Observed and Maximum Rates of Increase in Gray Whales, *Eschrichtius robustus*

STEPHEN B. REILLY

National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southwest Fisheries Center, 8604 La Jolla Shores Drive, La Jolla, California 92038

ABSTRACT

Shore station censuses indicate that the California stock of gray whales increased at an annual rate of 2.5% during 1967–1980, concurrent with an annual exploitation of approximately 1.2%, i.e. net reproduction was near 3.7% per year. In light of this net reproduction, vital-rate estimates for the *circa* 1967 population were re-evaluated. The most likely values during that period were: pregnancy rate of 0.467, mean age at sexual maturity of 8 years, adult survival of 0.945 and juvenile survival of 0.899. To estimate maximum net rate of increase, biologically defined limits of pregnancy rate, age at sexual maturation and juvenile survival were used to generate a Leslie matrix, with adult survival held constant at the 1967 level. The dominant eigenvalue of the matrix was calculated as 1.069. If a stable age structure can be assumed in populations at a very low level, this indicates a possible maximum net rate of increase approaching 6.7% per year.

INTRODUCTION

In the study of animal population biology the rate of increase exhibited by a reproductive stock is of interest in both applied and theoretical contexts. The maximum possible, or intrinsic rate of increase, and the realized rate under a set of definable and measurable conditions have relevance both for the study of population dynamics in general and for the management of exploited mammal populations.

In this study I have estimated the maximum rate of increase for the California stock of gray whales from what is known or can be inferred of the stock's vital rates, utilizing a population projection matrix. The observed rate of increase was calculated directly from data collected during annual shore station censuses. In the course of estimating the rates of increase, our state of knowledge of much of the reproductive biology of the stock has been reviewed, with new estimates made for some vital rates. Dependence of the rate of increase on population density or some related factor is tacitly assumed here. Data do not presently exist to test this assumption for gray whales.

Observed rate of increase, as measured through sighting censuses, is addressed here first. All available time series of sighting censuses were reviewed for applicability as indices of change in population size. Results from this section are then utilized in the following sections, in the estimation of vital rates and finally of maximum rate of increase. These results have potential interest in interpreting the assumed 'recovery' of the stock from severe depletion, in evaluating the effects of contemporary exploitation by the Soviet subsistence fishery, and in estimating the potential impact of major perturbations resulting from natural or man-induced changes on the calving and feeding grounds.

As part of their monographic study, Rice and Wolman (1971) reviewed information available up to 1970 on rate of increase. From Point Loma censuses of the 1950s they estimated an annual increase of 12.2%. This is re-estimated below. Rice and Wolman (1971) also estimated an annual rate of increase of 0.8% from the 1954–1964

Baja lagoon censuses. These data are also reviewed here.

Chapman (1981) estimated observed rate of increase from two of the time series examined here: early Pt Loma shore counts (10.4%) and Baja lagoon aerial counts (8.0%).

Previous studies which treated gray whale vital rates include Blokhin (1979; 1982), Ohsumi (1976), Rice and Wolman (1971), Zenkovich (1934; 1937), Zimushko (1969a; 1969b; 1970; 1971; 1973) and Zimushko and Ivashin (1980). Findings from these studies are reviewed below, with new estimates produced in some cases.

DATA SOURCES

Sighting time series

Data exist from four series of censuses of gray whale population size: three from shore-based counts of southbound migrating whales and one from aerial censuses of whales on their winter grounds along Baja California. For two of the four with interpretable data, rate of increase was estimated using exponential regression techniques.

Vital rates

Two data sources exist for the estimation of gray whale vital rates: from a series of whales examined by Rice and Wolman (1971) during the 1960s and from animals examined in the Soviet subsistence fishery during the 1960s, early 1970s and 1978–1980.

During 1959 through 1969 Rice and Wolman (1971) examined 316 gray whales collected off the coast of central California, between Half Moon Bay (37° 30′ N) and Point Reyes (39° 00′ N). Whales were captured *en route* both north and south (Table 1). The majority of collections were made during 1964 through 1969, with a mean collection date of 1967. For vital rate estimation, in both Rice and Wolman's analysis and here, the entire series was pooled over collection years in order to maximize sample sizes. It is possible that one or all vital

Table 1

Dates of capture for 316 gray whales collected off the central coast of California for Rice and Wolman (1971), used here for estimation of vital rates

Dates	Number of whales taken	Direction of migration
23–26 Feb. 1959	2	North
23–30 Mar. 1962	4	North
14–25 Mar. 1964	20	North
22–29 Mar. 1966	26	North
14 Dec. 1966–19 Jan. 1967	95	South
21 Feb.–9 Mar. 1967	30	North
14–25 Jan. 1968	35	South
26 Feb.–11 Mar. 1968	24	North
2–11 Apr. 1968	7	North
20 Dec. 1968–9 Jan. 1969	50	South
2–16 Mar. 1969	23	North

rates changed during the 10 years sampled (1959–69). If so, statistics estimated from the pooled data are at best representative of the mean rates and may also be biased.

Ohsumi (1976) utilized the Rice and Wolman (1971) estimates of pregnancy rate, age at sexual maturity and adult mortality in a simulation study. He estimated juvenile mortality from their data using a simple balance equation. An alternative method to estimate juvenile mortality is proposed below.

Soviet scientists have examined a sample of animals taken in the subsistence fishery in the Bering and Chukchi Seas. A limited amount of information has been reported in a number of short communications. For the years since 1948, total Soviet landings have been reported (Ivashin and Mineev, 1981; Blokhin, 1979; 1982). For 1965 through 1980, sex ratio and proportion mature of landed animals have been reported (Zimushko and Ivashin, 1980; Blokhin, 1982) (Table 2). Frequencies of pregnant females were reported for 1965–1970 (Zimushko, 1969a) and 1978–1980 (Blokhin, 1982). Zenkovich (1937) listed some information on pregnancies from a 1933–1936 series of Bering/Chukchi Sea specimens. For growth and related parameters, analyses and conclusions with varying and limited amounts of supporting data have been published (Zimushko, 1969a; 1969b; 1970; 1971; 1973; Zimushko and Ivashin, 1980; Blokhin, 1979; 1982).

The 1965–70 series of vital-rate estimates from the Soviet data represent roughly the same time period as the Rice and Wolman series and should be comparable from that standpoint. For 1978–1980 the proportion of mature females which were pregnant in catch sub-samples was reported (Blokhin, 1982). Sample sizes were given only for the 1980 data.

Below I review comparative estimates for pregnancy rate, age at sexual maturation, adult and juvenile survival (mortality) rates. New estimates are made here for all but age at sexual maturation.

METHODS

Age determination

As with other baleen whales, earplug laminae have been the primary measure of age in gray whales (Rice and Wolman, 1971; Zimushko, 1973). For adult females, ovarian corpora have also been used. Both time scales are subject to assumptions that are partially or totally untested, including regularity in time of deposition of marks and persistence of marks throughout life. Rice and Wolman estimated that one earplug layer was deposited per year, except for the first year of life, when two layers were deposited. Their interpretation is followed here.

The one-year pattern is in agreement with Roe's (1967) conclusions for fin whales. Zimushko (1969a 1969b; 1971; 1973), however, suggested that two layers per year were deposited in gray whales. This interpretation implied a halved life span (about 30 years at most), sexual maturation at 4.5 years with a minimum of 3 years, and a doubled ovulation rate (in relation to Rice and Wolman's interpretation). In later Soviet papers (Zimushko and Ivashin, 1980; Blokhin, 1979; 1982) the two-layers-per-year interpretation is no longer cited. Lacking new information, the interpretation of Rice and Wolman appears to be the most reasonable.

Notable problems with earplug ageing of gray whales are that the plugs are 'readable' in only about half of the individuals and that there may be fading of juvenile-deposited layers in later life (Rice and Wolman, 1971). Because of these problems, Rice and Wolman used the frequency of corpora in the ovaries of adult females as an alternate scale (discussed below).

Vital rates

Adult survival was estimated in this study and by Rice and Wolman (1971) using the methods of Chapman and Robson (1960). Alternate estimates with older whales truncated were made here in response to Rice and Wolman's (1971) concern that age determination of these 'older' whales was relatively imprecise.

Indirect methods must be employed to estimate juvenile survival. This is because in both the Soviet fishery (Zimushko and Ivashin, 1980) and probably to a lesser extent in the California scientific collections (Rice and Wolman, 1971) juvenile whales were selected against.

Table 2

Gray whales captured in the Soviet subsistence fishery from the Bering and Chukchi Seas, which were sampled for (at least) measurement and sex identification. From Zimushko and Ivashin (1980) and Blokhin (1982)

		1965	66	67	68	69	70	71	72	73	74	75	76	77	78	79[1]	80
Adult	F	47	16	16	31	11	56	1	21	73	74	73	84	4	8	?	44
Juvenile	F	41	2	8	1	2	10	1	1	4	14	40	11	6	7	?	26
Adult	M	39	19	30	10	4	69	2	3	89	80	30	57	?	?	?	19
Juvenile	M	17	4	10	6	1	6	0	0	6	11	28	11	?	?	?	9
Total no.		144	41	64	48	18	141	4	25	172	179	171	163	19	31	?	98

[1] For 1979 the sample size examined for age/sex status was not reported.

Prior to conducting his simulation of population trends, Ohsumi (1976, Equation 4) estimated juvenile mortality (where mortality is the negative logarithm of survival) using a two-age-class balance equation (also occasionally used by the International Whaling Commission's Scientific Committee):

$$1 - e^{-(M+F)} = (P/2) e^{-(M'+F) X_m}$$

where M' = juvenile mortality, M = adult mortality, P = pregnancy rate, F = fishing mortality and X_m = age at sexual maturation. This model assumes no net recruitment, equal vulnerability of juveniles and adults to fishing death, and population lumped into two age classes. Since we have estimates of gray-whale population growth and the range of ages during which sexual maturity is attained, it is possible to estimate juvenile survival more accurately, using this additional information.

As an alternative balance model to estimate juvenile survival, I have used a Leslie (1945) population-projection matrix,[1]

$$L = \begin{vmatrix} f_0 & f_1 & \cdots & f_k \\ S_0 & 0 & \cdots & 0 \\ 0 & S_1 & \cdots & 0 \\ 0 & 0 & . S_{k-1} & 0 \end{vmatrix}$$

where the elements of the top row are age-specific fecundities, the elements of the subdiagonal are age-specific survivals, and $k+1$ specifies the number of age classes. Here $k+1$ was set at 40, since approximately 98% of the population is 40 or younger (Rice and Wolman, 1971). Rate of increase can be dealt with implicitly when using a Leslie matrix, since the dominant eigenvalue λ (see Leslie, 1945) is the antilog of rate of increase: $\lambda = e^r$.

With values set for λ, f (fecundity vector) and adult survival, the characteristic equation for the Leslie matrix can be solved iteratively for S_0, the juvenile survival rate.

Even when only estimates of 'juvenile' and 'adult' rates exist, if a distribution of transition proportions between juvenile and adult stages can be approximated, recruitment to sexual maturity can be reflected as a gradual process. This introduces some of the advantages of a fully age-structured model.

In employing this age-structured technique, rates were assumed constant over large series of ages, i.e. 0–4 years for juveniles, 12+ years for adults. For the apparent transition period of 5–11 years of age, both fecundity and survival rates were changed gradually. The cut-points were defined by the age-at-sexual-maturation data, described in Vital Rates. To accomplish this, a function approximating the proportion of each age class sexually mature was defined, for a = age and x_m = median age at maturity, as

$$f(a) = \begin{cases} 0 & a = 0, 4 \\ (a-5) \cdot (0.5/X_m - 5) & a = 5, X_m \\ 0.5 + (11-a) \cdot (0.5/11 - X_m) & a = X_m + 1, 11 \\ 1.0 & a > 11 \end{cases}$$

The result is a vector r with elements on the interval (0, 1) which are the proportions of each age group sexually mature, and $f(a)$ set at 0.5 at the defined age at sexual

[1] Other, simpler methods could be used to estimate juvenile survival here, e.g. a Leslie matrix with all fully adult age classes collapsed into one term. The full matrix approach was used for consistency with a larger, complementary study (Reilly, 1981) in which population projection was done.
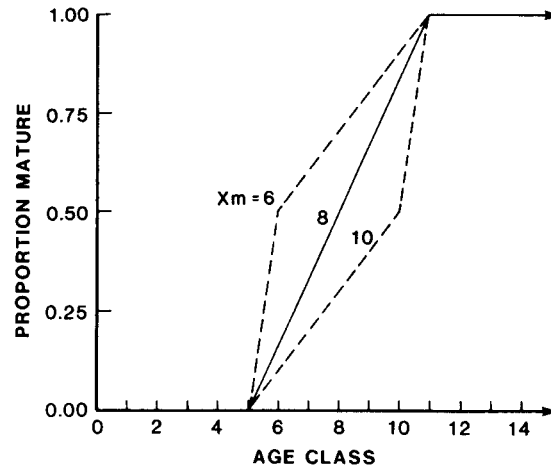

Fig. 1. Examples of vectors of proportions of each age class mature, for mean ages at sexual maturity of 6, 8 and 10 years.

maturation X_m. Fig. 1 illustrates the vector r for three values of age at maturation (X_m). The vector of age-specific fecundities was then generated by multiplying r by half the pregnancy rate and by juvenile survival, to estimate female young surviving through their birth year:

$$f = r \cdot (P/2) \cdot S_j$$

The vector of age-specific survivals (s) was generated by defining a transition between juvenile (S_j) and adult survival (S_a) as

$$s = (S_a \cdot r) + [S_j \cdot (1 - r)].$$

(In the current use, we are attempting to estimate S_j).

The gradual recruitment of age classes to the mature population during the transition years 5 through 11 is a closer representation of variability to be expected in the process of maturation in a mammalian population than simple knife-edged recruitment. To complete the procedure, a Leslie matrix (2) was defined using s and f.

Juvenile survival (S_j) was estimated by setting S_a, P, X_m and λ, and iteratively changing S_j until the characteristic equation for (2) was solved for λ to within a minimum tolerance of 0.001.

Rate of increase

Maximum rate of increase was also estimated using the Leslie matrix. To accomplish this, S_j, P, and X_m were set at values which were identified here as biological limits that would be approached as population density approached zero, assuming that these vital rates are variable in a density-dependent manner. Adult survival (S_a) was assumed not to be density-dependent here, following the arguments of Fowler (1981) and Eberhardt and Siniff (1977). The maximum rate of increase was then calculated from the dominant eigenvalue of the resulting matrix.
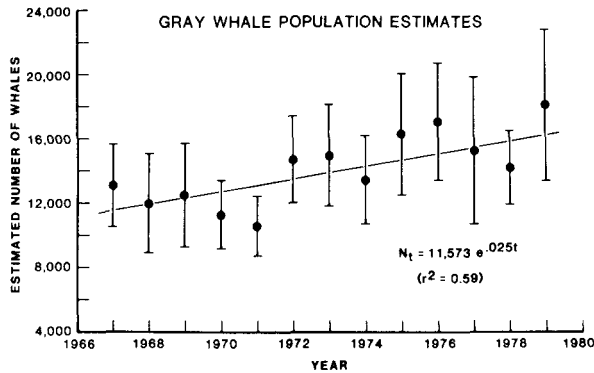
Fig. 2. Gray-whale population estimates and 95% confidence limits
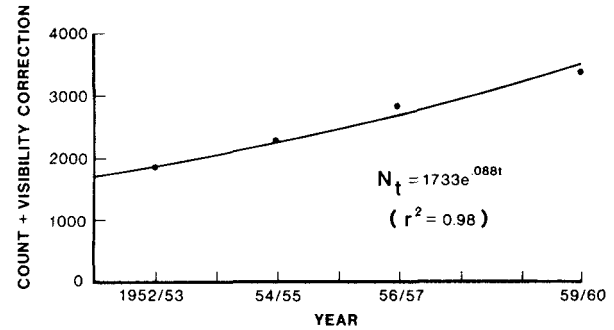from Monterey shore censuses, 1967–68 through 1979–80.

Fig. 3. Gray-whale population estimates from four Point Loma shore
censuses during the 1950s.

SIGHTING TIME SERIES: OBSERVED RATES OF INCREASE

Monterey shore censuses

Of the four time series of sighting-census data, the Monterey shore censuses appear to be the best for measuring the rate of change in population size. This is because it is a series of 13 consecutive censuses (1967–68 through 1979–80) of southbound migrants, during which consistent and well documented counting and data recording methods were used. Also, annual variability, due to changing weather and visibility conditions, and intra- and interobserver biases were addressed at least in part (Reilly, Rice and Wolman, 1980; 1983). A potential limitation of this series as an index of change in population size is that the census site was moved a few miles south from the original location after the seventh year. However, the two sites were very similar in seaward sighting perspective, and the data showed no significant differences between locations; group size distributions recorded at the two stations were not different, and the offshore distance distributions showed much less variation between locations than between years at either location (Reilly *et al.*, 1980; 1983).

The rate of change in population size during the 13 years censused was 2.5% per year (s.e. = 0.96) (Fig. 2). When the approximately 1.2% annual harvest in the Soviet subsistence fishery during these same years is also considered, an annual net reproduction of near 3.7% is indicated. (The term 'net reproduction' is used here to describe net rate of increase plus removals by humans).

Hubbs/Scripps shore censuses

Beginning in 1946–47 at the Scripps Institution of Oceanography (near San Diego, California) students under the direction of Carl L. Hubbs were stationed on top of a classroom building. The amount of effort and the methods applied are not clear from the secondhand accounts available (Walker, 1949; Gilmore, 1960). The recorded counts in 1946–47 through 1951–52 (omitting 1950–51) were 250, 500, 600 and 800. An increase is clear. If the methods and efforts were fairly constant (which is doubtful, given the 100% increase in the 2nd year) and

if the migration corridor was unchanged during this time, an exponential rate of increase of 20% per year was occurring. This seems unlikely. I consider these data unreliable, having so little accompanying information on effort expended and methods used.

Early Point Loma shore censuses

Beginning in 1952–53 a census of southbound migrants was conducted from Point Loma (San Diego, California) intermittently until 1959–60. Gilmore (1960), who supervised the efforts, eliminated two of the first five annual counts from consideration, due to irregularity of methods and/or effort. Rice (1961) reported the results of the final (1959–60) count for the series. The value of these data as an index is contingent upon the validity of Gilmore's (1960) and Rice's (1961) schemes to correct for whales missed due to poor visibility. Gilmore (1960) subjectively estimated the percent reduction in visibility each day to upwardly adjust his counts, while Rice (1961) drew a smooth curve on a figure connecting the higher count days. Consequently, the data from 1959–60 are not strictly comparable to those from previous years.

Another problem with the Point Loma data, perhaps the most serious, is the likelihood that the proportion of the population passing close enough to shore to be seen changed throughout the years covered, due to increasing nearshore boat traffic (Rice, 1965; Reeves, 1977; Gilmore, 1978). If one were to disregard the above inconsistencies and use the four 'good' censuses from the 1950s to estimate the rate of change during the decade, an exponential rate of 8.8% per year is indicated (Fig. 3). This is lower than Chapman's (1981) estimate (10.4%) because he used the authors' final population estimates (which include further unstandardized corrections) rather than just the raw data corrected for visibility as used here. Rice and Wolman's (1971) estimate of 12.2% annual increase from the same data probably represents a miscalculation.

There were five further censuses conducted at Point Loma intermittently between 1967–68 and 1978–79. These were not analyzed in detail by Reilly *et al.* (1980; 1983) due to the above unaddressed questions regarding the distribution of, and changes in, the migratory

corridor. Further, the methods used during the later Point Loma series differed somewhat from the early efforts there and are therefore not reasonably considered as part of a single time series.

Baja lagoon aerial censuses

There have been a number of aerial counts conducted on the winter grounds during the past 30 years. These were begun in 1952 by Carl L. and Laura Hubbs, and repeated by them and others during most years through 1964 (Hubbs and Hubbs, 1967; Gilmore, 1960). Gard (1974; 1978) conducted similar counts during 1970, '73, '74, '75, and '76. Recently, Rice, Wolman, Withrow and Fleischer (1981) and Rice, Wolman and Withrow (manuscript) conducted aerial counts on the winter grounds in 1980 and 1981, respectively.

As with the early shore censuses, the aerial counts were not conducted in a consistent manner. As discussed by Rice et al. (manuscript), reliable estimates from aerial counts in and outside the calving lagoons can be obtained only if many replicate surveys are made within a short time period, at the same time each year, along standardized census tracks at standardized altitude and speed, under good visibility conditions. With the exception of the very latest, none of the annual aerial surveys meet any of the requirements, except that most were conducted sometime during February. Rice et al. (manuscript) feel that these early efforts are consequently, 'worthless for estimating population sizes and trends'. Consequently, no rate of increase estimates are produced here from the lagoon aerial counts. Previously published estimates from this series include 0.8% per year (1954–64, $n = 4$, Rice and Wolman, 1971), and 8.0% (1952–59, $n = 4$, Chapman, 1981).

In summary, of four available time series of gray whale sighting surveys, only one is reliable enough to allow estimation of rate of change in population size: the Monterey 13-year series. The early Scripps series are not interpretable given present information. The 1950s Point Loma counts are of questionable value as an index of change due to unstandardized methodology. The Baja Lagoon aerial counts have even more severe methodological inconsistencies. The Point Loma series from the 1950s, perhaps the most reliable of the three sources other than Monterey, indicates a rate of increase of 8.8% per year. The possibility of the population achieving an 8.8% per year rate of increase is considered below in relation to vital rate estimates.

VITAL RATES AND MAXIMUM RATE OF INCREASE

In this section I review available information pertinent to gray whale vital rates, present slightly different estimates for the circa-1967 pregnancy rate and adult and juvenile mortality and use the existing estimate for age at sexual maturation. Then, the maximum rate of increase is inferred from the vital-rate values assumed for the near-zero population level, by use of a Leslie matrix. This rate is an estimate of the asymptotic or potential for the population, equivalent to r_s of Caughley (1977).

Age at sexual maturity

Both Rice and Wolman (1971) and Zimushko (1969a; 1971) used evidence of ovulation or pregnancy as evidence of maturity in females. Rice and Wolman found immature females with as many as 12 earplug layers and mature ones with as few as six. The median number of layers at maturity was nine. Zimushko also concluded that nine layers was the approximate time of attainment of maturity for females. The minimum number of layers in a mature female was eight in the Soviet sample, and the maximum in an immature individual was 12. The disparity in minimum layers for maturity was most likely due to sampling error. Only 34 females were examined by Zimushko (1969a), while Rice and Wolman (1971) examined a total of 140 females (not counting fetuses), of which 68 had readable ear plugs.

For the detection of maturity in males, Rice and Wolman relied solely on histological examination of the testes for evidence of spermatogenesis. Zimushko (1969a; 1971) examined a sub-sample histologically (apparently nine of 23, but this is not clear), using percent of seminal ducts open as a criterion of maturity. He combined this with an analysis of growth rate of testes weight to conclude that males reach maturity at approximately 11.1 m in length (Zimushko, 1971). Ranges in numbers of earplug laminae at maturity are not clearly stated for males from these studies. Rice and Wolman found essentially the same timing in males as in females. The median number of earplug layers at maturity was 9, the minimum 6 and the maximum 12.

Following this approach, then, gray whales became sexually mature at a median age of 8 years, a minimum age of 5 years, and a maximum of 11 years.

Population pregnancy rate

The independent data sets available on life history should allow two independent estimates of pregnancy rate for the circa-1967 population: one from the summer feeding grounds and one from the migration past central California. There are problems with the estimates produced from both, however. A revised estimate for this time period has been calculated here. Blokhin (1982) reported pregnancy rate statistics from the 1978, 1979, and 1980 harvests. These results are compared below to the pregnancy rate information for the late 1960s. A number of issues relative to an accurate determination of current and maximum pregnancy rate are problematic. These include ovulation rate, accurate ageing (discussed above), length of and possible overlap in gestation and lactation, and sampling biases.

In the sampling of migrating gray whales conducted by Rice and Wolman (1971) one important component of the population was missed due to the timing of the captures (e.g. Poole, 1984): post-partum females with calves of the year. There also appeared to be biases toward late pregnant females captured during the southward migration. Consequently, direct estimation of population pregnancy rate from their data is not possible.

Rice and Wolman (1971) examined a total of 116 mature females (Table 3). Late pregnant females headed south and post-partum females headed north were excluded from their computations of pregnancy rate

Table 3

Reproductive state of sexually mature female gray whales examined by Rice and Wolman (1971), classified by direction of migration

South		North	
Condition	Number	Condition	Number
Late pregnant	56	Post-partum	2
Recently ovulated	28	(non-lactating)	
		Early pregnancy	22
		Resting	8

Table 4

Percent of mature females which were pregnant from Soviet gray-whale catches for four consecutive years (P), 1965–1968 from Zimushko (1969), with sample sizes for each year (n) inferred from Zimushko and Ivashin (1980; Table 3), and a chi-squared test of differences in proportion pregnant between years

	Year				
	1965	1966	1967	1968	Total
P	46.3%	56.3	33.3	53.1	46.7%
$n(P)$	22	9	9	17	57
$n(\text{not } P)$	25	7	18	15	65

$\chi^2 = 3.055$, d.f. $= 3$, $P = 0.617$ (not significant).

because of the apparent biases mentioned above. They assumed that all 28 recently-ovulated animals headed south had conceived and that the number of females impregnated the previous year (giving birth in the current 'year' and absent from the samples) was approximately equal to the number assumed pregnant in the 'current' year. Consequently, 50 were in effect added to the denominator of the ratio of pregnant to total from the sub-sample (50/58), to produce $P_1 = 50/58 + 50 = 0.463$.

There are two aspects of Rice and Wolman's pregnancy rate estimation that may be in error. First, the assumption of one pregnant (post-partum) female missed for each 'pregnant' (recently ovulated or early pregnancy) whale in the sample appears valid for northbound captures but not for southbound. Second, it is probably unreasonable to assume that all corpora lutea observed represented pregnancies. Alternative interpretations are possible, but these also require conjecture.

Data from the Soviet fishery may help to clarify the issue of the circa-1967 pregnancy rate. Zimushko (1969b) reported percent pregnant by year for four years (1965 through 1968). From Zimushko and Ivashin (1980, Table 3) the sample sizes can be inferred (Table 4). Zimushko (1969b) speculated from this four year series that the proportion pregnant oscillates on a two-year cycle: one year above 50%, one year below. From this he further speculated that only a proportion of the population was on a two-year breeding cycle and that other females gave birth two, three or even four years in a row before resting for a year. Contributing to this picture was Zimushko's early (1969a; 1969b; 1971; 1973) interpretation of ageing, i.e. two layers accumulated per year.

I conducted a chi-squared test of differences in proportions pregnant between years in the Soviet data (Table 4). An hypothesis of equal proportions between

years cannot be rejected. Pooling the data over years, then, gives:

$$p_2 = 57/122 = 0.467$$

with variance

$$\begin{aligned} \text{var}(p_2) &= (0.467)(1 - 0.467)/121 \\ &= 0.00205. \end{aligned}$$

This is quite close to Rice and Wolman's (1971) original estimate (0.463) from the California series. If the sampling was unbiased, this estimate should be a valid representation of the pregnancy rate, being based upon 122 captures of adult females. The 95% confidence limits are (0.376, 0.558).

The variation between years in proportion pregnant in the 1965–1968 data from the summer grounds is possibly due to temporal sampling differences. This is suggested by the data and analyses of Blokhin (1982) for the years 1978–1980. He found a strong decreasing trend in proportion of mature females which were pregnant, by month from July through October, in the Soviet subsistence-fishery captures. The July proportion was near 0.90, declining to near 0.10 in October (Blokhin, 1982; Fig. 2). The overall pregnancy rate during the 3 years is not directly calculable, since the raw data were reported only for 1980. In that year the pregnancy rate was 0.52. For 1978 and 1979 only proportions were reported, without sample sizes: 0.30 for 1978 and 0.84 for 1979. Blokhin mentioned that seasonality was probably responsible for the wide distance between these estimates, sampling for 1978 having been predominantly late in the summer while sampling for 1979 was predominantly early in the summer. The mean of the three proportions is 0.55. It is possible that this is an accurate estimate, but an examination of the components of the calving interval (below) suggests that a rate greater than 0.5 is unlikely. Sampling bias toward pregnant females is suggested here. This also casts some doubt on the accuracy of the earlier summer-range data as well.

It is interesting to note that the proportion pregnant appears to be positively corrected with the proportion sexually mature in the three annual samples reported by Blokhin (1982): 1978 had 46% mature and 30% pregnant; 1979 had 87% and 84%, while 1980 had 63% and 52%. This also suggests that much of the inter-year variation in pregnancy rates is due to sampling problems.

For maximum pregnancy rate (or minimum calving interval), Rice and Wolman (1971) estimated 0.5 (2 years), while Zimushko (1969a; 1969b; 1971) estimated that it is greater than 0.5 (less than 2 years). Apparently these authors had differing interpretations of the components of the calving interval, i.e. length of gestation, and the possibility of overlapping lactation and/or gestation with ovulation. The minimum calving interval biologically possible is an important factor in the estimation of maximum rate of increase. Consequently the separate components of the calving interval are reviewed below.

Lactation period

The lactation period is indicated to be approximately 7 months, from collection dates of weaned calves reported from the summer feeding grounds (Zenkovich, 1937; Tomilin, 1957). Nearly all calves collected during August

and later, by the above sources, were weaned, having solid food but no milk in their stomachs. No data exist to examine possible trends in lactation period with time or changing population size.

Gestation period

Rice and Wolman estimated the gestation period to be 13 months, using the curve-fitting method of Hugget and Widdas (1951). This method assumes fetal growth to fall into two phases: an initial slow period followed by a longer, much faster period of growth. The later part of the gestation period is estimated from empirical data on fetal sizes and calendar date. Estimation of the initial phase is not as straightforward. Based upon an analysis of the state of development of two embryos, Rice and Wolman (p. 79) estimated the initial phase to last 75 days. The empirically estimated phase was 325 days, so their estimate of the total period was 400 days, or about 13 months.

Zimushko and Ivashin (1980) approached this situation in a different, slightly more qualitative manner. On a 'circular graph' of months of the year they plotted the sizes of fetuses by month. They concluded that the period is less than 12 months, not 13. Their figure shows the mean conception date to be in mid-February. This is about 11 months from the mean birth date of 20 January (Rice et al., 1981). It appears, however, that Zimushko's technique does not take the initial, slow phase of fetal growth (Laws, 1959) into account. Zimushko's extrapolated conception date (February) is in fact near the date at which the line from the 'linear' growth phase in Rice and Wolman's (1971; Fig. 29) analysis meets the origin. Also, all adult females taken by Rice and Wolman on the southward migration (except those with near-term fetuses) had fresh large corpora lutea. This indicates that they had at least ovulated, if not conceived. No embryos were found in these females. This could have been due to the small size of a new conceptus. Alternatively, all of these individuals could have ovulated again during the same season. This second alternative is not supported by the available data on ovulation rate (see below).

For gestation period, then, available data are not entirely conclusive. More work is desirable on estimation of the early phase of fetal growth. A period somewhat greater than 12 months appears most likely at this time.

Frequency and timing of ovulation

A simple linear regression of number of corpora lutea and c. albicantia vs. number of ear-plug laminae for 49 female gray whales results in the following equation (Table 5; data from Rice and Wolman, 1971):

$$\text{No. corpora} = (0.518) \cdot (\text{no. layers}) - 0.891$$
$$(r^2 = 0.614)$$

The slope of 0.518 is not significantly different from 0.5 ($t = 0.334$ $p = 0.65$) (Fig. 4). If multiple sequential ovulations were a common phenomena, a higher rate of ovulation would be expected. These data appear to support the concept of a 2-year minimum breeding cycle. Certainly not all ovulations would result in pregnancies.

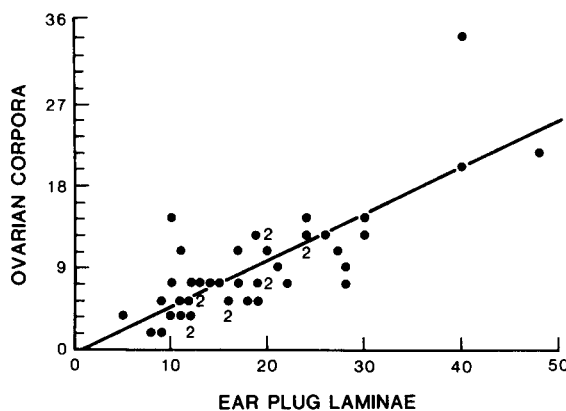Another factor to be considered in determining the

Fig. 4. Relationship between frequencies of ear-plug laminae and ovarian corpora for 49 gray whales. The slope = 0.518 ($r^2 = 0.614$).

length of the female reproductive cycle is the occurrence of either a post-lactation or post-partum ovulation/conception. A post-lactation ovulation/conception appears unlikely, given the relative uniformity in size of fetuses with time of year (Rice and Wolman, 1971; Zimushko and Ivashin, 1980) and the overall fairly precise, annual timing of the gray whale migration schedule. Given that Rice and Wolman (1971) observed no enlarged follicles in ovaries from 56 southbound females with near-term fetuses, a common post-partum ovulation also appears unlikely. It apparently does occur on some occasions, though, since Zimushko (1969a) reported the capture of seven simultaneously lactating and pregnant females from the Soviet fishery. The total sample size from which these seven were drawn was not stated and is difficult to infer from the text. As no near-term females were found to exhibit signs of imminent ovulation from the California specimen series, however, I consider this a relatively uncommon event.

When discussing life history characteristics in relation to ovarian scars, it is important to remember that there are still uncertainties involved: (a) ovulation may not be a regular, semi-annual event, (b) ovulation rate may change with age, and (c) it is unknown if all corpora persist throughout life (Perrin and Donovan, 1984).

Age-specific pregnancy rates

Zimushko (1970) examined the ovaries of 70 mature female gray whales. He distinguished two types of corpora albicantia: those of ovulations which had resulted in pregnancy, and those which had not.[2] From this he inferred a declining fecundity with age, as represented by a decreasing ratio of the corpora of pregnancy to those of non-pregnancy in older whales (Zimushko, 1973). No sample size was given for testing this hypothesis. A ratio of 1:1 for whales 12.0–12.5 m long, and 1:2.5 for females of 13.1–13.5 m was reported. A figure was presented by Zimushko (1973) with data for nine points (reproduced in Zimushko and Ivashin, 1980) to illustrate this concept. Unfortunately, the points cannot be read from the figure without conjecture, and

[2] Ivashin (1984) describes methods used by Soviet scientists for classifying corpora.

no means of substantiating the changing ratio is available. Regarding the basic premise, that two types of corpora albicantia can be distinguished for gray whales, Rice (pers. comm. 1981) states that Zimushko's method is faulty and that no clear consistent difference exists (see also Perrin and Donovan, 1984; Ivashin, 1984).

Laws (1961) could distinguish no such differences in fin whale corpora. Mizroch (1981) found no decline in proportion pregnant with age in an analysis of a large series of Southern Hemisphere baleen whale reproductive data. I have assumed fecundity constant for adult (beyond 11 years of age) gray whales, lacking conclusive evidence to the contrary. This controversy is not likely to be settled without substantial histological research on gray whale corpora.

In summary, neither the pregnancy rates for circa-1967 and 1978–80 nor maximum pregnancy rates can be unambiguously determined from available information. The data on ovulation rate and ovarian condition of southbound migrating females point to a two-year minimum cycle. It is not entirely clear what the gestation period is, but the best available data point to a period greater than 12 months, also supporting a two-year minimum cycle. The report of seven simultaneously pregnant and lactating females captured from the feeding grounds (Zimushko, 1969a) bears further verification, including accessory data on the size of the sample from which these were drawn. They point to an inconsistency in our understanding of gray whale reproductive biology as yet unresolved.

Adult survival rate

The Rice and Wolman (1971) samples provided the only information available on adult survival rate (S_a). From their data (Table 5), apparent adult survival rate (A) can be estimated from the frequencies of individuals per age class. If the population is stable in age structure, stationary in size and has not been subject to exploitation, this should be an unbiased estimate of adult survival. The California stock of gray whales had most likely been under exploitation continually since pre-history (Mitchell, 1979). There is no way of knowing if the age structure was stable in the mid 1960s, but the population was probably increasing in size. Consequently, while apparent survival (A) has been estimated with some degree of certainty here, the proportions of this estimate ascribable to growth (G) and exploitation (F) are less certain.

Rice and Wolman preferred the use of ovarian corpora to estimate apparent adult female survival and reported a Chapman–Robson (C–R) estimate of 0.921 ('$M = 0.082$'). Using earplug laminae and the entire adult series (8 years and older), their C–R estimates were 0.909 for females and 0.922 for males.

Earplug laminae are the reference time scale for ovarian corpora; the relation is linear and significant (see above) but not remarkably so, with $r^2 = 0.614$. Both time scales are questionable but of interest, because only about one half of the earplugs were readable and because readings for older animals may not be accurate (Rice and Wolman, 1971).

To obtain variances to facilitate comparisons (not presented in Rice and Wolman, 1971), I have recalculated C–R survival rates from age-class frequencies for four

Table 5

Age composition of gray whales from Rice and Wolman (1971) based upon ovarian corpora and earplug laminae as time scales

Estimated age (years)	Ovarian corpora		Ear-plug laminae		
	No. corpora	No. individuals	No. laminae	No. females	No. males
1			2	5	3
2			3	2	5
3			4	1	2
4			5	2	4
5			6	4	3
6			7		5
7			8	5	7
8	1	8	9	3	3
9			10	3	5
10	2	15	11	3	6
11			12	5	3
12	3	12	13	4	6
13			14	1	6
14	4	11	15	1	2
15			16	3	
16	5	9	17	2	4
17			18	1	3
18	6	11	19	3	3
19			20	5	3
20	7	11	21	1	6
21			22	1	4
22	8	6	23		2
23			24	4	1
24	9	8	25		1
25			26	1	
26	10	5	27	1	
27			28	2	1
28	11	3	29		2
29			30	2	
30	12	5			
31					
32	13	4	33		1
33					
34	14	2	35		1
35					
36	15	2			
37			38		1
39			40	1	4
40			41	1	
46	20	1	47		1
47			48	1	
50	22	1			
51					
57			. 58		1
69	.		70		1
76	35	1			
77					

cases: males and females separately, using laminae and all data; females using laminae but truncating 'older' (30 years and older) whales; and females using corpora (Table 6). Adult male survival (0.920, s.e. = 0.012, $n = 49$, not in Table 6) is significantly different from adult female survival ($Z^2 = 5.0$, $P < 0.01$). Since only female survival is of interest for the rate-of-increase calculations, the sexes were treated separately and males not considered further here.

Following Robson and Chapman (1961), a comparison of C–R and Heincke estimates at ages 8–12 showed no under-representation of those age classes ($Z^2 = 0.55$, 0.47, 0.38, 0.15, respectively; none significant at $\alpha = 0.05$). Consequently 8 years is a valid starting point for C–R computations.

Table 6

Estimates and standard errors of apparent adult female survival from frequency per age class using ear-plug laminae and ovarian corpora counts as age indicators, with and without truncation of age-30 and older individuals (original data from Rice and Wolman, 1971). A is the mean apparent survival rate and Z the corresponding apparent mortality coefficient

	Ageing technique	
Data	Ovarian corpora	Ear plug laminae
All 8+ years females	0.918 ± 0.007	0.910 ± 0.012
8–30-years females		0.908 ± 0.012
	$\bar{A} = 0.912$ ($Z = 0.092$)	

There is no well defined criterion with which to select one of the three available estimates of female survival as the best estimate (Table 6). All are quite close, however, and overlap in 95% confidence intervals. A simple average of the three was calculated: $\bar{A} = 0.912$ ($Z = 0.092$) where A is apparent survival (Z is total instantaneous mortality), including effects of population growth (G) and fishing mortality (F). The female data are fitted well by a geometric series with $A = 0.912$ ($X^2 = 34.27$, $d.f. = 29$, $P = 0.77$), validating the use of the C–R statistics.

Following Ohsumi (1976) I have estimated natural mortality (M) by subtracting population growth (G) and fishing mortality (F) from apparent total mortality (Z): $M = Z - (F + G)$. However, determining F and G during the time period of interest (about 40 years prior to 1967, since about 98% of the population was 40 or less in 1967 – Table 5) is at best a gross approximation.

Reported catches for 1927–1967 (summarized in Reilly, 1981) averaged only about 80/year, but they are reported to have increased to over 100/year during the 20 years immediately preceding 1967. There is no direct estimate of the population size or the precise nature of its changes during this period. An estimate does exist of $F + G$ for the 13 years following 1967. For lack of better information, I tentatively assumed $F + G$ constant at the same rate prior to 1967 as that measured for 1967–1980, or about 0.037. From $Z = -ln$ (0.912) = 0.092 and from (1), M was approximated as $M = 0.092 - 0.037 = 0.055$ ($S = 0.946$).

Juvenile survival rate

With other vital rates set at their presumed circa-1967 values ($P = 0.469$, $S_a = 0.946$, $X_m = 8$, $\lambda = 1.037$) juvenile survival S_j was estimated to be 0.893 (Table 7). This corresponds to a mortality coefficient of 0.113. Using the two-compartment model (1) and slightly different values for vital rates, Ohsumi (1976) estimated the juvenile mortality coefficient to be 0.167, notably higher than my estimate of 0.113. This latter estimate is hopefully more accurate, because (1) Ohsumi's (1976) estimate of pregnancy rate was probably too low; (2) his

[3] F was set at 0.0175 = 179/10,242 from the average kill 1955–1966 (Zimushko and Ivashin, 1980) and from the average population size during those years as extrapolated from the exponential model estimated for the years covered by the Monterey census by Reilly et al. (1983).

Table 7

The ranges of pregnancy rate (P), juvenile survival (S_j), adult survival (S_a) and age at sexual maturation (X_m) determined here for two different population levels, with dominant eigenvalues (λ) for each set. S_j was adjusted to yield $\lambda = 1.037$ for circa 1967. For near zero,[2] P was adjusted to yield $\lambda = 1.09$, holding S_a and X_m at near-zero[1] levels

Population level	P	X_m	S_j	S_a	λ
Near zero[2]	0.642	5	0.940	0.945	1.090
Near zero[1]	0.500	5	0.940	0.945	1.069
Circa 1967[3]	0.469	8	0.893	0.945	1.037

[1] For maximum P of 0.50.
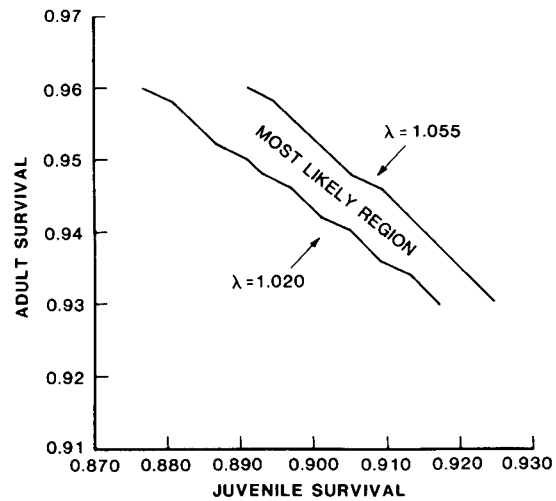[2] For maximum P of 0.642.
[3] Approximately 12,500.

Fig. 5. Relationship between juvenile survival, adult survival and per capita rate of increase for the circa-1967 gray-whale population. A best estimate of 0.893 for juvenile survival corresponds to adult survival of 0.945 and $\lambda = 1.037$.

estimate of adult mortality rate was probably too high; and (3) population growth was not accounted for in his estimation procedures.[3]

The estimate of juvenile survival produced here is dependent on the accuracy of my estimates of other vital rates. In Fig. 5 the sensitivity of estimates of S_j to values of adult survival and rate of increase is examined. The figure shows a region defined by $S_a = 0.945 \pm 0.015$ and $\lambda = 1.037 \pm 0.018$. Within these boundaries juvenile survival varies from about 0.878 to about 0.924. The central value of this 'most likely region' is, by definition, 0.893.

Maximum rate of increase

The maximum rate of increase which could be achieved by gray whales is dependent on the extremes approached by other vital rates as density nears zero. For pregnancy rate, if a two-year minimum calving interval is assumed, the maximum rate will be 0.5. Given the range in

observed ages at sexual maturation from 5 to 11 years, it seems reasonable to assume that the population median or mean age at sexual maturation would approach 5 years at minimum. Since adult survival (assumed density-independent here) was estimated to be 0.946, it is assumed that juvenile survival would approach but probably not equal or surpass this rate. Consequently a value of 0.940 was assumed for this exercise. Given this set of vital rates (Table 7) and a Leslie matrix constructed as in (2), a dominant eigenvalue of 1.069 was calculated. This equals a maximum rate of increase of approximately 6.7% per year for the California stock of gray whales, if a stable age structure can be assumed in populations at very low levels.

Considering the uncertainty encountered here in defining maximum pregnancy rate, and the possible rate of increase of 8.8% per year implied by early Pt Loma censuses, it is of interest to determine what the pregnancy rate must be to result in an 8.8% rate of increase. Holding the other vital rates at their previous extremes, pregnancy rate must be 0.64 for $\lambda = 1.09$. It does not seem likely that the population pregnancy rate could exceed the ovulation rate, calculated at 0.518. However, sufficient information does not exist on maximum pregnancy rate to dismiss the higher P and λ values considered here.

CRITIQUE AND SUMMARY

This study reviewed all available information on realized rate of increase from four series of sighting censuses and on vital rates and related biological topics from two specimen series and a number of previous analyses. It then utilized information from both topics to estimate the maximum rate of increase that gray whales might achieve.

Although gray whales are perhaps the best studied of all baleen whales, much research is still needed to satisfactorily describe their life history and population dynamics. The length of gestation, verification of ageing, flexibility in ovulation and conception, and (ultimately) the minimum calving interval are among the major topics requiring further research. Estimates of juvenile survival and maximum rate of increase produced here are contingent on the validity of estimates and assumptions made regarding other aspects of the life history. Future findings from direct observation may indicate a reassessment of juvenile survival and maximum rate of increase. The following outline summarizes the information reviewed and (in some instances) the parameters re-estimated here.

Observed rates of increase

1. The Monterey shore censuses conducted annually from 1967–68 through 1979–80 indicate a net rate of increase of 2.5% per year. If the removals from the Soviet subsistence fishery are considered as well, the mean net productivity was approximately 3.7% per year.

2. Census series from Scripps in the late 1940s, Point Loma in the 1950s through 1970s and from the calving grounds are not reliable as indices of population change.

Vital rates

3. Life-history data for the estimation of vital rates are available from two sources: a series collected by Rice and Wolman (1971) off the central California coast, and a limited sample from the Soviet subsistence fishery. All available data appear to apply roughly to the 1967 population.

4. The mean age at sexual maturation was 8 years, with a range of ages from 5–11 years for both sexes.

5. The population pregnancy rate *circa* 1967 was estimated here to be 0.467 with a standard error of 0.045.

6. There is some uncertainty regarding the gestation period, but available data suggest a minimum period somewhat greater than 12 months.

7. The *circa*-1967 ovulation rate was 0.518/year (s.e. = 0.059).

8. Lactation appears to have been near 7 months in duration.

9. The minimum calving interval is probably near 2 years. A report of seven simultaneously pregnant and lactating females on the summer grounds needs further investigation.

10. Female adult survival rate was estimated to be 0.945, corresponding to a mortality coefficient of 0.056. Juvenile survival was estimated to be within the range 0.878–0.924, with a best estimate being 0.893, corresponding to a mortality coefficient of 0.113.

11. Adult male survival is significantly higher than adult female survival, as calculated using ear-plug laminae as indicators of age.

Maximum rate of increase

12. The asymptotic maximum or intrinsic rate of increase for the stock is estimated to approach 6.7% per year as population density approaches zero.

REFERENCES

Blokhin, S. A. 1979. On the status of the gray whale stocks in the coastal waters of the Chukotka Peninsula. *Rep. int. Whal. Commn* 29: 335–6.

Blokhin, S. A. 1982. Investigations on gray whales taken off Chukotka in 1980. *Rep. int. Whal. Commn* 32: 375–380.

Caughley, G. 1977. *Analysis of Vertebrate Populations*. Wiley-Inter-science, New York. 234 pp.

Chapman, D. G. 1981. Evaluation of marine mammal population models. pp. 277–296. *In*: C. W. Fowler, and T. D. Smith, (eds), *Dynamics of Large Mammal Populations*. John Wiley and Sons, New York, Chichester, Brisbane, Toronto, Singapore. 477 pp.

Chapman, D. G. and Robson, D. S. 1960. The analysis of a catch curve. *Biometrika* 16: 354–68.

Eberhardt, L. L. and Siniff, D. B. 1977. Population dynamics and marine mammal management policies. *J. Fish. Res. Bd Can.* 34: 183–90.

Fowler, C. W. 1981. Density dependence as related to life history strategy. *Ecology* 62(3): 602–10.

Gard, R. 1974. Aerial censuses of gray whales in Baja California lagoons, 1970 and 1973, with notes on behavior, mortality and conservation. *Calif. Fish and Game* 60(3): 132–44.

Gard, R. 1978. Aerial census and a population dynamics study of gray whales in Baja California during the 1976 calving and mating season. Rep. on MMC-79/09 (*NTIS Rep.* PB 275 295). 20 pp.

Gilmore, R. M. (and Rice, D. W. – ed.). 1960. A census of the California gray whale. U.S. Fish Wildl. Serv. Spec. Sci. Rep. Fish. 342, 30 pp.

Gilmore, R. 1978. Some news and views of the gray whale, 1977. Part 2. Migration south and north along and between the islands of southern California. *Whale Watcher* 12(2): 9–13.

Hubbs, C. L. and Hubbs, L. C. 1967. Gray whale censuses by airplane in Mexico. *Calif. Fish and Game* 53(1): 23–7.

Hugget, A. St. G. and Widdas, W. F. 1951. The relationship between mammalian foetal weight and conception age. *J. Physiol.* 114: 306–17.

Ivashin, M. V. 1984. Characteristics of ovarian corpora in dolphins and whales as described by Soviet scientists. (Published in this volume.)

Ivashin, M. V. and Mineev, V. N. 1981. The history of gray whale harvessting off Chukotka. *Rep. int. Whal. Commn* 31: 503–05.

Laws, R. 1959. The foetal growth rates of whales, with special reference to the fin whale, *Balaenoptera physalus* Linn. *Discovery Rep.* 31: 327–486.

Laws, R. 1961. Reproduction, growth and age of southern fin whales. *Discovery Rep.* 31: 327–486.

Leslie, P. H. 1945. On the use of matrices in certain population mathematics. *Biometrika* 33: 183–212.

Mitchell, E. D. 1979. Comments on magnitude of the early catch of east Pacific gray whale (*Eschrichtius robustus*). *Rep. int. Whal. Commn* 29: 307–14.

Mizroch, S. A. 1981. Further notes on Southern Hemisphere baleen whale pregnancy rates. *Rep. int. Whal. Commn* 31: 629–33.

Ohsumi, S. 1976. Population assessment of the California gray whale. *Rep. int. Whal. Commn* 26: 350–9.

Perrin, W. F. and Donovan, G. P. (eds). 1984. Report of the Workshop. (Published in this volume.)

Poole, M M. 1984. Preliminary assessment of annual calf production in the gray whale, *Eschrichtius robustus*, from Pt. Piedras Blancas, California. (Published in this volume.)

Reeves, R. R. 1977. The problem of gray whale (*Eschrichtius robustus*) harrassment: at the breeding lagoons and during migration. *NTIS Rep.* No. PB 272 506, 60 pp.

Reilly, S. B. 1981. Population Assessment and Population Dynamics of the California Gray Whale, *Eschrichtius robustus*. Ph.D. Dissertation, U. of Washington, Seattle. 265 pp.

Reilly, S. B., Rice, D. W. and Wolman, A. A. 1980. Preliminary population estimate for the California gray whale based upon Monterey shore censuses, 1967–68 to 1978–79. *Rep. int. Whal. Commn* 30: 359–68.

Reilly, S. B., Rice, D. W. and Wolman, A. A. 1983. Population assess-

ment of the gray whale, *Eschrichtius robustus*, from California shore censuses, 1967–1980. *Fish. Bull., U.S.* 81(2): 267–81.

Rice, D. W. 1961. Census of the California gray whale. *Norsk Hvalfangsttid.* 50: 219–25.

Rice, D. W. 1965. Offshore southward migration of gray whales off southern California. *J. Mammal.* 46(3): 500–1.

Rice, D. W. and Wolman, A. A. 1971. The life history and ecology of the gray whale (*Eschrichtius robustus*). *Am. Soc. Mammal. Spec. Publ.* 3, 42 pp.

Rice, D. W., Wolman, A. A., Withrow, D. E. and Fleischer, L. 1981. Gray whales on the winter grounds in Baja California. *Rep. int. Whal. Commn* 31: 477–93.

Rice, D. W., Wolman, A. A. and Withrow, D. E. (Manuscript). Distribution and numbers of gray whales on their winter grounds.

Robson, D. S. and Chapman, D. G. 1961. Catch curves and mortality rates. *Trans. Am. Fish. Soc.* 90: 181–9.

Roe, S. H. J. 1967. The seasonal formation of laminae in the ear plug of the fin whale. *Discovery Rep.* 35: 1–30.

Tomilin, A. G. 1957. *Zveri SSSR i prilezhaschikh stran. Zveri vostochnoi Evropy i severnoi Azii. IX kitoobraznye.* Akad. Nauk, Moscow, 756 pp. [Translated in 1967 as *Mammals of the USSR and adjacent countries.* Vol. IX. Cetacea by the Israel Program for Scientific Translations, Jerusalem, 717 pp.]

Walker, T. 1949. Nursery of the gray whales. *Natural History* 58(6): 248–56.

Zenkovich, B. A. 1934. Materialy k poznaniyu kitoobraznykh dal'nevo-stochnykh morei (Seryi Kaliformiiskii kit – *Rachianectes glaucus* Cope). (Research data on Cetacea of far eastern seas – the California gray whale – *R.g.* Cope). *Vestnik Akad. Nauk SSSR, Dal'nevostochnyi Fil.* 10: 9–25.

Zenkovich, B. A. 1937. Esche o serom kaliforniiskom kite (*Rachianectes glaucus*, Cope 1864). (More on the California gray whale (*R.g.*, Cope, 1864)). *Vestnik Akad. Nauk SSSR, Dal'nevostochynyi Fil.*, 23: 91–103.

Zimushko, V. V. 1969a. (Data on the reproduction of gray whales.) *Thesis to 4th All-Union Conf. on Marine Mammals, Moscow.*

Zimushko, V. V. 1969b. (Some data on the biology of the gray whale.) pp. 93–7. In: *Marine Mammals* (A collection of articles from the 3rd All-Union Conf. on Marine Mammals, Moscow. Arseniev, V. A., Zenkovich, B. A. and Chapskii, K. K. (eds).

Zimushko, V. V. 1970. (Materials on the determination of the yellow bodies traces in gray whales (*Eschrichtius robustus* Erx. 1777).) (*Zool. Zh.* 49(7): 1073–1080.

Zimushko, V. V. 1971. Some data on the reproduction of gray whales. *Proc. ATLANTNIRO* 39: 44–53.

Zimushko, V. V. 1973. Age determination of the gray whale (*Eschrichtius gibossus* Erx. 1777). *TINRO Proc. Pac. Sci. Res. Inst. of Mar. Fish and Ocean* 71: 295–300.

Zimushko, V. V. and Ivashin, M. V. 1980. Some results of USSR investigations and whaling of gray whales (*Eschrichtius robustus* Lilljeborg, 1861). *Rep. int. Whal. Commn* 30: 237–46.