

POPULATION BIOLOGY AND STATUS
OF EASTERN PACIFIC GRAY WHALES: RECENT DEVELOPMENTS

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Abstract. Gray whales (*Eschrichtius robustus*) of the eastern Pacific stock are perhaps the best-known population of baleen whales, but uncertainties remain concerning many aspects of their population biology. The most recent abundance estimate (1987/88) of 21 113 (SE 688) may be the most accurate and precise available for any baleen whale population; but the estimated confidence interval is problematic, most likely not reflecting all relevant sources of error. The population is estimated to have increased at an annual rate of 3.2% (SE 0.5%) during the 20-yr period 1967/68 to 1987/78, during which annual harvests of about 174 whales were taken by the Soviet aboriginal fishery. Data from this fishery indicate a steep decline in pregnancy rates during 1987 to 1990, from a relatively stable level during the preceding 20 yr. Three approaches have been used to determine the status of this population: back-calculation, dynamic response, and Bayesian estimation of parameters for a simple population dynamics model. None of these approaches produced unequivocal results, but the back-calculation produced reasonable trajectories of abundance through time with either a tripling of carrying capacity since 1846 or a 50% minimum increase in recorded catches. All uncertainty considered, the population is probably above its 1846 level, when commercial exploitation began, and may now be approaching current carrying capacity. The combination of net productivity exceeding 4% and indications that the population is nearing carrying capacity are consistent with the hypothesis that for most large mammals, maximum net productivity occurs at high population levels.

INTRODUCTION

Gray whales (*Eschrichtius robustus*) are perhaps the world's best studied baleen whales. Their abundance, distribution, behavior, life history, and ecology have been the subjects of numerous investigations. There are, however, important aspects in all these topics that are still poorly understood or controversial. In this paper I review progress during the past 7-8 yr resulting from efforts to understand their population biology, with

emphasis on information relevant to determining their present status. As discussed below, it is not entirely clear what should be used as a standard to evaluate present status.

Two distinct populations of gray whales are recognized, the western Pacific and eastern Pacific stocks. This review is concerned only with the eastern Pacific stock. The western Pacific stock, with very few surviving individuals, is clearly endangered (Klinowska 1991, Braham and Donovan 1992), but may have never numbered more than a few thousand. (Two Atlantic stocks are now extinct.) In April 1990 the International Whaling Commission (IWC) convened a meeting to conduct a "comprehensive assessment" of the status of gray whales (IWC 1990). I have drawn heavily from the papers and proceedings of that meeting in this review. Three major topics are covered: abundance and trends, biological parameters, and quantitative attempts to determine status.

ABUNDANCE AND TRENDS

There have been many field programs to estimate gray whale abundance, as reviewed by Reilly (1984*b*) for efforts up to 1980, and by Dahlheim and Rugh (1990) for subsequent efforts. There are three types of survey data: aerial surveys of the winter range in Mexican waters, shore-based sighting surveys along the coast of upper California during the north and south migrations, and aerial or ship surveys on the summer range in the Bering and Chukchi Seas. Of these surveys, only one is sufficiently reliable for estimation of abundance and trends in abundance. This is the annual survey of the south migration conducted since 1967/68 from points near Monterey, California. The other efforts were incomplete, covered variable parts of the population, and lacked sufficient corroborative data to allow reliable estimates of relative or absolute abundance (Reilly 1984*b*). Two counts from a coastal point of northbound migrants have shown promise for estimating annual calf production (Poole 1984) but these counts have not been made in recent years.

Sixteen annual surveys were conducted near Monterey during the 21-yr period ending in the winter of 1987/88 (Reilly et al. 1983, Breiwick et al. 1988). To make these counts, one or two observers viewed migrating whales from a bluff-top position 21 m above the water. Migrating groups or "pods" were in view for about one-half hour. As the pods passed the counting station, the observers recorded estimates of the number of individuals in the pod and their distance offshore, along with information on sighting conditions. This protocol was followed during all daylight hours, sampling about 10 of 24 h each day (Dahlheim and Rugh 1990).

Estimating abundance from the recorded counts involves correcting for: (1) pods missed entirely in the nearshore area, (2) pods missed due to their distance offshore, (3) pods missed due to poor visibility conditions, (4) those passing during unmonitored periods at night, (5) others missed before and after the census period, and (6) miscounting of individuals within sighted pods (Reilly 1984*b*, Breiwick et al. 1988).

In analyzing the first 13 years' data, Reilly et al. (1983) applied the following solutions to the six problems listed above. Only counts from days with "good or better" sighting conditions (Beaufort 4 or lower) were used. A gamma probability density function (PDF) was fit to each year's daily sighting data. Migration rates were estimated

from this PDF for days with poor visibility and for days before the beginning and after the end of the survey. Whales passing at night were estimated by a simple proportionality constant, assuming no difference between day and night migration rates. Aerial surveys indicated that about 20% of passing pods were missed as a function of their distance offshore. Experiments indicated consistent negative biases in counting numbers within sighted pods, and appropriate corrections were applied. Abundance estimates ranged from a low of 10 414 for 1971/72 to a high of 17 577 for 1979/80, with coefficients of variation (CV) of about 11%. The population exhibited a significant annual increase of 2.5% during 1967/68-1979/80, concurrent with an annual harvest of about 1.2% in the Soviet aboriginal fishery.

Three additional surveys were conducted, in the winters of 1984/85, 1985/86 and 1987/88 (Breiwick et al. 1988). Data from the 1984/85 and 1985/86 surveys suggested a different distribution of pods migrating offshore from the survey site compared to those of the previous 13 yr. To check this, the aerial surveys of 1978/79 and 1979/80 were replicated in 1987/88 (Withrow 1990). The aerial data were very similar to those collected earlier, but the 1987/88 shore count distribution was farther offshore than in the pre-1981 efforts. The 1987/88 shore and aerial distributions were not statistically different, indicating that the shore observers did not consistently miss whales as a function of their distance offshore that year. The discrepancy between the shore-based distributions from the early years and the more recent 3 yr is a problem, especially in attempts to measure trends over the entire 21 yr period (discussed below).

Rugh et al. (*in press*) tested the assumption of Reilly et al. (1983) that essentially all passing pods were seen within 1.5 nautical miles (2.7 km) of the shore during periods of unhampered visibility, by running two independent, parallel counting operations during the 1987/88 migration. They used mark-recapture methods to estimate that about 26% of passing whales were missed by the shore counts, even during periods of good visibility and within 10.5 nautical miles. Swartz et al. (1987) radio tagged 12 gray whales during the south migration past central California, and found that night and day migration rates were not different, supporting the assumption used earlier in abundance estimation.

Other differences in treating the recent 3 yr counts included the fit of Hermite Polynomial models to the migratory timing data (rate of pods passing per hour) instead of gamma models. These models were used to predict migration rates during all unmonitored periods, including nights, daylight hours with poor visibility, and the "tails" of the migration. This was done by integrating the area under the fitted model, and comparing this sum to the totals from the observed periods. The ratio of these sums was used as an estimate of the proportion of pods missed during unmonitored periods. The recorded number of pods was then scaled up by this ratio estimate. Breiwick et al. (1988) also assumed the actual number of pods counted to be subject to variability that was greater than that of a poisson distribution by a factor estimated from the fit of the Hermite Polynomial, and estimated a SE for this factor. The corrections applied and their SE are listed in Table 1 for the 1987/88 absolute abundance estimate of 21 113.

This abundance estimate is perhaps the most accurate of any for a large whale population. In comparison to ship or aerial surveys of pelagic species, or breeding/feeding area counts of dispersed populations of humpback and right whales, a relatively large proportion of the gray whale population is actually observed. This is made possible by the mild winter climate at the survey site, and the migration of the vast

majority of the population past Monterey, very close to shore. The problems of estimating total abundance from recorded shore counts have been addressed for decades, with many refinements achieved (Rice and Wolman 1971, Reilly et al. 1983, Reilly 1984b, Breiwick et al. 1988, Buckland 1990).

I am not so confident in the magnitude of the 1987/88 abundance estimate's SE. In particular, the SE for the Hermite Polynomial model's correction factor for unmonitored periods is suspiciously small with a CV of 0.003 for that correction. This implies that it is possible to estimate the number of pods passing during over 60% of the migration to within less than 1% of the true number with 95% confidence, given the observed rates during the other 40% of the migration. In my opinion, the process of variance estimation for the 1987/88 abundance estimate, and subsequent application of this process to the rest of the time series, requires some reevaluation. Examination of Fig. 1 provides empirical evidence that the SEs estimated as in Breiwick et al. (1988) are too small. The 95% confidence limits of adjacent years do not overlap in four cases. This disparity is most extreme for 1971/72 versus 1972/73. Although the specific variance components that have been quantified may be technically correct, there are clearly other, unquantified components of variance. S. T. Buckland (*personal communication*) suggested that these SE estimates might be considered as lower bounds, and that upper bounds could be obtained from the mean residual of the annual estimates in Fig. 1 from the fitted, exponential line.

TABLE 1. Corrections applied, their standard errors (SE) and coefficients of variation (CV) for the 1987/88 estimate of gray whale abundance, from Breiwick et al. (1990).

| Parameter | Estimate | SE | CV |
|--------------------|----------|-------|-------|
| pods seen | 2902 | 81.1 | 0.028 |
| unmonitored time | 20.574 | 0.009 | 0.003 |
| mark-recapture | 1.260 | 0.014 | 0.011 |
| pod size + bias cf | 2.243 | 0.027 | 0.012 |
| Abundance | 21 113 | 688 | 0.033 |

Buckland (1990) also had to contend with the apparent inconsistencies in offshore distribution from the pre- and post-1981 shore surveys in his estimation of trend over the entire 21-yr period. Because the distributions from aerial surveys prior to 1981 showed no substantial differences from that collected after 1981, Buckland (1990) believed that the most likely explanation for the differences in the shore data was a consistently large negative bias in distance estimation by land-based observers during the first 13 yr. In support he cites the use in post-1981 surveys of binoculars with reticles (etched lines in

the lenses corresponding to known angles and therefore estimable distance categories). Lacking a satisfactory method to correct for this explicitly, he assumed there were no interannual trends in bias in detecting pods with distance, or in the true proportion of whales passing out of sight from land.

Buckland (1990) estimated relative abundance for years prior to 1987/88 by scaling up recorded counts with the Hermite Polynomial correction factor (for unmonitored periods) and multiplying by the average pod size. For 1987/88 an estimate of absolute abundance was made by further applying the correction factors for pod size bias, and for pods missed entirely (from the mark-recapture estimate). The other years were then scaled up for trend estimation by the ratio of the relative to absolute estimates for 1987/88. A regression of natural logs of abundance on time, weighted by the inverse of the variances, yielded an estimate of 3.21% (SE=0.55%) for the annual rate of increase during 1967/68-1987/88 (Fig. 1). The population approximately doubled in size during the 21 yr monitored. The mean annual catch of 174 whales in the Soviet aboriginal fishery (Blokhin 1984, 1989, 1990) represents just under 1% of the mean abundance during this 21 yr period. The combination of increase and catch indicates a mean net productivity of about 4%.

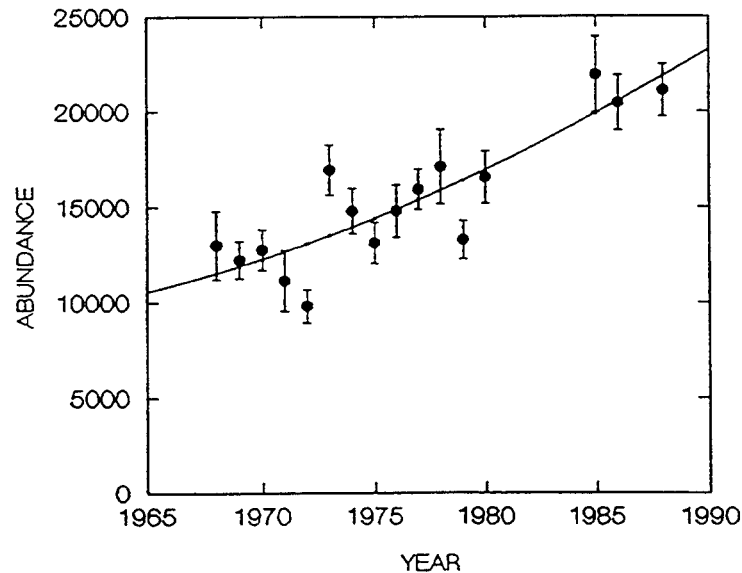


Fig. 1. Gray whale abundance estimates with 95% confidence intervals, by year, from Monterey shore censuses. Fitted line is from exponential regression weighted by reciprocals of squared standard errors (Buckland 1990).

BIOLOGICAL PARAMETERS

Do biological parameters have relevance in determining status of cetaceans? This

question has been debated extensively in recent meetings of the IWC's Scientific Committee (e.g., IWC 1990:119-130). Because of the considerable uncertainty in estimates of biological parameters, it is advisable to use assessment methods that are neither dependent upon nor sensitive to them (de la Mare 1990, IWC 1977). For example, use of the dynamic response method (Goodman 1988) requires only abundance indices. Assessment methods involving the fitting of a population model to abundance data require information on birth and death rates, and on the form of density dependence. A commonly-applied example is "back-calculation" (e.g., Smith and Polacheck 1979), which fits a population dynamics model to a history of catches. The simplest applications of back-calculation collapse effects of birth and death into simple stock-recruitment models. Even for these very simple models it is necessary to examine the sensitivity of results to assumptions about recruitment rates and the form of density dependence.

With some basic, general assumptions about density dependence, the monitoring of trends in one or more biological parameters may provide qualitative (but not conclusive) information on population size relative to carrying capacity (K). It is axiomatic that as a population approaches K , its birth rates will decrease and/or mortality rates will increase. Eberhardt and Siniff (1977) proposed a likely scheme for the direction and order of change in several vital rates as density changes. Unfortunately, we do not yet have adequate data from any cetacean population to test their hypotheses, which were derived from other mammals and theory.

Table 2 lists values of five vital rates accepted by the IWC in its 1990 "comprehensive assessment" of gray whale status (references in Braham and Donovan 1992). Nothing has been published to date allowing the detection of possible changes in mortality rates or ages at sexual maturity. It may be possible to make new estimates of adult mortality rates from the Soviet aboriginal fishery, but this has not been attempted. In contrast, pregnancy rates have been reported for most years' catches since 1965 (Blokhin 1984, 1989, 1990, 1991, Zimushko and Ivashin 1980). Annual reports to the IWC from the past four years (1987-1990) suggested a decline, which would be expected

TABLE 2. Gray whale biological parameters, from the report of the 1990 International Whaling Commission comprehensive assessment of gray whale status (Braham and Donovan 1992).

| | |
|-------------------|---|
| Gestation period: | 418 days |
| Sexual maturity: | 9 yrs median (range 6-12 yrs) 6 yrs median (range 5-9 yrs) |
| Ovulation rate: | ca. 00.5/yr |
| Pregnancy rate: | 0.47/yr (0.38-00.56): from catch data, 1965 - 1968 0.48/yr (0.46-00.50): from photo-ID, 1977 - 1982 |
| Mortality rates: | M = 0.055 (♀ adult): from catch data M = 0.046 (♂ adult): " " " M = 0.112 (juvenile): from balance equation |

to occur in a population nearing K . I combined the available data, estimated simple binomial variances for each annual rate, and plotted the results (Fig. 2a). There does appear to have been a substantial decline in recent years. A linear model exhibits a decline that is significantly different from zero ($F=27.9$, $P<.001$, $r^2=0.76$), but the data are better fit by a non-linear (quadratic) model, as plotted in Fig. 2a ($F=59.3$, $P<.001$, $r^2=0.87$). Fig. 2b shows the pregnancy rates plotted against predicted abundance estimates from Buckland's (1990) exponential model (same as fitted line in Fig. 1). The observed range of rates centered near 0.45 (but with wide confidence limits) during years up to 1986, in agreement with both Rice and Wolman's (1971) estimate of 0.46 from 316 whales captured off California, and Jones (1990) estimate of 0.48 from photo-ID studies.

I fit a simple, generalized exponential model to the pregnancy rate and abundance estimates of Fig. 2b. The specific model used was: $P_t = P_0 (1 - (N_t/K)^Z)$, where P_t is pregnancy rate at time t , $P_0 = 0.5$ is the maximum equilibrium rate (Reilly 1984a), and K is carrying capacity, set speculatively at 25 000 for this exercise (see below). The best fit, drawn in Fig. 2b, was obtained with $Z = 4.4$. If one speculated further that this was the only density dependent vital rate, this would imply that the maximum net productivity level (MNPL, that level which yields maximum net production) $\approx 68\%$ (in the absence of age-structure effects). There are too many untested assumptions in this fitting exercise to use the results for decision making. Nevertheless, it is interesting to note that if K is

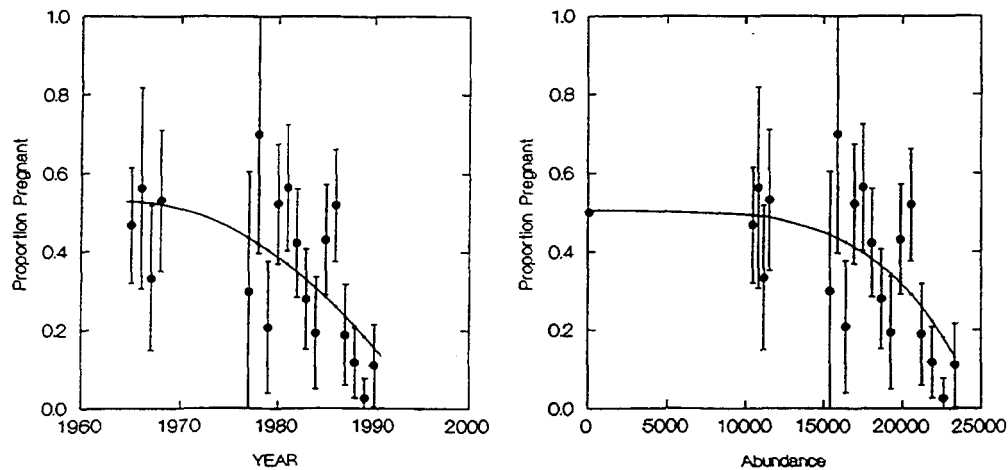


Fig. 2. a. Gray whale pregnancy rates, with binomial 95% confidence limits, by year, from the Soviet aboriginal fishery (Blokhin 1984, 1989, 1990, 1991, and Zimushko and Ivashin 1980). b. Gray whale pregnancy rates with 95% confidence limits by estimated population sizes. Pregnancy rates from Blokhin (1984, 1989, 1990, 1991), Breiwick et al. (1989), and Withrow (1990); abundance estimates from exponential increase model fit to Monterey census data from Breiwick et al. (1989).

in the mid-20 thousands, pregnancy rates appear to be responding similarly to predictions by Fowler (1987) that most density-dependent response is expected to occur in levels above 50% for most large mammals.

A major concern in interpreting the pregnancy rates from the Soviet fishery is possible sampling bias. Blokhin (1989) presents summary tables showing marked differences in pregnancy rates by subarea within the fishery zone around the Chuckchi Peninsula, and a steep decline in rates by month from almost 60% in July to 12% in November. Before the apparent annual trend can be accepted, it is essential that an analysis be conducted to account for effects of location and month of capture. This is not possible given the published summary statistics.

STATUS DETERMINATION

Reference level?

Assessment of a population's status requires agreement upon a reference level, or K , for comparison with the present population level. This is not a problem for populations with a short history of exploitation. For gray whales it is not clear what the reference level should be. Commercial exploitation began in 1846 (Henderson 1972), over 140 yr prior to the most recent census. A further complication arises from the aboriginal fisheries for gray whales, which date back to at least the 16th Century (Mitchell 1979, Mitchell and Reeves 1990). Consequently, the stock was not in an unharvested state in 1846. Ideally, we would be concerned only with the present K , as in the dynamic response method. As discussed below, this method has other limitations for the gray whale case, so we must still select the most appropriate reference level.

Back calculation

This method fits a population dynamics model to a history of catches, back to a point in time prior to exploitation. The abundance at this point is interpreted to be the carrying capacity (Breiwick et al. 1984, de la Mare 1990). Back calculation requires an estimate of current absolute abundance, through which the trajectory must pass, or a series of estimates to be fitted by the trajectory. For gray whales, we have a current absolute abundance estimate, a recent series of abundance estimates, and additional qualitative information to help evaluate trajectories. There is good historical documentation of a rapid decline in abundance following the peak of commercial exploitation, to a state of commercial "extinction" in the late 19th Century (Henderson 1972, 1984).

Early attempts to apply back-calculation to assess the status of gray whales were made by Ohsumi (1976), Reilly (1981), Cooke (1986) and Lankester and Beddington (1986). In general, these efforts were not successful in reconciling the catch history with the current abundance, recent increase, and standard models of density dependence. Reilly (1981) reported one model that appeared to produce a reasonable trajectory, but that result was extremely sensitive to the rather complex modelling structure used.

Butterworth et al. (1990b) repeated this exercise with a simpler population model,

the "hitter-fitter" model of de la Mare (1989), and updated catch statistics. Similar to Reilly (1981) and Lankester and Beddington (1986), this back-calculation explicitly included pre-1846 aboriginal exploitation. Initial runs with just the reported catch levels produced abundance trajectories much like those of the earlier efforts, with a decline during 1967-1981, and a minimum above 12 000 in the late 1800s, clearly not matching available data. Two modifications produced trajectories that were reasonable: a tripling of K during the period (considered very unlikely by the IWC Scientific Committee) or a scaling-up of the catch histories for aboriginal or commercial catches by more than 100%. Even with these changes, a productivity rate (MSY) greater than 3% at MNPL was also required. Estimates of K resulting from the acceptable runs ranged from 23 000 to about 35 000. It seems reasonable to assume that the early aboriginal kills were 100% higher than documented, given the recent, extensive review by Mitchell and Reeves (1990). If accurate, these results indicate the 1988 population of 21 113 was between 70% and about 88% of K . These results alone, however, are probably not sufficient to make a status determination, given the uncertainty involved (Braham and Donovan 1992).

Dynamic response (DR) and related methods

This approach fits simple functions to series of abundance data (relative or absolute) to test for an inflection, under the assumption that such a change in growth rate represents passage through MNPL (Goodman 1988, Gerrodette 1988). The simplest application of the method is to fit a quadratic function and examine the sign of the second order term. Boveng et al. (1988) describe a method of "local" fitting, i.e., to overlapping subsets of the series, followed by examination of the second order coefficients. A growing population passing through MNPL will have positive values initially, then cross the zero line and have negative values. Only positive values indicate status below MNPL.

Gerrodette and DeMaster (1988) applied dynamic response analysis to the 1967-1980 gray whale abundance series of Reilly et al. (1983) and concluded there was evidence that the population passed through MNPL during the sampled period. Boveng (1992) repeated this dynamic response analysis with similar methods, but included the most recent three census points. He concluded that there was no reliable information in the series on the stock's status. Boveng (1992) noted two possibilities to explain this result: the data may be too "noisy" to reflect density-dependent curvature, or the stock may, in fact, have been near MNPL at the midpoint of the sampled interval. Gerrodette (1988) showed that for populations at or somewhat above MNPL the probability of correctly determining status drops to near 0.5.

Butterworth et al. (1990a) applied a variation of the dynamic response method to the same data. They fit logistic and cubic models to the full series (a "global" fit), to test for points of inflection. They found that the cubic model followed what must be local noise in the series, causing spurious, repeated changes in sign of the coefficients. The logistic model fit very similarly to the exponential model shown here in Fig. 1, actually curving upward. Butterworth et al. (1990a) concluded that the probability was not large that the population passed through MNPL during the interval. Based on results of Butterworth et al. (1990a) and Boveng (1992) the dynamic response approach appears to provide little useful information for determining this population's status. It may be, as Boveng notes, that the power of this technique is unacceptably low for populations with

maximum growth rates less than 10% per year.

Goodman (1990) developed and applied a Bayesian approach to determining status from a series of abundance estimates. Unlike the dynamic response analyses, he postulated a modified logistic population dynamics model, and used the data series to improve estimates of K and r (intrinsic rate of increase) from uniform prior distributions set over wide ranges (20 000-50 000 for K , 0.03-0.08 for r). He concluded that there was little additional information in the Monterey census series to improve the prior distributions. The posterior distribution for K had a slight mode at about 23 000, but the distribution was so broad that substantially higher or lower values for K were also quite plausible. Goodman (1990) concluded that, based on the data, it would not be prudent to accept that the true value of K is in any particular subset of the plausible range.

CONCLUSIONS

The dynamic response and related methods have very attractive general properties for status determination: not relying on biological data, and determining status in terms of current K . Unfortunately, they provided little help for the gray whale case. It is difficult to envision another cetacean population for which we will have better abundance indices. In general, these methods may not be appropriate for cetaceans. Perhaps with the addition of more annual estimates there will be sufficient curvature in the abundance series for these methods to succeed.

For the present we are left with both back-calculation results that do not successfully complete a status determination without a substantial modification to the catch record and with MSY rate values that are considered somewhat controversial (e.g., IWC 1977:34). If we accept Henderson's (1972, 1984) careful, conservative reconstruction of the early commercial fishery and its effects on gray whale abundance, likely population sizes in 1846 were in the range of 12 000 to 15 000. The 1988 population was very likely above this range. We must, however, decide if the 1846 population is the appropriate standard, or if we should look even farther back in time prior to aboriginal exploitation. Should preindustrial exploitation by native people be considered part of the natural environment? A more acceptable approach would be to use current K as our standard, but we have no unequivocal, quantitative information about this.

The apparent decline in pregnancy rates is quite interesting and should be verified by a more detailed analysis. There is also some preliminary information cited by Stoker (1990) that the benthic fauna upon which gray whales feed is recently showing signs of over-exploitation. Stoker (1990) stated that recent, unpublished benthic investigations in the Chirikov Basin have noted a significant decline in amphipod populations, particularly of the larger adults, beginning about 1986-1987. If verified, this may be additional evidence that the gray whale population is nearing the limits of its environment.

Recent reviews by the IWC (Braham and Donovan 1992) and International Union for the Conservation of Nature (Klinowska 1991) have concluded that the eastern Pacific population is not in immediate danger of extinction. Gray whales are now legally classified as "endangered" in the U. S. under the Endangered Species Act, but this is

under reconsideration. I see no evidence that this population is in danger of extinction, and agree with the suggestions (e.g., Brownell et al. 1989) to remove it from the "endangered" classification under the U.S. Endangered Species Act. It is not entirely clear where it is in relation to its current K , but the back-calculation assessment and additional, preliminary information suggest that it is probably above MNPL and approaching K .

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