

Biological parameters for pygmy blue whales

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ABSTRACT

The basic biological parameters of blue whale populations are poorly known. To fill this gap, new estimates of the length-at-age relationship and natural mortality, and female age at sexual maturity and inter-birth interval were obtained for pygmy blue whales (*Balaenoptera musculus brevicauda*). The analyses are based on Soviet and Japanese ovarian corpora data and earplug data, assuming that one growth layer is added to earplugs each year. Length-at-age is estimated from Soviet length and earplug data in a Bayesian framework; the best fit equation is $l = 21.9(1 - \exp[-0.080(t + 16.2)])$ for females and $l = 21.1(1 - \exp[-0.089(t + 15.5)])$ for males; 95% credibility intervals are additionally presented for each age. Female length at sexual maturity was estimated to be 9.9 yr (95% credibility interval 9.0–11.0) from Soviet data and 9.9 yr (95% CI 8.0–11.8) from the less numerous Japanese data. A regression of earplug layers against ovarian corpora provided an estimate of 2.6 yr (95% CI 2.2–3.0) for the inter-ovulation interval, which is argued to be close to the inter-birth interval for pygmy blue whales. Natural mortality, estimated from age frequencies, is about 0.06 yr^{-1} (95% CI 0.05–0.07), with inconsistent variability between sexes and data sources. Taken together, these estimates of the biological parameters imply that the natural rate of increase for pygmy blue whales was less than 2% per annum in the 1960s.

INTRODUCTION

Despite a century of modern whaling that depleted blue whale (*Balaenoptera musculus*) populations worldwide to a small fraction of their original abundance levels (Clapham *et al.*, 1999; Branch *et al.*, 2004), surprisingly little is known about blue whale biology, including the relationship between age and length, age at sexual maturity, inter-birth interval, and adult and calf survival. Two main methods exist for obtaining estimates of these parameters, photo-identification studies and biological data from historical catches.

Long-term photo-identification studies provide a non-lethal way of estimating a variety of biological parameters. Photo-identification studies have yielded abundance estimates (Calambokidis and Barlow, 2004), and movement patterns (Calambokidis *et al.*, 1990; Sears and Larsen, 2002), and adult survival (Ramp *et al.*, 2006), but estimates of calving intervals, age at sexual maturity and juvenile survival have to date proven harder to obtain for blue whales from photo-identification studies.

Historical catches could have provided estimates of all of the vital parameters, if ageing methodology had been developed earlier. Unfortunately, most of the >378,000 blue whale catches worldwide were taken before reliable methods of ageing mysticetes from earplug laminae were developed in the 1950s (Purves, 1955; Laws and Purves, 1956). Earplug laminae (layers) are accumulated at a rate of one per year, and have been validated by examining the monthly widths of the most recent layer (Roe, 1967; Lockyer, 1974, 1984), although early papers (and even some more recent papers) assumed that two earplug layers are added per year (e.g. Chittleborough, 1959; Laws, 1961). The only published blue whale earplug data are for pygmy blue whales (*B. m. brevicauda*), which were described only in the late 1950s (Ichihara, 1961, 1963, 1966) and subsequently exploited by both Japan and the USSR. Pygmy blue whale earplug data are inadequate in some respects because the Japanese fleets largely adhered to the minimum length regulations of 70 ft (21.3 m), resulting in few records being available for the length at sexual maturity of 63 ft (19.2 m) (Ichihara, 1966; Sazhinov, 1970; Branch and Mikhalev, accepted), while the Soviet fleets disregarded many of the international regulations in place at that time and their real operations and associated data were not disclosed to the Western world until the 1990s (Yablokov, 1994; Zemsky *et al.*, 1995; Yablokov *et al.*, 1998).

Here I briefly review the history of past estimates of the age-length relationship, age at sexual maturity, calving interval, and adult and calf survival, and then obtain new estimates (except for calf survival) by re-analysing published Japanese data (Ichihara and Doi, 1964; Ichihara, 1966), and by presenting and analysing previously undisclosed Soviet data from Sazhinov (1980).

REVIEW OF PAST STUDIES

In this section I briefly review previous estimates of biological parameters for all populations of blue whales, including pygmy blue whales.

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Age-length relationship

Estimation of the relationship between age and length for blue whales passed through two phases: before earplug data and after earplug data. In the first phase, blue whales were thought to grow rapidly and reach sexual maturity at a young age. The paper by Mackintosh and Wheeler (1929) is key—these authors were the first to meticulously measure hundreds of Antarctic blue whales (*B. m. intermedia*). By plotting foetal and calf lengths against catch date, they showed that Antarctic blue whales have a distinct reproductive season, pairing in June–July and calving in April–May, from which they inferred a growth curve. Their key findings are that the gestation period is a little more than 10 months, females are 7 m long when born (measured from the tip of the snout to the notch in the tail), and they then grow rapidly before weaning at about 7 months old and 16 m long (males are somewhat shorter). These findings are uncontroversial. Mackintosh and Wheeler’s mistake was in the growth rate they assumed after weaning, based on modes in length frequencies. They concluded that female Antarctic blue whales were just over 2 yr old when they reached sexual maturity at 23.7 m.

The next major attempt at ageing Antarctic blue whales was Laurie’s (1937) investigations of ovarian corpora. On ovulation, a corpus luteum is formed in the ovary, which gradually dwindles to a permanent body called the corpus albicans. Ovarian corpora are the total of the corpora lutea and corpora albicantia and are thought to provide a record of lifetime ovulations (Mackintosh and Wheeler, 1929; Laurie, 1937). Laurie (1937) differentiated between recent corpora and old corpora, assuming that the recent corpora were produced within the past year, and hence that there are on average 1.13 ovulations per year, while admitting that “no positive proof could be advanced” for this conclusion. Looking back in hindsight, it is clear that modes in the frequencies of corpora were over-interpreted, and that the “recent” corpora could actually have been produced several years previously. Laurie noted that physical maturity (when growth in length ceases) occurs at 11–12 ovarian corpora, and based on the assumptions about corpora accumulation inferred that physical maturity occurred 10–11 yr, and that maximum age was 30 yr with no sign of a climacteric (end of fertility) at older ages. No change to the estimated age at sexual maturity of 2 yr was suggested.

Mackintosh and Wheeler’s estimate that the age at sexual maturity was 2 yr was challenged by Ottestad (1950), who found several distinct peaks in Antarctic blue whale catch length frequencies, interpreted as distinct age classes, which would imply that age at sexual maturity was 4 yr for females and 3 yr for males. The statistical evidence for these peaks seems lacking, especially given data issues like rounding to the nearest 5 ft. These results were used by Ruud and Jonsgård (1950) to cast doubt on Mackintosh and Wheeler’s estimate of 2 yr. Ruud and Jonsgård (1950) examined tracings of the shape of the longest baleen plates from the gum to the tip. They interpreted major undulations in these tracings as yearly growth patterns in, from which they inferred that the growth rate after weaning was substantially slower than assumed by Mackintosh and Wheeler (1929). From this, they estimated that female age at sexual maturity was 5 yr, with a range of 3–7 yr.

When the method of ageing by earplug laminae was developed, it soon became clear that all of these methods (length frequencies, ovarian corpora, baleen plate tracings) substantially over-estimated growth rates after weaning. The key study is by Ichihara (1966) who plotted earplug laminae against length for both Antarctic and pygmy blue whales. Unfortunately the published Fig. 9 displays the earplug data in groups of four laminae, and the original data are not tabled (except for 32 pygmy females and 48 pygmy males under 70 ft), nor are the equations for the fitted curves provided in the paper. Nevertheless, the figure clearly suggests that both pygmy and Antarctic blue whale females reach sexual maturity at about 10 yr. Ohsumi (1979) refers to earplug data from “a limited number” of Antarctic blue whales, from which the age at sexual maturity is about 10 yr, but does not present the original data. Finally, Lockyer (1981) obtained ear plug data from 20 female and 16 male Antarctic blue whales which “supported” the estimate of 5 yr for age sexual maturity obtained by Ruud and Jonsgård (1950). Again, however, the original data were not presented and their current whereabouts are unknown, according to a personal communication from C. Lockyer.

Recently, a number of key Soviet papers and the original Soviet logbooks from the period of illegal whaling, have been made available. These included substantial data on Soviet catches of pygmy blue whales (Zemsky and Sazhinov, 1982; Mikhalev, 2000; Branch and Mikhalev, accepted). A key paper is Sazhinov (1970) which estimates that the length of sexual maturity for pygmy blue whales is about 19.2 m, and notes that two 19.2 m pygmy blue whales had 9 and 11 earplug laminae respectively, implying the age at sexual maturity must be 9–11 yr for pygmy blue whales.

In summary, it is well accepted that the gestation period is somewhat greater than 10 months, weaning occurs 7 months after birth, and the age at sexual maturity for female Antarctic and pygmy blue whales is about 10 years. What is still missing, and estimated in this paper, is raw data for earplug laminae and lengths, and an age-length equation with estimated uncertainty about the length at each age.

Calving interval

Long-term photo-identification data have not yet been collected to estimate calving intervals. The long-term study in the Gulf of St Lawrence is unsuitable for this purpose because although the catalogue included 362 whales by 2002, only 13 calves had been observed (Ramp *et al.*, 2006). Therefore, historical catch data have been used to estimate the calving interval for blue whales. Mackintosh and Wheeler (1929) noted that for Antarctic blue whales, the gestation period is a little more than 10 months, and it takes another 7 months until weaning. Given that most calves are born in a defined period (April–May), and that

females are very rarely lactating and pregnant at the same time, this places a lower bound on the calving interval of 2 yr. From the high proportion of pregnant females among sexually mature females, they concluded that the majority of Antarctic blue whales calve every 2 yr while not excluding the possibility that some calve every 3 yr (Mackintosh and Wheeler, 1929). The ovarian study by Laurie (1937) concluded that they could calve as often as every 2 yr, but a substantial proportion may breed every 3 yr, and Laurie therefore proposed that the average calving interval is 2.5 yr.

An upper bound on the calving interval can be obtained by examining the relationship between ovarian corpora counts and age (measured by earplug laminae): the ovulation rate is the slope of a plot of ovarian corpora against age. Based on limited data, Ohsumi (1979) used this method to estimate an ovulation rate of 0.40 (once every 2.5 yr) for Antarctic blue whales from a limited number of whales caught in 1956/57–1958/59, but did not provide the original data or present confidence intervals for this estimate.

Adult and calf survival

Few estimates of adult survival, and none for calf survival, have been published. The standard method in fisheries is to obtain a large number of age samples from a pristine population. A frequency distribution will reveal a descending frequency at increasing ages; by plotting log-frequency, the absolute value of the slope (from highest frequency to maximum age) will be the natural mortality. When Japanese pygmy blue whale earplug data were analysed in this way, the resulting estimate of natural mortality (M) was 0.055 for males, 0.052 for females, and 0.05 for both sexes combined, assuming one earplug layer is produced per year (Ichihara and Doi, 1964). These correspond to annual survival rates ($S = e^{-M}$) of 0.946 for males, 0.949 for females and 0.95 for both sexes combined. No confidence interval was associated with these estimates. For northern blue whales (*B. m. musculus*), a long-term photo-identification study in the Gulf of St Lawrence, Canada, yielded an estimate of survival of 0.975 (95% CI 0.960–0.985), although the authors note that upward bias may result from including long sightings records, and downward bias from permanent emigration from the study area (Ramp *et al.*, 2006).

Calf survival rates have never been estimated for blue whales, although it seems logical that juvenile survival should be less than adult survival, since suckling calves would die if their mothers died. Of the four photographically identifiable calves sighted in the Gulf of St Lawrence population, none were resighted, thus these data cannot be used to estimate survival (Ramp *et al.*, 2006).

METHODS

Data

Soviet earplug data were provided by Y. Mikhalev from Sazhinov (1980); the original manuscript could not be obtained. The data consisted of pairs of lengths (0.1 m intervals) and counts of earplug laminae, separately for males ($n = 218$) and females ($n = 170$). No data on location, year, expedition code or corpora count were available. However, nearly all of the pygmy blue whale biological information recovered to date consisted of Soviet catches during the 1961/62 to 1971/72 seasons in the Indian Ocean (Branch and Mikhalev, accepted).

Japanese earplug data were obtained from Table 11 in Ichihara (1966), which lists earplug laminae and ovarian corpora (corpora lutea plus corpora albicantia) for females under the 70 ft legal minimum length (62–69 ft, 18.9–21.0 m, $n = 32$). Further data in the form of frequencies of earplug laminae counts were provided in Ichihara and Doi (1964) for males ($n = 410$) and females ($n = 335$) during the 1960/61–1962/63 whaling seasons. No information was available for location or expedition code for either dataset, and length and corpora counts were only available for the Ichihara (1966) dataset.

Length at age

Length at age for male and female pygmy blue whales was estimated by fitting growth models to the Soviet length and earplug laminae data from Sazhinov (1980). Three models were examined: the von Bertalanffy, Gompertz and logistic. The von Bertalanffy growth equation provided the best fit and therefore the other models are not considered further. Growth curves were fit separately to males and females, assuming that one earplug lamina is added per year of life (Lockyer, 1984). The von Bertalanffy equation is:

$$(1) \hat{l}_i = l_{\infty} (1 - e^{-\kappa(t_i - t_0)})$$

\hat{l}_i is the predicted length (in m) for whale i

l_{∞} is the asymptotic maximum length

κ is the growth rate (yr^{-1})

t_i is the observed age of whale i (in yr)

t_0 is a parameter to be estimated

Assuming that differences between predicted length and observed length are normally distributed, the negative log likelihood to be minimized, ignoring constants that are independent of the model parameters, is given by:

$$(2) -\ln L = n \ln \sigma + \sum_{i=1}^n \frac{(\hat{l}_i - l_i)^2}{2\sigma^2}$$

l_i is the observed length of whale i (in m)

σ is the estimated standard deviation

A Bayesian framework is employed to provide estimates of the model parameters, with broad uniform priors: $l_\infty \sim U[15, 30]$, $\kappa \sim U[0, 10]$, $t_0 \sim U[-100, 100]$, and $\sigma \sim U[0.01, 10]$. Model fits and posterior distributions were obtained in AD Model Builder (Otter Research Ltd, 2004), by running Markov Chain Monte Carlo chains for 1.2 million iterations, discarding the first 0.2 million draws, and then subsampling evenly to obtain 5000 posterior draws. The autocorrelation among the resulting posterior draws was <0.02 for all parameters.

Posterior 95% credibility intervals for mean length at each age were obtained from the posterior distributions of the model parameters l_∞, κ, t_0 . In addition, 95% posterior predictive intervals were obtained by additionally accounting for the standard deviation σ estimated for each draw.

Age at sexual maturity based on Soviet data

Age at sexual maturity is estimated from the Soviet data by combining previous estimates of the length at which 50% of the whales become sexual maturity: 19.2 m (95% credibility interval 19.1–19.3 m) (Branch and Mikhalev, accepted), with the age-length analysis in the previous section. To obtain a distribution of the age at sexual maturity, the following process is repeated $i = 1$ to 5000 times, once for each of the posterior draws in the length-at-age model in the previous section: (1) a length l_i is randomly drawn from a $N(19.2, 0.051^2)$ distribution, representing the distribution of length at sexual maturity, (2) the age estimate t_i corresponding the length l_i is calculated from the i th posterior draw of l_∞, κ, t_0 using Equation 3 below, a rearrangement of Equation 1, and (3) the 95% credibility intervals are calculated from the resulting 5000 t_i values.

$$(3) t_i = t_{0,i} - \frac{1}{\kappa_i} \ln \left(1 - \frac{l_i}{l_{\infty,i}} \right)$$

Age at sexual maturity and interval between ovulations, Japanese data

An alternative estimate of age at sexual maturity for females is obtained from data in Ichihara (1966). Ovarian corpora are a permanent record of lifetime ovulations, while earplug laminae record the age of the whale. A linear regression of earplug laminae against ovarian corpora therefore reveals two pieces of information: the intercept is the age at which the average pygmy blue whale has zero ovarian corpora (i.e. the age at sexual maturity), while the gradient is the interval between ovulations, which is an upper bound on the inter-birth interval. To avoid introducing bias into the regression analysis, whales with zero ovarian corpora were excluded (these could be any age under the age at sexual maturity).

Estimating natural mortality

Natural mortality was estimated for males and females from the Soviet (Sazhinov, 1980) and Japanese (Ichihara and Doi, 1964) data. Estimates were made for males and females separately and pooled, and from data from both countries both separately and pooled. Natural mortality was estimated by regressing log-frequency of age against age. If natural mortality is constant with age, the slope of the regression will be -1 multiplied by natural mortality. Because of minimum length regulations and for commercial reasons, whalers selected for larger and older whales, therefore the frequency of younger whales is lower than the true frequency in the population; for this reason the regression was conducted only between the age with the highest frequency (estimated from the mode of a lognormal distribution fitted to the age frequency), and the maximum age.

RESULTS

Length at age

The von Bertalanffy growth model provided a good fit to the Soviet data (Figure 1). Estimates of κ, t_0 , and σ were similar between males and females (Table 1), but asymptotic maximum length, l_∞ , was significantly shorter ($P = 0.004$) for males (21.1 m) than for females (21.9 m). Estimated length at each age for males and females is reported in Table 2.

Female age at sexual maturity

Based on Soviet data ($n = 170$ for age-length relationship, $n = 1272$ for length at sexual maturity), the estimated age at sexual maturity for female pygmy blue whales is 9.9 yr (95% credibility interval 9.0–11.0 yr). There was a high correlation between age and corpora count in the Japanese data ($r^2 = 0.88$, $n = 28$, Figure 2), resulting in an estimated age at sexual maturity of 9.9 yr (95% CI 8.0–11.8 yr).

Inter-ovulation interval

Based on the regression between age and corpora counts (Figure 2), the interval between ovulations is 2.6 yr (95% CI 2.2–3.0 yr), implying an ovulation rate of 0.39 yr^{-1} (95% CI 0.34–0.45 yr^{-1}). Not all ovulations result in pregnancy, and not all pregnancies result in birth, therefore this estimate should be higher than the inter-birth interval.

Natural mortality

Estimated natural mortality for both sexes combined is 0.060 (95% CI 0.052–0.069) from the Soviet data and 0.059 (95% CI 0.054–0.065) from the Japanese data (Table 3, Figure 3). When data from both sources are combined, the estimate increases slightly to 0.064 (95% CI 0.059–0.069). Estimates obtained from each sex separately are generally slightly lower, but there is no consistent pattern for one sex to have a lower natural mortality than the other. Therefore, a consensus from these estimates is that natural mortality for both sexes is about 0.06 (95% CI 0.05–0.07).

DISCUSSION

Length at age

The von Bertalanffy growth equation estimated here in a Bayesian framework is similar to that obtained by Ichihara (1966). Maximum length is 21.9 m (95% interval 21.5–22.5 m) for females, compared to 21.6–21.9 m estimated by Ichihara; and 21.1 m (95% interval 20.7–21.5 m) for females, compared to 20.4–20.7 m estimated by Ichihara. The key advance here is that credibility intervals have been estimated both for the parameters of the growth equation and also for the predicted lengths at each age.

Female age at sexual maturity

The age at sexual maturity is estimated to be 9.9 yr from both the Japanese and Soviet data, which is an eerie coincidence. More Soviet data are available, hence the narrower 95% intervals of 9.0–11.0 yr compared to 8.0–11.8 yr from the Japanese data. These results agree with the estimates of 10 yr inferred by Ichihara (1966) and by Sazhinov (1980) for pygmy blue whales. The overall conclusion therefore, is that pygmy blue whales reach sexual maturity at 10 yr, with 95% intervals of 9–11 yr. It should be noted that the age at first parturition will be slightly later, because not all sexually mature females become pregnant, not all pregnant females give birth, and because the gestation period of 10–11 months needs to be taken into account. For these reasons, age at first parturition is about a year later than the age at sexual maturity, i.e. 11 yr (95% interval 10–12 yr).

Calving interval

The inter-ovulation interval is estimated to be 2.6 yr (95% CI 2.2–3.0 yr), differing little from previous calving interval estimates of 2–3 yr (Mackintosh and Wheeler, 1929; Laurie, 1937; Ohsumi, 1979). The ovulation rate places an upper bound on the calving interval, because some ovulations may not result in pregnancy and some pregnancies may not end in live birth. However, it should be pointed out that there is no independent validation that corpora albicantia are formed from every ovulation and not only from pregnancies. In dolphins, as in large mysticetes, it has long been believed that every ovulation results in a corpus albicans being formed. However, weekly ultrasound scans of a captive bottlenose dolphin (*Tursiops aduncus*) over 11 years revealed that this individual ovulated at least 18 times but only three corpora albicantia were present in its ovaries upon death—corresponding to the three times that this female became pregnant (Brook *et al.*, 2002). If this is true for large mysticetes then corpora albicantia are only formed upon pregnancy. Regardless whether this is true for blue whales or not, the very low rate of accumulation of ovarian corpora in blue whales (less than once every two years) suggests that either there is no regular ovulation interval and ovulation is induced only upon mating, or that permanent ovarian corpora are only accumulated on pregnancy and not on ovulation, as in the captive bottlenose dolphin.

Natural mortality

The estimate of natural mortality of 0.06 (0.05–0.07) from the combined Japanese and Soviet data is slightly higher than obtained by Ichihara and Doi (1964) of 0.05, and is considerably higher than the estimate of 0.025 (95% CI 0.015–0.040) for northern blue whales in the Gulf of St Lawrence. This estimate assumes that the age distribution in the older ages was stable and not yet affected by whaling mortality, which is a reasonable assumption because whaling on pygmy blue whales had only been conducted for 2–3 seasons (affecting only the relative frequencies of the youngest 2–3 age groups) for the Japanese data, and for 3–11 seasons for the Soviet data. Since the mortality estimates were obtained from age 11 upwards (except for females from the Soviet data, which had the *lowest* natural mortality), whaling mortality probably did not bias these estimates.

Possible population rate of increase

Assuming an inter-calf interval of 2.6 yr, age at first parturition of 11 yr, sex ratio of 0.5, and an adult survival rate of 0.94, the implied rate of increase can be obtained using the equations in Branch *et al.* (2004). The resulting rate of increase is zero for a calf survival of 0.58 (likely much lower than the actual calf survival rate) and 2.0% for a calf survival of 0.94 (the same as adult survival). Therefore, if the parameter estimates in this paper are correct, pygmy blue whales in the 1960s were capable of increasing at only a slow rate of <2%.

ACKNOWLEDGEMENTS

T.A.B. is grateful for funding for this project from the International Whaling Commission, and wishes to thank Y. Mikhalev for providing the earplug data in Sazhinov (1980), L. Flynn for translating Sazhinov (1970), and I. Mikhalev for translating email exchanges with Y. Mikhalev.

REFERENCES

- Branch, T.A., Matsuoka, K. and Miyashita, T. 2004. Evidence for increases in Antarctic blue whales based on Bayesian modelling. *Mar. Mamm. Sci.* 20:726-754.
- Branch, T.A. and Mikhalev, Y.A. accepted. Regional differences in length at sexual maturity for female blue whales based on recovered data from illegal Soviet whaling data. *Mar. Mamm. Sci.*
- Brook, F.M., Kinoshita, R. and Benirschke, K. 2002. Histology of the ovaries of a bottlenose dolphin, *Tursiops aduncus*, of known reproductive history. *Mar. Mamm. Sci.* 18:540-544.
- Calambokidis, J. and Barlow, J. 2004. Abundance of blue and humpback whales in the Eastern North Pacific estimated by capture-recapture and line-transect methods. *Mar. Mamm. Sci.* 20:63-85.
- Calambokidis, J., Steiger, G.H., Cubbage, J.C., Balcomb, K.C., Ewald, C., Kruse, S., Wells, R. and Sears, R. 1990. Sightings and movements of blue whales off Central California 1986-88 from photo-identification of individuals. *Rep Int Whal Commn Spec. Iss.* 12:343-348.
- Chittleborough, R.G. 1959. Determination of age in the humpback whale, *Megaptera nodosa* (Bonnaterre). *Australian Journal of Marine and Freshwater Research* 10(2):125-143.
- Clapham, P.J., Young, S.B. and Brownell, J.R. 1999. Baleen whales: conservation issues and the status of the most endangered populations. *Mammal Rev.* 29:35-60.
- Ichihara, T. 1961. Blue whales in the waters around Kerguelen Island. *Norsk Hvalfangst-Tidende* 50(1):1-20.
- Ichihara, T. 1963. Identification of the pigmy blue whale in the Antarctic. *Norsk Hvalfangst-Tidende* 52(6):128-130.
- Ichihara, T. 1966. The pygmy blue whale, *Balaenoptera musculus brevicauda*, a new subspecies from the Antarctic. Pages 79-111 in K. S. Norris, editor. Whales, dolphins, and porpoises. University of California Press, Berkeley and Los Angeles.
- Ichihara, T. and Doi, T. 1964. Stock assessment of pigmy blue whales in the Antarctic. *Norsk Hvalfangst-Tidende* 53(6):145-167.
- Laurie, A.H. 1937. The age of female blue whales and the effect of whaling on the stock. *Discovery Reports* 15:223-284.
- Laws, R.M. 1961. Reproduction, growth and age of southern fin whales. *Discovery Reports* 31:327-486.
- Laws, R.M. and Purves, P.E. 1956. The ear plug of the Mysticeti as an indication of age with special reference to the North Atlantic fin whale (*Balaenoptera physalus* Linn.). *Norsk Hvalfangst-Tidende* 45(8):413-425.
- Lockyer, C. 1974. Investigation of the ear plug of the southern sei whale, *Balaenoptera borealis*, as a valid means of determining age. *J. Cons. int. Explor. Mer* 36(1):71-81.
- Lockyer, C. 1981. Growth and energy budgets of large baleen whales from the Southern Hemisphere. Pages 379-487 in *Mammals in the Seas, Volume III, General Papers and Large Cetaceans*. Food and Agricultural Organization of the United Nations, Rome.
- Lockyer, C. 1984. Age determination by means of the earplug in baleen whales. *Rep Int Whal Commn* 34:692-698.
- Mackintosh, N.A. and Wheeler, J.F.G. 1929. Southern blue and fin whales. *Discovery Reports* 1:257-540.
- Mikhalev, Y.A. 2000. Whaling in the Arabian Sea by the whaling fleets *Slava* and *Sovetskaya Ukraina*. Pages 141-181 in A. V. Yablokov and V. A. Zemsky, editors. Soviet Whaling Data (1949-1979). Center for Russian Environmental Policy Marine Mammal Council, Moscow.
- Ohsumi, S. 1979. Interspecies relationships among some biological parameters in cetaceans and estimation of the natural mortality coefficient of the Southern Hemisphere minke whale. *Rep Int Whal Commn* 29:397-406.
- Otter Research Ltd. 2004. An introduction to AD Model Builder Version 7.1.1 for use in nonlinear modeling and statistics. Report available from www.otter-rsch.com.
- Ottestad, P. 1950. On age and growth of blue whales. *Hvalrådets Skrifter* 33:67-72.
- Purves, P.E. 1955. The wax plug in the external auditory meatus of the Mysticeti. *Discovery Reports* 27:293-302.
- Ramp, C., Bérubé, M., Hagren, W. and Sears, R. 2006. Survival in blue whales *Balaenoptera musculus* in the Gulf of St. Lawrence, Canada. *Mar. Ecol. Prog. Ser.* 319:287-295.
- Roe, H.S.J. 1967. Seasonal formation of laminae in the ear plug of the fin whale. *Discovery Reports* 35:1-30.

- Ruud, J.T. and Jonsgård, Å. 1950. Age studies on blue whales taken in Antarctic seasons 1945-46, 1946-47 and 1947-48. *Hvalrådets Skrifter* 33:5-66.
- Sazhinov, E.G. 1970. Sexual and physical maturity of pygmy blue whales (*Balaenoptera musculus brevicauda*). Pages 34-40 *Whales of Southern Hemisphere (Biology and Morphology)*. AtlantNIRO, Kaliningrad.
- Sazhinov, E.G. 1980. Pygmy blue whales. Science Academy USSR, Kiev, and Zoology Institute, Kaliningrad. PhD dissertation.
- Sears, R. and Larsen, F. 2002. Long range movements of a blue whale (*Balaenoptera musculus*) between the Gulf of St. Lawrence and West Greenland. *Mar. Mamm. Sci.* 18:281-285.
- Yablokov, A.V. 1994. Validity of whaling data. *Nature* 367:108.
- Yablokov, A.V., Zemsky, V.A., Mikhalev, Y.A., Tormosov, V.V. and Berzin, A.A. 1998. Data on Soviet whaling in the Antarctic in 1947-1972 (population aspects). *Russian Journal of Ecology* 29:38-42.
- Zemsky, V.A., Berzin, A.A., Mikhalev, Y.A. and Tormosov, D.D. 1995. Soviet Antarctic pelagic whaling after WWII: review of actual catch data. *Rep Int Whal Commn* 45:131-135.
- Zemsky, V.A. and Sazhinov, E.G. 1982. Distribution and current abundance of pygmy blue whales. Pages 53-70 in V. A. Arsen'ev, editor. *Marine Mammals*. All-Union Research Institute of Marine Fisheries and Oceanography, Moscow. Translated by V.S. Gurevich in February 1994, translation edited by M.A. Donahue and R.L. Brownell, Jr., as Southwest Fisheries Science Center Administrative Report LJ-94-02, available from NMML, sonja.kromann@noaa.gov.

Table 1. Soviet age-length data for pygmy blue whales from Sazhinov (1980). Lengths in m, ages are earplug laminae which are in yr (assuming one lamina was produced per year).

Females								Males							
Age	Length	Age	Length	Age	Length	Age	Length	Age	Length	Age	Length	Age	Length	Age	Length
2	16.0	8	18.4	15	20.0	28	20.4	1	14.8	9	19.4	15	20.7	20	19.7
2	16.5	9	16.1	15	20.3	28	20.7	1	15.1	9	19.7	15	20.8	20	19.8
2	16.5	9	16.6	15	20.6	28	20.9	1	16.0	9	19.9	16	18.9	20	20.0
2	16.6	9	18.0	15	20.6	28	21.0	1	16.0	10	18.7	16	19.3	20	20.0
2	16.6	9	19.2	15	21.4	28	22.9	1	16.1	10	18.7	16	19.4	20	20.2
2	16.6	9	20.2	16	19.8	29	20.0	2	16.0	10	18.7	16	19.4	20	20.8
2	16.8	9	20.2	16	19.8	29	21.4	2	16.7	10	19.3	16	19.6	21	19.6
2	16.9	10	18.2	16	19.9	30	20.8	2	17.4	10	19.5	16	19.8	21	20.0
2	17.6	10	19.0	16	20.5	30	21.0	3	15.8	10	19.7	16	19.9	22	19.6
2	17.7	10	19.5	16	20.5	30	21.0	3	16.8	10	19.8	16	20.0	22	20.0
3	16.0	10	20.0	16	21.2	30	22.4	3	17.0	10	19.8	16	20.1	22	20.2
3	16.1	11	18.4	17	19.8	30	23.3	4	16.0	11	19.1	16	20.3	22	20.5
3	16.4	11	18.8	17	20.4	30	23.4	4	16.0	11	19.2	16	20.7	22	20.7
3	16.4	11	18.9	18	18.6	31	21.1	4	17.0	11	19.5	17	19.1	22	21.4
3	16.5	11	19.2	18	19.2	31	22.4	4	17.4	11	19.6	17	19.3	23	19.7
3	17.0	11	19.6	18	19.6	32	20.7	4	17.5	11	19.8	17	19.3	23	19.7
3	17.0	11	20.2	18	20.2	32	21.6	4	17.7	11	19.8	17	19.7	23	19.9
3	17.2	11	20.2	18	20.4	33	20.3	4	18.0	11	20.2	17	19.9	23	19.9
3	17.6	12	18.4	18	20.0	33	21.4	4	18.1	12	18.7	17	20.1	23	20.4
3	17.7	12	18.8	18	23.0	34	21.3	4	18.2	12	19.0	17	20.2	23	20.5
3	17.8	12	19.0	19	20.5	35	21.2	4	18.3	12	19.4	17	20.4	23	20.6
4	16.2	12	19.4	20	21.8	35	21.5	4	18.4	12	19.7	17	21.4	23	21.1
4	17.1	12	19.4	22	20.7	35	22.5	5	16.6	12	20.6	18	19.0	24	19.4
4	17.8	12	19.8	23	21.2	36	21.2	5	16.9	13	19.5	18	19.4	24	20.0
4	17.9	12	19.8	24	20.2	36	22.4	5	17.4	13	20.0	18	19.6	24	20.2
4	18.4	12	20.4	24	20.7	36	22.6	5	17.5	14	17.6	18	19.6	24	20.3
4	18.4	12	21.0	25	20.1	36	22.6	5	18.0	14	18.0	18	19.6	24	20.3
4	18.5	13	20.0	25	20.3	37	21.7	5	18.6	14	18.5	18	19.9	24	20.5
4	18.7	13	20.2	25	20.5	37	22.5	5	18.6	14	19.1	18	20.0	24	20.6
5	18.3	13	20.3	25	21.2	38	21.0	5	19.0	14	19.2	18	20.0	24	21.1
6	17.6	13	20.4	25	21.3	38	21.3	6	17.6	14	19.3	18	20.3	24	21.2
6	19.3	13	20.7	25	21.6	39	21.3	6	18.6	14	19.3	18	21.3	24	21.2
7	17.0	14	19.4	25	22.8	43	20.6	7	17.0	14	19.8	19	19.2	25	19.8
7	18.2	14	19.5	26	20.2	43	21.8	7	18.2	14	19.9	19	19.2	25	20.2
7	18.2	14	19.5	26	20.3	43	22.0	7	18.6	14	19.9	19	19.2	25	20.3
7	18.3	14	19.6	26	20.5	45	22.3	7	18.7	14	20.0	19	19.5	25	20.5
7	18.8	14	19.7	26	20.6	50	20.2	7	18.9	15	17.5	19	19.8	25	20.7
7	18.8	14	19.9	26	20.6	56	23.2	7	19.2	15	18.9	19	19.9	25	20.8
7	19.2	14	20.7	26	20.9			7	19.4	15	19.4	19	19.9	25	21.3
7	19.2	14	21.0	27	20.7			8	17.6	15	19.5	19	20.0	25	21.9
7	19.3	14	22.0	27	22.0			8	18.8	15	19.7	19	20.1	26	20.3
7	19.3	15	19.8	27	22.0			8	19.3	15	19.8	19	20.1	26	20.9
7	19.5	15	19.9	27	22.1			9	18.2	15	20.1	19	20.3	27	19.2
8	18.3	15	20.0	28	20.0			9	18.8	15	20.3	20	19.3	27	19.9

Table 2. Frequencies of ages of male and female pygmy blue whales from Ichihara and Doi (1964), assuming that age equals the number of earplug laminae.

Age	Male	Female	Total	Age	Male	Female	Total
1	0	0	0	38	10	4	14
2	1	0	1	39	7	0	7
3	0	1	1	40	12	1	13
4	2	0	2	41	5	3	8
5	3	2	5	42	8	1	9
6	1	2	3	43	7	4	11
7	3	3	6	44	1	3	4
8	4	6	10	45	5	3	8
9	2	7	9	46	8	0	8
10	10	3	13	47	3	3	6
11	8	6	14	48	5	1	6
12	7	9	16	49	2	4	6
13	5	7	12	50	4	2	6
14	7	11	18	51	5	1	6
15	13	16	29	52	3	2	5
16	10	12	22	53	4	1	5
17	10	9	19	54	1	1	2
18	8	14	22	55	1	0	1
19	13	14	27	56	2	2	4
20	15	12	27	57	2	1	3
21	12	19	31	58	1	1	2
22	13	11	24	59	1	0	1
23	10	10	20	60	2	1	3
24	9	10	19	61	3	0	3
25	13	14	27	62	1	0	1
26	9	10	19	63	1	1	2
27	10	13	23	64	0	1	1
28	9	11	20	65	0	1	1
29	15	12	27	66	1	0	1
30	7	6	13	67	0	0	0
31	9	3	12	68	1	0	1
32	11	7	18	69	0	0	0
33	13	8	21	70	1	0	1
34	9	7	16	71	1	0	1
35	9	5	14	72	2	0	2
36	11	7	18	73	1	0	1
37	8	6	14	Total	410	335	745

Table 3. Posterior estimates and 95% credibility intervals for the von Bertalanffy growth curve for pygmy blue whales, based on Soviet length and age data from Sazhinov (1980).

Sex	Maximum length l_{∞}		Growth rate κ		Scaling parameter t_0		Standard deviation σ	
Female	21.9	(21.5; 22.5)	0.080	(0.061; 0.102)	-16.2	(-21.5; -12.2)	0.85	(0.76; 0.95)
Male	21.1	(20.7; 21.5)	0.089	(0.068; 0.115)	-15.5	(-20.7; -11.5)	0.74	(0.67; 0.82)

Table 4. Estimated length (m) at age for male and female pygmy blue whales: posterior median, 95% credibility intervals, and 95% posterior predictive intervals.

Age	Female			Male		
	Median	95% credibility interval	95% predictive interval	Median	95% credibility interval	95% predictive interval
1	15.9	(15.3; 16.4)	(14.1; 17.6)	15.8	(15.2; 16.3)	(14.3; 17.3)
2	16.4	(15.9; 16.8)	(14.7; 18.1)	16.3	(15.8; 16.7)	(14.7; 17.8)
3	16.8	(16.4; 17.1)	(15.1; 18.5)	16.7	(16.3; 17.0)	(15.2; 18.2)
4	17.2	(16.9; 17.5)	(15.5; 18.9)	17.0	(16.8; 17.3)	(15.6; 18.5)
5	17.5	(17.3; 17.8)	(15.9; 19.2)	17.4	(17.2; 17.6)	(15.9; 18.8)
6	17.9	(17.7; 18.1)	(16.2; 19.5)	17.7	(17.5; 17.9)	(16.2; 19.2)
7	18.2	(18.0; 18.4)	(16.6; 19.9)	18.0	(17.8; 18.2)	(16.6; 19.5)
8	18.5	(18.3; 18.7)	(16.8; 20.2)	18.3	(18.1; 18.4)	(16.8; 19.7)
9	18.7	(18.6; 18.9)	(17.1; 20.4)	18.5	(18.3; 18.7)	(17.0; 19.9)
10	19.0	(18.8; 19.2)	(17.3; 20.7)	18.7	(18.6; 18.9)	(17.2; 20.2)
11	19.2	(19.0; 19.4)	(17.6; 20.8)	18.9	(18.8; 19.1)	(17.4; 20.4)
12	19.4	(19.2; 19.6)	(17.7; 21.1)	19.1	(18.9; 19.3)	(17.6; 20.5)
13	19.6	(19.4; 19.8)	(17.9; 21.3)	19.3	(19.1; 19.4)	(17.8; 20.7)
14	19.8	(19.6; 20.0)	(18.1; 21.5)	19.4	(19.3; 19.6)	(18.0; 20.9)
15	20.0	(19.8; 20.1)	(18.3; 21.6)	19.6	(19.4; 19.7)	(18.2; 21.0)
16	20.1	(19.9; 20.3)	(18.4; 21.8)	19.7	(19.5; 19.8)	(18.2; 21.2)
17	20.2	(20.1; 20.4)	(18.5; 21.9)	19.8	(19.7; 20.0)	(18.4; 21.3)
18	20.4	(20.2; 20.5)	(18.7; 22.0)	19.9	(19.8; 20.1)	(18.5; 21.4)
19	20.5	(20.3; 20.7)	(18.8; 22.2)	20.0	(19.9; 20.1)	(18.6; 21.5)
20	20.6	(20.4; 20.8)	(18.9; 22.3)	20.1	(20.0; 20.2)	(18.7; 21.5)
21	20.7	(20.5; 20.9)	(19.0; 22.3)	20.2	(20.1; 20.3)	(18.7; 21.6)
22	20.8	(20.6; 21.0)	(19.1; 22.4)	20.3	(20.1; 20.4)	(18.8; 21.7)
23	20.9	(20.7; 21.0)	(19.2; 22.6)	20.3	(20.2; 20.5)	(18.9; 21.8)
24	21.0	(20.8; 21.1)	(19.3; 22.7)	20.4	(20.3; 20.5)	(18.9; 21.9)
25	21.0	(20.9; 21.2)	(19.4; 22.7)	20.5	(20.3; 20.6)	(19.0; 22.0)
26	21.1	(20.9; 21.3)	(19.5; 22.8)	20.5	(20.4; 20.6)	(19.0; 21.9)
27	21.2	(21.0; 21.3)	(19.5; 22.9)	20.6	(20.4; 20.7)	(19.1; 22.0)
28	21.2	(21.0; 21.4)	(19.6; 22.9)	20.6	(20.5; 20.7)	(19.1; 22.1)
29	21.3	(21.1; 21.5)	(19.6; 23.0)	20.6	(20.5; 20.8)	(19.2; 22.1)
30	21.3	(21.1; 21.5)	(19.6; 23.0)	20.7	(20.5; 20.8)	(19.2; 22.1)
35	21.5	(21.3; 21.8)	(19.9; 23.2)	20.8	(20.6; 21.0)	(19.3; 22.3)
40	21.6	(21.4; 21.9)	(20.0; 23.3)	20.9	(20.7; 21.2)	(19.5; 22.4)
45	21.7	(21.4; 22.1)	(20.0; 23.4)	21.0	(20.7; 21.3)	(19.4; 22.4)
50	21.8	(21.4; 22.2)	(20.1; 23.5)	21.0	(20.7; 21.3)	(19.5; 22.5)
55	21.8	(21.5; 22.3)	(20.1; 23.5)	21.0	(20.7; 21.4)	(19.6; 22.5)
60	21.9	(21.5; 22.3)	(20.2; 23.6)	21.0	(20.7; 21.4)	(19.5; 22.6)

Table 5. Natural mortality (M) estimates and 95% confidence intervals for pygmy blue whales. The regression to estimate M was conducted over the data range indicated, which was from the modal age to the maximum age. Japanese data were from Ichihara and Doi (1964) and Soviet data from Sazhinov (1980).

Data source	Sex	n	Age range	M	95% CI	r^2	P
Japan + USSR	Male + female	1133	17–73	0.064	(0.059; 0.069)	0.93	< 0.001
Japan + USSR	Male	628	18–73	0.054	(0.048; 0.061)	0.86	< 0.001
Japan + USSR	Female	505	16–73	0.059	(0.052; 0.066)	0.84	< 0.001
Japan	Male + female	745	20–73	0.059	(0.054; 0.065)	0.91	< 0.001
Japan	Male	410	22–73	0.049	(0.042; 0.056)	0.79	< 0.001
Japan	Female	335	19–73	0.054	(0.047; 0.061)	0.81	< 0.001
USSR	Male + female	388	11–59	0.060	(0.052; 0.069)	0.80	< 0.001
USSR	Male	218	14–59	0.056	(0.045; 0.066)	0.72	< 0.001
USSR	Female	170	6–59	0.039	(0.029; 0.048)	0.57	< 0.001

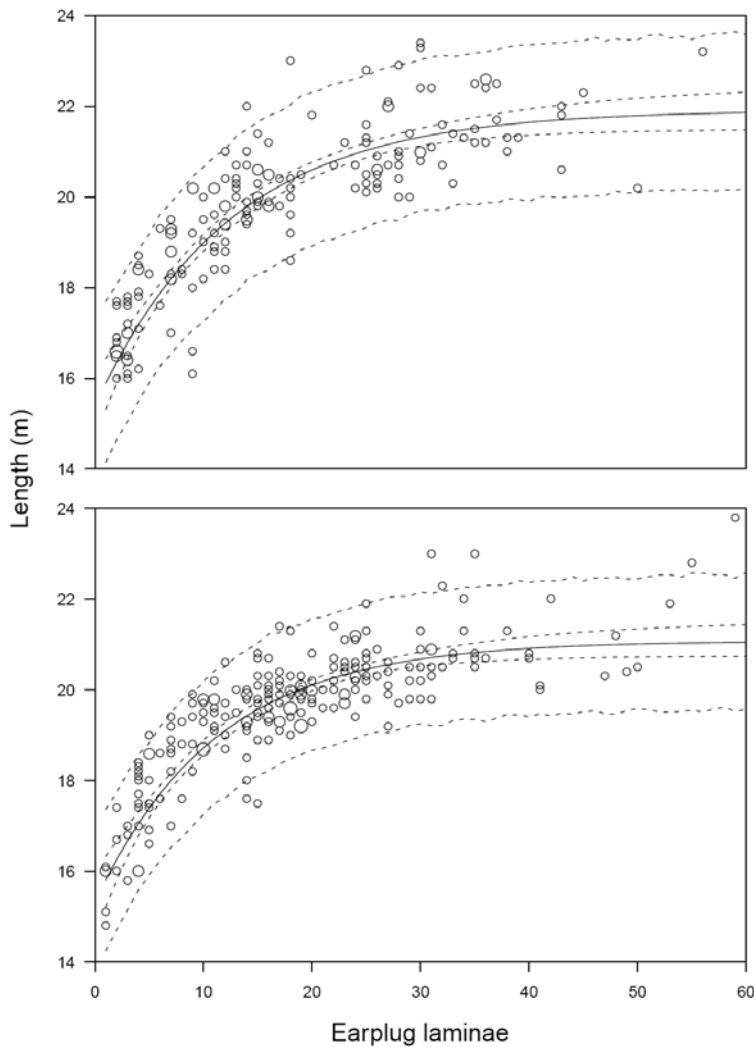


Figure 1. Relationship between length (m) and age (measured in earplug laminae) for female (top panel) and male (bottom panel) pygmy blue whales caught in Soviet expeditions. Circles represent the data, with sizes proportional to the frequency recorded at each point. Model fits are represented by the posterior median (solid line), 95% posterior error about the median (innermost dashed lines), and posterior predictions for length (outer dashed lines). Data were provided by Y. Mikhalev from Sazhinov (1980).

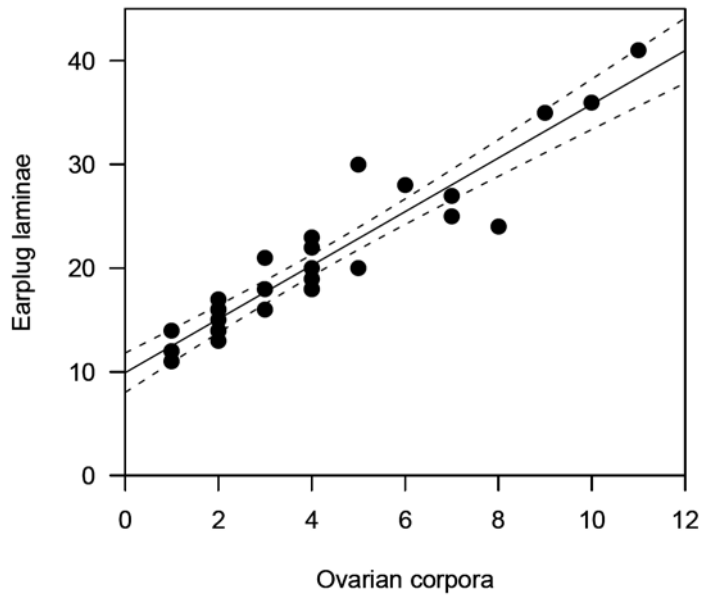


Figure 2. Mean and 95% confidence intervals for the regression between ovarian corpora and earplug laminae (age) for pygmy blue whales shorter than 70 ft listed in Ichihara (1966). The equation is $y = 2.59x + 9.91$, $r^2 = 0.88$, $n = 28$. Pygmy blue whales with zero ovarian corpora were omitted from the regression analysis.

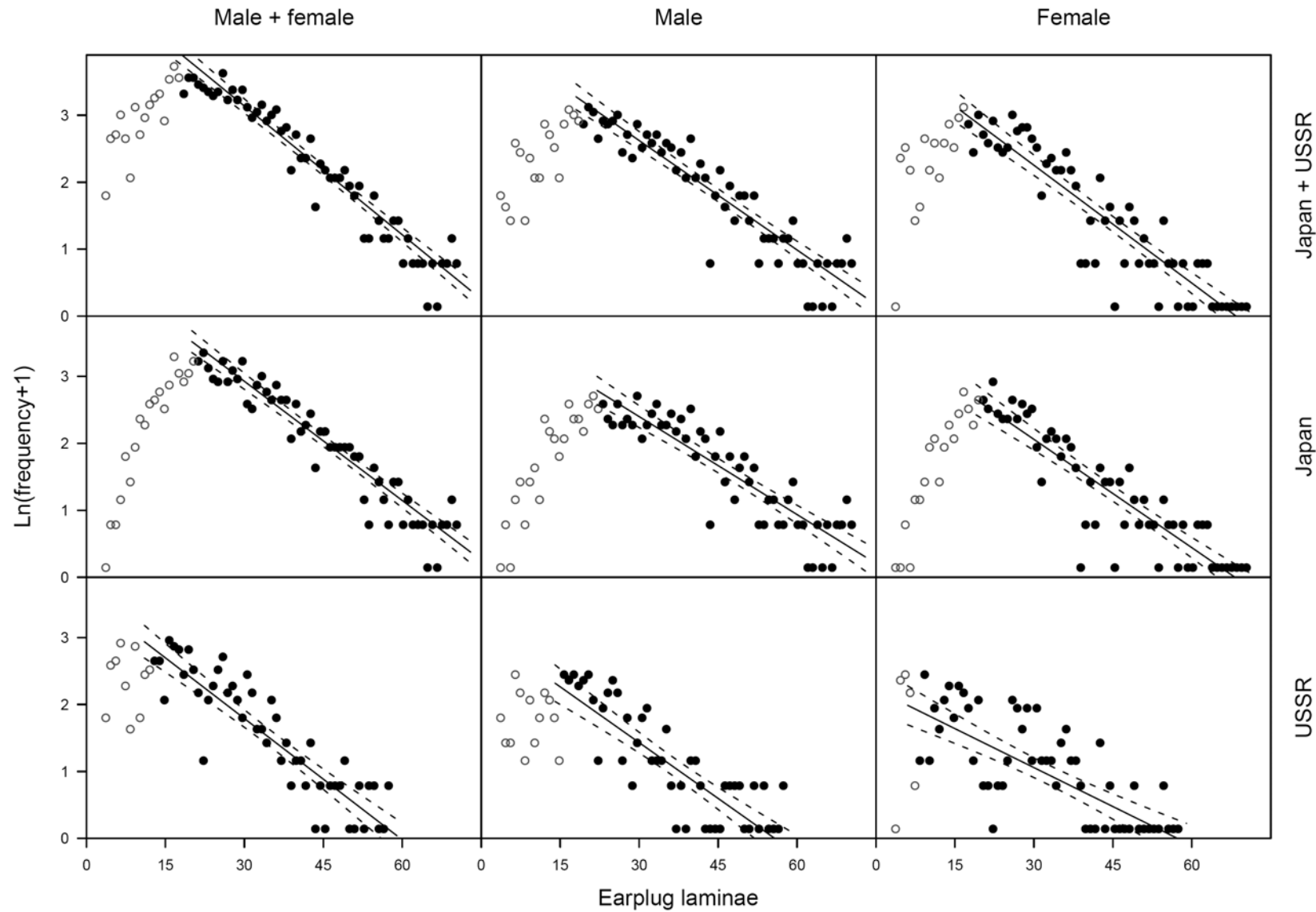


Figure 3. Regression of log-frequency against earplug data, used to estimate natural mortality. The regression (solid line) and 95% confidence intervals (dashed lines) are shown; solid circles were used in the regressions, while open circles were not included. Model estimates are given in Table 3.