.001$). Tukey/Kramer *post hoc* tests revealed that all samples differed significantly (Fig. 13). These results indicate that gray whale condition, as indexed by the relationship between L_t and W_m, declined steadily during the winter migration and that northbound lactating females were the narrowest or in the poorest nutritive condition of all categories.

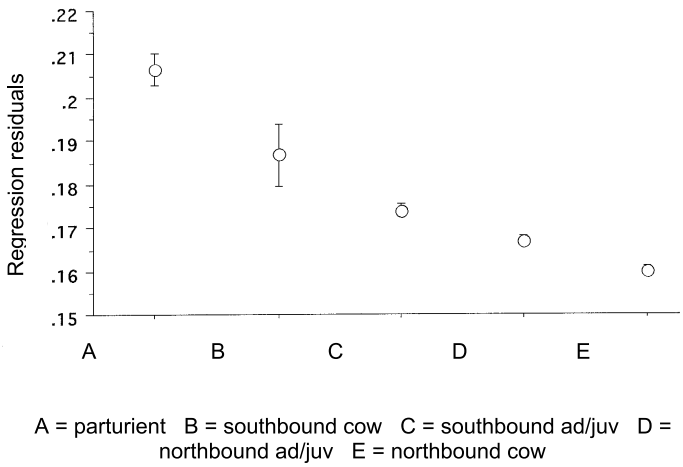


Fig. 13. Plot of means of residuals from regressions of length (x) on width (y) for all gray whales for which these two features could be measured. Calves of the year were excluded from this dataset. Error bars are + 2 standard errors of the mean values.

To test the hypothesis that RW_m was the same between the five categories of whales described in the previous paragraph, a linear regression of RW_m on L_t was performed. The means of the resulting residuals were then compared (ANOVA). The location of W_m was found to vary significantly between whale categories ($F = 40.046$, $P < 0.001$). Results of Tukey/Kramer *post hoc* tests indicated that for parturient females and southbound cows (the two categories of whales that were widest relative to their length) the location of their greatest width was farther from their rostrum than for all other categories of gray whales (Fig. 14). For the near-term pregnant females the foetus probably accounts for some of this change in shape, but for southbound cows these data indicate that the extra fat carried by these females was reflected in a change in width that is closer to the fluke than in other southbound or northbound whales.

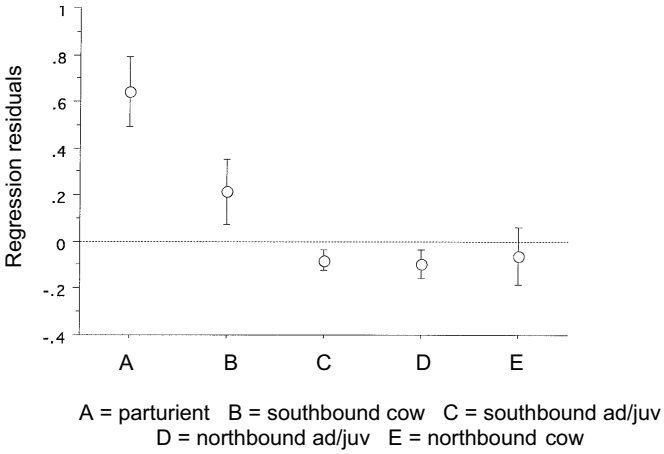


Fig. 14. Plots of means of residuals from regression of length (x) on distance from the tip of the rostrum to the widest point (y) on all gray whales for which these two features could be measured. Calves of the year were excluded from this dataset. Error bars are + 2 standard errors of the mean values.

DISCUSSION

The findings of partial temporal segregation in southbound gray whales by size and reproductive condition are consistent with those published by Rice and Wolman (1971) from analysis of whales sampled through a hunt over 25 years earlier. Early migrants were longer on average and more likely to be parturient than those passing later. Small juveniles were most common after the peak of the migration. Although no southbound cow/calf pairs were located during Rice and Wolman's (1971) study, in this study calves represented about 5% of the southbound sample. Shelden *et al.* (1997) found that up to 4.4% of the southbound gray whales sighted during aerial surveys near Monterey Bay were neonates and suggested that the apparent increase in births north of the lagoons may be associated with the delays in the migration reported over the past few decades (Rugh *et al.*, 2001; Buckland and Breiwick, 2002).

The median calving date within the Southern California Bight was estimated as 13 January. This date falls between the median calving date estimates of 10 January by Rice and Wolman (1971) based on foetal growth rates, and 27 January proposed by Rice *et al.* (1981) from the temporal distribution of calves in Laguna Ojo de Liebre, Mexico. Although the estimate 13 January date for gray whales is the only estimate based on counts of parturient and recent post partum females, its validity for the eastern North Pacific population depends on the untested assumption that the probability of a near-term female giving birth is more related to the duration of her pregnancy than to her location.

Making the assumption that a female mammal is pregnant, based on her shape alone, can be risky. However, the identification of parturient female gray whales from the relationship between their length and maximum width is supported by several findings made from the examination of specimens taken in fisheries. Fishery data revealed that near-term pregnant gray whales had greater girth to length ratios than any other group of southbound gray whales and that pregnant females were most common early in the

southbound migration (Rice and Wolman, 1971). In addition, results from examination of gray whales taken in the Arctic and off California agree that female gray whales reach sexual maturity at a length of about 11.1m (Rice and Wolman, 1971; Blokhin, 1984; Yablokov and Bogoslovskaya, 1984). This study found that some of the southbound gray whales photographed were exceptionally wide relative to their length, these wide whales were most common early in the southbound migration, and that all of these whales were >11.1m in length. In addition, no exceptionally wide whales were found in any of the photographs of gray whales returning northward from the calving lagoons. Because of the consistency of the findings from the fishery and the photogrammetric sample, it is likely that the anomalously wide whales photographed were near-term pregnant females.

While no pattern of temporal segregation by size and sex was found in the northbound migration, as reported from specimens, the early migration sample may have been collected too late in the season to capture the northbound newly pregnant females. Rice and Wolman (1971) noted that these females pass Central California within a two-week period that peaks around 28 February and, although gray whales appear to be migrating later than they did in the 1960s (Rugh *et al.*, 2001; Buckland and Breiwick, 2002), the March 11 flight may have missed this first pulse of northbound whales. No cows with calves were found to migrate with the adults and juveniles that make up the first phase of the northbound migration, as also reported by Poole (1984).

Although no correlation was found between the lengths of southbound gray whale cows and their associated calves, there was a positive linear relationship between the lengths of northbound cows and calves. These results suggest that length at birth is independent of size of the mother, but calves of larger (probably older) cows grow at a faster rate than those of smaller females. However, southbound data include measurements of only 15 cow/calf pairs and the lack of correlation in these pairs of measurements may be the result of the small sample size. The average length for the 15 newborn calves (4.6m) is closer to estimates of size at birth based on measurement of near-term foetuses (4.6m) from Rice and Wolman (1971) and of live-captured calves (4.7m) (Norris and Gentry, 1974) than it is to the average of lengths for stranded calves (4.4m) summarised by Jones and Swartz (1984). Rice (1983) suggested that compression of the intervertebral disks might cause body length to shrink after birth, thus explaining the difference between data from foetuses and stranded newborns. The results here and recent data from stranded calves (Pacheco, 1998) indicate that the difference between these datasets is more likely the result of higher mortalities (and therefore strandings) amongst smaller, possibly premature calves. A similar pattern of potential size bias towards small calves in data from strandings was reported for southern right whales (Best and Rüther, 1992).

Based on their analysis of the data taken from the whales captured along the California coast, Rice and Wolman (1971) estimated that gray whales reached a length of about 8.5m at weaning and averaged 9.3m by the following winter. Their estimate of length for one-year-old whales was based on the assumption that the smallest whales in the sample were yearlings. These small gray whales had two growth layer groups in their ear plugs, and more recent research has shown that gray whales lay down a single layer each year (Blokhin and Tiupeleev, 1987). Sumich (1986) reviewed data from stranded specimens, some photogrammetric data and growth of a captive gray whale calf and concluded that gray whales reach a length of 5.6m at three months, are 7m at weaning and attain a length of 8.0m at one year. Sumich (1986) assumed that the hiatus in lengths of stranded neonates in the 6-7m range represented the difference in lengths between calves of the year and one-year-old whales. In a more recent study, Sumich *et al.* (2001) published growth data for a second gray whale calf that was raised in captivity. This calf reached a length of about 6m at three months and 9m at one year.

In this study, gray whale calves photographed in late April, at an age of about three months, averaged 7.1m in length, not 5.6-6m as suggested above. The lack of stranded specimens in the 6-7m size range is likely to reflect greater survivorship of calves that reach this size. Based on data from 9-10 month old gray whales reported by Blokhin (1990; 1997) and a single gray whale cow with a calf photographed off Alaska (8.33m) on 6 July 1998 (Perryman unpublished data), gray whales are estimated to be between 8.0 and 8.5m when weaned. We believe, as suggested by Sumich (1986), that growth in young gray whales slows at weaning and that the length of yearling gray whales average 8.5m, as originally suggested by Rice and Wolman (1971). The estimate of the mean length of yearling gray whales is based on the interpretation of the overall length distribution of photographed whales and must be taken with caution until a larger sample of lengths for whales of known age is available.

Gray whales do not feed significantly during their winter migration. Rice and Wolman (1971) estimated that gray whales passing San Francisco on their way north weigh about 11-29% less on average than they did passing the same site on their way south. A detectable pattern of reduction was found in the relationship between maximum width and length that mirrors the pattern of change in nutritive condition reported from specimens. Southbound parturient females were found to be widest relative to their length and northbound lactating females were the narrowest. For whales that were not parturient or with a calf, southbound gray whales were significantly wider than those migrating north. These findings indicate that the documented changes in overall nutritive condition in gray whales associated with fasting for approximately 60 days can be detected in measurements from photographs. It was also found that the location of the widest point on a gray whale changes with reproductive and nutritive condition. These results imply that, for stranded gray whales and those taken in fisheries, axillary girth might be a less informative measurement than maximum girth coupled with the distance from the rostral tip to the site of this measurement. Published results on both fin and sei whales also indicate that girth measurements taken near mid-length or even farther posterior may be more reflective of changes in condition than those taken at the apex of the pectoral fin (Lockyer *et al.*, 1985; Lockyer, 1987; Víkingsson, 1990).

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