Branch Trevor (Orcid ID: 0000-0003-4308-8930)
Monnahan Cole (Orcid ID: 0000-0003-0871-6700)

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ARTICLE

Sex ratios in blue whales from conception onward: effects of space, time, and body size

Trevor A. Branch[1] | Cole C. Monnahan[1,2]

[1]School of Aquatic and Fishery Sciences, University of Washington, Seattle, Washington

[2]Current address: Resource Ecology and Fisheries Management, Alaska Fisheries Science Center, National Oceanic and Atmospheric Administration, Seattle, Washington

Correspondence

Trevor A. Branch, School of Aquatic and Fishery Sciences, Box 355020, University of Washington, Seattle, WA 98195.

Email: tbranch@uw.edu

ABSTRACT

Deviations from equal sex ratios in mammals can reveal insights into sex-specific growth, survival, movements, and behavior. We assessed blue whale (*Balaenoptera musculus*) sex ratios based on 21,542 fetal and 311,901 whaling records, finding that males were slightly but significantly more common than females (51.3% fetal, 52.1% postnatal). Antarctic catches shifted from 52.4% male before 1951 to 48.0% male thereafter, even though larger females were preferentially targeted by whalers and should have declined. The southernmost land stations caught more males than those in southern Africa, and at land stations, sex ratios shifted subtly over the course of a year. Pelagic catches demonstrated spatial structure in sex ratios, including more males being caught in the Ross Sea. In utero, the smallest females were often misidentified as males, and there was some evidence for higher prenatal male mortality. Once born, medium-sized blue whales within each region were more often male, while the longest were nearly all female; explained entirely by females growing faster and reaching longer sizes. Overall, though, sex ratios are remarkably close to equality across time, space, and length; with any deviations best explained by faster female growth and size-selective whaling.

KEYWORDS

Antarctic blue whale, *Balaenoptera musculus*, Northern Hemisphere, pygmy blue whale, sex ratios, Southern Hemisphere

1 | INTRODUCTION

In most mammal species, males and females are present in nearly equal numbers, both at birth and throughout most of their lifespan (Parkes, 1926). The evolutionary pressures behind this are straightforward: if genes arose that resulted in one sex becoming more common than the other, then the rarer sex would have higher lifetime reproductive success than the more common sex, and the genes for the common sex would dwindle (Fisher, 1930). Exceptions to this rule occur most spectacularly in haplodiploid insect species such as bees and wasps (Hamilton, 1967), but not in mammals. Subtler differences in sex ratios at birth can be expected if one sex undergoes higher mortality after birth, because natural selection should then favor more births of that sex to ensure equal sex ratios during prime reproductive years—explaining the slight but significant preponderance of males at birth in humans (e.g., Parkes, 1926). There can also be evolutionary pressure for changes in sex ratios when reproductive output for one sex increases when parental investment is high: under good conditions, that sex should be favored; while under poor conditions, the other sex should be favored (Trivers & Willard, 1973). For example, the largest male elephant seals command large harems and can produce many pups each season, while small males produce none. Female elephant seals reliably produce one pup per year regardless of size. Thus, there is selective pressure for larger females to invest in raising (larger) male offspring, while smaller females should produce more female pups (Arnbom, Fedak, & Rothery, 1994).

The theories outlined above have been joined by a plethora of additional sex-ratio theories, provoking the wry observation that: “Because theory predicts equal production of the two sexes, any deviation from equality invites interpretation, and prods the imagination of theoreticians” (Myers, 1978). Good general reviews are available of theories invoked to explain deviations from equal sex ratios at birth (Clutton-Brock & Iason, 1986; Hardy, 1997); among which are theories that outline the role in sex ratio determination of environmental variability (Charnov, Los-den Hartogh, Jones, & van den Assem, 1981), male attractiveness (Booksmythe, Mautz, Davis, Nakagawa, & Jennions, 2017), female dominance (Clutton-Brock, Albon, & Guinness, 1986), and competition for local resources (Hardy, 1997).

Fetal sex ratios offer some hope in understanding how differences in sex ratios actually arise in mammals. To control sex, females must either alter sperm passage, select sperm when fertilization occurs, or more frequently abort fetuses of one sex (Hardy, 1997). There is considerable evidence for differential prenatal mortality between sexes (Creasy, Crolla, & Alberman, 1976; Parkes, 1926), which likely depends on population densities and fecundity (Kruuk, Clutton-Brock, Albon, Pemberton, & Guinness, 1999), although others theorize that the timing of insemination in relation to estrous cycles, and hormone levels also play a role (Krackow, 1995). None of these theories have provided a workable method for artificial selection of female-biased sex ratios in farmed species (Hardy, 1997). Furthermore, such methods suffer from the “file-drawer effect” (e.g., Møller & Jennions, 2001): when an experiment happens by chance to produce a sex ratio significantly different from equality, it is more likely to be published than the many studies finding nonsignificant results that languish in (computer) file drawers.

While sex ratios at birth reveal selective pressures, postnatal sex ratios can reveal far more. From birth to death, sex ratios will differ: by age if one sex has higher survival than the other; by body length if growth rates vary by sex; seasonally if migration timing differs by sex; by area if there are sex-specific migration pathways or tendencies (Druskat, Ghosh, Castrillon, & Bengtson Nash, 2019; Kasamatsu & Ohsumi, 1981; Laidre, Heagerty, Heide-Jørgensen, Witting, & Simon, 2009); and across years due to human selection if catches preferentially target one sex (e.g., Beddington & May, 1980). Thus, a careful examination of sex ratios across age, length, day, area, and year can reveal much about the growth patterns, movements, and behavior of a given species.

Large cetaceans offer some of the most extensive sex-ratio data available, obtained during large-scale whaling in the 20th century. From the late 1920s onward, regulations required whalers to record the species, date, position, length, sex, and pregnancy status of each whale in addition to the length and sex of any fetuses. These data have been used to infer sex-specific migration pathways for several whale species, but not yet for blue whales (*Balaenoptera musculus*). In sperm whales (*Physeter macrocephalus*), lone larger males are found closer to the poles, while females and smaller males are more common in large groups in temperate regions (Mikhalev, 2019). The opposite pattern is found in minke whales (*Balaenoptera acutorostrata*), where females are more common close to the poles: in the Antarctic, females comprise more than 80% of whales south of 70°S (Kasamatsu & Ohsumi, 1981); and off west Greenland, more than 90% at 72°N (Laidre et al., 2009). For humpback whales (*Megaptera novaeangliae*), males dominated catches in temperate Australian waters (60%–73% male), but comprised less than half (43%) of Antarctic catches (Chittleborough, 1965).

However, interpretation of postnatal sex ratios from whaling is complicated by whaling selectivity and regulations. In general, whalers preferred large and fat whales since they produced more oil than small whales, and the gunners were incentivized by rewards to target them. Since female blue whales are larger, these incentives would generally increase female catches over male catches. In the early years in the Antarctic, though, both whaling boats and shore-side equipment was insufficient to handle the largest of whales, resulting in smaller blue whales being preferred at South Georgia and the South Shetlands (Anonymous, 1920; Harmer, 1921; Hinton, 1915), and thus sex ratios should be male-dominated in those catches. Whaling regulations would also likely have played a role in observed sex ratios given the bans on taking females accompanied by calves (lactating females), reducing female catches, and minimum length regulations imposed in the 1930s (70 ft for blue whales). Minimum lengths in turn led to “whale stretching,” where observers misreported undersized whales as being just equal to the minimum length (e.g., Branch, Abubaker, Mkango, & Butterworth, 2007), increasing male catches. However, there were no incentives to misreport blue whale sex, which is therefore likely to be reliable.

Fetal sex ratios from whaling data show a slight excess of males for fin, Antarctic minke, blue, sperm, and humpback whales (50.6%–52.7% male) and near even ratios for sei whales (*Balaenoptera borealis*; 49.7% male), though only the values for fin and blue whales are significantly greater than 0.5 despite large sample sizes (Table 1). Fetal sex data were collected by a wide variety of whaling expeditions—only some of which contained experienced biologists—and the data for the smallest fetuses have often been questioned. Notably, fetuses smaller than 5 in. (13 cm) are likely to be overlooked (Brinkmann, 1948; Hjort, Lie, & Ruud, 1934; Mizue & Jimbo, 1950); sei whale fetuses smaller than 5 cm cannot be sexed visually (Gambell, 1968); and the relatively large clitoris of small female fetuses may be mistaken for a penis (Gambell, 1968, 1972), although in Antarctic minke whales, males are substantially underrepresented at lengths ≤10 cm (Kato & Shimadzu, 1983).

Here, we delve into the sex data for blue whales held by the International Whaling Commission (IWC) to investigate how sex ratios in blue whales change from conception onward as a function of year, day, region, and length. A variety of models are used to investigate how sex ratios vary with each of these factors, and a conceptual model is developed to explain the relation between postnatal length and sex ratios.

2 | MATERIALS AND METHODS

2.1 | Data summary

Data for 321,284 individual blue whales were obtained from the

July 18, 2016, version of the IWC's individual catch database (Allison, 2016). Of these, sex is noted for 311,901 blue whales, with the remainder coded as "unknown." No blue whales were recorded as hermaphroditic. Catches were allocated into five regions, and separate analyses conducted for those caught from land stations and during pelagic (open-water) whaling.

2.2 | Allocation of catches by region and subspecies

Blue whale catches were allocated to five regions that were examined separately (Figure 1), first dividing catches among subspecies: Antarctic (*B. m. intermedia*), pygmy (*B. m. brevicauda*), Southeast Pacific (unnamed subspecies), and northern blue whales (*B. m. musculus*), and then further separating northern blue whales into two regions: North Pacific and North Atlantic. The boundary between North and Southeast Pacific catches was set at 2ºN, although no sex data were available for catches between 2ºN and 22ºN. Blue whales from the northern Indian Ocean (putative subspecies *B. m. indica*) were combined with pygmy blue whales from the southern Indian Ocean from 30ºE eastwards to 160ºW into a single "pygmy" category since there are multiple acoustic call types with considerable geographic overlap in this region (Branch, Monnahan, Širović, Balcazar, Barlow et al., 2019), but blue whale length is similar throughout this region (Branch & Mikhalev, 2008).

The southern demarcation between Antarctic and pygmy blue whales has been the subject of considerable study (Branch et al., 2007; Branch, Mikhalev, & Kato, 2009; Ichihara, 1966; Kato, Miyashita, & Shimada, 1995), and this boundary was based on the most recent analysis of length frequencies (Branch et al., 2019). However, 66 blue whales were coded as “pygmy blue whale” and caught just south of this boundary (53°S). Of these, five were south of 60°S (at 31°E, 149°E, and 165°E), and one was longer than the maximum pygmy blue whale length. These five were coded as Antarctic blue whales. The remaining 61 were coded as pygmy blue whales, since they were caught in waters close to other pygmy blue whale catches (54–57°S, 44–87°E); and almost all (54 of 61) were caught December 5–24, 1964, by the Soviet fleet *Yuri Dolgoruky*.

All South Atlantic catches were assumed to be Antarctic blue whales based on morphometrics (Branch et al., 2007; Branch et al., 2019; Mackintosh & Wheeler, 1929) and song type

(Samaran, Berne, Leroy, Moreira, Stafford et al., 2019; Shabangu, Findlay, Yemane, Stafford, van den Berg et al., 2019), but are split between southern “feeding” grounds (south of 47°S) and northern “breeding” grounds (north of 47°S). Catches taken from Durban are not included in the main regional categories since it is unknown whether these are pygmy or Antarctic blue whales (Branch et al., 2007; Branch et al., 2019; Gambell, 1964).

2.3 | Testing if sex ratios differ from equality

Confidence intervals for plotting were calculated from binomial distributions using the binom.bayes function in package binom (Dorai-Raj, 2015) in R (R Core Team, 2020). If sex ratios were equal among sexes, and the samples truly independent, 1 in 20 such confidence intervals would be expected to not include 0.5. Given the large number of confidence intervals plotted in this study, we focus our results on testing only whether overall sex ratios differed from equality, and on cases where sex ratios were often dominated by one sex.

2.4 | Annual changes in sex ratio by region

Sex ratios were calculated by year or whaling season for whales of all lengths in each of the regional groupings. For Southern Hemisphere pelagic whaling, whaling seasons (July 1 to June 30) were used, but calendar years (January 1 to December 31) were used for Southern Hemisphere temperate land stations and for the Northern Hemisphere.

2.5 | Patterns in land stations

At land stations, large numbers of whales were captured near the same location, allowing for analysis of daily and annual changes in sex ratio independent of latitude and longitude. Expedition codes associated with land stations were obtained from the IWC’s annual catch database, with land stations in the same island group combined, and analyses conducted separately for land stations recording more than 1,000 sexed blue whales (Figure 1): South Georgia (33,557), South Shetlands (14,876), Saldanha Bay (5,501), Durban (2,487), South Orkneys (1,613), and Walvis Bay (1,059). Catches at all these land stations were Antarctic blue whales except for Durban, where an unknown portion were pygmy blue whales.

Sex ratios at a given location should change over the course of a year if the sexes have segregated migrations, as seen in humpback whales (Chittleborough, 1965; Druskat et al., 2019; Franklin, Franklin, Brooks, & Harrison, 2018). Daily patterns were examined at land stations with more than 5,000 catches, for all days where 25 or more whales were sexed, with data for each day of the year summed across all years.

For each land station, four models predicting sex ratio on each day were compared: (1) equality, with predicted proportion of males $\hat{p}_{\text{male}} = 0.5$; (2) constant sex ratio, $\hat{p}_{\text{male}} = r_{\text{mean}}$, where the proportion of males was constant, but could differ from 0.5; (3) linear, $\hat{p}_{\text{male}} = a + b(d - d_{\text{mid}})$, with *a* and *b* being estimated parameters, *d* being the day of the year (1–366), centered on d_{mid}, the middle day of the whaling season (183.5 for Saldanha Bay, and 1 for the other two stations); and (4) a sine wave model given by the following equation:

$$\hat{p}_{\text{male}} = r_{\text{min}} + (r_{\text{max}} - r_{\text{min}})\left[0.5\sin\left(2\pi\frac{d-d_{\text{max}}}{365} + 0.5\pi\right) + 0.5\right] \tag{1}$$

where r_{max} is the maximum proportion of males, reached on day d_{max}, and r_{min} is the minimum proportion of males. This model assumes an annual cycle, and hence the predicted proportions on day 1 and day 366 is identical. Parameters for the four models were estimated using maximum likelihood estimation (MLE), assuming binomial likelihood, by finding parameter values that minimized the following negative log-likelihood (–ln*L*) after removing constants:

$$-\ln L = \sum_{d}\left[(n_{d,\text{male}} - n_d)\ln(1-\hat{p}_{d,\text{male}}) - n_{d,\text{male}}\ln\hat{p}_{d,\text{male}}\right] \tag{2}$$

where $n_{d,\text{male}}$ is the number of males on day *d*, n_d is the total number of male and female whales on day *d*, and $\hat{p}_{d,\text{male}}$ is the predicted proportion of males on day *d* from each of the models. Models were compared using Akaike’s Information Criterion (Akaike, 1973), with the best model having the lowest AIC, and other models having some support from the data if their AIC is within 10 units (i.e., ΔAIC < 10) (Burnham & Anderson, 2002).

2.6 | Spatial patterns in Antarctic catches

Spatial patterns require substantial data, and therefore spatial models were only fit to feeding area catches of Antarctic blue whale (Figure 1). This included 273,022 whales from both land stations and pelagic catches south of 53°S. We used the VAST package (Thorson & Barnett, 2017), reporting estimates of approximately smooth spatial surfaces of encounter rates of males (i.e., male to female sex ratio). The VAST model is built in the modeling platform Template Model Builder (TMB; Kristensen, Nielsen, Berg, Skaug, & Bell, 2016), which is a statistical framework for frequentist estimation of mixed effects models. VAST estimates latent Gaussian Markov random fields using the stochastic partial differential equations (SPDE; Lindgren, Rue, & Lindstrom, 2011) approach of the INLA software package (Lindgren & Rue, 2015). INLA approximates smooth surfaces with a specially constructed, discrete mesh leading to similar estimates but much faster estimation time. The net result is that the probability of encountering a male, $p(s)$ can be predicted at any point in the spatial domain s from $p(s) = \text{logit}^{-1}[\beta + \omega(s)]$. Here, the estimated fixed effects are the intercept (β), the marginal spatial variance, and the spatial decorrelation range used to construct the spatial covariance matrix Σ, for the spatial random effects $\omega \sim MNV(0, \Sigma)$ represented as a Gaussian Markov random field. The random effects were integrated by TMB using the Laplace approximation, such that MLEs were found by minimizing the negative log of the marginal likelihood (Skaug & Fournier, 2006).

VAST analyses were conducted on three data groupings: (1) all years and months combined; (2) separately for each month; and (3) separately for yearly groupings chosen to represent the first years of pelagic whaling (1925–1930), the pre-World War II whaling era (1931–1940), post-World War II era (1944–1052), and the period when blue whales were heavily depleted, there was a shift to more females in the catches, and there was substantial Soviet whaling (1953–1973). For the yearly groupings the year denotes the year in which the whaling season started, i.e., 1925 represents 1925/1926. For all models, the subsetted data were fitted independently for the processes of creating a spatial mesh, estimating parameters, and making predictions at locations near observed data for visualizing spatial fits. Spatial effects were included in all models, since the model fitted to all years and months that included spatial effects explained the data far better than one without spatial effects (ΔAIC = 763).

2.7 | Fetal sex ratios by region and length

Detailed records of fetal length and sex were extracted from the

IWC database, and sex ratio calculated for broad regions, and by region and length (in feet) for Antarctic and pygmy blue whales (the two regions with sufficient data). Feet were used instead of metric measurements, since this was the required unit of measurement from the late 1920s onward for Norwegian vessels and from the 1930s for all nations (e.g., Ruud, 1956).

Two major factors are hypothesized to affect fetal sex ratios: (1) inaccurate sex identification in very small fetuses resulting in either an excess of males (Gambell, 1968) or females (Kato & Shimadzu, 1983), and (2) higher fetal mortality rates for males, as reported in humans (Creasy et al., 1976; Parkes, 1926).

Five models were developed to predict fetal sex ratio from fetal length: (1) equality, with predicted proportion of males $\hat{p}_{\text{male}} = 0.5$; (2) constant sex ratio, $\hat{p}_{\text{male}} = r_{\text{mean}}$, where the proportion of males was constant; (3) constant plus misidentification at lengths shorter than 5 ft; (4) linear change in sex ratio $\hat{p}_{\text{male}} = a_{10} + b(L - 10)$ where a_{10} is the sex ratio at L = 10 ft, and a_{10} and b are estimated parameters; and (5) linear plus misidentification at all lengths. MLE values were found for model parameters, assuming binomial likelihood, and the best model selected using AIC.

Sex misidentification was modeled by defining L_{50} and L_{95} as the lengths at which 50% and 95% of females are correctly identified, and assuming that a logistic selectivity equation can predict the probability of correctly identifying females (p_{correct}) as follows: $p_{\mathrm{correct}} = \{1 + \exp[-\ln 19(L - L_{50})/(L_{95} - L_{50})]\}^{-1}$. If the actual proportion of males is $\hat{p}_{\mathrm{male}}$, then after misidentification is taken into account, the observed proportion of males would be $\hat{p}^{*}_{\mathrm{male}} = \hat{p}_{\mathrm{male}} + (1 - \hat{p}_{\mathrm{male}})(1 - p_{\mathrm{correct}})$.

2.8 | Postnatal sex ratios by length

Female baleen whales grow larger than males, and therefore should be more prevalent at larger sizes. To test this hypothesis, sex ratios were calculated by length for 1-ft bins. In addition, we developed a conceptual model of sex ratio by postnatal length.

To accurately model sex ratio by postnatal length requires estimates of survival rate by age and sex, length at age and sex, and pregnancy rate. Not all these parameter estimates are available since they rely on accurate age information, but the most reliable ageing technique (laminae in earplugs) was developed only in the 1950s (Laws & Purves, 1956; Purves, 1955). As a result, age data are currently only available for pygmy blue whales (Branch, 2008; Ichihara, 1966). Estimates of the age-length relationship are further biased by the lack of data for whales shorter than the 70 ft minimum length limit, and by “whale-stretching” whereby whales shorter than 70 ft were nevertheless listed as being 70 ft long (e.g., Branch et al., 2007).

Therefore, instead of fitting a model to observed sex ratios by postnatal length, we developed a conceptual age-structured model that predicts patterns in sex ratios by length, using plausible equilibrium parameter values and age-length relations for Antarctic blue whales. The model estimates the number of whales for ages 0–80 year, with no plus group (i.e., individuals are assumed to die after age 80). Noncalf survival was set to S_a = 0.935, and calf survival to S_j = 0.74 based on the middle of the plausible range estimated for humpback whale

$$N_0 \;=\; N_{\text{eq}} / \left(1 + S_j + S_j \sum_{i=1}^{79} S_a^i\right)$$

calves (Zerbini, Clapham, & Wade, 2010), and both were assumed equal for males and females. The proportion of females at birth (q_f) was assumed to be 0.5. Population size was set to N_{eq} = 239,000—the prewhaling abundance of Antarctic blue whales (Branch, Matsuoka, & Miyashita, 2004)—which is obtained when the number of births is . Numbers at age are $N_1 = N_0 S_j$, and $N_{i+1} = N_i S_a$ for subsequent ages. The age at maturity was assumed to be T_m = 10 years (Branch, 2008; Branch et al., 2004). The value of noncalf survival (S_a = 0.935), ensures that the pregnancy rate, $p_r = N_0 / \left(q_f \sum_{i=T_m}^{80} N_i \right) = 0.324$, is similar to the 0.334 estimated for eastern North Pacific blue whales (Atkinson, Gendron, Branch, Mashburn, Melica et al., 2020), which are near to prewhaling levels, but at the low end of other estimates of 0.33–0.50 (Branch, 2008; Branch et al., 2004; Ohsumi, 1979; Sears, Ramp, Douglas, & Calambokidis, 2013).

Few published data are available to estimate length at age for Antarctic blue whales, but there are some indications of length at key ages. Males and females are born at 7.0 m (23 ft) and weaned 7 months later at 16.0 m (52.5 ft) (Mackintosh &

Wheeler, 1929). Female Antarctic blue whales reach sexual maturity at ~23.7 m (77.8 ft) (Branch & Mikhalev, 2008; Mackintosh & Wheeler, 1929), and males at 22.6 m (74.1 ft) (Mackintosh & Wheeler, 1929), both at age 10 years (Branch, 2008; Ichihara, 1966). Growth ceases at physical maturity, which occurs in mature females with ~11 ovarian corpora (Brinkmann, 1948; Laurie, 1937). Since corpora are added every ~2.5 years after sexual maturity (Branch, 2008; Ohsumi, 1979), physical maturity is assumed to occur at 35 years. In the conceptual model we assumed that females reach physical maturity at 26.8 m (88 ft), and males at 24.4 m (80.1 ft). Growth rates are assumed to be the same for both sexes before weaning, but thereafter females grow faster. A feature of baleen whales is their extremely rapid early growth (first 2–3 years) followed by much slower growth rates, as reported previously for Antarctic minke whales, fin whales, sei whales, and blue whales (Aguilar & Lockyer, 1987; Best & Lockyer, 2002; Laws, 1961; Lockyer, 1981a,b). Such curves are not easily fit by a smooth growth function such as the von Bertalanffy equation (von Bertalanffy, 1938). Instead, through a combination of trial and error and smoothed model fits, we created plausible length-at-age values for each sex (Table 2) that went through the data points above and also (1) did not have sudden discontinuities, (2) had length increments that declined smoothly with increasing age, (3) growth ceased at age 35 with physical maturity, and (4) displayed rapid growth in the first 2–3 years.

It should be noted that the observed rapid growth after birth led early researchers to believe that blue whales became sexually mature at 2–3 years old (Laurie, 1937; Mackintosh & Wheeler, 1929), but this notion has since been dispelled by earplug ages (Branch, 2008; Ichihara, 1966; Rice, 1963), the realization that a single light-dark pair of earplug laminae represents one year of age in baleen whales (e.g., Best, 2011; Roe, 1967), and long-term photo-identification studies (Gabriele, Lockyer, Straley, Jurasz, & Kato, 2010).

Length frequency distributions were obtained from numbers at age in the age-structured model, the mean length at age for males and females (Table 2), and the assumption of a lognormal distribution around mean length with a standard deviation of 0.04, 0.05, 0.06, or 0.07. Predicted sex ratios by length were then calculated from these length frequency distributions.

3 | RESULTS

3.1 | Overall sex ratios in catches

The proportion of males among all catches was 0.521, 95% CI [0.520, 0.523], comprising 149,264 females and 162,637 males. For all regions, the proportion of males (p_{male}) was more than 0.5, and for all regions except the North Atlantic, there was a significant excess of males: Antarctic (n = 284,546, p_{male} = 0.521, $p < 10^{-16}$), pygmy (n = 10,265, p_{male} = 0.514, p = 0.0039), SE Pacific (n = 2,467, p_{male} = 0.531, p = 0.0025), North Atlantic (n = 1,953, p_{male} = 0.501, p = 0.96), and North Pacific (n = 2,327, p_{male} = 0.573, $p < 10^{-12}$).

3.2 | Annual changes in sex ratio by region

Antarctic blue whale catches were 27–144 times greater than in the other regions, resulting in greater power to detect changes in annual sex ratios in the Antarctic (Figure 2). Across all year-region combinations, 48 were significantly male-dominated, and 13 significantly female-dominated (Figure 2, test outlined in Section 2.3). There are no noticeable trends in any region except for the Antarctic where nearly all seasons up to 1950/51 were male-dominated (n = 262,809, p_{male} = 0.524, $p < 10^{-16}$), but thereafter all seasons except one were female-dominated or near parity (n = 19,246, p_{male} = 0.480, $p < 10^{-8}$).

3.3 | Overall and daily patterns in land stations

Within the Southern Hemisphere, temperate “breeding” land stations had catches dominated by females, although Walvis Bay was not significantly different from parity: Walvis Bay (n = 1,059, p_{male} = 0.474, p = .097), Saldanha Bay (n = 5,501, p_{male} = 0.472, $p < 10^{-5}$), and Durban (n = 2,487, p_{male} = 0.464, p = .0004). Conversely, the southern “feeding” land stations were close to parity (South Georgia) or strongly biased towards males: South Georgia (n = 33,557, p_{male} = 0.498, p = 0.56), the South Orkneys (n = 1,613, p_{male} = 0.598, $p < 10^{-15}$), and the South Shetlands (n = 14,876, p_{male} = 0.555, $p <10^{-16}$).

When examined by day, at Saldanha Bay sex ratios were fairly constant across the season, with consistently more than 50% of the catch comprising females, including eight days with significantly more females and only one day with significantly more males (Figures 3 and 4). The best model estimated a linear decline from 49.3% males on June 1 to 45.0% male on October 1, but the constant model (ΔAIC = 6.42) and sine wave model (ΔAIC = 4.14) also had some support from the data (Table 3).

For South Georgia, there were more females in October, more males in December and January, and then more females from March onwards (Figures 3 and 4), best fitted by a sine wave (Table 3). The selected model predicted the highest proportion of males (51.5%) on January 4, and the lowest proportion (41.6%) on July 8. However, these predictions are driven by the numerous catches in summer. During the austral winter (June 1–August 31), the sine wave model predicts an average of 42.2% males, which is much lower than the observed 46.8% males (*n* = 109).

At the South Shetlands, catches favored males throughout, with 32 days having male proportions significantly greater than 50%, and zero days where females significantly dominated catches (Figures 3 and 4). The sine wave model and linear model had nearly equal support from the data (Table 3), and both estimated a decline in male proportions from the start of major whaling on November 1 (57.9% for the linear model and 59.8% for the sine wave model) to April 1 (52.9% and 54.5%, respectively).

3.4 | Spatial patterns in Antarctic catches

For Antarctic blue whales south of 53ºS, there is strong evidence for spatially varying sex ratios: VAST models with spatial effects had AIC values 763 units better than VAST models without spatial effects. The most visible of these effects is the dominance of males in the region around the Ross Sea (170ºE–170ºW; Figure 5), but there are also other regions where either males or females are more commonly caught, and this pattern persists across months (Figure 6). Monthly patterns show how the retreat of sea ice during October to March influenced whaling, which also shifted closer to the Antarctic continent during this period (Figure 6). When the data are divided into different whaling periods it is clear that the pronounced male dominance in the Ross Sea was primarily a function of post-World War II whaling (1944–1952; Figure 7); also visible is the shift around the Antarctic from male-biased catches to female-biased catches.

3.5 | Fetal sex ratios by region and length

Across all recorded fetuses, 51.3% were male and this differed significantly from equality (11,045 males, 10,497 females, 95% CI [0.506, 0.519], *p* = .0002). When separated by region, the male proportion was not significantly different from 0.5 in the

North Pacific ($n = 95$, $p_{\text{male}} = 0.432$, $p = .22$), North Atlantic ($n = 48$, $p_{\text{male}} = 0.5$, $p = 1.00$), or for pygmy blue whales ($n = 842$, $p_{\text{male}} = 0.485$, $p = .39$), but was significantly greater than 0.5 in the Antarctic ($n = 20{,}557$, $p_{\text{male}} = 0.514$, $p < 10^{-5}$).

Fetal sex ratios differed significantly from equality only at the smallest lengths, and only for Antarctic blue whales, where males were significantly more common for six of the eight smallest length groups in feet (Figure 8). For fetuses smaller than 1.5 ft in Antarctic blue whales, 68.6% were male ($n = 156$, $p_{\text{male}} = 0.686$, $p < 10^{-6}$).

The best fit to the Antarctic blue whale fetal data included a linear decline in the proportion of males with increasing length, together with misidentification of small females as males (Table 3, Figure 9). This model was 5.37 AIC units better than a simple linear model without misidentification; and both models with linear declines were substantially better (>19 AIC units) than corresponding models assuming a constant sex ratio (Table 3). The two models including misidentification of sex fit the data better than models without misidentification, estimating that >50% of females are correctly sexed at lengths greater than 0.26 or 0.28 ft; and >95% are correctly sexed at lengths greater than 2.65 ft (constant model) or 1.93 ft (linear model). The constant model with misidentification estimated that the male proportion in fetuses is 51.1%, while the linear model with misidentification estimated that males are more common than females at lengths up to 12 ft, after which females are more common.

Additional fetal analyses found that fetal sex ratio did not change with mother length, but the longest one-third of mothers had longer fetuses than the shortest one-third of mothers—by as much as 1–2 ft in the latter half of the austral summer. There was some evidence for sexual dimorphism in fetal growth, but this was slight, resulting in female fetuses being no more than 2–5 cm longer than males on a given day of the year. None of these factors explain the decline in male proportions with longer fetal lengths.

3.6 | Postnatal sex ratios by length

For all regions, sex ratios were close to equality at the smallest postnatal lengths, male-dominated at intermediate lengths, and thereafter female-dominated (Figure 10). The crossover from male to female domination occurred at 83 ft for Antarctic blue whales, 68 ft for pygmy blue whales, 75 ft for the Southeast Pacific, 76 ft for the North Atlantic, and 78 ft for the North Pacific.

The conceptual model of sex ratios by lengths relied on length-at-age curves for Antarctic blue whales that represent the key features of blue whale growth: females grow faster and to longer lengths than males, but males and females are born at about the same length (Figure 11). The resulting simulated length frequencies have more males at intermediate lengths and more females at longer lengths (Figure 12). The mode around 56.5–57.0 ft (Figure 12) represents age-1 blue whales, which are substantially shorter than age-2 individuals (63–64 ft), and is more prominent when the *CV* of length at age is assumed to be small (0.04–0.05). The conceptual model predicts sex ratios by postnatal length (Figure 13) that embody key features in the observed data (Figure 10): sex ratios are close to equality for the smallest lengths (<60 ft), rise to >60% male at intermediate lengths (67–77 ft), switches to female dominance at longer lengths (81 ft), and thereafter the proportion of males declines to near zero, with the most rapid decline occurring with a small *CV* of length at age. This general pattern mimics that seen in each region, although the switch to female dominance occurs at 83 ft in the actual data for Antarctic blue whales compared to 81 ft in the conceptual model for Antarctic blue whales.

4 | DISCUSSION

Overall, male blue whales are slightly more prevalent than females in both fetal (51.3% male) and postnatal (52.1% male) data, with both values being significantly greater than 50%. These estimates are based on large sample sizes of 21,542 and 311,901 respectively, far greater than available for wild terrestrial species (Clutton-Brock & Iason, 1986). The only comparably rich data are for domesticated sheep (~49% male at birth) and cattle (~52% male at birth) (Clutton-Brock & Iason, 1986), and of course for humans, where males average 51.5% of births (Grech, Savona-Ventura, & Vassallo-Agius, 2002). Whale species clearly provide exceptionally rich data sets to test sex ratio theories.

4.1 | Annual changes in sex ratio by region

Annual sex ratios in Antarctic blue whale catches display a striking shift from being slightly male dominated (52.4% male) up to the 1950/51 season, to being either female-dominated or near parity thereafter (48.0% male). This subtle but significant shift from males to females occurred at a point when Antarctic blue whale abundance had declined to 8% of prewhaling levels, and continued whaling would result in a further decline to 0.15% of prewhaling levels in 1973 (Branch et al., 2004). A shift in sex ratio from males to females in catches is puzzling since whalers preferred to catch the larger and more profitable females, and it would be expected that female numbers would decline over time due to overexploitation, resulting in an increase in the proportion of males in catches, not a decrease. Furthermore, although whalers were shifting northward to focus on catching fin whales instead of blue whales (Branch, Lobo, & Purcell, 2013), our spatial models did not find more females in catches further from the Antarctic ice. Instead, more females were caught in all regions in later years. In part, the shift from males to females may reflect selectivity patterns of Soviet whalers during 1958–1973 when they operated in contravention of international regulation, ignoring the 70-ft minimum size limit and the ban on catching females accompanied by calves (e.g., Ivashchenko & Clapham, 2014; Yablokov, Zemsky, Mikhalev, Tormosov, & Berzin, 1998). Another possible explanation is sex-specific changes in survival, behavior, or age at maturity as a result of the changes in available food given depletion in whale populations.

In other whale species, sex ratios have generally been stable over time (Holt, 1977), except for sei whales and sperm whales. Sei whales shifted from female to male dominance over time, and this shift was not subtle, changing from under 40% male in catches from 1949–1950 to 1961–1962 to over 50% male from 1963–1964 on (Holt, 1977). In sperm whales, catches were concentrated near the poles where large lone males dwell, while the smaller females living in temperate regions were protected by minimum size limits and a Southern Hemisphere ban on pelagic whaling north of 40°S. The net result was a substantial decline in males, possibly sufficient to leave too few males to mate with all of the females (Beddington & May, 1980; Clarke, Aguayo, & Paliza, 1980). The hypothesized large shift in sperm whales (from 50% to 17% male) would be far greater than the subtle shift from 52% to 48% male in Antarctic blue whales. The sperm whale findings are complicated somewhat by both Soviet and Japanese whalers misreporting the sex of sperm whale catches in some years (e.g. Clapham & Ivashchenko, 2016; Ivashchenko & Clapham, 2014).

4.2 | Overall and daily patterns in land stations

Land stations at Walvis Bay, Saldanha Bay, and Durban (all in southern Africa) were slightly female-dominated (46%–47% male), South Georgia evenly split (50% male), and males dominated in the southernmost stations (South Orkneys, 60% male; South Shetlands, 56% male). These differences most likely reflect two opposing patterns. First, there was a well-known preference of whalers for shorter blue whales prior to 1920 in the southern stations of South Georgia, South Orkneys, and South Shetlands (Anonymous, 1920; Harmer, 1921; Hinton, 1915), and male Antarctic blue whales are more prevalent at these lengths (61% male for lengths 70–82 ft). Second, in the southern African land stations (especially at Walvis Bay and Saldanha Bay), catch lengths were characteristically comprised of a smaller peak at 80–95 ft including many large females, and a larger peak at 60-

70 ft comprising young juveniles, at lengths where sex ratios are close to equality. The southern African region is thus likely to be both a calving area for female Antarctic blue whales, and an area frequented by juvenile blue whales for several years after weaning.

Statistically significant daily shifts in sex ratios in Saldanha Bay (linear decline), South Georgia (sine wave) and South Shetlands (sine wave or linear decline), may result from the interplay of selectivity (shorter whales preferred in earlier years), the shrinking of the whaling season over time (from year round to just a few months), and the years in which whaling took place. Given the relatively modest daily trends, however, these data provide little or weak evidence for sex-specific migration in blue whales.

4.3 | Spatial patterns in Antarctic catches

For pelagic catches of Antarctic blue whales, there were no clear latitudinal or longitudinal spatial patterns in sex ratios, with sex ratios being slightly male dominated in most regions and time periods. The one exception was in the Ross Sea (170°E–170°W), where males were substantially more common than females. These patterns are much subtler than the strong latitudinal gradients in sex ratio reported for sperm whales, minke whales, and humpback whales. In sperm whales, almost all sightings (and catches) in the Antarctic comprise lone males, while temperate regions are dominated by schools of females and immature males (e.g., Best, 1979; Branch & Butterworth, 2001; Mikhalev, 2019). Antarctic minke whale catches also display strong latitudinal segregation by sex, shifting from 80% male north of 60ºS to less than 20% male south of 70ºS (Kasamatsu & Ohsumi, 1981); and minke whales off West Greenland also show a shift towards females nearer the poles, from 80% male at 59ºN to >90% female at 72ºN (Laidre et al., 2009). Humpback whales are also well-known to have sex-segregated migrations (Chittleborough, 1965): for example, in Hervey Bay, Australia, 75% are female, and this may be a strategy to minimize male harassment of mature females (Franklin et al., 2018); although in general humpback migrations to Australian breeding areas are male-dominated, ranging from 57% to 85% male depending on the year (Druskat et al., 2019).

4.4 | Fetal sex ratios by region and length

After accounting for sex misidentification at the smallest sizes, an estimated 51.1% of Antarctic blue whale fetuses are male, a result that is similar to the slight male bias in fin, minke, sperm, Antarctic blue, and humpback whales reported in other studies (Table 1), and also similar to the slight male bias found in humans (Parkes, 1926).

There was clear evidence of misidentification of small females as males in the data for Antarctic blue whales. Misidentification affects only the smallest fetuses (under 2–3 ft), which have previously been noted to be problematic for inexperienced observers in sei whales (Gambell, 1968, 1972) and Antarctic minke whales (Kato & Shimadzu, 1983). Clearly, for accurate fetal sex determination at these small lengths, genetic methods are needed instead of visual assessment.

In addition, there was a statistically significant decline in the proportion of males with increasing fetal length. Most likely this is due to higher in-utero mortality of males, a phenomenon that has been proposed or demonstrated in humans (Creasy et al., 1976), in a wide variety of mammals (Clutton-Brock & Iason, 1986; Parkes, 1926; Trivers, 1985), and in long-finned pilot whales (Desportes, Andersen, & Bloch, 1994). Trivers (1985, p. 276) provides estimates of higher male mortality in utero for whales by “Seger et al. in prep.” but the underlying methods and results remain unavailable. However, data for Antarctic minke whales (Kato & Shimadzu, 1983) do include significantly fewer large males than expected at longer lengths (>220 cm, 16 males, 32 females, p = .01). Clearly, a reexamination of historical whaling data is needed to test if other whale species have higher in utero male mortality.

A variety of other hypotheses for declining male proportions with increasing fetal length were also briefly examined but discarded. One possibility is that female blue whales grow faster than males in utero, thus if pregnant females leave the Antarctic for feeding grounds at similar times, a greater proportion of long fetuses in Antarctic catches would be female. A comparison of fetal length by sex and day of the year showed the well-known increase in length by day (Laws, 1959), but the very small increases in female fetal lengths at a given date were insufficient to explain the trend in sex ratio with fetal length. Another possibility is that larger mothers may have more rapidly growing fetuses and choose to invest in female offspring (Clutton-Brock et al., 1986; Trivers & Willard, 1973). It is true that larger Antarctic blue whale mothers do have substantially larger fetuses on a given date (either because their fetuses grow faster or because they conceive earlier in the year), but there is no evidence in the data for fetal sex ratios varying by mother length (T.A.B., unpublished analysis).

4.5 | Postnatal sex ratios by length

In all regions, males were more frequent at intermediate lengths and females more common among the longest individuals. This pattern is explained by differential growth rates between the sexes, as exemplified by the conceptual model. In the conceptual model this was the only factor that differed between sexes, and reproduced the bump in male proportions at intermediate lengths and the increase in females at the longest lengths. Extensions to this model would require model fitting over time to dynamic changes in length frequencies, rather than relying on an equilibrium age-structured model.

4.6 | Data limitations

One take-home message from the relation between sex ratio and postnatal length is that care needs to be taken when interpreting sex ratios in catches. Any change in whaling selectivity, caused by a change in incentives to catch larger whales, the implementation of minimum length regulations (generally at 70 ft), or the flouting of minimum length regulations by the Soviet whalers, will alter overall sex ratios in catches. Several key issues were identified that alter our understanding of sex ratios in blue whales. The misidentification of small female fetuses as males was resolved by developing a model of observed sex ratios assuming sex misidentification at small sizes. The issue of whaling selectivity due to minimum length regulations and other incentives to avoid or target blue whales by size, can also be addressed through an extension of the conceptual model of length at age that incorporates whaling removals and projects the population forward in time. Additional modeling is also needed to account for the ban on catching lactating females during whaling, first required by Norwegian whaling law in 1929 for the Antarctic, and later applied internationally in 1937, although this may not be a major issue for Antarctic blue whales, since calves are born in April–May and weaned in November–December (Mackintosh & Wheeler, 1929), generally before the peak pelagic whaling period (January–March).

4.6 | Conclusions

Despite the caveats related to data limitations, the current investigation uncovered a variety of interesting trends. Notably, females increasingly dominated in Antarctic catches over the years; sex ratios varied systematically with latitude among the land stations, and across days of the year for each land station; the proportion of males declined with increasing fetal length, and increased and then declined with postnatal lengths in catches. We plan to extend the current work to other large cetaceans to determine if these are general patterns or are specific to blue whales.

The current paper does offer some practical advice for population modeling of blue whales. Antarctic blue whales are currently the focus of an in-depth assessment by the International Whaling Commission. Since variations in sex ratio are only slight across space, time, and length, such models do not need to be sex-specific for an accurate assessment of blue whale population status.

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AUTHOR CONTRIBUTIONS

Trevor A. Branch: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; software; validation; visualization; writing–original draft; writing–review and editing. **Cole C. Monnahan**: Conceptualization; formal analysis; methodology; software; validation; visualization; writing–review and editing.

ORCID

Trevor A. Branch	https://orcid.org/0000-0003-4308-8930
Cole C. Monnahan	https://orcid.org/0000-0003-0871-6700

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TABLE 1 Fetal sex ratios reported in previous papers for large whale species. Here p_{male} = proportion of males; p is the probability of observing the listed proportion of males if the true proportion was 0.5. Only species with published values based on $n \geq 2{,}000$ were included. Records here are the largest published analyses found each species.

Species	Region	Males	Females	n	p_{male}	95% CI	p	Source
Sei	South Africa + Antarctic	9,340	9,465	18,805	0.497	0.490, 0.504	.37	Gambell (1968)
Fin	Antarctic	6,787	6,267	13,054	0.520	0.511, 0.529	5.5×10^{-6}	Mackintosh (1942)
Minke	Antarctic	5,629	5,486	11,115	0.506	0.497, 0.516	.18	Kato & Shimadzu (1983)[a]
Blue	Antarctic	5,374	4,821	10,195	0.527	0.517, 0.537	4.5×10^{-8}	Mackintosh (1942)
Sperm	Global	1,983	1,887	3,870	0.512	0.497, 0.528	.13	Best et al. (1984)
Humpback	Australia + Antarctic	1,073	990	2,063	0.520	0.498, 0.542	.07	Chittleborough (1965)

[a] For fetal lengths ≥ 10 cm, since lengths 1–10 cm had anomalously few males (p_{male} = 0.2012, n = 1,267).

TABLE 2 Assumed length-at-age values for male and female Antarctic blue whales (in ft), used in the conceptual model of sex ratio by length.

Age	Males	Females
0	23.0	23.0
1	56.5	57.0
2	63.0	64.0
3	66.2	68.0
4	68.7	70.5
5	70.5	72.5
6	71.8	73.8
7	72.4	75.0
8	73.0	76.0
9	73.6	76.9
10	74.1	77.8
11	74.6	78.6
12	75.1	79.4
13	75.6	80.2
14	76.0	80.9
18	77.5	83.4
19	77.8	83.9
20	78.1	84.4
21	78.4	84.9
22	78.6	85.3
23	78.8	85.7
24	79.0	86.1
25	79.2	86.4
26	79.4	86.7
27	79.5	87.0
28	79.7	87.2
29	79.8	87.4
30	79.9	87.6
31	80.0	87.7
32	80.0	87.8

15	76.4	81.6	33	80.1	87.9
16	76.8	82.2	34	80.1	88.0
17	77.1	82.8	35+	80.1	88.0

TABLE 3 Maximum likelihood estimates (MLEs) for models fitted to the daily trends in sex ratio in catches at the three most important land stations (Saldanha Bay, South Georgia, and the South Shetlands). Parameters are: sample size (n); number of model parameters (k); mean proportion of males (r_{mean}); intercept (a) and slope (b); day of highest male proportion (d_{max}); and the lowest (r_{min}) and highest (r_{max}) proportion of males in the catches. The ΔAIC is the difference between the AIC for each model and the AIC for the best model; thus, the best model has ΔAIC = 0.

Station	**Model**	**Parameter estimates (MLEs)**	***n***	***k***	**AIC**	**ΔAIC**
Saldanha Bay	Equality	$r_{\mathrm{mean}} = 0.5$	5,439	0	7,540.06	22.44
	Constant	$r_{\mathrm{mean}} = 0.471$	5,439	1	7,524.03	6.42
	Linear	$a = 0.482$, $b = -0.00035$	5,439	2	7,517.61	0.00
	Sine wave	$d_{\mathrm{max}} = 88.8$, $r_{\mathrm{min}} = 0.453$, $r_{\mathrm{max}} = 0.512$	5,439	3	7,521.75	4.14
South Georgia	Equality	$r_{\mathrm{mean}} = 0.5$	33,554	0	46,515.72	40.17
	Constant	$r_{\mathrm{mean}} = 0.498$	33,554	1	46,517.37	41.83

	Linear	$a = 0.499$, $b = -0.000038$	33,554	2	46,516.86	41.32
	Sine wave	$d_{max} = 4.1$, $r_{min} = 0.416$, $r_{max} = 0.515$	33,554	3	46,475.55	0.00
South Shetlands	Equality	$r_{mean} = 0.5$	14,542	0	20,159.49	190.57
	Constant	$r_{mean} = 0.556$	14,542	1	19,981.54	12.62
	Linear	$a = 0.560$, $b = -0.00033$	14,542	2	19,969.78	0.86
	Sine wave	$d_{max} = 235.6$, $r_{min} = 0.535$, $r_{max} = 0.627$	14,542	3	19,968.92	0.00

TABLE 4 Maximum likelihood estimates (MLEs) of model parameters for models predicting sex ratio as a function of fetal length (in feet). Better models have lower AIC, with the best model indicated by ΔAIC = 0. Parameters are: sample size (n); number of model parameters (k); mean proportion of males (r_{mean}), length at which 50% and 95% of females are correctly recorded as female (L_{50} and L_{95} in feet); intercept (a) and slope (b); and proportion of males at length 10 ft (r_{10}).

Model	**Parameter estimates (MLEs)**	n	k	**AIC**	**ΔAIC**
1 Equality	$r_{\text{mean}} = 0.5$	20,572	0	28,498.05	52.08
2 Constant	$r_{\text{mean}} = 0.514$	20,572	1	28,483.29	37.31
3 Constant + misid.	$L_{50} = 0.26$, $L_{95} = 2.65$, $r_{\text{mean}} = 0.511$	20,572	3	28,465.76	19.78
4 Linear	$b = -0.0045$, $r_{10} = 0.511$	20,572	2	28,451.35	5.37
5 Linear + misid.	$L_{50} = 0.28$, $L_{95} = 1.93$, $b = -0.0039$, $r_{10} = 0.509$	20,572	4	28,445.98	0.00

FIGURE 1 Regions used to group blue whale catches (points) for the sex ratio analyses, with major land stations labeled. Note that some (*n* = 61) pygmy blue whale catches fall just south of the Antarctic–pygmy boundary in the region 44°–87°E. The dashed line in the South Atlantic separates known breeding and feeding regions for Antarctic blue whales. Catches around Durban are colored black since it is currently unknown if these were pygmy or Antarctic blue whales.

FIGURE 2 Sex ratios (proportion male) by year in each major region. Days that differ significantly from an equal sex ratio (indicated by the horizontal dashed line) are highlighted in blue (male-dominated) or red (female-dominated). For the Southern Hemisphere pelagic whaling, year was defined as the start year of the whaling season (i.e., 1960 for the 1960/1961); for all other regions, year is calendar year. Points are plotted only for year-region combinations with 25 or more sexed whales, and catches around Durban are excluded.

FIGURE 3 Daily patterns in sex ratios (proportion male) for the three land stations with the most catches. Almost all whaling was conducted in winter at Saldanha Bay and in summer at South

Georgia and the South Shetlands. Points are plotted only for days with 25 or more whales. Days that differ significantly from an equal sex ratio (indicated by the horizontal dashed line) are highlighted in blue (male-dominated) or red (female-dominated).

FIGURE 4 Models fitted to daily patterns in sex ratios (proportion male) for the three land stations with the most Antarctic blue whale catches, showing all data year round (points), and maximum likelihood predictions for the four models: equality (male proportion 0.5), constant (male proportion estimated but the same for every day), linear, and sine wave. Linear models were fitted starting in January 1 for Saldanha Bay, and July 1 for the other two stations.

FIGURE 4 Models fitted to daily patterns in sex ratios (proportion male) for the three land stations with the most Antarctic blue whale catches, showing all data year round (points), and maximum likelihood predictions for the four models: equality (male proportion 0.5), constant (male proportion estimated but the same for every day), linear, and sine wave. Linear models are fitted starting in January 1 for Saldanha Bay, and July 1 for the other two stations.

FIGURE 5 VAST model predictions for sex ratio (proportion of males) for Antarctic blue whales for all data south of 52ºS combined. Each point shows a prediction near observed data, with color representing sex ratios.

FIGURE 6 Monthly VAST model predictions for sex ratio (proportion of males) for Antarctic blue whales, for the 6 months with the greatest catches. Each point shows a prediction near observed data, with color representing sex ratios.

FIGURE 7 VAST model predictions for sex ratio (proportion of males) for Antarctic blue whales for four time periods of pelagic whaling: 1925–1930, 1931–1940, 1944–1952, and after 1952. Each point shows a prediction near observed data, with color representing sex ratios.

FIGURE 8 Proportion of males in each fetal length bin (in feet) for Antarctic blue whales and pygmy blue whales. Points are plotted only for length bins with 25 or more whales. Lengths that differ significantly from an equal sex ratio (indicated by the horizontal dashed line) are highlighted in blue (male-dominated); there were no female-dominated lengths.

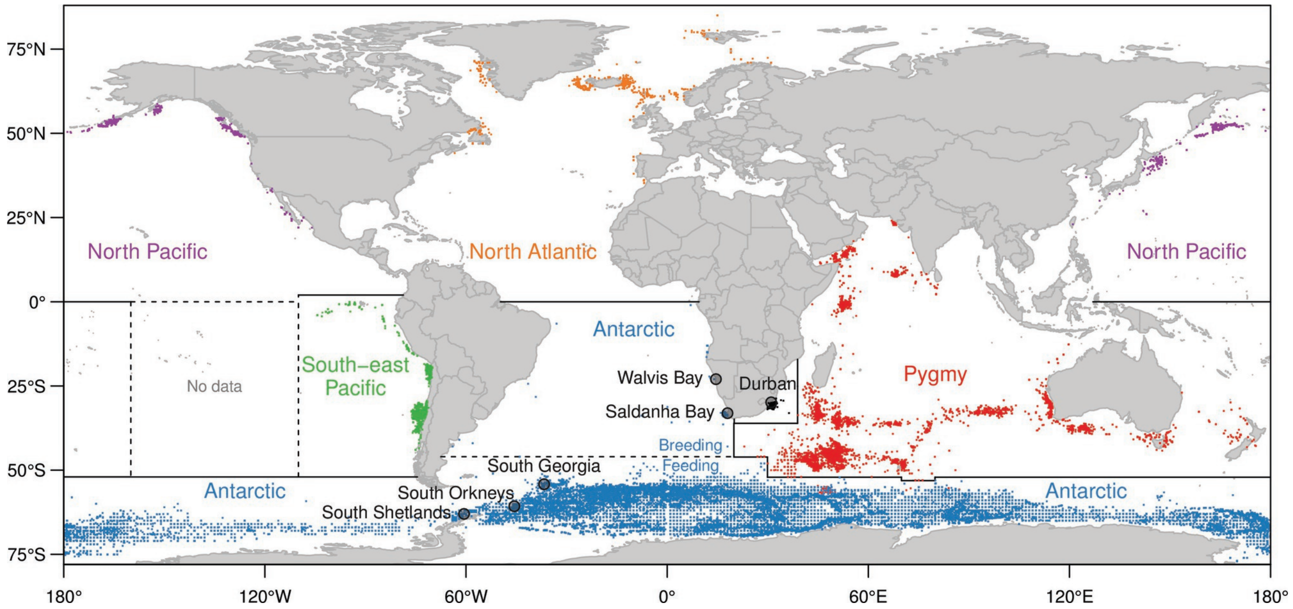
FIGURE 9 Predictions of fetal sex ratio as a function of fetal length, for five models of Antarctic blue whales. 1: Equality, assuming the proportion of males is 0.5. 2: Constant model estimating a constant sex ratio regardless of fetal length. 3: Constant with misidentification model, which assumes that female fetuses smaller than 5 ft in length could have been misidentified as male, with a logistic function for misidentification that increases the rate of misidentification as size declines. 4: Linear, where sex ratio changes linearly with fetal length. 5: Linear with misidentification model, which assumes a linear change in fetal sex ratio with length in addition to a logistic function for misidentification (at all lengths). Parameter values are given in Table 2.

FIGURE 10 Mean and 95% confidence intervals for proportion of males by length (postnatal) for blue whales from different regional groupings. Sex ratios differing significantly from equality (the horizontal dashed line) are colored in blue (male-dominated) or red (female-dominated). Points are plotted only for length bins with 25 or more whales. For some points, sample sizes are so high that confidence intervals are subsumed within points.

FIGURE 11 Plausible length at age for female (red) and male (blue) Antarctic blue whales, used in the conceptual model of sex ratio by length, shown here with a lognormal standard deviation of 0.04 around the mean values. The smallest lengths are those assumed for 1-year-old blue whales.

FIGURE 12 Plausible length frequencies for Antarctic blue whales at prewhaling equilibrium with lognormal *CV* at length at age of 0.04–0.07. In this conceptual model, the parameter values were: population size 239,000; adult survival 0.935/year; calf survival 0.74/year; proportion of females at birth 0.5; age at maturity 10 years; resulting pregnancy rate at equilibrium of 0.32/year; and length-at-age as depicted in Figure 11.

FIGURE 13 Predicted sex ratios for Antarctic blue whales at prewhaling equilibrium from the conceptual model, with lognormal *CV* at length at age of 0.04–0.07.



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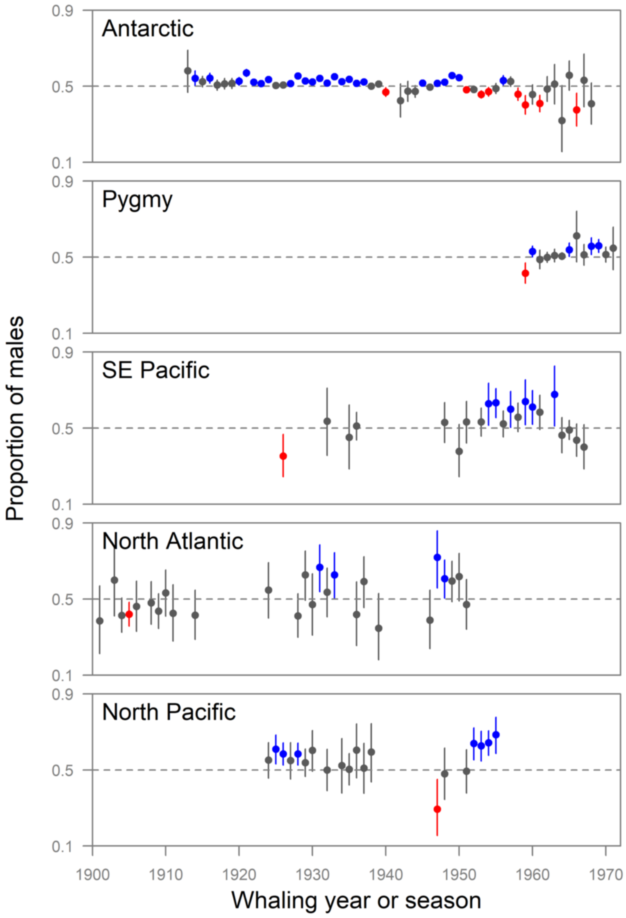

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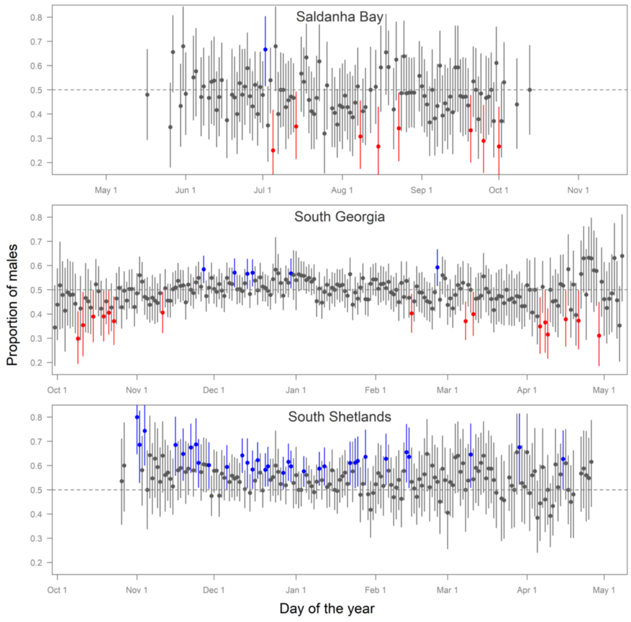

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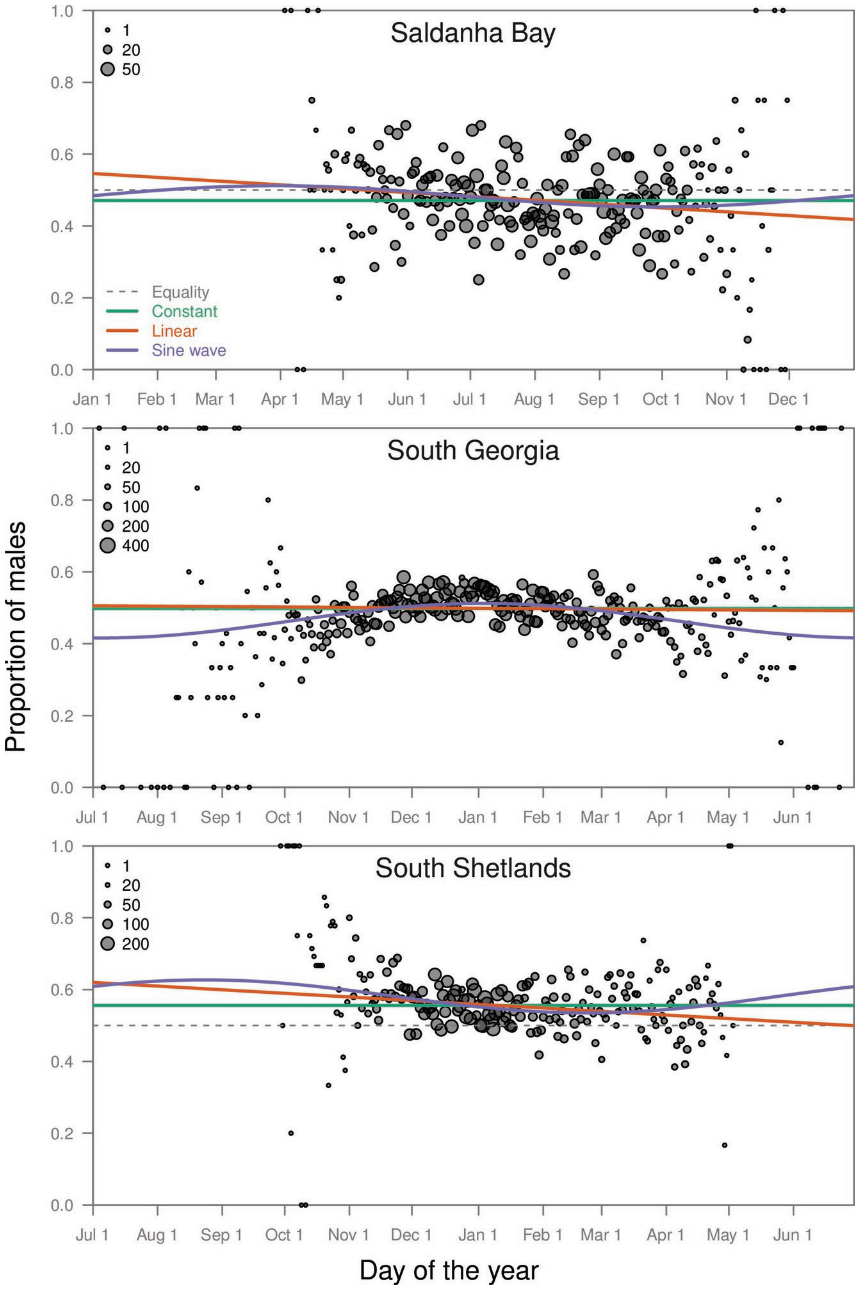

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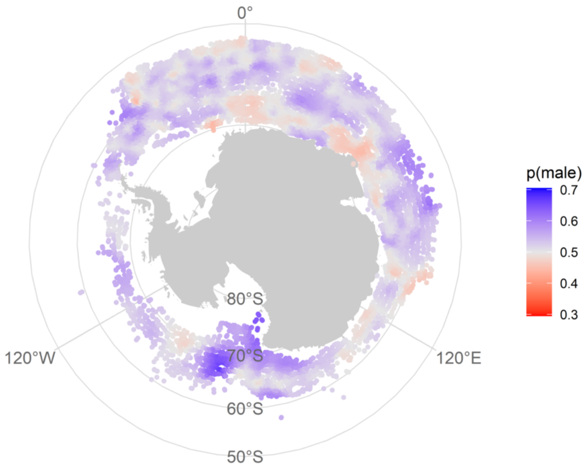

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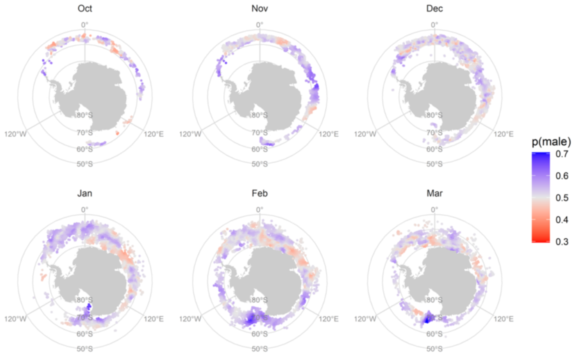

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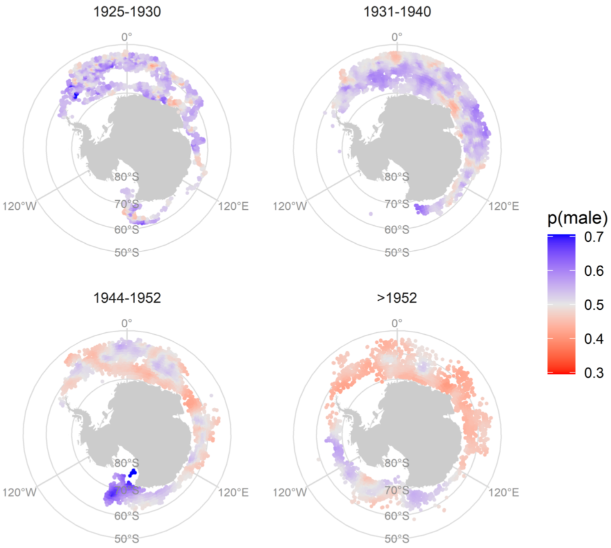

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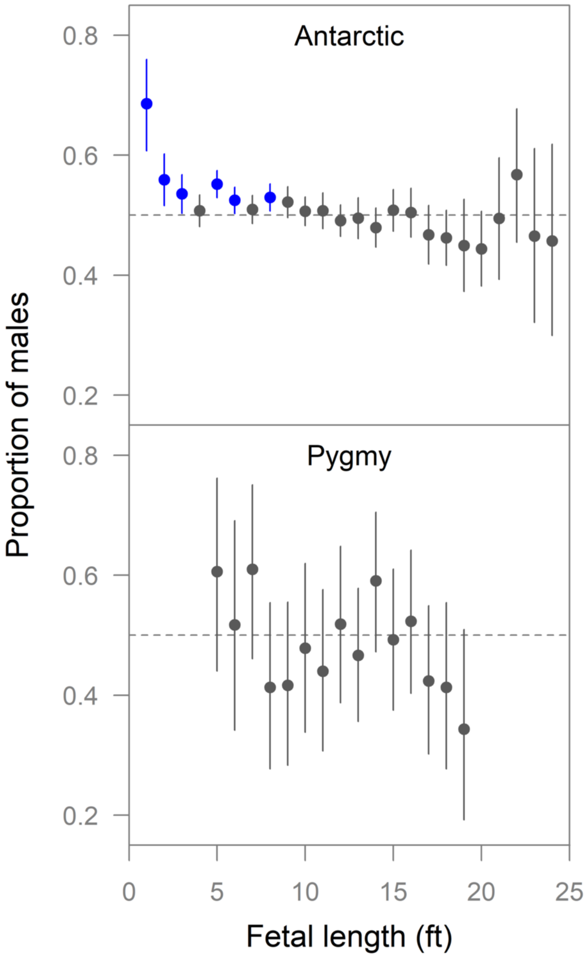

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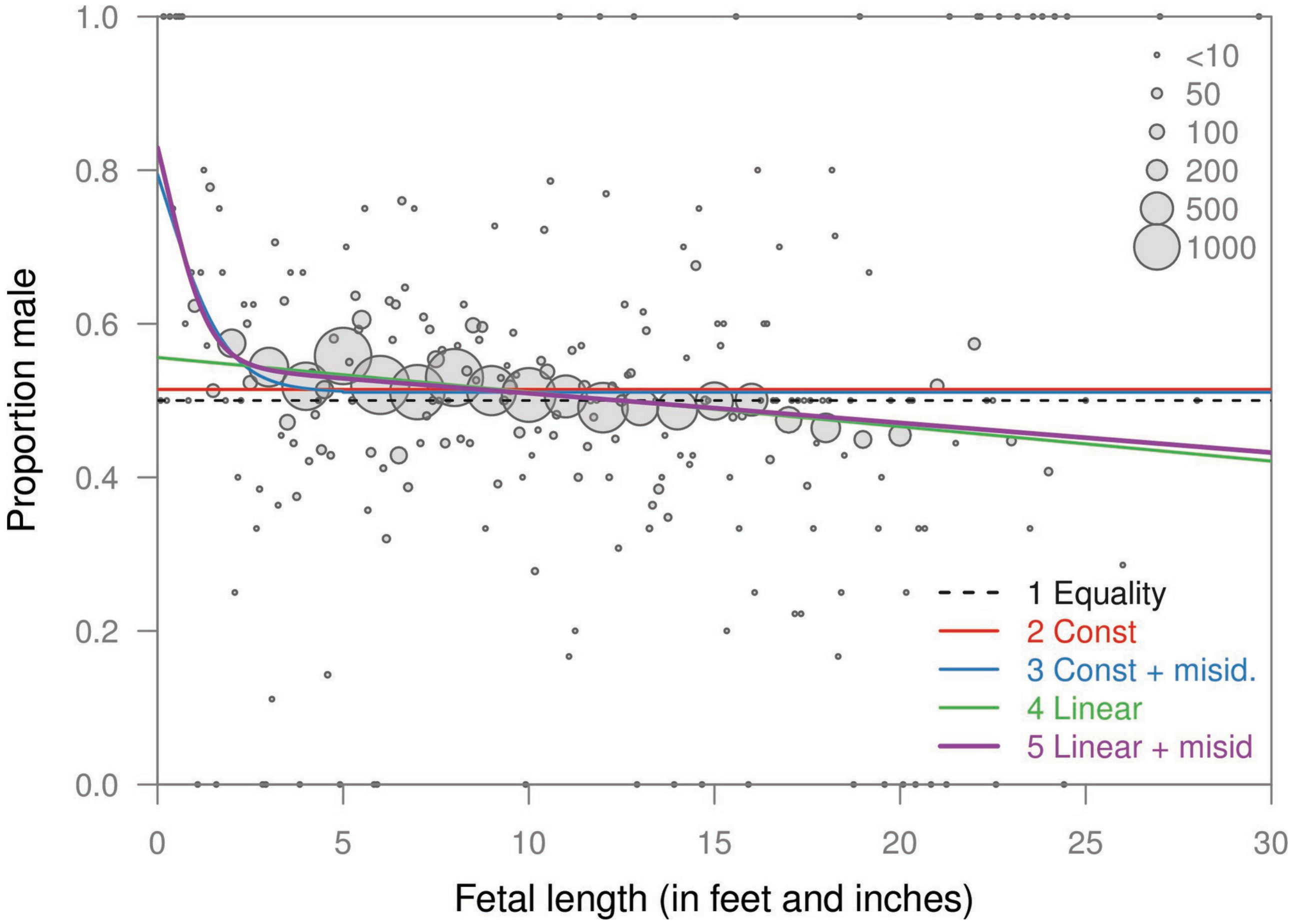

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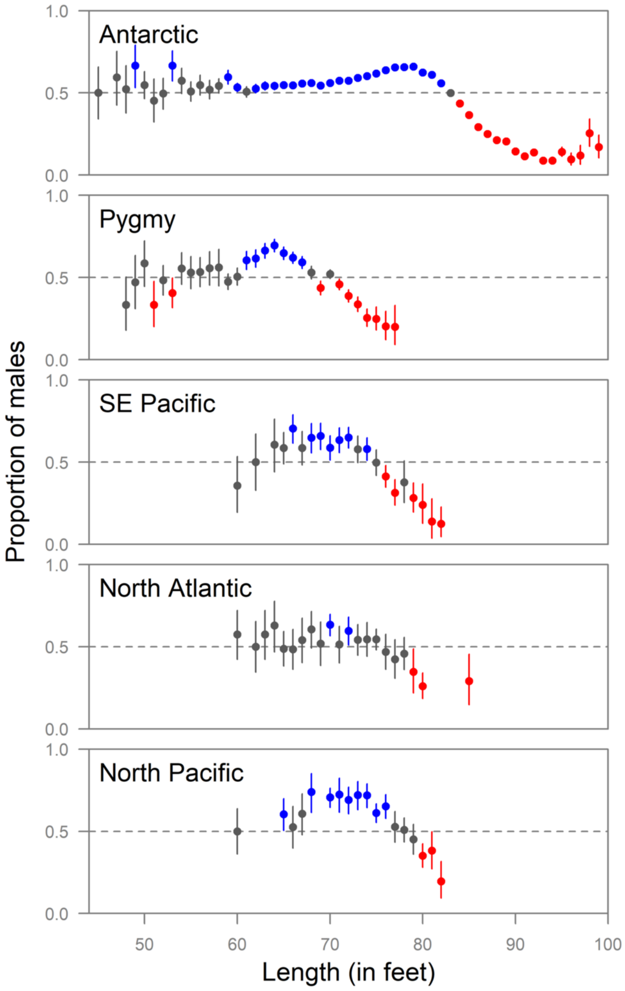

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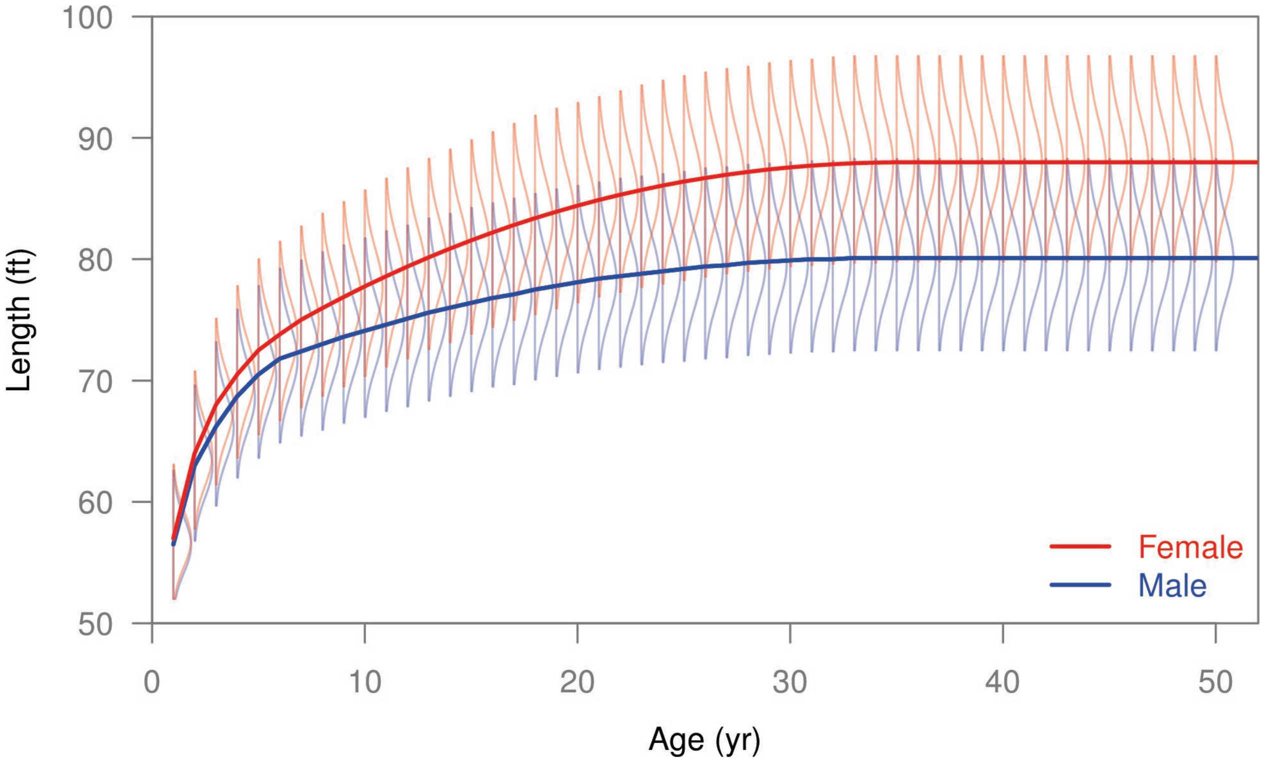

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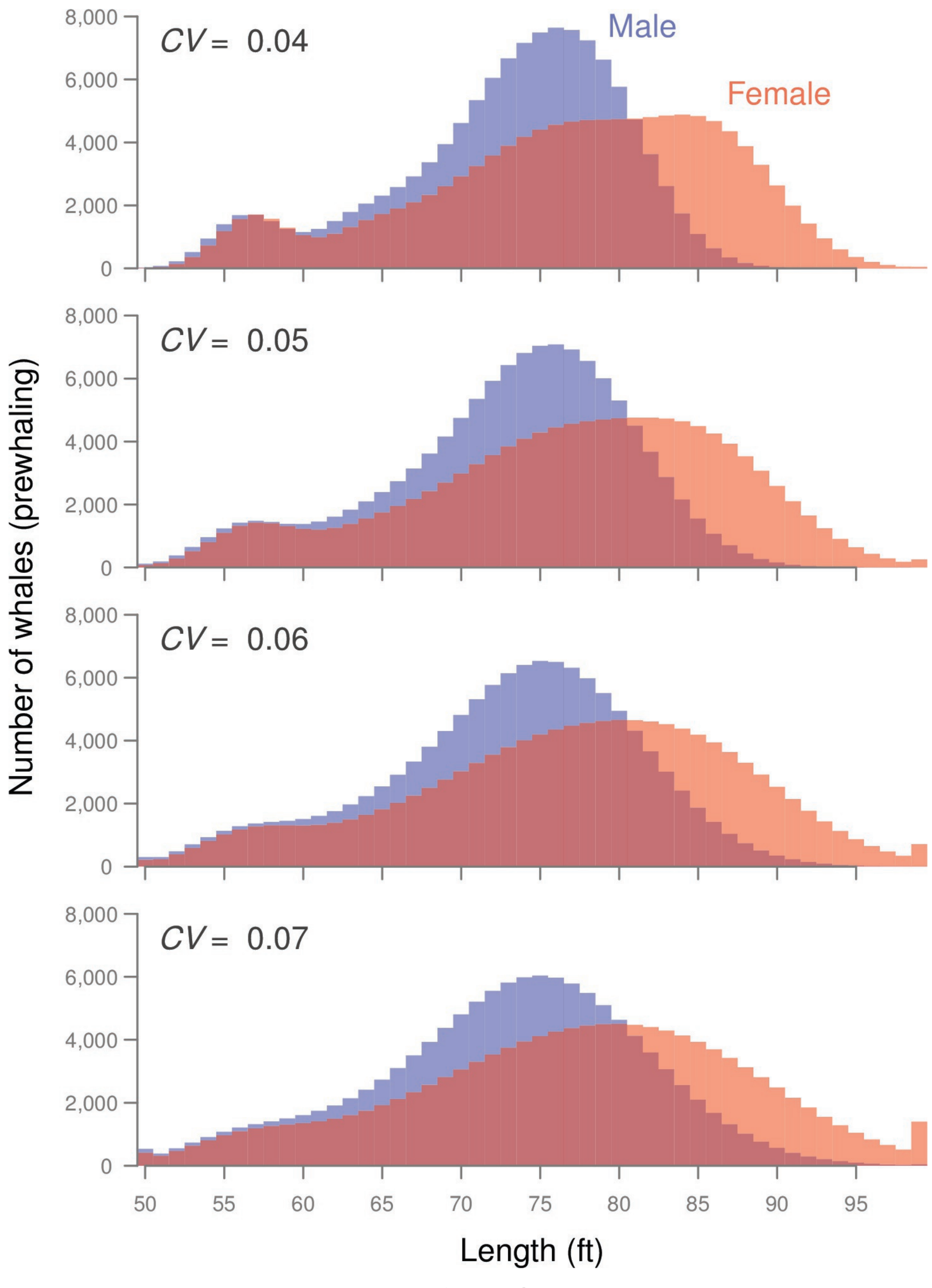

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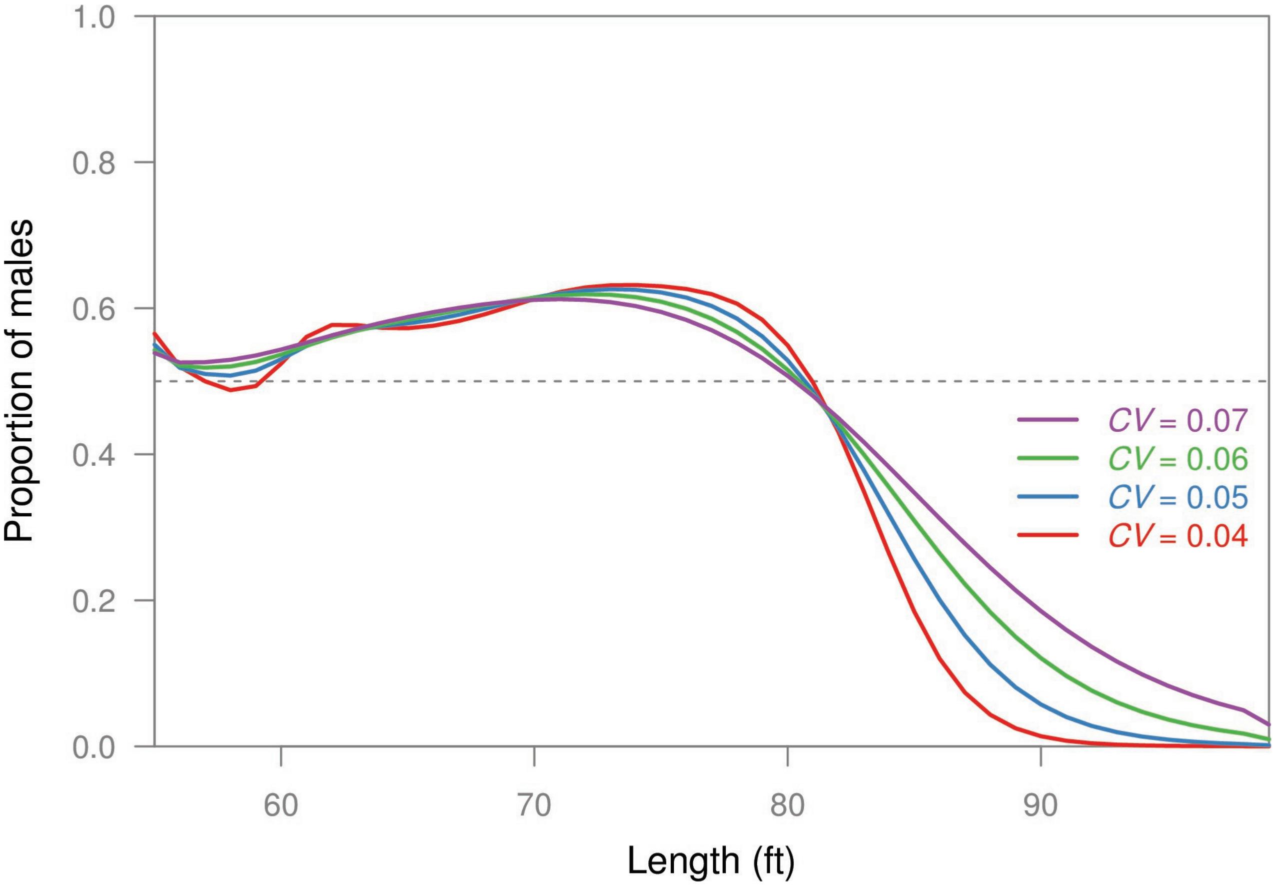

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