

# Biologically plausible rates of increase for Antarctic blue whales

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## ABSTRACT

Basic biology limits the possible rate of increase in natural populations. Simply put, no population closed to immigration can increase more rapidly than is allowed by survival rates, pregnancy rate, age at first parturition, and the proportion of female births. Using a basic equation that relates values of these parameters to the implied rate of increase, a biologically plausible distribution and an upper bound are estimated for rates of increase in Antarctic blue whales (*Balaenoptera musculus intermedia*). The literature is reviewed to obtain distributions for each of the input parameters: adult survival  $S \sim N(0.963, 0.02^2)$ , calf survival  $S_j \sim N(0.84, 0.15^2)$ , annual pregnancy rate  $p \sim U(0.33; 0.5)$ , age at first parturition  $t_p \sim N(10, 2^2)$ , and the proportion of births that are female  $q_f \sim N(0.473, 0.001^2)$ . Lower and upper bounds were also placed on  $S$ ,  $S_j$ , and  $t_p$ ; most important of these is the restriction that  $S_j < S$ . The resulting distribution for the instantaneous annual rate of increase is  $\sim N(0.040, 0.019^2)$  with an upper 99<sup>th</sup> percentile of 0.082, corresponding to annual rates of increase  $\sim N(0.041, 0.019^2)$  and 0.085 respectively. Estimated rates of increase from surveys of Antarctic blue whales (7.4% from JARPA, 8.2% from IDCR/SOWER) are close to this theoretical maximum of 8.5%, and have 95% confidence intervals that exceed the biological maximum possible rates.

## INTRODUCTION

Rates of increase in any population are limited by biology, providing a key piece of information that can be incorporated in population assessments. The key biological factors are survival rates, inter-birth intervals, age at first parturition, and the proportion of females in the population, which can be combined using a simple equation to provide estimates of both the average and maximum possible rates of increase for biological populations. When this method is applied to humpback whales (*Balaenoptera novaeangliae*), biologically plausible average rates of increase are 4.7% per annum (Clapham *et al.*, 2006) and the maximum rates are 12.6% (Clapham *et al.*, 2001), 13.8% (Brandão *et al.*, 2000) and 10.6% (Clapham *et al.*, 2006); when applied to southern right whales (*Eubalaena australis*), the average rate of increase of 7.2% almost exactly matches the growth rate of 6.9% per annum from surveys (Best *et al.*, 2005); and when applied to Antarctic blue whales (*B. m. intermedia*), the average annual rate of increase is 4.3%, and the maximum rate is 11.9% (Branch *et al.*, 2004).

Since the Antarctic blue whale distribution was published (Branch *et al.*, 2004) new data have been presented for several of the biological parameters, particularly for survival in northern blue whales (*B. m. musculus*) (Ramp *et al.*, 2006), and for survival, age at first parturition, and inter-birth intervals in pygmy blue whales (*B. m. brevicauda*) (Branch, 2008b); and many studies have been published for other mysticetes. Here, we update the previous estimates of average and maximum rates of increase for Antarctic blue whales.

## METHODS

### Equation for estimating rate of increase

The Euler-Lotka equation, derived from Leslie matrix theory, can be used to directly estimate the instantaneous rate of increase from biological parameters (Brandão *et al.*, 2000):

$$e^{t_p \delta} = e^{(t_p - 1) \delta} S + p q_f S_j S^{t_p - 1},$$

where:

$\delta$  is the instantaneous rate of increase,

$t_p$  is the age at first parturition (yr), assumed to be one year after the age at sexual maturity,  $t_m$

$S$  is adult survival rate

$S_j$  is first-year survival rate

$p$  is the annual pregnancy rate, or the inverse of the inter-calf interval

$q_f$  is the proportion of births that are female

Estimated distributions were obtained for each of the parameters from a literature review of known blue whale biology and the biology of other large mysticetes. To obtain the distribution for the rate of increase, Monte Carlo simulations were conducted where 50,000 sets of values were drawn from the parameter distributions and  $\delta$  calculated for each. The maximum possible rate of increase for Antarctic blue whales is assumed to be the upper 99<sup>th</sup> percentile of this distribution. The highest

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rate recorded for any one draw would be misleading, because this would increase as the number of draws increased, whereas the 99<sup>th</sup> percentile is a stable estimator.

### IWC catch database

The IWC individual catch database has recently been updated and now includes corrected Soviet catches (C. Allison, IWC individual catch database Version 3.5, 11 February 2008). For several of the parameters, data from the database is extracted. In each case, only the data for blue whales south of 56°S are used, because in this region >99% of blue whales are Antarctic blue whales according to length frequencies of sexually mature females (Branch *et al.*, 2007a) and relationships between length and ovarian corpora (Branch *et al.*, 2008).

### Age at first parturition ( $t_p = t_m + 1$ )

Most available estimates are for mean age at sexual maturity,  $t_m$ , which is generally presumed to be about 1 yr before mean age at first parturition,  $t_p$  (e.g. Brandon *et al.*, 2007). Existing estimates of the age at sexual maturity,  $t_m$ , are sparse for Antarctic blue whales. The best method for ageing mysticetes is by counting earplug layers, a method pioneered in the 1950s (Purves, 1955; Laws and Purves, 1956). Earlier papers interpreted these layers by assuming that two earplug layers were added each year (e.g. Chittleborough, 1959), but later analyses examining monthly changes in earplug formation have confirmed that only one earplug layer is added per year for a variety of mysticetes (Roe, 1967; Rice and Wolman, 1971; Lockyer, 1972, 1974, 1984). Earplugs were rarely collected before this ageing method was developed, and as the Antarctic blue whale population was substantially depleted by this time, only limited earplugs were collected before the ban on catching Antarctic blue whales was implemented in the early 1960s. As a result, estimates of  $t_m$  are based on limited data for Antarctic blue whales, and although good estimates are available for pygmy blue whales, no estimates are available for any other blue whale population.

The little that has been published on earplug ageing of Antarctic blue whales is contradictory. Ohsumi (1979) reports that limited Antarctic blue whale earplug data imply  $t_m = 10$  yr, and the few data points plotted in Figure 9 of Ichihara (1966) for Antarctic blue whales also seem to imply that  $t_m$  is about 8–12 yr. However, Lockyer (1981), aged earplug of 20 females and 16 males (data not reported) and states that  $t_m$  is 5 yr, noting that this estimate is consistent with estimates of  $t_m$  from baleen plates made by Ruud and Jonsgård (1950) and Nishiwaki (1952).

For pygmy blue whales, estimates of  $t_m$  come from Japanese and Soviet data. Japanese data presented by Ichihara (1966) include ovarian corpora and earplug counts for 32 females shorter than the legal minimum catch length (70 ft, 21.3 m). These data were reanalysed by regressing ovarian corpora counts against earplug laminae counts, resulting in an estimate of  $t_m = 9.9$  yr (95% CI 8.0–11.8) (Branch, 2008b). Most of the Soviet whaling on pygmy blue whales was illegal (Yablokov, 1994; Mikhalev, 2000), and analyses on these data have been unknown in the West until recently. Part of the Soviet pygmy blue whale data were analysed in a paper by Sazhinov (1970), only recently translated into English, and the author reported that the length at sexual maturity is 19.2 m and that two female blue whales that were 19.2 m long, each with one corpus luteum, had 9 and 11 earplug layers respectively, implying that  $t_m = 9$ –11 years. The complete Soviet ovarian corpora data from the recovered original logbooks, recently analysed, confirm that the length at maturity is 19.2 m (95% credibility intervals 19.1–19.3 m) (Branch and Mikhalev, accepted). When combined with the complete earplug data presented in Sazhinov's PhD dissertation (Sazhinov, 1980), only recently obtained, the estimate of  $t_m$  was 9.9 yr (95% credibility interval 9.0–11.0) for female pygmy blue whales (Branch, 2008b), essentially confirming the preliminary estimates of Sazhinov (1970).

Rather more extensive data are available for humpback whales than for other mysticetes due to the recent surge in photo-identification studies. In the Gulf of Maine, age at first calving,  $t_m + 1$ , is 5.92 yr (95% CI 5.47–6.37) (Clapham, 1992). In south-eastern Alaska, though, age at first calving is substantially higher:  $t_m + 1$  is 11.8 yr (95% CI 10.3–13.3) (Gabriele *et al.*, 2007). If the results of Chittleborough (1959) are reinterpreted assuming that there is one growth layer laid down in the earplug per year, as is now believed (e.g. Best, 2006), then the age at sexual maturity was 8–12 yr off Australia in the mid-20<sup>th</sup> century.

Estimates of  $t_m$  for other mysticetes show a similar range of estimates. For fin whales (*B. physalus*),  $t_m$  apparently declined from 10–11 yr in the 1930s to 6–7 yr during 1960–65 (Lockyer, 1972). For sei whales (*B. borealis*),  $t_m$  also declined from 11–11.5 yr before 1935 to 8.4 yr in the 1960s in the Antarctic (Lockyer, 1974) and  $t_m$  was 8.2 yr (95% CI 7.3–9.0 yr) in 1962–63 in South African waters (Best and Lockyer, 2002). Antarctic minke whale (*B. acutorostrata*) estimates of  $t_m$  declined from ~11 yr for cohorts born in the 1950s to 7 yr for those in the 1970s (Thomson *et al.*, 1999). North Atlantic right whales (*Eubalaena glacialis*) produce their first calves at  $t_m + 1 = 9.53$  yr (95% CI 8.39–10.67) (Kraus *et al.*, 2001), compared southern right whale estimates of  $t_m + 1 = 7.69$  yr (95% CI 7.06–8.32) for South Africa (Best *et al.*, 2005); and  $t_m + 1 = 9.1$  yr (95% CI 8.5–9.9) for Península Valdés, Argentina (Cooke *et al.*, 2001). Eastern Pacific gray whales mature at  $t_m = 8$  yr (range 5–11 yr) (Reilly, 1984). A much higher estimate of  $t_m$  of 20 yr (95% CI 14–26) is obtained from the Bering-Chukchi-Beaufort Seas population of bowhead whales (Brandon *et al.*, 2007), which is known to contain very long-lived whales (e.g. George and Bockstoce, 2008).

In summary, the limited data available for Antarctic blue whales supports  $t_m = 10$  yr, but one study indicates  $t_m$  could be 5 yr; data from pygmy blue whales strongly supports  $t_m = 10$  yr (95% CI 9–11 yr); and  $t_m$  for humpback, fin, sei, northern right, southern right and Antarctic minke whales has ranged from 5 yr to 11 yr, with most recent estimates falling in the 6–9 yr

range. It is difficult to amalgamate these contradictory assessments in a consistent manner. Although the most likely value of  $t_m$  for Antarctic blue whales is 10 yr, other evidence supports a lower value for  $t_m$ . To introduce the possibility of a lower  $t_m$ , one year is subtracted from the most likely value, and a high standard deviation of 2 yr is assumed, thus  $t_m \sim N(9, 2^2)$  and  $t_p \sim N(10, 2^2)$ . To prevent the high standard deviation resulting in draws of  $t_p$  falling outside the range observed for species other than bowhead whales, draws from this distribution were bounded to lie within the interval [5, 12] yr.

### Adult survival rate ( $S$ )

Survival rates have not been calculated for Antarctic blue whales. For pygmy blue whales, the estimated survival rate from combined age frequencies of Soviet and Japanese data is 0.94 (95% CI 0.93–0.95) (Branch, 2008b). For northern blue whales in the Gulf of St Lawrence, a long-term photo-identification study produced an estimate of 0.975 (95% CI 0.960–0.985) (Ramp *et al.*, 2006). For North Pacific blue whales, survival was 0.927–0.951 based on earplug layers collected in 1957–1965, but this is a lower bound on survival in the absence of whaling given the long history of whaling on this population (Ohsumi, 1979).

Estimates of adult survival for other mysticetes vary considerably, but are generally higher than the 0.94 estimated for pygmy blue whales. Survival rates for South African right whales are 0.990 (95% CI 0.983–0.997) (Best *et al.*, 2005); for Argentine right whales, 0.981 (95% CI 0.971–0.991); for Bering-Chukchi-Beaufort bowhead whales, 0.984 (95% credibility interval 0.948–1.000) despite annual whaling mortality of 0.005 (Zeh *et al.*, 2002); for western Pacific gray whales, 0.951 (95% CI 0.917–0.972) (Bradford *et al.*, 2006), or 0.97 (95% CI 0.96–0.98) (Cooke *et al.*, 2005); for Gulf of Maine humpback whales (most recent estimate): 0.950 (95% CI 0.928–0.972) (Clapham *et al.*, 2003); for Hawaiian humpback whales, 0.963 (95% CI 0.944–0.978) (Mizroch *et al.*, 2004); for southeastern Alaskan humpback whales, 0.957 (95% CI 0.943–0.967) (Mizroch *et al.*, 2004); and for Prince William Sound humpback whales, 0.984 (95% CI 0.954–0.995) (Mizroch *et al.*, 2004).

For north Atlantic right whales, adult survival was estimated to be 0.979 (95% CI 0.973–0.985) during 1980–1992 (Knowlton *et al.*, 1994), but are now thought to have declined over time from 0.99 in 1980 to 0.94 in 1994, resulting in a prediction of extinction in at most 191 yr (Caswell *et al.*, 1999). When separated by stage, the survival of mothers declined from 0.95 to 0.63 during 1980–1995, while non-mother adult females had constant survival of 0.99 during 1980–1995 (Fujiwara and Caswell, 2001). However, given that since these estimates were published, this population has increased from under 300 (Fujiwara and Caswell, 2001) to 396 in 2006 (Anon, 2006), survival rates have probably increased again in recent years.

In summary, there are two blue whale survival estimates, neither from Antarctic blue whales. The Gulf of St Lawrence estimates are closer to the estimates from other mysticetes, while the estimates from pygmy blue whales are lower than for all other species. A weighting of 2:1 is applied to the Gulf of St Lawrence: pygmy blue whale mean estimates, to obtain an overall mean of 0.963, while a broad standard deviation of 0.02 is assumed, i.e.  $S \sim N(0.963, 0.02^2)$ . Bounds of [0.927; 0.990] reflect the lower limit for North Pacific blue whales, and the maximum survival rate of 0.990 for South African right whales.

### First-year survival rate ( $S_j$ )

Calf survival rates have never been estimated for blue whales, but Branch *et al.* (2004) and Brandão *et al.* (2000) assumed that calf survival should be less than adult survival, since suckling calves would presumably die if their mothers died. Although this assumption is retained here, North Atlantic right whale calf survival was consistently *higher* than the survival of mothers during 1980–1995 (declining from 0.96 to 0.85 compared to declines from 0.94 to 0.63 for mothers) (Fujiwara and Caswell, 2001).

Calf survival rate estimates in other mysticetes vary greatly: 0.99 (95% CI 0.97–1.00) for Argentine southern right whales (Cooke *et al.*, 2001); 0.85–0.96 for north Atlantic right whales (Fujiwara and Caswell, 2001); 0.875 (range 0.828–0.922) for Gulf of Maine humpback whales (Barlow and Clapham, 1997); 0.818 (95% CI 0.482–0.977) for Pacific humpback whales (Gabriele *et al.*, 2001); 0.734 (95% CI 0.518–0.95) for South African southern right whales (Best *et al.*, 2005); and either 0.701 (95% CI 0.492–0.850) (Bradford *et al.*, 2006) or 0.73 (90% credibility interval 0.61–0.83) for western Pacific gray whales (Cooke *et al.*, 2005).

Estimates for this parameter are based entirely on other species. The mean of the population means is 0.84. The upper bounds of those estimates range from 0.83 to 1.00, and these upper bounds are close to the adult survival estimate assumed above for most populations, while lower bounds range from 0.492 to 0.97. Values for  $S_j$  were therefore assumed to be distributed  $\sim N(0.84, 0.15^2)$  with bounds of [0.492,  $S$ ]. The upper bound is based on adult survival,  $S$ , to ensure that juvenile survival is always less than adult survival, as discussed above.

### Annual pregnancy rate ( $p$ )

Ongoing photo-identification studies have not yet produced estimates of the inter-calf interval (the inverse of the pregnancy rate) for blue whales. Many studies have recorded pregnancy rates, which vary between 0.11 and 0.84 (Laws, 1961; Mizroch, 1981), with a mean of 0.43 (SD = 0.17) (Branch *et al.*, 2004), but these estimates are not as direct an estimate of pregnancy rates as might be imagined, because it was illegal to catch females with calves and because of likely segregation by reproductive class both by time and in space. Ovulation rates have been calculated by regressing ovarian corpora counts against earplug laminae, producing inter-ovulation estimates of 2.5 yr (no CI calculated) for Antarctic blue whales caught in 1956/57–1958/59 (Ohsumi, 1979) and 2.6 yr (95% CI 2.2–3.0) for pygmy blue whales caught in the early 1960s (Branch,

2008b). Although the rate of accumulation of ovarian corpora places a theoretical upper bound on the pregnancy rate, both of these estimates are based on very small sample sizes.

All studies on blue whales have concluded that the inter-calf interval is 2–3 yr (e.g. Mackintosh and Wheeler, 1929; Laurie, 1937; e.g. Mackintosh, 1942; Tomilin, 1967). The upper bound of 3 yr essentially comes from the high observed pregnancy rates in the catches. The lower bound of 2 yr follows directly from observations that pairing occurs in June–July and calving in May–June the following year, and weaning only occurs 7 months after birth (Mackintosh and Wheeler, 1929; Mackintosh, 1942). Assuming that females only rarely are simultaneously lactating and pregnant, it is improbable that female Antarctic blue whales could give birth annually. In the IWC catch database, there are 25,515 pregnant females, 173 lactating females and only 2 records of females both lactating and pregnant. However, it should be noted that multiple instances of annual calving has been reported both for Alaskan humpback whales (Straley *et al.*, 1994) and for east Australian humpback whales (Kaufman *et al.*, 2006), including one east Australian female observed with a calf for five consecutive years.

It should be noted that multiple births are ignored here since it is unlikely that more than one fetus would survive to maturity. Excluding multiplets would have negligible effect in any case: in the IWC database, there were 24,560 single fetuses, 206 twins, 5 triplets and 1 quadruplet, for an average of 1.009 fetuses per pregnancy, similar to previous estimates of 1.007–1.008 (Risting, 1928; Tomilin, 1967).

Inter-calf intervals are available for other species of mysticetes, with the greatest information available for humpback whales. For humpbacks off east Australia, the mean calving interval was 2.39 yr (95% CI 2.20–2.62) (Kaufman *et al.*, 2006); off California, 2.30 (95% CI 1.85–3.04) (Steiger and Calambokidis, 2000); in south-eastern Alaska, 2.78 (95% CI 2.31–3.52) (Baker *et al.*, 1992); in the Gulf of Maine, 2.56 yr (95% CI not given) (Clapham *et al.*, 2003); and around Hawaii, 1.72 (95% CI 1.33–2.44) (Baker *et al.*, 1987). North Atlantic right whales have experienced fluctuations in the inter-calf interval from 3.67 yr (95% CI 3.46–3.89) during 1980–1992 (Knowlton *et al.*, 1994), to over 5 yr in 1993–1998 (Kraus *et al.*, 2001) decreasing to 3.2 yr in 2006 (Anon, 2006). Southern right whales have inter-calf intervals of 3.15 yr (95% CI 3.11–3.18) off South Africa (Best *et al.*, 2005); 3.28 (95% CI 3.16–3.40) off southern Australia (Burnell, 2001); and 3.35 (95% CI 3.25–3.45) at Peninsula Valdéz, Argentina (Cooke *et al.*, 2001).

The above summary of available information sheds little light on what is a reasonable value to assume for Antarctic blue whales average annual pregnancy rates. The most likely values of  $0.39\text{--}0.43\text{ yr}^{-1}$  are problematic because of their underlying assumptions or small sample sizes, while the “upper bound” on inter-calving intervals for pygmy blue whales imposed by the inter-ovulation interval has wide 95% confidence intervals ranging from 2.2 to 3.0 yr. In light of these uncertainties, I decided to assume a uniform interval between 2 and 3 yr for the inter-calving interval, corresponding to  $p \sim U(1/3, 1/2)$ .

### Proportion of births that are female ( $q_f$ )

A previous review of published estimates (Branch *et al.*, 2004) found that 5,637 out of 11,942 fetuses examined were female ( $q_f = 0.472$ ) and that the catches listed in the same sources comprised 87,098 females out of 184,280 ( $q_f = 0.473$ ) (Mackintosh, 1942; Nishiwaki and Oye, 1951; Tomilin, 1967). That review noted that sexed catches represent a near census of the population since virtually all Antarctic blue whales were caught.

The IWC catch database was examined for sex ratios south of  $56^\circ\text{S}$ . More sexed whales were contained in the database than presented in previous sources (229,023), of which 108,332 were female, thus  $q_f = 0.473$  is identical to the previous estimate. The proportion of females among sexed fetuses (9,643 out of 19,915) is slightly higher than previously estimated:  $q_f = 0.484$ .

Since nearly all of the catches listed in the database were sexed (98.8%), and the catches comprised a virtual census of the population, the sex ratio in the catch (0.473) is assumed to be the best estimate of the proportion of whales that are female. Given the high sample sizes, the binomial distribution is practically identical to a normal distribution, therefore the 95% CI is 0.471–0.475, and this factor is distributed  $q_f \sim N(0.473, 0.001^2)$ .

## RESULTS

The distribution of values for  $\delta$ , the instantaneous rate of increase, is  $N(0.040, 0.019^2)$ , with a maximum rate (the 99% quantile) of 0.082. These correspond to annual rates of increase of 0.041 (SD = 0.019) and 0.085 respectively.

## DISCUSSION

The estimated distribution for the instantaneous rate of increase (mean 0.040, sd = 0.019) is similar to that obtained for Antarctic blue whales previously (mean 0.043, SD = 0.019) by Branch *et al.* (2004), but the maximum of 0.082 is considerably lower than previously assumed (0.12). If the distribution was incorporated as a prior on the rate of increase (or the maximum taken to be an upper bound), this would decrease the estimated rate of increase in Branch *et al.* (2004).

Based on surveys, the estimated current rate of increase for Antarctic blue whales is 8.2% per year (95% CI 1.6–14.8%) from the IDCR/SOWER surveys (Branch, 2008a), and 7.4% per year (CV=1.19) from the JARPA surveys (Matsuoka *et al.*, 2006). These survey-based estimates are close to the maximum annual rate of 8.5% and a substantial proportion of the confidence intervals of these estimates are above the maximum estimated here. It might be tempting to conclude from these

surveys that Antarctic blue whales are increasing at near maximal possible rates, but the confidence intervals around these survey-based rates of increase are high, and include substantial probability of lower rates of increase.

The biologically plausible distributions developed in this paper rely heavily on biological parameters for pygmy blue whales and other mysticete species, which may not be directly applicable to Antarctic blue whales. Given that Antarctic blue whales were depleted to much lower levels than pygmy blue whales (Branch *et al.*, 2007b), it is possible that they may have a lower age at first parturition, higher survival, or shorter inter-calf interval, because of the relatively lower densities and higher food availability. If so, the rates of increase estimated here would be biased low. In support of this idea, age at first parturition appears to have declined for fin, sei and minke whales in response to depletion by whaling (Lockyer, 1972, 1974; Thomson *et al.*, 1999; Best and Lockyer, 2002), although these findings have been questioned by Mizroch (1981).

As pointed out by Branch *et al.* (2004), the estimates obtained here assume that the distributions for each of the input parameters are independent, except for the constraint that calf survival must be smaller than adult survival. For purists this is problematic, but the practicality of the matter is that no data exist to estimate a variance-covariance matrix between each of the parameters for any whale population, let alone Antarctic blue whales. In any case, reducing the uncertainty in the estimated values of the input parameters would most likely have a greater impact on the estimated rate of increase, than attempting to estimate the variance-covariance matrix of the parameters. Therefore, we assume independence between these parameters, as other authors have done in the past (Best *et al.*, 2001; Clapham *et al.*, 2001; Branch *et al.*, 2004; Clapham *et al.*, 2006).

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