POPULATION ASSESSMENT OF THE GRAY WHALE, *ESCHRICHTIUS ROBUSTUS*, FROM CALIFORNIA SHORE CENSUSES, 1967-80

STEPHEN B. REILLY,[1,2] DALE W. RICE,[1] and ALLEN A. WOLMAN[1]

ABSTRACT

Estimates of abundance by year were developed for the California-Chukotski stock of gray whales, from a 13-year consecutive series of shore censuses, conducted near Monterey, Calif. Annual estimates of population size range from a low of 10,414 for 1971-72 to a high of 17,577 for 1979-80. Standard errors are about 10% of population estimates. During the 13 years censused, the population increased annually by 2.5%, concurrent with a 1.2% harvest in the Soviet subsistence fishery, indicating a 3.7% net annual productivity.

Seasonal migratory timing was relatively constant during the study period. Gamma probability density function models of the annual migrations past Monterey had an overall mean day of 9 January, with a range from 8 to 19 January. A slight depression in mean hourly count for 0070-0800 h, during 1978-79 and 1979-80, contrasted with a constant mean hourly count through 10 daylight hours during the previous 11 years. Aerial surveys of the offshore distribution of southward migrating whales during 1979-80 agreed closely with those reported for 1978-79, indicating that 40% pass within 1 mile (1.6 km) of shore and 90% within 2 miles (3.2 km). In the shore censuses, about 20% of the passing whales were missed due to their distance offshore.

The estimation of population size for large whales has traditionally been based upon information derived from exploitation, e.g., catch per unit effort, mark-recapture, or related data (Allen 1980). Because of the recent decline in exploitation of marine mammals, assessment techniques based upon sighting surveys are increasing in importance (Eberhardt et al. 1979). The annual migration of the California stock of gray whales, *Eschrichtius robustus* (Lilljeborg 1861), makes it especially well suited to assessment by means of sighting surveys. Assessment studies on this stock can potentially aid in the development of sighting survey field and analysis techniques, especially those in which the observer is stationary and the population mobile. This paper presents some recent developments in the use of shore-based census data for whale population assessment, and the results of the 1979-80 gray whale census. Revised population estimates for the previous 12 annual censuses are also reported, along with a consideration of change in population size during the period 1967-80.

Each year during the northern winter the California stock of gray whales migrates from feeding waters in the Bering and Chukchi Seas, south along the west coast of North America, to calving areas in Mexical waters (Fig. 1); the stock returns to the Arctic in the spring (Rice and Wolman 1971). In many places along the route, the whales pass very close to land (Gilmore 1960; Pike 1962; Rice and Wolman 1971; Rugh and Braham 1979). Consequently, it is feasible to census the migrating whales visually from strategic points along the shore.

Early shore-based censuses were summarized by Reilly et al. (1980). Systematic censuses of southward migrating gray whales were initiated during the winter of 1967-68 at both Point Loma (lat. 32°40'N; 130 m above sea level) in San Diego, Calif., and at Yankee Point (lat. 36°29'N; 23 m above sea level) near Monterey, Calif. The San Diego count was conducted intermittently until 1977-78, for a total of 5 yr. The San Diego data were not analyzed in this study because an unverified proportion of the population passes far offshore south of Point Conception (Rice 1965) and because the migration route may have been influenced by increased boat traffic (Rice 1965; Reeves 1977). The Monterey census was conducted each year for 13 yr up to and including 1979-80. Beginning in 1975-76 the counting station was moved 3.7 km south to Granite Canyon (21 m above sea level) due to real estate development of the Yankee Point site. The Monterey data were used as the basis for this study, because they form a continuous time series and are less complicated by coastal geography and boat traffic than the San Diego data.

[1]National Marine Mammal Laboratory, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE., Seattle, WA 98115.

[2]National Marine Mammal Laboratory, Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way NE., Seattle, Wash.; present address: Southwest Fisheries Center La Jolla Laboratory, National Marine Fisheries Service, NOAA, 8604 La Jolla Shores Drive, La Jolla, CA 92038.

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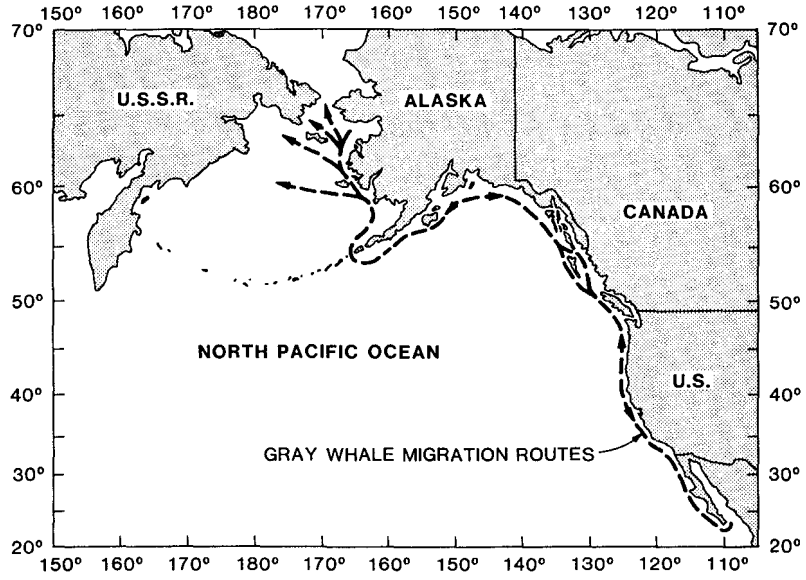

FIGURE 1.—The approximate migration route of the California stock of gray whales.

To estimate total abundance by extrapolating from recorded counts of passing whales one must determine the following:

1) What proportion of the population, if any, passes beyond sight of the observers? Does this change with time or experience? How does the observer's accuracy in estimating the distance to passing whales vary with distance?
2) Are there diel variations in migration rate? How can daylight counts be used to estimate the number of whales passing at night?
3) How do weather (visibility) conditions affect census results?
4) Does the observer's ability to count the number of individuals within a passing group vary with group size?
5) Are the initiation and termination of the migration fully represented in the data?

During the 1978-79 southward migration we conducted two types of verification experiments aimed at addressing the questions of points 1 and 4 above. These were reported in detail in Reilly et al. (1980). In one experiment we tested 12 observers simultaneously for accuracy in estimating distances to and numbers within 50 events in which whales passed the Granite Canyon station. The observers estimated the distance offshore to within one of seven predefined distance intervals, as during the actual annual censuses (see Methods). We found significant heterogeneity between observers for both distance and count estimates. Given this heterogeneity, there were also consistent biases recorded: In placing whales to within correct intervals out to 1 mi (1.6 km) and beyond 1.5 mi (2.4 km), and in estimating the true number of individuals present in groups of one whale, and four or more. Further analysis of this data (Reilly 1981) indicated that "experienced" observers were on average no more accurate than inexperienced observers, but somewhat more precise.

A second experiment was conducted during 1978-79 to characterize the width of the migration corridor offshore from the Monterey counting stations (Reilly et al. 1980). A small aircraft flew a series of transects perpendicular to the coast in the vicinity of the stations, recording locations of sighted whales (Fig. 2). The results indicated that, contrary to previous assumptions and characterizations of 95% of the population passing within 1.6 km (Rice and Wolman 1971; Sund and O'Connor 1974), we found only about 40% within 1.6 km, with significant numbers passing offshore between 1.6 and 4.5 km. This experiment was repeated during 1979-80, with results reported here.

Regarding night migration rate (point 2 above), after a review of all available information, we accepted an assumption of a constant 24-h rate. Contrary to the earlier report of Ramsey (1968), we found no evidence of a diurnal fluctuation from the shore census data. During the 1979-80 migration a new (prototype) infrared image sensor, supplied by the U.S. Department of Defense, was tested at Granite Canyon. As with previously tested night-vision devices (Reilly et al. 1980), it proved unsatisfactory.

The possible effect of visibility conditions on cen-

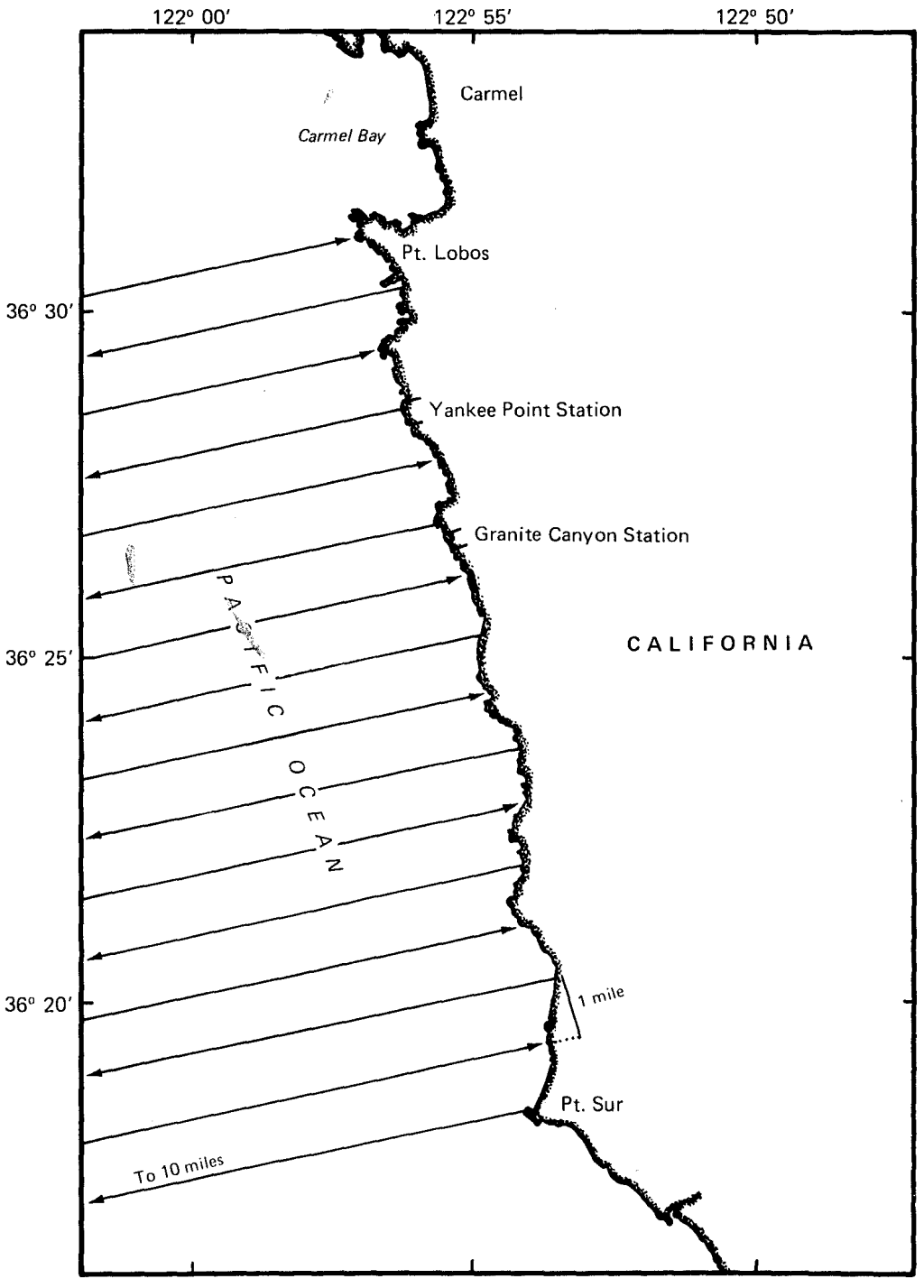

FIGURE 2.—The California coast south of Monterey, showing census stations and aerial transect lines for gray whale study

sus results was not addressed in Reilly et al. (1980). We report here a quantitative appraisal of this effect, and account for it in our abundance estimation.

METHODS

Field Methods: Shore Census

The exact seasonal duration of the annual census changed only slightly from year to year, but it usually began on or before 10 December and ended on or after 6 February (59 d). The watch was conducted between 0700 and 1700 h, 7 d a week, by two observers who alternated 5-h shifts.

The observers watched to the north for southward swimming whales to come into view. At first sighting of a whale or group of whales the time was recorded and an initial estimate was made of the number of whales in the group. The whales were kept under observation until they were directly offshore from the station, usually about 0.5 h later. At that time a final estimate of the number present was recorded, along with the time and an estimate of the distance of the animals offshore. Distance estimates were classified in seven intervals: 0-0.25; 0.25-0.50; 0.50-0.75; 0.75-1.0;1.0-1.5; 1.5-2.0; 2.0+ mi. Beaufort Sea state, wind direction, and notes on visibility conditions were recorded continuously throughout the day. Binoculars (7 × 50) were used regularly. Beginning in 1978-79, visibility conditions were assigned one of six ordinal categories (Table 1) for each pod observed. For data prior to 1978-79, visibility conditions were classified to within these categories during the analysis, based upon information recorded systematically during the censuses.

TABLE 1.—Gray whale census—Granite Canyon visibility codes.

Code	Condition	Description
01	Excellent	Clear day, or high clouds. No glare. Horizon visible. Effective sighting distance = 3+ mi.
02	Very good	Clear or some cloud cover. Some glare, surface ripple. Effective sighting distance = 2-3 mi.
03	Good	Some fog, haze, low clouds. Some interference from chop, surf, or glare. Effective sighting distance = 1-2 mi.
04	Fair	Fog, full overcast, light rain, haze with glare. Frequent whitecaps. Effective sighting distance = 0.5-1 mi.
05	Poor	Moderate rain or fog, large surf, bad glare, etc. Effective sighting distance = 0.25-0.5 mi.
06	None	Combination of conditions make it very difficult or impossible to see even the closest (within 0.5 mi.) whales. Heavy rain, dense fog, near darkness, etc.

Analysis Methods: Shore Census

Occasionally during the censusing, only one of the standard two sighting times per group (when first seen and when directly offshore) was recorded. Frequently when an observer came on duty at 0700 h there were whales directly offshore and no "north time" was recorded. In addition, at the end of the day at 1700 h, whales which had not yet passed directly in front of the station were often sighted to the north, and no "south time" was recorded. To correct for missing time records, a mean difference between the two times was calculated for each observer individually. Missing time records were then generated from this average, and the single time record available. The time when the animals were directly offshore was then used to categorize data for time of day analyses. Only sightings with this time falling between 0700 and 1700 h were used for abundance estimation.

The results of the 1978-79 and 1979-80 half-day observation periods were investigated by analysis of variance (ANOVA) for differences between observers and between morning vs. afternoon periods on rate of recording animals, as was previously done (Reilly et al. 1980) for the 1967-68 through 1977-78 data. We also examined the two most recent censuses for possible changes in hourly rates of recorded counts, as done previously for the 1967-68 through 1977-78 data. Again, we looked for significant depressions in the counts both at the ends of the 5-h observer periods (as an indication of observer fatigue) and at the beginning and end of the day (as an indication of daylight-mediated change in migration rate).

For any migratory species which can be censused feasibly from a fixed point, the distribution of daily counts, transformed to proportions for each migration, can be viewed profitably as a time-density distribution and modeled by various probability density functions (Mundy 1979). We previously assumed a normal distribution (Reilly et al. 1980) for all years pooled. Problems with this approach were that mean days between years were not equal and that a slight but consistent skewness occurred causing lack of fit. Consequently we have replaced the normal distribution with the more flexible gamma distribution (Pearson's Type III; Bury 1975) and modeled each year separately. The time-density model for each migration was then employed in three ways:

1) To estimate the number of whales having passed the station before the first and after the last day of the census (the "tails").
2) As a standard for comparison with observed daily results, in a determination of if, and to what degree, conditions associated with the six visibility categories affect census results.

3) To estimate the proportion of the population passing the census station on days for which the visibility conditions were worse than a critical value, as determined by the results of the visibility analysis (2).

The data on pod-size estimation from all years were examined both for differences between years and for a pattern in distance from shore.

The offshore distance frequency distribution of observations was investigated for significant differences between the two locations, as a preliminary to post facto application of correction factors for whales missed offshore.

Field Methods: Verification Experiments

The aerial transects to determine the offshore distribution of the migratory corridor were repeated in 1979-80 following our previous methods (Reilly et al. 1980). We flew a Cessna 172[3] aircraft at 305 m (1,000 ft) altitude, at a speed of 145 km/h (90 mi/h), along a series of predefined tracklines (Fig. 2). These lines were situated along a 25 km stretch of the coast which included both the Yankee Point and Granite Canyon census stations. Distances of whales from shore were calculated from the timed difference between their position and the shore edge, and the plane's speed. During 1979-80 we flew a total of 13 flights for 34 h, in periods of good to excellent visibility. Flights were continued until a number greater than the minimum sample size of whales was obtained (330) for 90% precision in correctly classifying the population into the seven distance intervals used in the shore census (Reilly et al. 1980). Sample-size determination was based upon Cochran's (1977:74-76) formulae for sampling for proportions. Data from the 1974-75 shore counts were used as a presample of the proportions expected within the distance intervals from shore. The seven-interval experimental design also presented the opportunity to analyze the data in a pooled, less demanding interval scheme, with resulting higher precision in estimating the within-interval proportions.

Additive bias corrections were previously determined from the results of the observer bias experiments regarding estimation of the number of whales present in passing groups. Specifically for estimates of group size n (see Appendix 1 for explanation of notation)

$$E[n] = \hat{n} + b_n = \begin{cases} n + 0.350 & n = 1 \\ n + 0.00 & n = 2,3 \\ n + 0.333 & n \geq 4 \end{cases} \quad (1)$$

with variances as in Appendix 2.

Analysis Methods: Verification Experiments

Aerial sightings were analyzed for effects on offshore distance estimates from: differences between the two individual observers; the side of the plane from which the whales were seen; and the period of day (morning or afternoon flight) by ANOVA. The distance distributions from the 2-yr surveys were tested by χ^2 (chi-square) for the possibility of pooling.

To address the misclassification bias suggested by the results of the 1978-79 experiments, the data from those experiments were reanalyzed by using a less demanding classification scheme of three broad intervals: 0-0.75 mi (1.2 km); 0.76-1.5 mi (2.4 km); 1.6 mi + (2.6 km). From this characterization, a series of reclassification parameters (probabilities) were calculated, ρ_{ab}, being the proportion of whales estimated to be within interval a, that were determined to be actually passing within interval b. The actual census data, structured in the same three intervals, were restructured by application of these parameters as

$$\hat{m}_b = \sum_a (m_a \rho_{ab}), \quad (2)$$

where m_a includes the whales originally classified into interval a, and $\hat{m}_b$ comprises the whales redistributed into interval b, which were originally (erroneously) estimated to be in a. For example, for $a = 1$ and $b = 1$, sightings correctly classified into interval 1 are summed into the new $\hat{m}_{b=1}$. For $a = 2, b = 1$, sightings incorrectly classified during the censuses into interval 2 are reclassified, or summed, into $\hat{m}_{b=1}$. In the case of $a = 2, b = 1, \rho_{21} = 0.2367$ of the whales originally put in interval 2 would be placed into interval 1. The redistributed census data were then compared with the "true" distribution from the aerial surveys. As a simple correction factor, the ratio of the cumulative proportions seen within 2.4 km (1.5 mi) was calculated for each year (k):

$$h(k) = C_s/C_p. \quad (3)$$

A necessary assumption of this method is that at least during periods of good or better visibility, all groups of whales passing within 2.4 km (1.5 mi) were recorded.

[3]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Analysis Methods: Estimation of Abundance

In fitting the probability density functions to the census data, the unit used was the estimate of the proportion of the population passing during a 24-h day. The number passing on day j was estimated as

$$\hat{n}_j = (\Sigma E[n]/t_j) \cdot 24, \quad (4)$$

where $E[n]$ is the expected value of n, i.e., the estimate of the number per group, corrected for bias as in Equation (1). The relative proportion passing on day j was estimated as

$$\hat{p}_j = \hat{n}_j/\Sigma\hat{n}_j. \quad (5)$$

Model parameters were first estimated for each year using all data points regardless of recorded visibility conditions. Data were fit by the two-parameter gamma model

$$f(j;\alpha,\beta) = \frac{1}{\alpha \cdot \Gamma(\beta)} (j/\alpha)^{\beta-1} \exp\{-j/\alpha\} \quad (6)$$

for each migration separately. The parameters of the gamma distribution, their variances and covariance, were estimated by the method of maximum likelihood (Chapman 1956; Greenwood and Durand 1960). Equality of parameters between years was tested by the F statistic (Chapman[4]),

$$F = \frac{\Sigma (x - \bar{x})^2/n - 1}{\Sigma \text{ var } (x)/n} \quad (7)$$

for $x = \alpha, \beta$.

The distribution of $\hat{p}_j$ for each year was then used to determine the effect of visibility conditions on census results. An average visibility condition was calculated for each day from all of the recorded codes (Table 1). The difference (residual) between the observed and predicted relative proportions for each day was also calculated. An ANOVA was performed on the residuals with visibility categories as groups, along with multiple range tests (Duncan's, Student-Newman-Kuels, Scheffe's). These results were used, along with an examination of the mean squared errors for each category, to set a critical level of visibility conditions beyond which there was significant interference with accurate censusing. The data were then refit by the gamma distribution using only days with visibility codes less than the critical value as points. The new set of daily predictors ($\hat{p}'_j$) from the fitted gamma model were used in the further estimation procedures.

Then, as an alternate to Equation (2), the abundance for day j was

$$\hat{n}_j = \begin{cases} [(\Sigma E[n])/t_j]\ 24 & : \text{vis} \leq \text{critical value} \quad (8a) \\ \hat{p}'_j\ (\Sigma\hat{n}_j) & : \text{vis} > \text{critical value.} \quad (8b) \end{cases}$$

That is, for days with visibility conditions less than or equal to some critical level (with levels defined as in Table 1) the average hourly sighting rate, corrected for counting bias, multiplied by 24 h, was used as the estimate of the total number of whales passing. For days with visibility conditions worse than some critical value, the estimate of the number passing came from the expected proportion for the day (from the gamma distribution model of migratory timing for that year, p'_j) multiplied by the sum of the daily estimates from the first fitting of the gamma model.

For estimating the "tails" of the migration, a slight modification of the method of Mundy (1979) was used. This method was developed to predict total run size for salmon from intermediate results of counts, given that migratory timing can be modeled. The total "run" N_j was predicted by minimizing the least squares error function

$$\text{err} = \sum_j \left(\theta_j - \frac{\Sigma n_j}{N_j}\right)^2 \quad (9)$$

which was solved for $\hat{N}_j$ (N estimated by data cumulative to day j) by

$$\hat{N}_j = \sum_j (\Sigma n_j)^2/\Sigma n_j\theta_j. \quad (10)$$

Here Mundy uses θ_j as the cumulative proportion expected to have passed by day j, and we define θ_j as that quantity less the predicted proportion missed before the first day of each census.

The final form of the abundance estimate for each year k was then,

$$N_k = \{\sum_j (\Sigma n_j)^2/(\Sigma n_j) \cdot \theta_j\} h(k). \quad (11)$$

The variance for Equation (11) was estimated in two ways. The first, S^2_δ, outlined in Appendix 2, was derived from the component variances of the parameters used in the model, employing the Delta Method (Seber 1973). In the second method the data were subsampled in five 2-h samples/d. The five

[4]D. G. Chapman, Director, Center for Quantitative Science, College of Ocean Fishery Sciences, University of Washington, Seattle, WA 98195, pers. commun. March 1980.

estimates for the year were then calculated using Equation (11). A simple variance of these estimates about the mean estimate (S_R^2) was then calculated. Variances were compared for equality ($H_0: S_R^2 = S_0^2$) by the test statistic

$$\chi^2 = \frac{(n-1)S_R^2}{S_0^2}, \tag{12}$$

where χ^2 is distributed approximately as chi-squared (Freund 1962:371) with rejection regions $\chi^2 > \chi^2_{\alpha/2,n-1}$ or $\chi^2 < \chi^2_{1-\alpha/2,n-1}$.

Analysis Methods: Trends in Population Size

In order to test for a trend in population size during the 13-yr study period, two models were chosen for regression analysis. This first model was simple linear regression, the second was a weighted $\log_e$ model:

$$N_t = N_0 e^{rt}, \tag{13}$$

where N_t is population size in year t, N_0 is year zero, or 1967 for the shore census time series. Equation (13) was fit linearly as

$$\ln N_t = \ln N_0 + rt, \tag{14}$$

with weights calculated as an inverse function of the estimated variance of N_t in the log model:

$$\begin{aligned} \mathrm{Var}(\ln N_t) &\quad [f'(N_t)]^2 \mathrm{Var}(N_t) \\ &= \mathrm{Var}(N_t)/N_t^2 \\ &= w_t^{-1}. \end{aligned} \tag{15}$$

RESULTS

Shore Census Data Base

A histogram of group sizes as recorded from the 13 annual censuses is presented in Figure 3. The overall mean was 2.086 ($S^2 = 1.974, n = 23{,}749$). The mean group sizes by year are listed in Table 2. An ANOVA indicates that there are significant differences between the mean pod sizes recorded by year ($F = 8.282 > F_{12,\infty,0.05}$). Multiple range tests (Duncan's, Student-Newman-Kuel's, Scheffe's) show that 1967-68 and 1977-78 are different from each other and the rest, while all the others are homogeneous. In the 1967-68 census the unusually high mean is attributable to one of the two observers that year. His individual mean pod was 3.123 ($S^2 = 2.651$), and was significantly different from the other observer that year, whose mean was 1.886 ($S^2 = 1.959$: $t = 24.528 > t_{\infty,0.05}$). In 1977-78 however, the two observers did not differ significantly

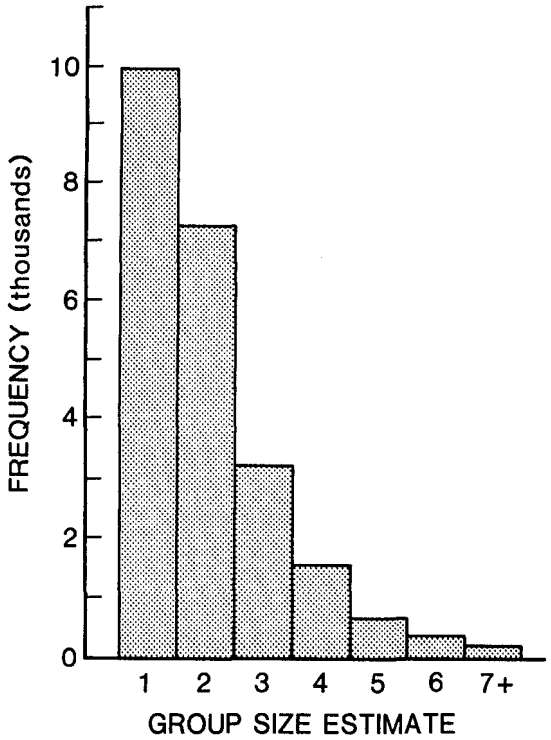

FIGURE 3.—Frequencies of group size estimates from Monterey gray whales census, 1967-68 through 1979-80, n = 23,678 observations.

TABLE 2.—Mean pod size estimates by year for the Monterey gray whale censuses, 1967-68 through 1979-80. Group membership identifies placement by multiple range tests into one of three nonsignificantly different subgroups.

Year	Mean pod estimate	SD	n	Group membership
1967-68	2.4970	3.5520	1239	3
1968-69	2.1471	2.2550	1509	2
1969-70	2.0900	2.2790	1643	2
1970-71	2.0330	1.6110	1652	2
1971-72	2.1630	1.8700	1272	2
1972-73	2.1400	1.6780	2041	2
1973-74	2.0990	1.7980	1859	2
1974-75	2.0710	1.9170	1855	2
1975-76	2.0620	1.7210	2086	2
1976-77	2.0660	1.5930	2296	2
1977-78	1.8250	1.2470	1996	1
1978-79	2.0040	2.3750	1960	2
1979-80	2.1030	1.7120	2341	2
Overall	2.0855	1.9736	23,799	

Analysis of variance

Source	df	ss	ms	F
Between groups	12	385.7561	32.1463	8.283[1]
Within groups	23,736	92,119.1877	8.8810	
Total	23,748	92,504.9438		

[1]Significant at $\alpha = 0.05$.

from each other in mean pod size estimated (1.842, 1.829, $t = 1.1442 < t_{\infty,0.05}$) and, consequently, the difference of this year's data from others cannot be credited to one aberrant observer.

There was a significant increase in mean group size as a function of distance from shore (Fig. 4) ($F = 97.28 > F_{5,231}$). A significant linear increase in the pooled data (Fig. 4) was also noted in 10 of the 13 individual years. In the remaining 3-yr data (1968-69, 1972-73, 1978-79), the average pod size peaked at about 0.6-0.9 km (1-1.5 mi) from shore, and decreased thereafter. This may be a real between-year difference in whale behavior, but is more likely a function of the varying abilities of the observers themselves.

There are highly significant differences between years in the frequency of observations recorded within offshore distance intervals ($\chi^2 = 2{,}340$, df = 24). For this analysis, a pooled three-interval distribution was used in light of the observer bias tests discussed above. Within both the Yankee Point location subset of years and the Granite Canyon subset there also exists significant heterogeneity in the offshore distribution ($\chi^2 = 1{,}077$, df = 14; $\chi^2 = 1{,}025$, df = 8, respectively). Given this, a difference between locations pooled over years ($\chi^2 = 239$, df = 2) is not surprising and also not particularly meaningful. Consequently, given the range of interyear variation, we cannot adequately test for interlocation differences in the migratory corridor and therefore have applied distance estimation corrections equally to data from both locations.

Within each year, the distribution of distance estimates was tested for a within-season change, since our verification experiments were conducted during roughly the middle third of the migration. For this, the data were divided into early (10-29 December), mid (30 December-18 January), and late (19 January-6 February) time periods. As with the first 11-yr data (Reilly et al. 1980), the 1978-79 and 1979-80 distributions have no seasonal differences indicated by contingency table analysis ($\chi^2 = 8.54, 7.13, < \chi^2_{4,0.05}$), but do have significantly different mean distance observations ($F = 16.34, 26.91 > F_{2,\infty,0.05}$). Consequently, as with the first 11 yr, only data from the middle third of the migration were used for comparison with aerial results in Equation (3).

No significant period differences were indicated for the 1978-79 and 1979-80 censuses, in the ANOVA testing for effects on numbers of whales recorded per 5-h shift, from variation between observers and from period (morning or afternoon). Similar results were obtained in the comparison of observers within each year ($F = 1.242, 2.003, F_{1,118}$). The data were

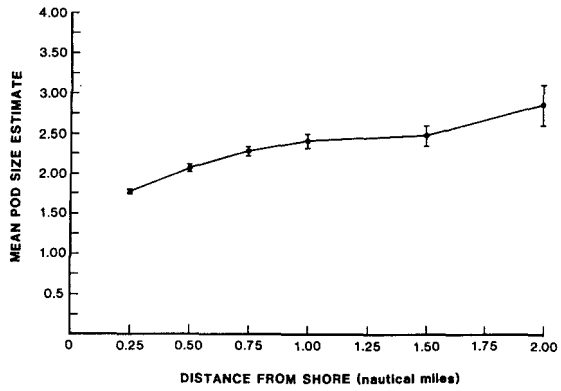

FIGURE 4.—Mean pod size estimates by distance from shore, with 95% confidence limits, from 13 annual gray whale census, 1967-68 through 1979-80, $n = 23{,}678$ observations.

therefore considered homogeneous for pooling over these factors.

The results from 1978-79 are somewhat different than the results from the first 11 yr, in the rate of whales recorded per hour of day. The mean counts show significant differences in an ANOVA ($F = 3.717 > F_{9,\infty,0.05}$) which are due to the depressed value for 0700-0800 h (Fig. 5). Multiple range tests (Duncan's, Student-Newman-Kuel's) indicate that the hourly means (other than that for 0700-0800 h) are homogeneous.

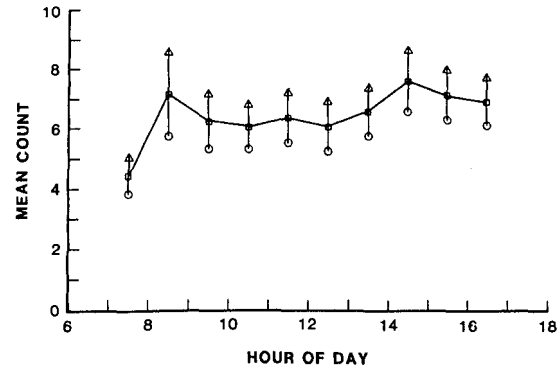

FIGURE 5.—Mean count of gray whales passing Granite Canyon Station by hour of day, with 95% confidence limits. 1978-79 and 1979-80 pooled, $n = 120$ d.

Modeling of Migratory Timing

Table 3 lists the parameters of the gamma distribution as calculated for all 13 yr, along with the mean days ($\simeq \alpha\beta$) and standard deviations ($\sqrt{\alpha \cdot \beta}$) of the annual migrations. As previously discussed, the

TABLE 3.—Parameters of the gamma models of migratory timing for each of the 13 annual gray whale censuses. $S_{\bar{x}}$ is the standard error of the scaled mean day.[1] α, β, their variances, and covariances are maximum likelihood estimates, as in Greenwood and Durand (1960).

Year	Mean day	$S_{\bar{x}}$	α	var(α)	β	var(β)	cov(α,β)	n^2
1967-68	11 January	10.05	6.0679	1.6862	3.7900	0.5758	42.4097	41
1968-69	19 January	11.13	4.8378	0.8033	6.4070	1.3028	59.0233	44
1969-70	08 January	11.68	5.0684	0.8400	6.3140	1.2042	60.8971	46
1970-71	10 January	13.09	6.6379	1.3877	4.9716	0.7036	61.9997	65
1971-72	14 January	14.58	7.9561	2.5758	3.5195	0.4367	51.3318	41
1972-73	16 January	15.16	8.8199	2.6032	3.7417	0.4094	60.7978	57
1973-74	14 January	14.47	7.5301	2.0797	4.3812	0.6278	61.4829	49
1974-75	12 January	13.12	5.6951	1.1374	5.7946	1.0430	62.5312	54
1975-76	09 January	13.09	6.0154	1.3424	4.9872	0.7662	56.3723	39
1976-77	12 January	13.17	5.6979	1.1356	5.9680	1.1456	64.5253	55
1977-78	09 January	14.10	6.7340	1.6036	4.6039	0.6833	57.9679	21
1978-79	11 January	14.38	7.1149	1.7302	4.6383	0.6598	61.7334	60
1979-80	14 January	12.82	5.1287	0.9149	7.2144	1.6887	70.8288	48

[1]The mean day is ($\alpha\beta$), scaled so that 10 December = 1.
[2]Number of days with visibility conditions of fair or better, used as points for the fit.

means and variances are not equal statistically. Following adjustment on the time scale so that mean days align, however, we cannot reject the hypothesis of equality of parameters for the gamma distribution between years. For the α's, $F = 1.33 < F_{12,\infty,0.05}$. For the β's, $F = 1.54 < F_{12,\infty,0.05}$, where the F statistics were calculated as in Equation (7). Figure 6 illustrates data on daily proportions of the population passing Monterey, pooled over the 13 yr, as fit by the cumulative gamma. The use of the gamma represents a marked improvement in fit over the normal distribution, which we employed previously (Reilly et al. 1980). The error sum of squares from gamma model was 0.0179, while that from the normal fit to the same data was 0.1998, one order of magnitude greater.

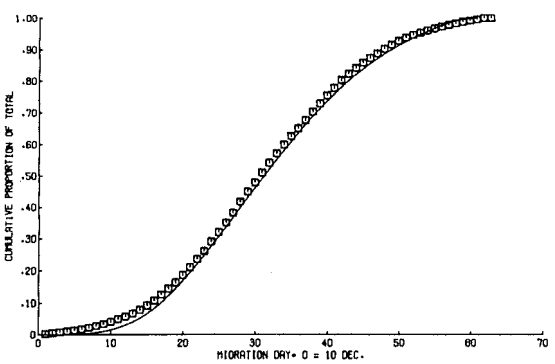

FIGURE 6.—Cumulative proportions of total count of gray whales by day (averaged) fit by the cumulative gamma function. Error sum of squares = 0.0179.

Effect of Visibility Conditions on Censusing

There are significant differences between visibility categories in the residuals (differences) of the observed from expected daily proportions of the population passing the census site (ANOVA: $F = 63.99 > F_{5,749,0.05}$). Three separate multiple range tests (Duncan's, Student-Newman-Kuel's, Scheffe's) gave the following nonsignificantly different subgroups of visibility codes, arranged in order of increasing magnitude of residuals:

1. visibility = 1, 2, 3
2. visibility = 1, 3, 4
3. visibility = 5
4. visibility = 6.

A simple interpretation of these results is that for conditions ranging from 1 (excellent) to 4 (fair), there is no significant interference from weather in shore censusing of gray whales. A plot of the mean squared residual for each category (Fig. 7) graphically illustrates this. Consequently, for days with average

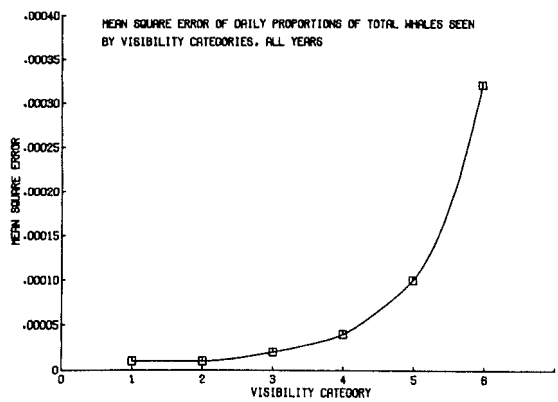

FIGURE 7.—Mean squared errors from comparison of daily proportions of total number of whales seen per season to proportions predicted by the gamma distribution, by visibility categories, all 13 yr included.

visibility of fair or better (<4) the total count for the day was estimated by Equation (8a), while for days with visibility of poor or worse (>4), it was estimated by Equation (8b). (The number of fair or better days recorded each year are listed in Table 3.)

Verification Experiments

The distance estimate data from the 1979-80 aerial survey were found to be homogeneous for pooling over sides of the plane, observers, and flight periods (Table 4). Further, the two separate years aerial data were homogeneous, and therefore pooled to form the model distribution (Table 5). This offshore frequency distribution was used as a standard for comparison with the annual observed distributions, as in Equation (3).

The values of ρ_{ab} (Equation (2)), the redistribution parameters calculated from the 1978-79 observer bias experiments, are listed in Table 6. The distance correction factors for each year $h(k)$ indicate that about 20% of passing whales are missed as a function of their distance from shore (Table 7). The cumulative proportions of the population estimated to have been observed during the census periods of around 2 mo, $\theta(k)$, indicate that between 80 and 96% of the population passed the census site during those periods (Table 7). That is, between 4 and 20% of the population passed on days before the initiation and after the termination of the annual counting efforts.

TABLE 4.—Analysis of variance for distances of sightings from shore from the 1979-80 aerial transects, with side of plane, period (morning, afternoon), and observer (Reilly, Wolman) as factors. None significant at $\alpha = 0.05$.

Source of variation	Sum of squares	df	Mean square	F
Main effects	0.385	3	0.128	0.253
side	0.062	1	0.062	0.122
observer	0.116	1	0.116	0.228
period	0.314	1	0.314	0.618
2-way interactions	1.131	3	0.377	0.743
side × obs	0.586	1	0.586	1.154
side × per	0.018	1	0.018	0.035
obs × per	0.621	1	0.621	1.224
Explained	1.516	6	0.253	0.498
Residual	124.792	246	0.507	
Total	126.308	252	0.501	

TABLE 5.—Numbers of whales observed within each of seven distance intervals from shore in aerial transects during 1978-79 and 79-80 with a χ^2 test of differences for pooling. $\chi^2 = 5.585 < \chi^2_{6,\,0.25}$.

Interval	Distance (mi)	1978-79 no. observed	1979-80 no. observed	Pooled (%)
1	0-0.25	14	11	2.91
2	0.26-0.5	36	33	8.02
3	0.6-0.75	41	42	9.65
4	0.76-1.0	74	88	18.34
5	1.1-1.5	148	167	36.63
6	1.6-2.0	74	61	15.69
7	2.1+	29	42	8.26
Total		416	444	

Population Estimates and Variances

The population size estimate from the 1979-80 census is 17,577, with a standard error of 2,364. Table 8 gives revised population estimates for each of the 13 yr using Equation (11), along with raw counts, variances (calculated as outlined in Appendix 2), and 95% confidence intervals (C.I.).

TABLE 6.—Values of the redistribution parameters, ρ_{ab}, and their variances.

Parameter	Value	Variance
$\rho 11$	0.6647	0.001288
$\rho 12$	0.3353	0.001280
$\rho 13$	0	0
$\rho 21$	0.2367	0.000602
$\rho 22$	0.7567	0.000614
$\rho 23$	0.0067	0.000002
$\rho 31$	0.0282	0.000386
$\rho 32$	0.8451	0.001844
$\rho 33$	0.1267	0.001558

TABLE 7.—Values of the sighting function $h(k)$, its variance, θ, the cumulative proportion predicted to have passed during the census period, and the variances of θ, for each of 13 annual gray whale censuses.

Year	$h(k)$	Var $h(k)$	θ_k	Var θ_k
1967-68	1.212	0.00958	0.8004	0.00434
1968-69	1.219	0.01143	0.9398	0.00094
1969-70	1.218	0.01076	0.9546	0.00069
1970-71	1.214	0.00889	0.9660	0.00052
1971-72	1.215	0.00619	0.8774	0.00207
1972-73	1.212	0.00857	0.9546	0.00069
1973-74	1.213	0.00848	0.9208	0.00128
1974-75	1.207	0.00642	0.9451	0.00085
1975-76	1.217	0.01112	0.9134	0.00141
1976-77	1.218	0.01170	0.9340	0.00104
1977-78	1.218	0.01607	0.9276	0.00116
1978-79	1.213	0.00659	0.9451	0.00085
1979-80	1.217	0.00929	0.9340	0.00104

TABLE 8.—Raw counts, final population estimates, their variances, standard deviations, and 95% confidence intervals for each of 13 annual grey whale censuses.

Year	Raw count	Population estimate	Variance (derived)	SD	95% confidence limits
1967-68	3,077	13,095	1,628,883	1,276	(10,593, 15,597)
1968-69	3,265	11,954	2,388,470	1,545	(8,925, 14,983)
1969-70	3,399	12,408	2,622,599	1,619	(9,234, 15,582)
1970-71	3,264	11,177	1,050,782	1,625	(9,168, 13,186)
1971-72	2,667	10,414	842,864	918	(8,615, 12,213)
1972-73	3,684	14,534	1,817,229	1,348	(11,892, 17,176)
1973-74	3,889	14,676	2,426,376	1,558	(11,623, 17,729)
1974-75	3,836	13,110	1,864,729	1,366	(10,434, 15,786)
1975-76	4,295	15,919	3,545,588	1,803	(12,228, 19,610)
1976-77	4,720	16,621	3,233,889	1,798	(13,096, 20,146)
1977-78	3,717	14,811	5,163,965	2,272	(10,357, 19,265)
1978-79	3,927	13,676	1,270,429	1,127	(11,467, 15,885)
1979-80	4,924	17,577	5,558,979	2,364	(11,943, 22,211)

Table 9 lists the mean of five subsample population estimates for each year, and the alternate variances (S_R^2) estimated from these, as well as statistics comparing variances from both methods. In 5 of the 13 yr, the variances from different methods are not equal, with the subsample estimates being generally larger. In all cases, however, the estimates are of the same general order of magnitude.

TABLE 9.—Mean estimates from five 2-h/d subsamples of each year's data, with variance (from the mean). These variances are compared with those derived for each year independently (col. 4) by χ^2 test.

Year	Mean estimate ($n = 5$)	Variance (from mean)	Variance (derived, Table 8)	χ^2
1967-68	12,301	2,326,235	1,628,883	5.7129
1968-69	11,336	474,113	2,388,470	[1]0.7940
1969-70	12,226	4,183,815	2,622,599	6.3011
1970-71	11,567	5,595,042	1,050,782	[1]21.2985
1971-72	9,745	956,377	842,864	4.5307
1972-73	15,532	9,522,245	1,817,229	[1]20.9600
1973-74	14,992	5,050,008	2,426,376	8.3252
1974-75	13,641	1,858,617	1,864,729	3.9869
1975-76	15,001	10,096,117	3,545,588	[1]11.3901
1976-77	15,833	920,392	3,233,889	1.1384
1977-78	13,588	515,923	5,163,965	[1]0.3996
1978-79	13,557	1,737,235	1,270,420	5.4698
1979-80	17,337	8,668,263	5,558,979	6.2373

[1]Significant at $\alpha = 0.05$.

Changes in Population Size, 1967-68 to 1979-80

There was a significant, positive rate of change in gray whale population size of 2.5%/yr during the 13 yr observed. The annual estimates are plotted, along with 95% C.I., in Figure 8. The unweighted simple linear model results are

$$N_t = 11{,}502.29 + 390.3 \cdot t. \qquad (16)$$

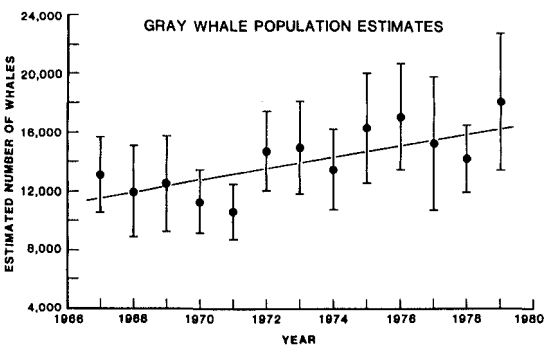

FIGURE 8.—Population estimates for the California stock of gray whales for 13 yr (1967-68 to 1979-80) with 95% confidence intervals. Fitted line is from exponential regression weighted by variances.

The coefficient of determination is 0.516, the slope is significant ($t = 3.427 > t_{11,0.05}$), and the 1980 population level estimate from this model is 16,186, with 95% C.I. (14,608, 17,763). The weighted $\log_e$ model results are

$$\ln N_t = 9.3313 + 0.02513 \cdot t. \qquad (17)$$

The retransformed intercept is 11,285 for the 1967 population level. The slope is also significant ($t = 2.61 > t_{11,0.05}$), and is an estimate of the net annual rate of increase. Expressed as a percentage, $r = 2.513$ with a standard error of 0.964. The estimated 1980 population level from this model is 15,647 with 95% C.I. (13,450, 18,201).

DISCUSSION

Five areas of investigation were mentioned at the beginning of this paper as necessary to extrapolate confidently from counts of whales passing during daylight hours to estimates of total population size. We have addressed four of these quantitatively: 1) Animals missed as a function of their distance from shore, 2) animals missed due to poor visibility conditions, 3) miscounting of the number per pod, and 4) whales passing before and after the census period. The fifth area, night travel rates (and extrapolation of daylight counts to cover these), has not been adequately addressed to date by direct observation. Our last 2-yr data show a lower count for 0700-0800 h. The low value for this hour can be interpreted in two ways: The counts may be reduced due to limited visibility during the first half of this hour before the sun is up over the coastal mountains, or the animals are in fact increasing their rate of travel as the sun rises, having slowed down at night. As discussed previously (Reilly et al. 1980), the small amount of direct evidence that does exist on night travel rates, from Cummings et al. (1968) and Rugh and Braham (1979), supports the concept of a constant 24-h rate. Lacking conclusive data on this, and for consistency, we have treated the abundance estimation for these last years in the same manner as the earlier years. That is, an hourly mean rate calculated for the 10 sampled hours is used to extrapolate over the 14 h of darkness each day. If in fact the rate is slower at night, then our estimates are biased upward by an unknown proportion. For example, if the whales slow down at night to about one-half of the daytime rate of travel, our estimate from 1979-80 would be reduced from 17,577 to 12,450. Estimates from the other 12 censuses would be similarly reduced. If the rate is indeed constant, and the depressed 0700-0800 h rates for

the last two censuses are a result of limited light, then our estimates for these 2 yr are biased downward, but only by a small amount.

Because the night rate is the single largest extrapolation of the estimation procedure, more direct evidence on this would be highly desirable. Perhaps radiotelemetric studies in progress by Mate and Harvey (1979)[5] will help to clear up remaining ambiguity on this point.

The mean estimated group size increased with increasing distance from shore. This prompts two varying interpretations: This result may be an accurate depiction of whale behavior, or it may be an indication of greater sightability of larger groups farther offshore. The correction used here for whales missed offshore is based upon the assumption of equal sightability of groups, independent of group size within 1.5 mi (2.4 km), during periods of unhampered visibility. If the distribution of group sizes is in fact uniform with respect to shore, and small groups are missed near the outside of the 1.5-mi (2.4 km) zone, our population estimates would be biased downward.

Even after correction for varying amounts of poor visibility conditions and proportions of the population missed offshore, there is a considerable amount of year-to-year variation within the significant increase noted here. This may be due to further effects of visibility conditions or to unaccounted variation between counters. It also may be due, in part, to varying proportions of the population overwintering north of the Monterey area during different years. An investigation into the possible relationships of the changes in migratory timing to seasonal environmental events in the Arctic Ocean and North Pacific is in progress and may help clarify this problem.

The annual estimates presented here are slightly higher than those reported earlier (Reilly et al. 1980), especially for years with many days of poor visibility, primarily due to correction for this factor. The variances presented are also of a slightly greater magnitude than those previously reported. These are probably a more realistic representation of the variation inherent in the estimates, because they now include consideration of variation from both the effect of visibility conditions, and the inconsistency of estimating distances to passing whales. The general magnitude of the derived variances was independently corroborated by the subsampling exercise.

Regarding the current population level, we have produced three estimates: 17,577 from the latest census, 16,186 extrapolated from a simple linear model of increase, and 15,647 extrapolated from the weighted log model of increase. The 95% confidence intervals of all three overlap the point estimates. Given the range of extrapolations employed, the most conservative route is to choose the lowest, 15,647, as the "best" estimate of current population size.

A statistically significant increase in population level of about 2.5%/annum was calculated from these census results. If one also considers the annual harvest of about 164 whales by the Soviet subsistence fishery near the Chukotski Peninsula (Ivashin and Mineev 1978; International Whaling Commission 1979), the total net annual rate of production was probably near 3.75% for the past 13 yr. To our knowledge, this is the first empirical substantiation of a net increase in size by a whale population which was under exploitation.

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APPENDIX 1.—NOTATION

$\hat{n}$ = estimate of the number of whales in a passing group.

m_a = number of whales estimated to be within interval a during the regular censuses.

$\hat{m}_b$ = number of whales classified into interval b after restructuring by Equation (2).

b_n = mean bias for estimates of the number of whales in pods of n individuals.

ρ_{ab} = the proportion of the whales estimated to pass within offshore distance interval a which are actually passing within interval b.

k = the year of the census, with the 1967-68 census scaled as year 1.

$h(k)$ = offshore distance distribution correction factor for year k.

C_s = cumulative proportion of whales sighted between the shore and 1.5 mi (2.4 km) during the regular census.

C_p = cumulative proportion of the population predicted to have passed between the shore and 1.5 mi (2.4 km), by aerial transect verification.

$\hat{n}_j$ = estimate of the total number of whales passing the census site during day j, from actual counts, or from the gamma distribution, depending upon the visibility conditions.

$\Sigma\hat{n}_j$ = sum of the daily estimates.

t_j = number of hours during which a watch was conducted on day j.

$\hat{p}_j$ = the relative proportion of the population estimated to have passed the station on day j, from direct observation.

$\hat{P}_j$ = the relative proportion of the population expected to have passed the station on day j, from the gamma model.

$\hat{\theta}_j$ = the cumulative proportion of the population expected to have passed the station up to and including day j, less the proportion which passed prior to the first census day.

α = scale parameter of the gamma distribution.

β = shape parameter of the gamma distribution.

a,b = intervals of distance from shore.

N = total number of whales in the population.

$\hat{N}_j$ = estimate of the total number of whales in the population from data cumulative to day j.

$\hat{N}_k$ = estimate of population total for year k, using data cumulative to the last day of the census.

S_0^2 = variance of the estimate of the population total derived from the components of the estimation model (Equation (11)) by the Delta Method (see Appendix 2).

S_R^2 = variance of the estimate of the population total from data subsamples.

APPENDIX 2.—VARIANCE ESTIMATION

For $\hat{n}_j = (\Sigma E[n]/t_j) \cdot 24$:

$$\text{var}\{E[n]\} = \begin{cases} 0.464 ; n = 1 \\ 0.000 ; n = 2,3 \\ 0.612 ; n \geq 4 \end{cases} \text{ from Reilly et al. (1980).}$$

$\text{var}(\hat{n}_j) = (24/t_j)^2 \cdot \{\Sigma \text{var} E[n]\}$, by the Delta Method (Seber 1973).

For $n_j = (\Sigma \hat{n}_j) \cdot p_j$:

$\text{var}(\hat{n}_j) = (\hat{p}_j)^2 \text{ var}(\Sigma \hat{n}_j) + (\Sigma \hat{n}_j)^2 \text{ var}(\hat{p}_j)$,

where $\text{var}(\Sigma \hat{n}_j) = \Sigma \text{var}(n_j)$ as above, assuming $\text{cov}(\hat{n}_j, \hat{n}_{j-1}) \simeq 0$, and

$\text{var}(\hat{p}_j) = (\delta p/\delta\alpha)^2 \text{var}(\beta) + (\delta p/\delta\beta)^2 \text{var}(\alpha) + 2(\delta p/\delta\beta)(\delta p/\delta\beta) \times \text{cov}(\alpha,\beta)$, by the Delta Method, and

$\text{var}(\alpha)$, $\text{var}(\beta)$, and $\text{cov}(\alpha,\beta)$ are estimated as in Greenwood and Durand (1960).

For $\hat{N}_k = (\sum_j \hat{n}_j)^2/\Sigma \hat{n}_j \cdot \theta_j) \cdot h(k)$:

$\text{var}(\hat{N}_k)$ is approximated by the Delta Method (as in $\text{var}(\hat{n}_j)$ and $\text{var}(\hat{p}_j)$), with component variances

$\text{var}(\theta) \simeq \theta(1 - \theta)/n$,

$\text{var}\{h(k)\} = (-C_p/C_s^2)^2 \text{ var}(C_p) + (1/C_p)^2 \text{ var}(C_s)$,

$\text{var}(C_p) = C_p(1 - C_p)/n$,

$\text{var}(C_s) = \text{var}(\hat{n}_b)$, in which

$\text{var}(\hat{n}_b) = b_a(\hat{n}_a/\Sigma \hat{n}_a)^2 \cdot \Sigma \text{var}(\rho_{a\,b})$, and

$\text{var}(\rho_{a\,b}) = \sum_a (\rho_{ab})(1 + \rho_{ab})/n_a$.