Estimates of abundance of the eastern North Pacific stock of gray whales (*Eschrichtius robustus*) 1997-2002

DAVID J. RUGH[*], RODERICK C. HOBBS[*], JAMES A. LERCZAK[+] AND JEFFREY M. BREIWICK[*]

Contact e-mail: dave.rugh@noaa.gov

ABSTRACT

The southbound migration of the eastern North Pacific stock of gray whales (*Eschrichtius robustus*) was documented by the National Marine Fisheries Service from 13 December 1997 to 24 February 1998, 13 December 2000 to 5 March 2001 and from 12 December 2001 to 5 March 2002. Research protocol was essentially identical to that used in previous surveys. This involved single observers independently searching for whales and recording data on effort and sighting time, location, count and direction-headed. In 1997/98, there were 2,346 pods (3,643 whales) counted during 435.0h of standard observational effort when visibility was recorded as fair to excellent. In 2000/01, a total of 1,694 pods (2,754 whales) were counted during 592.4h, and in 2001/02, there were 1,712 pods (2,800 whales) during 531.5h. The southbound migrations in 1997/98 and 2001/02 were normal, beginning in mid-December, centred on mid-January (mean dates=18 January 1998 and 15 January 2002 respectively) and ending by mid-February. However, in 2000/01 (mean date=25 January 2001) the migration was more protracted than any other migration observed in the past 25 years, with many whales still travelling south three weeks after the typical end date. Data analysis procedures were comparable to those used in previous years, with the exception of a new correction factor for night-time travel rates. Abundance estimates were 29,758 whales in 1997/98 (CV=10.49%; 95% log-normal confidence interval=24,241 to 36,531), 19,448 in 2000/01 (CV=9.67%; 95% log-normal confidence interval=16,096 to 23,498) and 18,178 in 2001/02 (CV=9.79%; 95% log-normal confidence interval=15,010 to 22,015). The abundance in 1997/98 was the highest estimate made since this project began in 1967/68. It was followed by two much lower estimates – probably related to the high mortality rates observed in 1999 and 2000. This whale population appears to be approaching the carrying-capacity of its environment.

KEYWORDS: GRAY WHALE; MONITORING; SURVEY – SHORE-BASED; ABUNDANCE ESTIMATE; TRENDS; MIGRATION; PACIFIC OCEAN; NORTHERN HEMISPHERE

INTRODUCTION

The National Marine Fisheries Service (NMFS) has conducted shore-based counts of the eastern North Pacific stock of gray whales most years since 1967 (Table 1) at Granite Canyon (or Yankee Pt), 13km south of Carmel, in central California. Access to this site is convenient, and the narrowness of the whales' migratory corridor in this area has permitted an efficient counting process that has been repeated through many seasons. All of these counts were done during the two-month southbound migration (from mid-December to mid-February), which is less protracted than the three-month northbound migration (from mid-February to late May). The predictability of the migration and routine nature of these counts contribute to inter-annual trend analyses. For example, Buckland and Breiwick (2002) showed there has been an increase of 2.5% per annum (SE=0.3%) between 1967/68 and 1995/96, and Wade and DeMaster (1996) have shown how this population may be approaching its carrying-capacity.

Tests of the counting procedure used in this study have included: (1) aerial surveys to document the distribution of whales relative to shore near Granite Canyon (Shelden and Laake, 2002); (2) high-power binoculars to monitor trends in offshore distribution (Rugh *et al.*, 2002); (3) corrections for estimates in pod size (Laake *et al.*, 1994); (4) paired, independent counting effort to estimate whales missed within the viewing area (Rugh *et al.*, 1990; 1993); (5) estimates of night travel rates via thermal sensor imaging (Perryman *et al.*, 1999); and (6) a study of migratory timing relative to this site (Rugh *et al.*, 2001).

The analytical techniques developed by Reilly (1981) to assess gray whale populations have been modified as more sophisticated algorithms have become available, such as Hermite polynomials to interpolate for unwatched periods (Buckland *et al.*, 1993), and improved estimates of variance (Hobbs *et al.*, 2004). For trend analyses, these improved techniques can be applied to all years so that analytical methods are consistent.

The primary objective of the field studies presented here has been to continue the standardised counts for purposes of extending the trend analyses, relying on single observers doing independent counts with minimal optical aids, as in the past. Of particular interest is that this may be the first large whale stock that has been monitored through the recovery process as it approaches its carrying-capacity. An additional incentive to conduct the study in 2000/01 and 2001/02 was to assess the abundance after two years (1999 and 2000) in which unusually high counts of dead gray whales had been reported (Le Boeuf *et al.*, 2000; Norman *et al.*, 2000; Gulland *et al.*, 2005). This monitoring is part of management recommendations following the removal of this stock from the list of endangered or threatened wildlife (Rugh *et al.*, 1999).

METHODS

Field methods

Systematic counts of gray whales were conducted throughout most daylight hours, covering most of the duration of the southbound migration past the Granite Canyon research station (Table 1). Three 3hr standard effort periods covered the nine daylight hours from 07:30 to 16:30. Observers were rotated to keep a balance of effort in each of the three shifts. A total of 10 people took part in the counts in 1997/98 and 10 in 2000/01, while 15 were involved in 2001/02 (see Acknowledgments). Observation sheds provided a writing platform with some protection from the elements. Average eye height above sea level was 22.5m.

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[*] *National Marine Mammal Laboratory, Alaska Fisheries Science Center, NMFS, NOAA, 7600 Sand Point Way NE, Seattle, Washington 98115 USA.*
[+] *Department of Physical Oceanography, MS#21, Woods Hole Oceanographic Institution,Woods Hole, Massachusetts 02543 USA.*

Table 1

Survey dates and gray whale abundance estimates from counts conducted by NMFS during the whales' southbound migration past Granite Canyon, California. The most recent estimates have a better assessment of standard error than was available in data collected during previous years. New abundance estimates incorporate a night-time correction factor adapted from Perryman *et al.* (1999).

Start dates	End dates	Cited abundance	SE	Source	New abundance	New SE	CV
18 Dec. 1967*	3 Feb. 1968	12,921	964	1	13,776	1,082	0.0785
10 Dec. 1968*	6 Feb. 1969	12,070	594	1	12,869	708	0.0550
8 Dec. 1969*	8 Feb. 1970	12,597	640	1	13,431	758	0.0564
9 Dec. 1970*	12 Feb. 1971	10,707	487	1	11,416	590	0.0517
18 Dec. 1971*	7 Feb. 1972	9,760	524	1	10,406	614	0.0590
16 Dec. 1972*	16 Feb. 1973	15,099	688	1	16,098	834	0.0518
14 Dec. 1973*	8 Feb. 1974	14,696	731	1	15,960	872	0.0546
10 Dec. 1974	7 Feb. 1975	12,955	659	1	13,812	781	0.0565
10 Dec. 1975	3 Feb. 1976	14,520	796	1	15,481	930	0.0600
10 Dec. 1976	6 Feb. 1977	15,304	669	1	16,317	818	0.0501
10 Dec. 1977	5 Feb. 1978	16,879	1,095	1	17,996	1,249	0.0694
10 Dec. 1978	8 Feb. 1979	13,104	629	1	13,971	753	0.0539
10 Dec. 1979	6 Feb. 1980	16,364	832	1	17,447	984	0.0564
27 Dec. 1984	31 Jan. 1985	21,443	1,182	1	22,862	1,379	0.0603
10 Dec. 1985	7 Feb. 1986	20,113	927	1	21,444	1,120	0.0522
10 Dec. 1987	7 Feb. 1988	20,869	913	1	22,250	1,115	0.0501
10 Dec. 1992	7 Feb. 1993	17,674	1,029	2	18,844	1,190	0.0632
10 Dec. 1993	18 Feb. 1994	23,109	1,262	2	24,638	1,475	0.0599
13 Dec. 1995	23 Feb. 1996	22,571	1,182	3	24,065	1,393	0.0579
13 Dec. 1997	24 Feb. 1998	27,958	2,853	4	29,758	3,122	0.1049
13 Dec. 2000	5 Mar. 2001	18,246	1,707	4	19,448	1,882	0.0967
12 Dec. 2001	5 Mar. 2002	16,848	1,599	4	18,178	1,780	0.0979

Source: 1=Buckland *et al.* (1993); 2=Laake *et al.* (1994); 3=Hobbs *et al.* (2004); 4=Rugh *et al.* (2003).
*Observation site was at Yankee Pt., 5km north of Granite Canyon.

Although the field of view covered >150°, observers generally searched through an arc of only 40-50° near the standard azimuth, a line perpendicular to the coastline (241° magnetic) intersecting the survey site. Standard search efforts were the same as in previous surveys (Rugh *et al.*, 1993). Each observer searched for whales independently and hand-recorded entries onto a data form. When a gray whale pod was first sighted within the primary viewing range, the time, horizontal bearing and vertical angle were recorded as a 'north sighting'. Magnetic compasses in *Fujinon* 7 × 50 binoculars provided the horizontal bearings, and 14 reticle marks in the binoculars provided vertical angles relative to the horizon (detailed in Rugh *et al.*, 1993; Kinzey and Gerrodette, 2001). A chart was available to help predict the time and vertical angle at which the pod would cross the standard azimuth. If possible, another sighting (the 'south sighting') was recorded when the whale(s) were close to the standard azimuth. Entries included time, horizontal bearing, vertical angle, and a pod size estimate, as well as any unusual behaviours and calf sightings. During periods of routine search effort, observers recorded the number of times each pod was sighted within the viewing area ('cue counts'). These counts were treated in the analysis as cues per pod and compared between seasons as a quantifiable index of relative visibility. Also, observers recorded start and end times of systematic search effort and times of environmental changes, which included visibility (subjectively categorised from 1 to 6 for excellent to unacceptable), sea state (Beaufort scale) and wind direction. Visibility was recorded as a sightability index, that is, a record of how well observers thought they could see whales, not the visibility of the horizon. Primary considerations in establishing visibility were: (1) observer attentiveness; (2) light level and direction; (3) rain or fog; and (4) sea state. During shift changes, observers conferred and agreed on visibility and Beaufort conditions.

In addition to the primary effort, a second, independent effort was conducted once or twice daily during January (when sighting rates were high[1]) for each of the three seasons reported here. The paired effort had a field of view and station conditions nearly identical to those of the primary effort. This provided an independent sighting record, allowing for comparisons between observers, and an estimation of the number of whales missed within the viewing area. The methods applied were as described in Rugh *et al.* (1993), which have been used since 1986 (Rugh *et al.*, 1990) during much or all of these shore-based studies.

The offshore distribution of whale sightings was documented through a shore-based 25 power binocular on a fixed-mount, as per Rugh *et al.* (2002). No correction factor, other than for probability of detection by distance, was applied for whales passing the site beyond 5.6km (3 n.miles) because aerial surveys conducted in the past have estimated that only 1.28% of the whale population travels beyond this distance (Shelden and Laake, 2002), considered to be the outer limit of the typical viewing area for shore-based observers.

Abundance analysis

Population abundance calculations from the observer counts followed the analytical procedures described in Hobbs *et al.* (2004). These methods account for: (1) whales that passed during periods when there was no observational effort (prior to and after the census season, at night or when visibility was poor); (2) whales missed within the viewing range during on-effort periods; (3) differential sightability by observer, pod size, distance offshore and various environmental conditions; (4) errors in pod size estimation; (5) covariance within the corrections due to variable

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[1] It has not proved cost effective to maintain two simultaneous efforts throughout the season, and the abundance algorithm includes a density dependent factor.

sightability by pod size; and (6) differential diel travel rates of whales. Although the methods used here are essentially the same as used in the past, a new correction factor for night travel rate has been included (see below) based on a study conducted by Perryman *et al.* (1999). Previous abundance analyses (e.g. Hobbs *et al.*, 2004) have used several different programs for synthesising the observational records. In order to streamline the analysis process, a new program was written (Lerczak, 2003) providing a common language (Visual Basic) and convenient outputs for use in analyses carried out in S-plus or R statistical programs. The same analysis routine was applied to each of the three seasons reported here.

Calculation of crossing times

The recorded sighting time and location closest to the standard azimuth (usually within a few degrees of 241°) were used to estimate the time and offshore distance at which each pod crossed this line. This was based on the assumption that southbound migrating gray whales travel at 6km/h (3kt) and maintain a course parallel to shore (c.f. Swartz *et al.*, 1987). The time from the beginning to the end of the survey season was partitioned into effort periods (time between 07:30 and 16:30 with visibility 4 or better and an observer on effort) and non-effort periods. Each sighting was assigned to the effort or non-effort period into which it fell as a function of the calculated time it crossed the standard azimuth. Whale sightings were eliminated from the analysis if they crossed this line prior to the start of an effort period or if they had not crossed the line by the end of an effort period.

Correction for missed pods

Corrections for whale pods missed within the viewing area during a systematic effort were estimated from the paired, independent observation records. These paired records provide capture-recapture data that were used to estimate the total number of pods passing the station while observations were underway. A scoring algorithm established by Rugh *et al.* (1993) defined matches between records based on time, offshore distance and pod size. Iterative logistic regression (Buckland *et al.*, 1993) was used to identify significant covariates to the probability of detecting a pod and to estimate the detection probability associated with each recorded pod. Possible covariates were observation site (north or south), effort period (1, 2 or 3), day, observer, distance offshore, pod size, sea state (Beaufort scale), wind direction and whales per hour averaged over each day. After establishing the matching record, all covariates were examined individually as binned categorical data. All covariates were then entered into the model, and a backward step-wise model selection was followed until no step decreased the Akaike Information Criterion (AIC). Once the best linear model fit was determined, interactions between each possible pair of the retained covariates were considered. The logistic regression model was used to estimate p_{ei}, the detection probability of the *i*th pod of size *e* passing during the effort periods of the survey. The total number of pods of size *e* passing during the effort periods of the survey, $\hat{M}_e$, and its variance were estimated as:

$$\hat{M}_e = \sum_{i=1}^{m_e} \frac{1}{p_{ei}}$$

$$Var\left(\hat{M}_e\right) = \sum_{i=1}^{m_e} \left[\frac{1-p_{ei}}{p_{ei}^2}\right] + D_\beta\left(\hat{M}_e\right)^T \hat{\Sigma}_\beta\, D_\beta\left(\hat{M}_e\right)$$

where m_e is the number of pods of size *e* sighted from the primary site, D_β ($\hat{M}_e$) is the vector of partial derivatives of $\hat{M}_e$ with respect to the vector of parameters, β, estimated in the logistic regression evaluated at $\hat{\beta}$, the vector of parameter estimates, and $\hat{\Sigma}_\beta$ is the estimated variance-covariance matrix of $\hat{\beta}$ (c.f. Borchers, 1996). The estimated total number of pods passing the field site while systematic efforts were underway, $\hat{M}$, is then:

$$\hat{M} = \sum_{e=1}^{E} \hat{M}_e \qquad Var\left(\hat{M}\right) = \sum_{e=1}^{E} Var\left(\hat{M}_e\right) + 2\sum_{j=1}^{E-1}\sum_{k=j+1}^{E} D_\beta\left(\hat{M}_j\right)^T \hat{\Sigma}_\beta\, D_\beta\left(\hat{M}_k\right)$$

where *E* is the largest observed pod size.

Bias in recorded pod sizes

Bias in the recorded pod size resulting from underestimation by observers is removed by an additive correction which has been estimated for each pod size, *e*, from data collected during earlier surveys (Laake *et al.*, 1994), with the variances and covariances calculated as in Hobbs *et al.* (2004). Corrected pod sizes were then summed by effort period with the sum rounded to the nearest integer so they could be used in the FORTRAN program *gwnorm*. In earlier gray whale analyses, observed pod sizes were used with *gwnorm*; however, in the present analyses, distributions of the estimated number of whales passing during an effort period were analysed via *gwnorm* so that the variance inflation factor was based on variation in the passage rate of whales rather than the passage of pods.

The total number of whales, W_e, passing the observation site during effort periods represented by pods of size *e*, was estimated as:

$$\hat{W}_e = \hat{M}_e\left(e + b_e\right) \qquad Var\left(\hat{W}_e\right) = Var\left(\hat{M}_e\right)\left(e + b_e\right)^2 + \hat{M}_e^2 \hat{\sigma}_{b_e}^2$$

where b_e is the estimated additive bias correction for *e* from Laake *et al.* (1994) and $\hat{\sigma}_{b_e}$ is the bootstrap estimate of the variance of b_e. The variance consists of two summands representing the estimation errors in $\hat{M}_e$ and b_e.

The total number of whales, *W*, passing the site during usable effort periods was estimated as:

$$\hat{W} = \sum_{e=1}^{E} \hat{W}_e,$$

$$CV\left(\hat{W}\right) = \frac{1}{\hat{W}}\sqrt{\sum_{e=1}^{E} Var\left(\hat{W}_e\right) + 2\sum_{j=1}^{E-1}\sum_{k=j+1}^{E}\left[\left(j + b_j\right) D_\beta\left(\hat{M}_j\right)^T \hat{\Sigma}_\beta\, D_\beta\left(\hat{M}_k\right)\left(k + b_k\right) + \hat{M}_j \hat{M}_k \hat{\sigma}_{b_{jk}}\right]}$$

where E is the maximum observed pod size and $\hat{\sigma}_{b_{jk}}$ is the bootstrap estimated covariance of b_j and b_k.

Correction for whales passing during off-effort periods (f_t)

The rate of whales passing the site was modelled by a normal distribution with Hermite polynomials added to adjust for skewness, kurtosis and higher moments (Buckland *et al.*, 1993). The model defines a bell-shaped rate function, *q*(*t*), of expected whales per day that was integrated to correct for periods when no search effort was underway. The correction factor, f_t, was defined as the ratio of the area under *q*(*t*) integrated over the entire survey period, *Q*, to the area under *q*(*t*) integrated only over effort periods. Although the histograms used to portray the seasonal distribution of sighting rates averaged data through each day, the model used to interpolate the generalised distribution was based on each effort period no matter how small. No corrections were applied for whales passing prior to or after the apparent start and end of the migrations based on the distribution of sighting rates for the respective season (Figs 1-3), and no correction was included for whales travelling beyond the viewing range of the shore-based observers because these factors appear to involve very few whales without satisfactorily quantifiable estimates.

Correction for nocturnal travel rates (f_n^*)

The correction for night travel rate, f_n = 1.020 (SE=0.023), used by Buckland *et al.* (1993), was based on data from three radio-tagged gray whales recorded by Swartz *et al.* (1987) during both day and night hours near Granite Canyon, excluding six other whales followed either during the day or the night. To further study diurnal variations in gray whale travel rates, Perryman *et al.* (1999) recorded thermal images of whales at Granite Canyon, California, while the census of the southbound migration was underway in January 1994, 1995 and 1996 (total sample size=116h by day; 146h by night). As with the tagging results, the imagery showed elevated travel rates at night, or put more accurately, depressed rates during the day, perhaps related to increases in non-migratory behaviour in daylight hours after 15 January (Perryman *et al.*, 1999)[2]. For calculations of abundance, median sighting dates were used instead of 15 January (which, on most years are virtually the same), because the median date may be more representative of the whales' behaviour than a calendar date. Accordingly, an additive correction factor $f_n^* = 1 + 0.28\, f\,(15/24)$ from Perryman *et al.* (1999) was applied, where f is the fraction of total whales migrating after the median date. Because this fraction is 0.5, the correction can be simplified to f_n^* = 1.0875 with SE=0.116 f (15/24)=0.0363. This SE term has been changed from the one in Perryman *et al.* (1999) in that the amount of night hours is 15/24 instead of 14/24, and the f term has been included (J. Laake, pers. comm.).

Synthesis

The total number of whales passing through the viewing area at Granite Canyon during effort periods, W, was multiplied by corrections for whales passing when no search effort was in effect (including periods with poor visibility), f_t, and differences in diurnal/nocturnal travel rates, f_n^*. Accordingly, the total abundance estimate, N is calculated as:

$$\hat{N} = W \cdot f_t \cdot f_n^*$$

The coefficient of variation, CV, is estimated by:

$$CV\left(\hat{N}\right) = \sqrt{\frac{\chi^2/df}{W} + CV^2\left(f_t\right) + CV^2\left(f_n^*\right) + CV^2\left(W\right)}$$

where χ^2/df is a variance inflation factor from fitting a Hermite polynomial to the sighting rates.

RESULTS

Sample size

Shore-based observations were conducted during most daylight hours from 13 December 1997 to 24 February

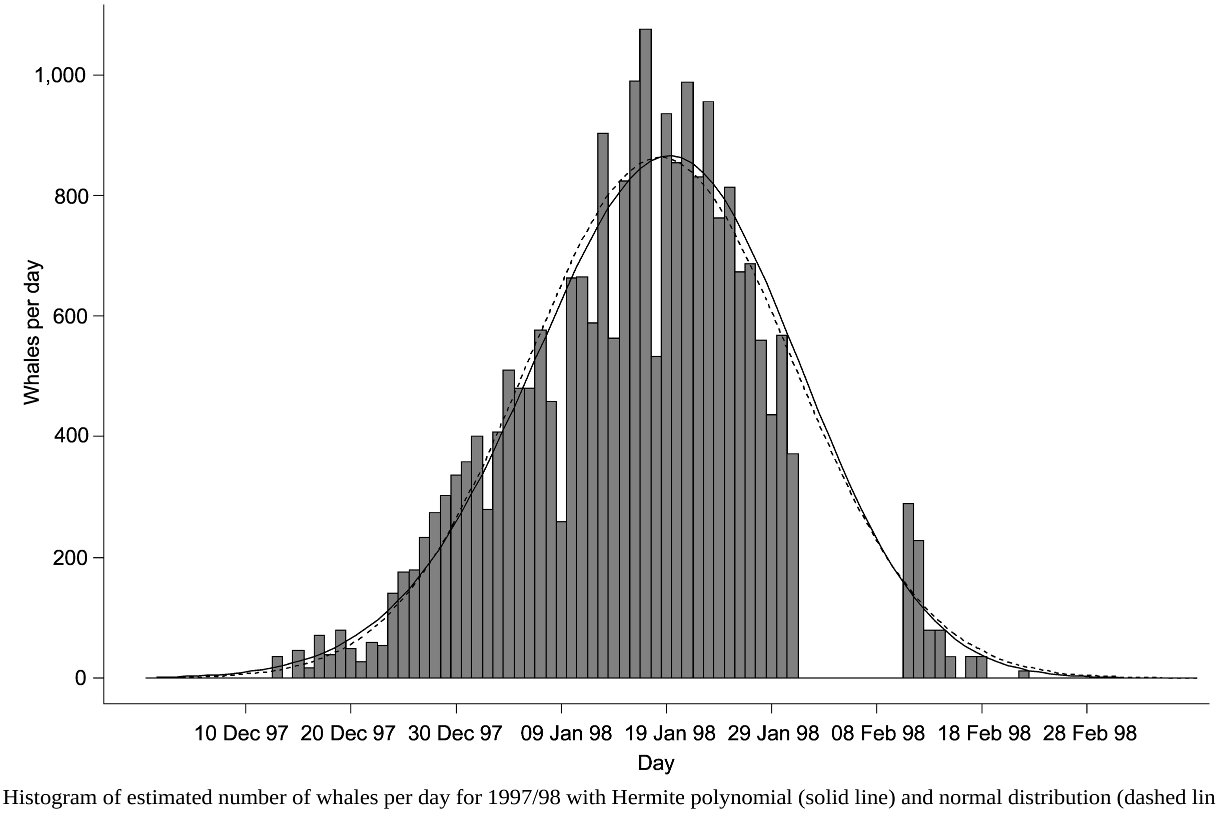

Fig. 1. Histogram of estimated number of whales per day for 1997/98 with Hermite polynomial (solid line) and normal distribution (dashed line) fitted to whales per effort period.

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[2] To confirm that there was a change in whale behaviour midway through the migration, the primary observational records were examined for milling whales and whales seen going north before 13 February 1998, 15 February 2001 and 18 February 2002, dates on which it appeared the northbound migration was underway. Of 37 gray whales seen deviating from their migration south, 30 (81%) of the deviations were after 15 January.

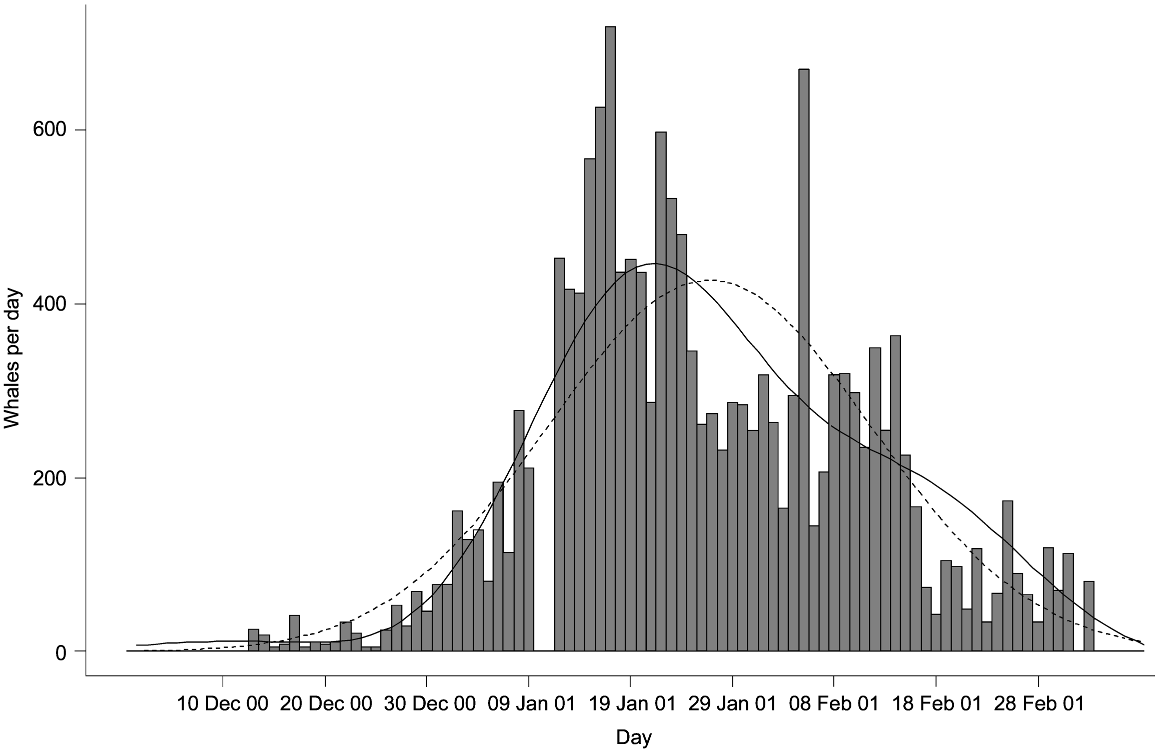

Fig. 2. Histogram of estimated number of whales per day for 2000/01 with Hermite polynomial (solid line) and normal distribution (dashed line) fitted to whales per effort period.

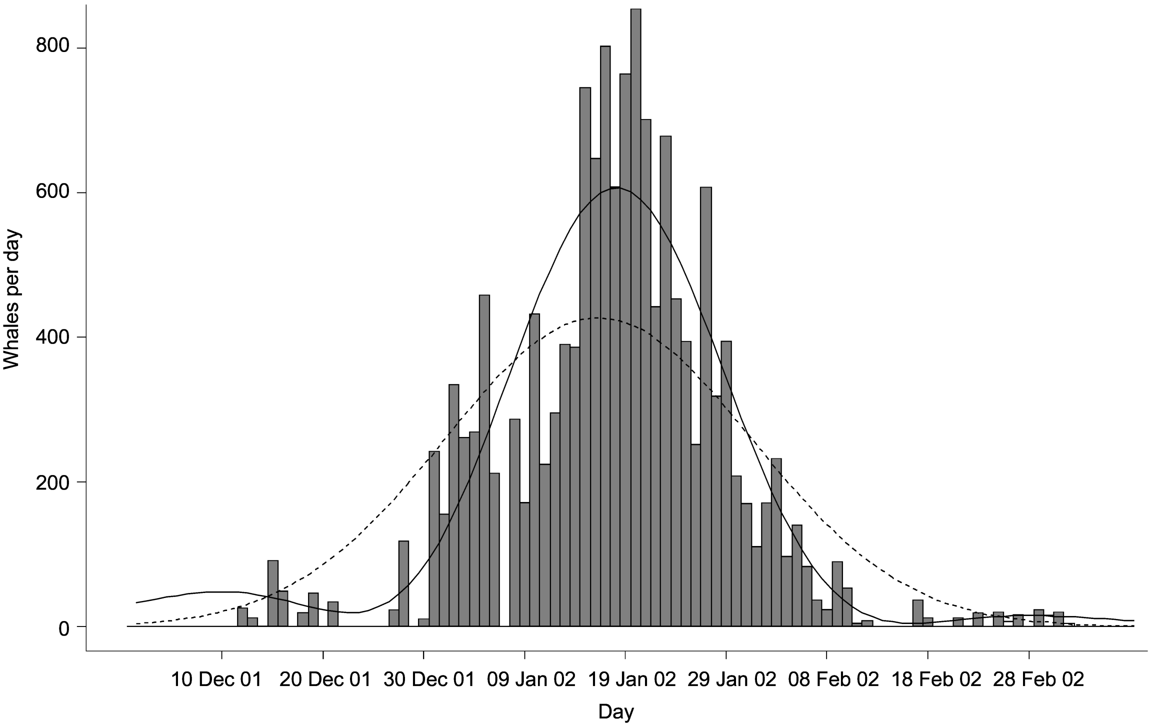

Fig. 3. Histogram of estimated number of whales per day for 2001/02 with Hermite polynomial (solid line) and normal distribution (dashed line) fitted to whales per effort period.

1998[3] (507.2h of effort), 13 December 2000 to 5 March 2001 (698.5h) and 12 December 2001 to 5 March 2002 (621.1h; Table 1). Southbound whales were seen throughout almost all of these days. During the 1997/98 study, a total of 2,346 pods of gray whales was recorded from the primary observation shed, compared to 1,694 in 2000/01 and 1,712 in 2001/02, despite the longer seasons in the latter two years. Searches were maintained from the secondary shed 3-26 January 1998 (173.9h and 1,325 pods), 29 December 2000 to 11 February 2001 (300.6h and 1,169 pods) and 2 January to 7 February 2002 (174.0h and 945 pods). In each of these years, there were respectively, 107.4h, 55.6h and 53.1h on the fixed, high-power binoculars.

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[3] No effort was conducted from 3 to 10 February 1998 due to unusually violent storm activity in the area. The road to the Granite Canyon study site was washed out, preventing any further survey work at that site for the remainder of the southbound migration period. On 11 February, the weather improved sufficiently to allow the establishment of an alternate site at Point Lobos State Park where the final two weeks of survey effort was conducted.

Visibility

Of the six subjective visibility categories, very little time was spent in excellent conditions (2.6h in 1997/98; 5.4h in 2000/01; 10.9h in 2001/02; Table 2). Accordingly, the small sample sizes in excellent conditions were not considered representative sighting rates. Larger sample sizes in the other categories indicated there were no real differences between visibilities 2-4, but sighting rates dropped in visibilities 5 and 6 (Fig. 4). As has been done in previous seasons (e.g. Hobbs *et al.*, 2004), categories 5 and 6 (72.3h in 1997/98; 106.1h in 2000/01; 89.6h in 2001/02) were deleted from further analyses and were treated as unwatched periods. The remaining categories (approximately 85% of the total effort) did not need to have any corrections applied as a function of visibility.

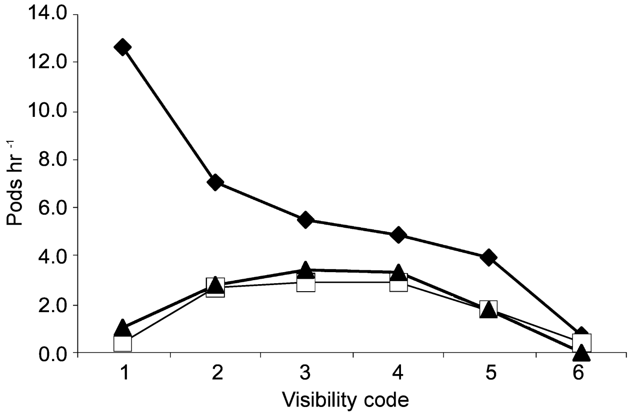

Fig. 4. Annual averages of gray whale pods seen in different visibilities (from excellent [1] to useless [6]; 1997/98 = diamonds; 2000/01 = squares; 2001/02 = triangles).

Table 2

Rates of sightings of gray whale pods as a function of visibility as recorded in the primary observation shed in 1997/98, 2000/01 and 2001/02.

Visibilities	Visibility code	Effort (h)	Number of pods	Pods h^{-1}	SE	Mean pod size	SE
1997/98							
Excellent	1	2.6	33	12.69	0.08	1.667	0.161
Very good	2	40.0	283	7.08	1.10	1.710	0.072
Good	3	162.6	901	5.54	0.42	1.594	0.036
Fair	4	230.0	1,129	4.91	0.32	1.546	0.030
Poor	5	61.0	240	3.94	0.45	1.500	0.061
Unacceptable	6	11.3	8	0.71	0.39	1.000	0.000
All effort	1-6	507.2	2,594	5.11	0.23	1.576	0.021
Usable effort	1-4	435.0	2,346	5.39	0.26	1.586	0.022
2000/01							
Excellent	1	5.4	2	0.37	0.25	1.500	0.500
Very good	2	83.1	223	2.68	0.43	1.874	0.075
Good	3	237.8	686	2.88	0.24	1.723	0.037
Fair	4	266.2	783	2.94	0.19	1.489	0.032
Poor	5	99.6	177	1.78	0.18	1.395	0.048
Unacceptable	6	6.5	3	0.46	0.27	1.000	0.000
All effort	1-6	698.5	1,874	2.68	0.12	1.611	0.022
Usable effort	1-4	592.4	1,694	2.86	0.14	1.635	0.024
2001/02							
Excellent	1	10.9	11	1.01	0.83	2.000	0.357
Very good	2	98.4	279	2.83	0.42	1.767	0.085
Good	3	238.5	814	3.41	0.36	1.677	0.035
Fair	4	183.7	608	3.31	0.34	1.515	0.036
Poor	5	85.8	151	1.76	0.35	1.325	0.053
Unacceptable	6	3.8	0	0.00			
All effort	1-6	621.1	1,863	3.00	0.19	1.611	0.024
Usable effort	1-4	531.5	1,712	3.22	0.21	1.636	0.025

The six visibility categories are subjective and might not have been consistently determined between seasons, therefore observers were asked to record the number of times each pod was seen (see Methods). These 'cue counts' provide an empirical indicator of relative visibility of whales. Accordingly, results show that cues/pod were closely correlated to visibility ($R^2 = 0.98$; $p<0.01$; Fig. 5). There were significant differences between years (mean ($\bar{x}$)=1.91 for 1997/98; 1.84 for 2000/01; 1.73 for 2001/02; $p<0.01$, ANOVA). This apparent decrease in annual averages suggests that sighting rates were generally better in 1997/98. However, this might instead be a reflection of differences between observers, many of whom were not available for more than one season, and many of the observers were new in the latter two years (see 'Observer Performance'). Since individual observers could have varying abilities or styles in recording sighting cues, the analysis of each observer's data between years is a more accurate comparison than pooling each year's results. Accordingly, cues pod^{-1} were compared between 1997/98 and 2000/01 and/or 2001/02 for each observer that participated in two or more of these three seasons. In all but 2 of 7 pair-wise ANOVA comparisons, there were significant differences ($p<0.05$ in each case), and among the five observers who did have inter-year differences, four had higher sighting rates in the latter two years. Therefore, visibility was probably better in 2000/01 and 2001/02 relative to 1997/98, so visibility changes do not explain the low counts made in the most recent seasons.

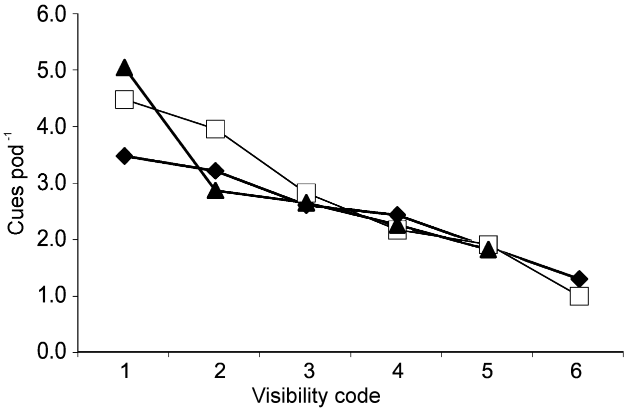

Fig. 5. Annual averages of cues/pod seen in different visibilities (from excellent [1] to useless [6]; 1997/98 = diamonds; 2000/01 = squares; 2001/02 = triangles).

Offshore distances

Several tests were run to establish whether or not inter-year differences in distance from shore were affecting changes in abundance estimates. Kendall's distribution-free test for independence (Hollander and Wolfe, 1973) showed no correlation ($p=0.36$) between average offshore distances (2.19, 2.09, 2.04, 2.33, 2.17, 2.20km, respectively) and abundance estimates (Table 1) for the years 1992-2002. This was the period when distances were established through binocular reticles (with given distances corrected to estimate the location of each whale pod when it crossed the standard azimuth at 241°) instead of uncalibrated estimates as recorded prior to 1992. ANOVA showed significant differences ($p<0.01$) in offshore distances within this period (1992-2002), but the largest mean distance of 2.33km occurred in 1997/98, the year with the highest abundance estimate, and distances in the most recent years ($\bar{x}$ =2.17 and 2.20km, respectively) were close to the average for all years ($\bar{x}$ =2.17km). Pooling distances from 1995-98 ($\bar{x}$ =2.17km; SE=0.012; *n*=5,946) and from 2000-02 ($\bar{x}$ =2.19km; SE=0.014; *n*=3,194) showed there were no significant differences (*t*-test; *p*=0.38). Therefore, the low abundance estimates in the latter two years cannot be described as a function of change in average distance from shore.

Perhaps average distances do not fully reflect variations in the proportion of the population missed as a function of distance because shore-based observers rarely could see whales beyond approximately 6km[4] (as estimated by aerial transects; Shelden and Laake, 2002). Accordingly, high-power binoculars were used to document whales passing beyond the perimeter of the standard search (Rugh *et al.*, 2002), often with good visibility as far as the horizon, 17km away. Although search effort ranged from 53 to 137h per season, this analysis was limited to only those periods when visibility was good throughout the viewing area (28.5, 48.5, 60.0, 22.8, 24.2hr for 1995, 1996, 1998, 2001, 2002 respectively). ANOVA of sightings per reticle showed no differences between these years (*p*=1.0), and χ^2 tests of sightings in 1.4km (0.75 n.miles) bins showed that the only significant differences (*p*<0.05) were between 2002 and both 1996 and 1998. In a *t*-test restricted to sightings beyond 5.6km, there were no significant differences (*p*=0.33) between pooled years (1995-98; $\bar{x}$ =7.45km; SE=0.39; *n*=20; and 2000-02, $\bar{x}$ = 8.98km; SE=1.44; *n*=8). It seems, then, that there is no evidence that the whale migrations in 2000/01 and 2001/02 were farther from shore than in other years, removing this as an explanation for the recent low abundance estimates.

Observer performance

When observers were compared through the paired sighting effort, it was evident that all missed a few whale sightings relative to the other observer. The paired records provided a means to compare many variables that may affect sighting rates. Individual categorical parameter fits of all covariates are shown in Table 3, indicating the respective correction factors. In a test of observer performance, averages in number of sightings recorded for each whale group (cues pod^{-1}) were compared among observers as a function of how many previous seasons of experience they had had with this project. In 1997/98, all of the observers were considered experienced, having had two or more seasons at Granite Canyon. In 2000/01, 5 observers were new, and 5 were experienced. In 2001/02, 6 were new, 3 had one season of experience, and 5 had several seasons. There was a direct correlation between experience and mean cues pod^{-1} (*p*<<0.01; ANOVA): first-time observers averaged 1.70 cues pod^{-1} (SE=0.02; *n*=3,019); during their second season observers averaged 1.77 cues pod^{-1} (SE=0.06; *n*=486); those with many seasons of experience averaged 2.08 cues pod^{-1} (SE=0.05; *n*=1,079). Furthermore, throughout their first season, observers showed an increase in cues pod^{-1} (*n*=11 observers; 3,019 observations; R^2=0.03; *p*<0.01), starting at 1.66 cues pod^{-1} and increasing to 1.84 by the 300th observation (most observers had at least 300 observations in a season).

Table 3

Covariates and fitted parameters estimated for the logistic regression of the probability of detection of whale pods by individual observers in 1997/98, 2000/01 and 2001/02.

Coefficient	Estimate	SE
1997/98		
Intercept	2.079	0.415
Site (N Vs S)	-0.360	0.165
Period 2	-1.958	0.157
Period 3	-2.313	0.297
Observer A	-0.523	0.406
Observer B	0.033	0.313
Observer C	-0.309	0.315
Observer D	-0.590	0.305
Observer E	-1.514	0.212
Observer F	-1.118	0.368
Observer G	-0.695	0.310
Observer H	-1.660	0.250
Observer I	-0.015	0.406
Pod size	0.290	0.073
Pods hr^{-1}	0.034	0.014
Distance	0.001	2.000×10^{-4}
Distance^2	-1.743×10^{-7}	3.008×10^{-8}
Cos (wind dir.)	0.227	0.113
2000/01		
Intercept	1.512	0.282
Period 2	-0.804	0.176
Period 3	-1.397	0.163
Observer A	0.784	0.334
Observer B	-0.296	0.283
Observer C	0.151	0.296
Observer D	-0.255	0.214
Observer J	-0.333	0.377
Observer K	-0.837	0.201
Observer L	0.597	0.262
Observer M	-0.544	0.192
Observer N	-0.703	0.207
Pod size	0.509	0.079
Beaufort	0.080	0.054
Pods hr^{-1}	0.047	0.017
Distance^2	-3.83×10^{-8}	1.452×10^{-8}
Cos (wind dir.)	1.701	0.462
Beaufort x cos (wind dir.)	-0.613	0.165
2001/02		
Intercept	3.863	0.604
Site (N vs S)	0.869	0.369
Period 2	-0.309	0.207
Period 3	-1.143	0.177
Observer A	-1.400	0.526
Observer B	-1.230	0.526
Observer C	-0.462	0.557
Observer F	-0.994	0.557
Observer H	-2.531	0.482
Observer L	-2.697	0.619
Observer N	-3.112	0.624
Observer O	-1.567	0.630
Observer P	-3.179	0.604
Observer Q	-1.543	0.516
Observer R	-2.787	0.600
Observer S	-1.858	0.491
Observer T	-1.945	0.662
Pod size	0.337	0.079
Beaufort	-0.041	0.071
Visibility	-0.189	0.092
Pods hr^{-1}	0.050	0.016
Distance^2	-4.886×10^{-8}	1.248×10^{-8}
Cos (wind dir.)	-1.204	0.576
Cos^2 (wind dir.)	-0.861	0.258
Beaufort x cos (wind dir.)	0.325	0.185

Migratory timing

The passing rate of the 1997/98 migration was nearly symmetrical around the peak on 18 January 1998 ($\bar{x}$ =day 49.4; SE=0.18, with day 1=1 December; Fig. 1). A Hermite polynomial with added terms up to order 3 was hardly different from the normal distribution for this year.

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[4] During the past three seasons, 0.37% of the observers' sightings were beyond 5.6km (34 sightings, or 1.51%, in 1997/98; 4 sightings, or 0.25%, in 2000/01; 3 sightings, or 0.19% in 2001/02). Maximum distances were 15.9, 7.2 and 9.3km for the respective years. These sightings, when applied to the corrections for missed whales, may in part compensate for the calculated 1.28% of the population estimated to be beyond 5.6km (Shelden and Laake, 2002).

The mean sighting date in 2000/01 was 25 January (day 55.9; SE=0.14), 10 days after the expected date of 15 January (Rugh *et al.*, 2001). However, a ‘peak’ in sighting rates occurred on 17 January, which is within the expected time frame (Fig. 2). Sighting rates were lower than expected (relative to 1997/98) through most of this migration, but rates were much higher than expected after 15 February, when the migration usually ends. A Hermite polynomial of order 6 was fitted to the temporal distribution of the 2000/01 sighting data. Unlike in previous years, when the sighting rates closely approximated a normal distribution, in 2000/01 there was a nearly exponential rise in sighting rates from the start of the census until the peak in mid-January, followed by a disordered period until rates dropped in early March. Prior to 2001, these gray whale surveys were usually terminated by mid-February (Table 1); however, in 2001 the survey was extended an additional three weeks because whales continued to pass the site in significant numbers through February and into March.

In 2001/02, the mean sighting date was 16 January (day 47.3; SE=0.16), which was virtually the same as most dates observed in the 1980s and 1990s (Rugh *et al.*, 2001). An apparent peak in sightings occurred on 20 January. A Hermite polynomial distribution (of order 6) had a normal, bell-shaped curve appearance and was approximately symmetrical around the mean date. In 2002 the survey was again conducted until 5 March to better compare with the survey effort in 2000/01; however, the migration ended in 2002 as it typically had in the past, on or about 15 February (Rugh *et al.*, 2001).

Pod size

The mean recorded pod sizes during periods when visibility was adequate (1-4) was 1.586 (SE=0.022), 1.635 (SE=0.024) and 1.636 (SE=0.025) for 1997/98, 2000/01 and 2001/02, respectively. Sighting rates relative to each pod size are shown in Table 4. Observers tend to underestimate pod size, therefore bias corrections were applied as per Laake *et al.* (1994), based on aerial studies of previous years. These corrected pod size estimates are shown in Table 4 without rounding (values used in the abundance estimates are slightly different because they were based on whole integers for the respective effort periods). Average pod sizes after bias correction were 2.40, 2.43 and 2.43.

Corrections for using Point Lobos State Park in 1998

During a severe winter storm in February 1998 (during an El Niño year), part of the road to Granite Canyon was washed out and was not repaired until 7 May. The storm’s duration meant that eight days went by without any search effort. By 11 February the weather abated enough to allow two observers a chance to resume the search, but without access to Granite Canyon. The observations were made at *ad hoc* sites in Point Lobos State Park, 9km north of Granite Canyon and 7km south of Carmel. Two sites were used during the final two weeks of the survey (11-24 February) until the southbound migration appeared to be over. One site, in a car park at approximately 6m altitude, was used when there was rain because observers could retreat into a parked car. The other site, at 25m altitude, was accessed by a footpath used by many tourists. This was considered the primary site but could only be used in mild weather because of the lack of protection from the elements.

It was unclear how comparable the results between Pt Lobos and Granite Canyon were, so in January 2002 two observers returned to Pt Lobos to conduct counts while counts were ongoing at Granite Canyon. Because the two sites are 9km apart, the average whale swimming at 6km h^{-1} takes 1.5h to reach Granite Canyon after passing Pt Lobos. Accordingly, data collected at Pt Lobos were compared to sightings made 1.5h later at Granite Canyon. During 8.8h of systematic searches on three days, 69 pods were sighted at Pt Lobos and 62 at the primary site at Granite Canyon. Recorded pod sizes were higher at Pt Lobos ($\overline{x}$ =2.09 whales pod^{-1}; SE=0.15) than at Granite Canyon ($\overline{x}$ =1.45; SE=0.09; p<0.001, Z=3.61), which provided a correction of 0.70 used to adjust the Pt Lobos counts relative to those of Granite Canyon. This correction is nearly the same value (0.67) as the average correction for pod sizes at Granite Canyon (Table 5). Therefore, it appears that the pod size estimates made at Pt Lobos were fairly accurate. The higher counts at Pt Lobos are probably because the whales were concentrated closer to shore ($\overline{x}$ =1.65km; SE=0.099; n=76) than at Granite Canyon ($\overline{x}$ =2.13km; SE=0.096; n=62; p<0.001; Z=3.51), where the continental shelf is somewhat wider. Whales on the southbound migration arrive at Pt Lobos after crossing Monterey Bay (which cuts eastward as much as 30km from a straight-line course across the mouth of the bay), Carmel Bay (which cuts 3km eastward) and Carmel Canyon (which is as much as 360m deep on a line connecting the outermost points of land). If gray whales use bathymetry to navigate, then these marine canyons cause them to move closer to shore.[5]

Abundance estimates

Uncorrected counts (m) of southbound gray whale pods seen during periods with good visibility (<5) during the primary effort are shown in Table 5 for 1997/98, 2000/01 and 2001/02 (2,347; 1,694 and 1,712, respectively). These counts of pods were multiplied by corrected pod sizes to estimate the number of whales (W =7,299; 5,053 and 5,103, respectively). These estimates were then corrected for whales passing between effort periods (f_t) and a differential night travel rate ($f_n^* = 1.0875$). In addition, the abundance estimate in 1997/98 has been corrected for counts conducted at Pt Lobos instead of Granite Canyon. This correction and the new program for matching sightings meant the previously circulated estimate for 1997/98 (26,635; CV=10.06%; 95% log-normal confidence interval = 21,878 to 32,427; Hobbs and Rugh, 1999) has been changed. Accordingly, the abundance estimate for 1997/98 is 29,758 whales (CV=10.49%; 95%; log-normal confidence interval (CI) = 24,241 to 36,531), the estimate for 2000/01 is 19,448 whales (CV=9.67%; 95%; CI = 16,096 to 23,498) and the estimate for 2001/02 is 18,178 whales (CV=9.79%; 95%; CI = 15,010 to 22,015). The lower bound of the 95% CI for the 1997/98 estimate (24,241) does not overlap with the upper bounds for the 2000/01 and 2001/02 estimates (23,498 and 22,015, respectively), indicating this to be a statistically significant drop.

Table 1 and Fig. 6 summarise estimates of gray whale abundance including standard errors (Table 1) and 95% log-normal confidence intervals (Fig. 6). Two regressions were run on these data, one from 1967/68 to 1997/98 and the other from 1967/68 to 2001/02. Assuming a Poisson error distribution with over-dispersion and a logarithmic link function, estimates of the average annual increase were 2.59% (SE=0.28%) and 1.86% (SE=0.32%), respectively.

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[5] Although it appears that gray whales pass closer to shore at Pt Lobos than at Granite Canyon, only the latter site has an unobstructed view from a sea cliff with vehicle access, nearby accommodations, restricted access for tourists, options for constructing observation sheds and a research facility appropriate for the gray whale census.

Table 4

Estimations of total numbers of whales passing during systematic observational periods (visibility ≤ 4) in 1997/98, 2000/01 and 2001/02.

Pod size	Number of recorded pods	Average correction for missed pods	Bias-corrected pod size	$\hat{M}_e$	$\hat{W}_e$	$CV\left(\hat{W}_e\right)$
1997/98						
1	1,535	1.364	1.941	2,094	4,065.2	14.48%
2	502	1.275	2.646	640	1,693.9	10.68%
3	177	1.197	3.607	212	764.0	12.12%
4	77	1.165	4.25	90	381.1	17.31%
5	23	1.204	5.25	28	145.4	19.31%
6	15	1.069	6.25	16	100.2	14.94%
7	8	1.046	7.25	8	60.7	15.00%
8	7	1.026	8.25	7	59.3	13.30%
9	2	1.018	9.25	2	18.8	18.75%
10	1	1.050	10.25	1	9.9	29.29%
All	2,347	1.320	2.40	3,098	7,298.5	9.45%
2000/01						
1	998	1.302	1.941	1,300	2,522.6	14.05%
2	459	1.211	2.646	556	1,470.6	10.12%
3	151	1.124	3.607	170	612.4	11.70%
4	49	1.081	4.25	53	225.1	17.21%
5	26	1.051	5.25	27	143.4	15.05%
6	7	1.037	6.25	7	45.4	17.14%
7	2	1.027	7.25	2	14.9	23.55%
8	1	1.013	8.25	1	8.4	26.84%
10	1	1.001	10.25	1	10.3	20.09%
All	1,694	1.250	2.43	2,115	5,032.5	8.46%
2001/02						
1	1,033	1.258	1.941	1,299	2,522.2	14.07%
2	432	1.247	2.646	540	1,425.5	10.30%
3	150	1.188	3.607	178	642.9	11.98%
4	65	1.122	4.250	73	309.9	17.04%
5	15	1.054	5.250	16	83.0	16.71%
6	11	1.049	6.250	12	72.1	15.46%
7	3	1.030	7.250	3	22.4	20.18%
8	1	1.043	8.250	1	8.6	31.53%
16	1	1.006	16.250	1	16.3	14.49%
All	1,711	1.240	2.43	2,123	5,103.0	8.46%

Table 5

Estimated abundance and intermediate parameters for the eastern North Pacific stock of gray whales counted at Granite Canyon.

	1997/98			2000/01			2001/02		
Parameter	Est.	SE	CV (%)	Est.	SE	CV (%)	Est.	SE	CV (%)
Total number of pods recorded by primary observers during effort periods with visibility ≤ 4 (*m*):	2,347			1,694			1,712		
Mean recorded pod size:	1.59	0.022	1.39	1.635	0.024	1.45	1.636	0.025	1.54
Corrected mean pod size:	2.40	0.018	0.77	2.43	0.019	0.80	2.43	0.021	0.86
Estimated number of whales passing during effort periods (*W*):	7,299	690	9.45	5,053	427	8.46	5,103	432	8.46
Correction for pods passing outside effort periods (f_t):	3.749	0.015	0.39	3.539	0.005	0.15	3.276	0.009	0.27
Estimated total number of whales without night travel correction (*Q*):	27,364			17,883			16,715		
Correction for night travel (f^*_n):	1.0875	0.036	3.33	1.0875	0.036	3.33	1.0875	0.036	3.33
Estimated number of whales passing Granite Canyon ($\hat{N}$):	**29,758**	3,122	10.49	**19,448**	1,882	9.67	**18,178**	1,780	9.79
95% CI	24,241-36,531			16,096-23,498			15,010-22,015		

A discrete, logistic model was also fit to the data:

$$N_{t+1} = N_t + R_{\max} N_t (1 - N_t / K) - C_t$$

where N_t is the abundance in year *t*, $R_{\max}$ is the maximum growth rate, *K* is the carrying-capacity and C_t is the catch in year *t*. The parameters of the model ($N_0 = N_{1967}$, $R_{\max}$ and *K*) were estimated by maximising the log-normal likelihood function. The estimated asymptote, *K*, was 26,290 (SE=1,562).

DISCUSSION

Gray whale abundance estimates made from data collected at or near Granite Canyon during southbound migrations showed an upward trend of 2.5% from 1967 to 1995

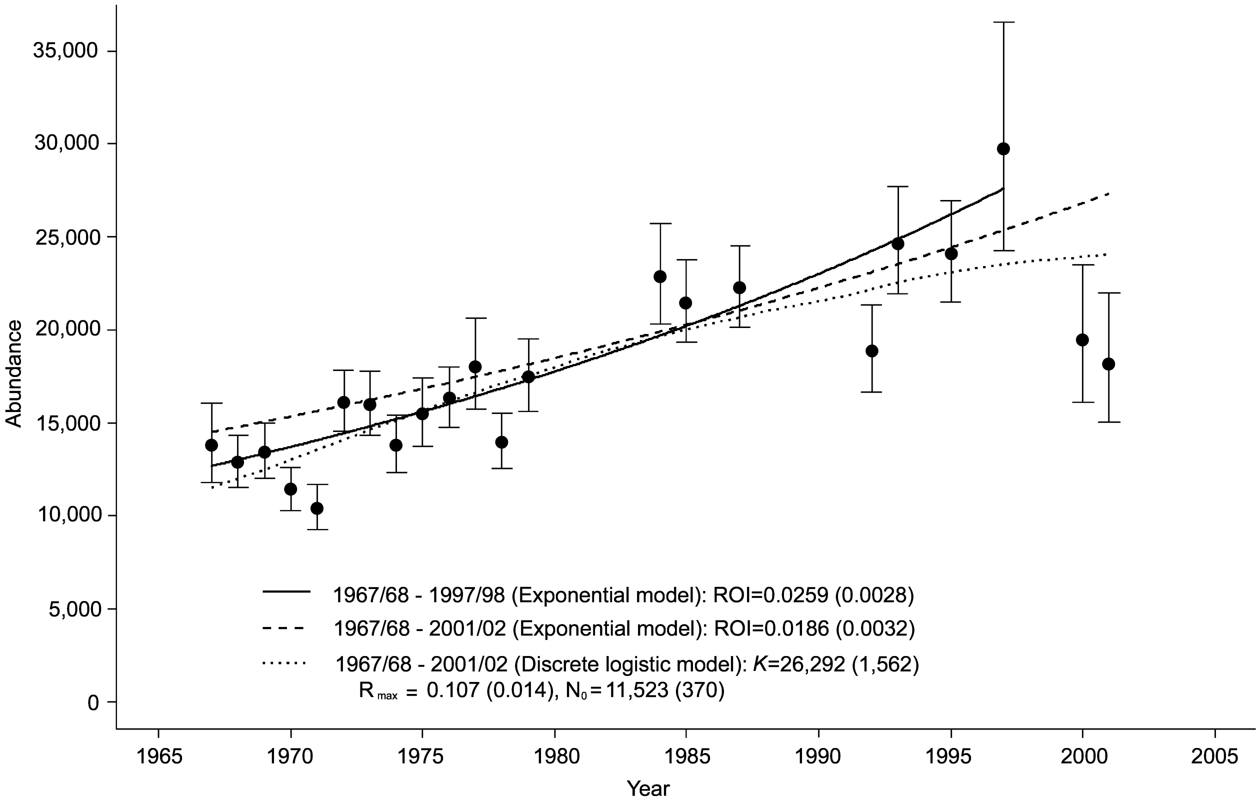

Fig. 6. Gray whale abundance estimates and 95% log-normal confidence intervals. The regression of abundance on time (1967/68 to 1997/98 and 2001/02), assuming a Poisson error distribution with over-dispersion and a logarithmic link function, gave estimates of average annual rate of increase (ROI) of 2.59% (SE=0.28%) and 1.86% (SE=0.32%). A discrete, logistic model was also fit to the abundance data (dotted curve), including parameter estimates and their standard errors (in parentheses) where K is the carrying-capacity, $R_{\max}$ is the maximum growth rate and N_0 is the abundance in the first year 1967/68).

(Buckland and Breiwick, 2002). This trend appeared to continue through 1997/98, but in 2000/01 and 2001/02, abundance estimates were well below this trend line. Although at first the low counts in 2000/01 were thought to be related to an unusual migration (see 'Migratory timing'), with whales continuing to go south long after the usual timeframe, the migration timing in 2001/02 appeared to be quite typical, and yet the abundance was still low. Both of these years (2000/01 and 2001/02) had estimates that were 65% and 61%, respectively, of the estimate made in 1997/98. Several possible explanations for the low estimates are presented here.

Visibility

If visibility was persistently lower in the 2000/01 and 2001/02 seasons relative to 1997/98, the year of the highest counts, then the recent counts might have been downwardly biased. Yet, there was no real difference in the percentage of time spent in adequate visibility (conditions 1-4) in 1997/98 (86%) and 2000/01 (85%) or 2001/02 (86%). Also, the number of sightings recorded per pod (cue counts) for observers who were available for multiple seasons, suggested that visibility was better in the more recent years than in 1997/98. Therefore, visibility does not explain the low encounter rates recorded in 2000/01 and 2001/02.

Change in offshore distribution

Data from the standard effort (using reticles in 7 × 50 binoculars) and from dedicated effort on fixed, high-power binoculars (25 × 150) showed there was no apparent offshore shift in the migration that could explain low encounter rates in 2000/01 and 2001/02 relative to previous years.

Observers

Approximately half of the observers were new in each of 2000/01 and 2001/02, and therefore it may be argued that their lack of experience led to lower sighting rates, explaining in part the low counts from these two years. Indeed, cue counts indicate that new observers made fewer sightings than experienced observers: the overall mean cues pod^{-1} showed a 4% drop in 2000/01 and 9% drop in 2001/02 relative to 1997/98, but this was far less than the observed drop in abundance. Although new observers had lower sighting rates than experienced observers, inter-observer differences were compensated for in the corrections for missed pods, to minimise bias. With sufficient overlap and testing among observers between seasons, it is not likely that changes in performance would explain the low counts recorded in the final two seasons.

Migratory change

The timing of the gray whale southbound migration past Granite Canyon has been phenomenally regular, with median dates consistently near 15 January in recent years, and generally ending in mid-February as the northbound migration begins (Rugh *et al.*, 2001). In 2000/01, however, the median migration date appeared to be 10 days late, and whales continued passing the station until the effort was terminated on 5 March, when counts of southbound whales had dropped to 0.7h^{-1}, and northbound counts had risen to 1.3h^{-1}. Small numbers of gray whales continued to travel south long after this date as was evident from shore-based surveys at Piedras Blancas, 130km south of Granite Canyon (W. Perryman, pers. comm.) and Pt Vicente, 485km south of Granite Canyon, near Los Angeles in southern California

(A. Schulman-Janiger, pers. comm.). Although the migratory timing in 2000/01 was unusual, the timing appeared normal in 2001/02, yet the abundance estimate was still low, and so the delayed migration in 2000/01 does not explain the low numbers. Of course, it is possible that in both years a significant portion of the population did not migrate as far south as Granite Canyon. Unexpectedly low abundance estimates also occurred in 1970/71, 1971/72, 1978/79 and 1992/93, yet each (except the first) was followed by several seasons with much higher estimates (Fig. 6). One of the explanations for the low estimate in 1992/93 was that varying proportions of the gray whale population remain north of Granite Canyon each year (Laake *et al.*, 1994). Perhaps in some years, such as in 2000/01 and 2001/02, many whales did not migrate as far south as Granite Canyon.

Abundance decline

If none of the other theories fully explain the low counts recorded recently, then the change may be attributed to being a true drop in the population size. This may have been indicated by a high mortality rate between the 1997/98 and 2000/01 censuses: 274 dead gray whales were reported in 1999 (Le Boeuf *et al.*, 2000; Norman *et al.*, 2000) and 368 in 2000 (Gulland *et al.*, 2005), significantly above the average rate of 38yr^{-1} from 1995-98 (Norman *et al.*, 2000). Of course, these stranding reports reflect only a small proportion of the total mortality rate. Visibly emaciated whales (Le Boeuf *et al.*, 2000; Moore *et al.*, 2001) and low calf production (Perryman *et al.*, 2002) are suggestive of a deterioration in available resources, such as benthic amphipods in the Bering and Chukchi seas (Le Boeuf *et al.*, 2000), perhaps associated with unusually high sea temperatures in 1997 (Minobe, 2002). However, several factors indicate this was an acute event, not a chronic situation or trend, because since then: (1) counts of dead gray whales (21 in 2001 and 26 in 2002; Gulland *et al.*, 2005) have dropped to levels below those seen prior to this event; (2) living whales no longer looked emaciated in 2001 (W. Perryman, pers. comm.); and (3) calf counts in 2002, a year after the event ended (gestation=13 months; Rice and Wolman, 1971), and in subsequent years were near or higher than averages for previous years (Perryman *et al.*, 2004; A. Schulman-Janiger, pers. comm.).

The drop in abundance following many years of increasing numbers invites speculation on this population's carrying-capacity. Gray whale abundance prior to commercial takes in the 19th century has been estimated at 30,000-40,000 (Scammon, 1874) or 15,000-20,000 (Henderson, 1972). Models projecting into the future have produced point estimates of carrying-capacity (K) based on the abundance data through 1995/96 ranging from 24,000 to 35,000 (Wade and DeMaster, 1996; 1998; Wade, 1997; 2002), but with broad credibility intervals. Wade and Perryman (2002) obtained more precise interval estimates of K by incorporating the abundance data through 2001/02, as well as data from surveys for calves during the northbound migration. Their 90% credibility interval incorporating the calf estimates through 2001 was 19,830 to 28,470, suggesting that currently the population is essentially at K.

After the heavy exploitation of gray whales, especially from 1855-74, the abundance may have dropped to only a few thousand animals (Henderson, 1972). This low abundance lowered the efficiency of the hunt, reducing further takes, but it has also led to conservation measures, which began in 1937 under the International Agreement for the Regulation of Whaling[6] (Reeves, 1984). Since that time, this stock of whales has demonstrated a remarkable recovery. During the documented period from 1967/68 to 1995/96, there was a 2.5% per annum increase in abundance estimates (Buckland and Breiwick, 2002). A plateau in this increase has been anticipated (Reilly, 1992; Wade, 1997), but through 1997/98[7], abundance estimates continued to rise almost linearly. Until 2000/01, there was only a suggestion of density-dependence beginning to occur (Wade and DeMaster, 1998), though it has been proposed that this whale stock was close to its equilibrium level (Wade, 2002; Wade and Perryman, 2002). Possibly, then, the abundance estimates from 2000/01 and 2001/02 were the first clear indication that the abundance was responding to environmental limitations, albeit temporarily exaggerated by unusual conditions in 1998 and 1999. It is anticipated that in the future, abundance estimates will rise and fall as the population finds a balance with the carrying-capacity of its environment.

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[6] International Convention for the Regulation of Whaling. 1946. (Dec 2, 1946), art. XI, 62 Stat. 1716, T.I.A.S. No. 1849, 161 U.N.T.S. 72, 4 Bevans 248, 249.

[7] The abundance estimate from 1997/98, which in Fig. 6 appears to be well above the others, may have been biased upwardly if interpolations overcompensated for missed observational periods that year (8 days were lost due to a severe storm, and on 14 days effort was conducted at an alternate site; i.e. Granite Canyon was used during only 70% of the season).

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