Modeling population status and demographic rates of baleen whales using historical whaling data

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Abstract

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Commercial whaling in the 20th century decimated the populations of many baleen whale species. Blue whales *(Balaenoptera musculus*) were especially impacted, with multiple populations whaled to near extinction, resulting in their current listing globally as Endangered by the IUCN. During whaling, extensive biological data were collected that, when combined with contemporary statistical methods, can be used to answer long-standing questions about baleen whale demography and population status. In this dissertation, I use historical data from whaling and contemporary Bayesian statistical methods to model baleen whale population dynamics and demography, with a particular focus on the highly exploited blue whale. In Chapter 1, I used a multi-state mark-recovery model to investigate population structure in Antarctic blue whales using historical mark-recovery data and found that they move frequently in the Southern Ocean, suggesting they are a single well-mixed circumpolar population. In Chapter 2, using the extensive fetal sex ratio data collected during whaling, I investigated ecological theories about adaptive sex ratio behavior, finding that longer rorqual (family Balaenopteridae) whale mothers have more female offspring. This suggests there is an advantage to being large that larger mothers pass on their daughters, likely stemming from the high costs of gestation and lactation for female baleen whales. In Chapter 3, I combined historical catch data and contemporary abundance estimates to build a population assessment model for Antarctic blue whales, finding that at the end of whaling they were at just 0.2% of pre-whaling levels, although their population size is currently increasing. Despite increasing, they are currently at less than 2% of pre-whaling levels so they still have many decades before they recover from whaling. In Chapter 4, using a global compilation of blue whale aging and reproductive data, I modeled age-length relationships and estimated reproductive rates for Antarctic, pygmy, and eastern North Pacific blue whales, finding that asymptotic lengths were longer for females than males across subspecies, and that Antarctic blue whales were the largest while pygmy blue whales were the smallest. In addition, I estimated pregnancy rates and age of sexual maturity for female eastern North Pacific and pygmy blue whales and, in Chapter 5, estimated natural survival for pygmy blue whales. These

projects provide a deeper understanding of blue whale population dynamics and demography and lay the groundwork for age-structured stock assessments of blue whales.

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Dedication

This dissertation is dedicated to the giant and mysterious blue whale

Introduction

Commercial whaling of baleen whales began in the 11th century, with the Basques, who pursued whales in small open boats, attacking whales with hand harpoons and lances. This early whaling was largely confined to the North Atlantic and Arctic (Reeves & Smith 2006). However, by the 18th and 19th centuries, commercial whaling had spread throughout much of the rest of the globe (Reeves & Smith 2006, Smith et al. 2012). By the 19th century, offshore whaling was dominated by American vessels, but many British and French companies were active too, as well as shore-based stations in many countries (Reeves & Smith 2006). Commercial whaling was largely characterized by boom-and-bust cycles—as each new whaling area was discovered, exploited species in those areas became depleted in only a few years, prompting whalers to search for new areas to hunt (Josephson et al. 2008, Scarff 2001, Smith et al. 2012). Open-boat whaling could only catch the slower-moving species of whales (right, bowhead, sperm, humpback, gray), but by the late 1860s, the invention of steam ships, exploding harpoons and compressed air, all of which allowed whalers to finally hunt the faster-moving rorqual (family *Balaenopteridae*) whales, ushered in the era of "modern" whaling (Tonnessen & Johnsen 1982). By the start of the 20th century, the only remaining unexploited region was the Southern Ocean (Smith et al. 2012). Southern Ocean whaling began on land stations but expanded in the 1920s to the use of factory ships with stern slipways—large floating factories with 500-person crews that could process whales on the ship deck anywhere in the world, accompanied by fleets of steam-powered whaling boats (Reeves & Smith 2006, Tonnessen & Johnsen 1982).

Commercial whaling in the Southern Ocean led to the sequential depletion of large cetaceans. Antarctic blue whales (*Balaenoptera musculus intermedia*) were the largest and most abundant and therefore became the most sought-after target of this whaling. As these dwindled, the continued pursuit of fin whales (*Balaenoptera physalus*) facilitated an even greater depletion of blue whales, as whalers targeting fin whales would catch blue whales when they came across them (Branch et al. 2013). When fin whales in turn became depleted, whalers switched to sei whales (*Balaenoptera borealis*) and then to Antarctic minke whales (*Balaenoptera acutorostrata*) (Patil et al. 2023).

The International Whaling Commission (IWC) was formed in 1946 to manage the whaling industry (https://iwc.int/commission/history-and-purpose). The initial convention set up whaling regulations that could be modified at annual meetings based on the optimal use of whale resources and updated scientific findings. This was one of the first attempts to create international management of a natural resource with an emphasis on science-based management (Burnett 2012). After several unsuccessful attempts at regulation, a moratorium on hunting Antarctic blue whales was finally implemented in 1965. However, Soviet whalers were already ignoring IWC regulations and continued to hunt illegally until 1973 (Berzin 2008, Ivashchenko & Clapham 2014). A moratorium on commercial whaling on all species was implemented in 1985.

During the period of modern whaling, more than two million whales were caught in the Southern Ocean alone (Clapham et al. 1999) depleting almost all baleen whale populations. Blue whales and other baleen whale species are currently listed as Endangered—and Antarctic blue whales as Critically Endangered—by the IUCN primarily due to this exploitation (Cooke 2018, Thomas et al. 2016). Despite the moratorium on commercial whaling in 1985, baleen whales still face many other threats including bycatch and entanglement in fishing gear, ship strikes, and changing krill availability due to climate change and ocean acidification (Clapham et al. 1999, Constable et al. 2014, Thomas et al. 2016). Additionally, anthropogenic noise can impact whales through hearing loss, masking, and behavioral changes (Blair et al. 2016, Castellote et al. 2012). Baleen whales are integral to marine ecosystems as essential parts of marine food webs and for their role in carbon sequestration (Roman et al. 2014)**.** To understand the true extent of the impacts of whaling and manage the recovery of baleen whale populations in the face of current threats, we need a better understanding of their population structure and demographic rates.

Starting in the 1920s, regulations required whalers to collect biological information on all landed whales. Early naturalists interested in whales were limited to studying the occasional bone or whale carcass that washed ashore. Whaling, however, provided an unprecedented flood of specimens for these researchers, allowing them to think about population-level characteristics of whales rather than just single specimens (Burnett 2012). Biologists joined crews on factory ships, and “hip-booted” and wearing crampons so as not to slip on the slippery flensing platforms, collected information on the morphology, stomach contents, sex, pregnancy, reproductive organs, and fetuses of whales. Standardized forms provided to whaling fleets allowed for data collection across different expeditions and whaling nations (Burnett 2012, Tonnessen & Johnsen 1982). These early data about baleen whales are currently unmatched by contemporary data collection methods but also come with challenges. For instance, whalers did not provide information about effort, only about where whales were caught, therefore there is no direct information in these data about where whales were searched for but not found. Additionally, later regulations required that harvested whales be longer than a minimum length. Whalers, however, sometimes ignored these regulations and any whales that were caught below this minimum length were simply reported as being at the minimum length, known as “whale stretching” (Best 1989, Branch & Mikhalev 2008). As another example, while fetuses of pregnant whales were examined and sexed, it has been hypothesized that sexing smaller fetuses was difficult and a bias in the sex of fetuses has been found for the smallest fetuses (Branch & Monnahan 2020, Gambell 1968, Kato & Shimadzu 1983).

Contemporary statistical methods can allow us to account for the challenges in these data and assess the population status and recovery of baleen whales. Bayesian methods allow for the incorporation of prior information and mathematically intuitive ways to combine likelihood functions so that models can share information across data sources (McCarthy 2007, McElreath 2015, Schaub & Abadi 2011). Additionally, advances in statistical software and Bayesian model-fitting algorithms allow for faster and more efficient model fitting (e.g., Ge et al. 2018, Kristensen 2024, Kristensen et al. 2016, Monnahan & Kristensen 2018). By combining these contemporary statistical methods with historical whaling data, we can leverage existing whaling data to understand the effects of whaling on exploited whale populations and derive demographic parameters that are important for assessing their recovery.

In this dissertation I use historical data from whaling to model baleen whale population structure and demography and obtain a better baseline understanding of their demography and population status. In Chapter 1, I fit a mark-recovery model to historical data from Antarctic blue whales, investigating movement rates and population structure in the Southern Ocean. In Chapter 2, I explore fetal sex ratios of exploited whale populations using generalized linear models to test for adaptive sex ratio behavior. In Chapter 3, I use an integrated stock assessment model to assess the population status of Antarctic blue whales. In Chapter 4, I compile blue whale age data from earplugs and ovarian corpora to estimate age-length relationships, pregnancy rates, and age at sexual maturity for global blue whale subspecies. Finally, in Chapter 5, I use catch-curve methods to estimate natural survival for pygmy blue whales using the compiled earplug and ovarian corpora data. These projects provide a deeper understanding of blue whale population dynamics and demography and lay the groundwork for age-structured stock assessments of Antarctic blue whales and future population assessments of other blue whale subspecies.

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Chapter 1. High historical movement rates of Antarctic blue whales on Southern Ocean feeding grounds estimated from Discovery mark data

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Abstract

Little is known about Antarctic blue whale *(Balaenoptera musculus intermedia*) movement and migration. In many baleen whale species, distinct populations arose due to inherited fidelity to migration routes between breeding and feeding areas. To assess whether population structure is present in the form of feeding area fidelity in Antarctic blue whales, we analyzed mark-recovery data with a multistate model to estimate historical interyear movement rates among the three ocean basins in the Southern Ocean (Atlantic, Indian, and Pacific) during 1926–1963. We found high probabilities of interyear movement in almost all directions: for blue whales in the Atlantic basin of the Southern Ocean, we estimated that each year 15% (95% interval: 0.66-46%) moved to the Indian and 29% (4%-49%) to the Pacific basins; from the Indian basin, 13% (3%-33%) moved to the Atlantic and 32% (14%-48%) to the Pacific basins; and from the Pacific basin, 28% (13%-46%) moved to the Indian, and 8% (1%-24%) to the Atlantic basins. These high estimated movement rates provide little evidence for population structure arising from basin-specific feeding ground fidelity by Antarctic blue whales.

1.1 Introduction

Baleen whales undertake some of the longest migrations of any mammal on earth (Corkeron & Connor 1999), with species such as humpback whales (*Megaptera novaeangliae*) traveling over 8,400 km between Antarctica and Central America (Rasmussen et al. 2007). The stereotype of mysticetes is that they migrate between high-latitude feeding grounds and low-latitude breeding and calving grounds, though the reason for these migrations is still widely debated (Corkeron & Connor 1999, Stevick et al. 2002, Geijer et al. 2016). Most of the debate centers around the benefits that low-latitude areas might provide, as whales often undergo months-long fasts to access them. Many hypotheses have been proposed, including that migrations may reflect historical patterns of prey distribution (Lipps & Mitchell 1976), calves may be better able to thermoregulate in warm waters (Clapham 2001, Rasmussen et al. 2007), calmer water may provide an easier environment for calves to swim in (Norris 1967), killer whale (*Orcinus orca*) predation on calves is reduced in lower latitudes (Corkeron & Connor 1999), and whales may need to conserve their body heat and molt in warm water (Pitman et al. 2020).

The stereotypical migration of baleen whales does not always hold, however, and there are more complex movement patterns than the basic low-to-high latitude pattern. There are populations of baleen whales that have year-round residency in warmer waters, including fin whales (*Balaenoptera physalus*) in the Mediterranean (Berube et al. 1998, Geijer et al. 2016) and the Gulf of California (Jiménez López et al. 2019) and blue whales (*B. musculus*) in the northern Indian Ocean (Cerchio et al. 2020). Additionally, many baleen whales seem to undergo differential or partial migration, where migration strategies vary among age classes, sexes, reproductive status, or among individuals (e.g., Brown et al. 1995, Craig et al. 2003, Soule & Wilcock 2013, Blevins et al. 2022). Migration strategies may also vary among populations, with some populations remaining year-round in a particular region and others following a more stereotypical low-to-high latitude migration pattern (Mizroch et al. 2009, Mizroch et al. 2016). Geijer et al. (2016) suggests that baleen whale migrations should be seen less as a single strategy, and more as a repertoire of strategies that range between complete migration and complete residency.

Cetacean movement and migration patterns can lead to population differentiation and structure even when there is a lack of geographic boundaries. Humpback whales, for instance, show site fidelity to ocean basins and follow similar migration routes throughout their life; these routes are maternally inherited and have produced population structure, with genetically distinct subpopulations in different ocean basins (Baker et al. 1990, Jackson et al. 2014). Understanding population structure in baleen whales is especially important because they were overexploited worldwide during 20th century whaling, with over two million killed in the Southern Ocean, and many are still listed as threatened or even endangered due to this exploitation (Clapham et al. 1999). Conservation applied at the population level ensures that a diversity of genetic, geographic, and life-history variation is represented, which increases the adaptive capacity of the species (Smith et al. 2018). This is the principle of “representation” and is used widely in the management of endangered species (Shaffer & Stein 2000). Protecting diversity in populations requires a thorough understanding of the population structure of baleen whales.

Antarctic blue whales (*B. m. intermedia*) were one of the principal targets of commercial whaling from 1904–1973, which caused them to be depleted from 239,000 to a low of 360 when whaling on this subspecies ended (Branch et al. 2004). Though the Antarctic blue whale population is estimated to be increasing at 7.3% per year (Branch et al. 2004), the most recent abundance estimate (in 2004) was less than 1% of their pre-exploitation levels (Branch 2007). It has long been assumed that Antarctic blue whales are comprised of a single circumpolar population, and this was the basis for previous assessments (Branch et al. 2004, Branch 2008). The key piece of evidence for a single circumpolar distribution of Antarctic blue whales is the existence of a characteristic blue whale song type, the Z-call, that is heard throughout the Southern Ocean (Miller et al. 2014, Shabangu et al. 2024). Song types are considered a reliable way to identify blue whales to population (McDonald et al. 2006) and have been used to distinguish populations of blue whales in other parts of the world, such as the Indian Ocean (Samaran et al. 2013) and North Pacific (Monnahan et al. 2014).

Additional lines of evidence for Antarctic blue whale population structure suffer from logistical constraints and small sample sizes. Genetic evidence for population structure in Antarctic blue whales is still ambiguous, and genetic samples have only been collected on the feeding grounds and not the breeding grounds (Sremba et al. 2012, Attard et al. 2016, IWC 2017). Photo-identification studies in the region suggest that Antarctic blue whales move widely throughout the Southern Ocean, though only 16 out of more than 500 identified whales have been resighted between years (Olson et al. 2022). Satellite tagging data are often used to study animal movement and could also provide evidence for Antarctic blue whale movements and inform population structure hypotheses. However, it has proven difficult to tag them in the Antarctic and the two Antarctic blue whales that have been satellite tagged do not resolve questions about population structure and migration (Andrews-Goff et al. 2022).

Overall, Antarctic blue whale movements and migration patterns remain uncertain. There is evidence that Antarctic blue whales undergo a low-to-high latitude migration, as indicated by the annual rise and fall of the population present in the Southern Ocean (Mackintosh 1966). In the 20th century, during the austral winter whaling seasons substantial numbers of Antarctic blue whales (>8,000) were caught off the coasts of Angola, Namibia, and the southwest coast of South Africa (Branch et al. 2007b), but not elsewhere in temperate Southern Hemisphere waters, perhaps because low-latitude whaling was concentrated in coastal and continental shelf waters with less effort offshore. More recently, Antarctic blue whales have been acoustically detected in the eastern tropical Pacific, the central Indian Ocean, off Australia and northern New Zealand, as well as off the coasts of Namibia and Angola (Stafford et al. 2004, McDonald et al. 2006, Branch et al. 2007b, Samaran et al. 2013, Thomisch et al. 2019, Torterotot et al. 2020). However, Antarctic blue whale calls are detected in the Southern Ocean year-round, which may indicate that some individuals remain in the Southern Ocean year-round or that the timing of migration differs between individuals (Branch et al. 2007b, Širović et al. 2009, Thomisch et al. 2016). Antarctic blue whale calls have also been heard in temperate waters off Namibia during the summer, providing additional evidence for variability in migration timing, or suggesting that some individuals skip migration and remain in temperate waters in summer (Thomisch et al. 2019). The low number of recorded calls and sightings of blue whales during winter months suggests that blue whales are widely dispersed offshore rather than congregating on low-latitude coastal breeding grounds like humpback and gray whales (*Eschrichtius robustus*) (e.g., Swartz et al. 2006, Rasmussen et al. 2007).

If Antarctic blue whales generally follow consistent migration routes and show long-term site fidelity to ocean basin feeding and breeding grounds, this could lead to population structure (Figure 1.1a). However, it is also possible that Antarctic blue whales have less consistent migratory routes and do not form distinct subpopulations due to defined movement patterns. Branch et al. (2007b) noted that the year-round distribution of Antarctic blue whales corresponds to areas with high densities of euphausiids, suggesting that foraging opportunities might drive migratory routes rather than fidelity to specific breeding grounds. Memory of previously successful and stable foraging sites has led to some degree of consistency in migratory routes in north-east Pacific blue whales (Abrahms et al. 2019), and between Australian feeding areas and Indonesian breeding areas in eastern Indian Ocean blue whales (Double et al. 2014, Möller et al. 2020). However, the Southern Ocean offers a very broad distribution feeding ground, and so may facilitate population mixing widely among feeding areas. Mixing in the feeding areas would not prevent population structure arising from geographic separation on the breeding grounds (Figure 1.1b), as has been seen for humpback and fin whales (Berube et al. 1998, Schall et al. 2021); conversely, gray whales mix on the breeding grounds but have feeding grounds spread more than 5,000 km apart from the Salish Sea to Kamchatka (Weller et al. 2012, Mate et al. 2015). If Antarctic blue whales are mixed in both the feeding and breeding areas, then they comprise a single circumpolar population (Figure 1.1, c-d**)**.

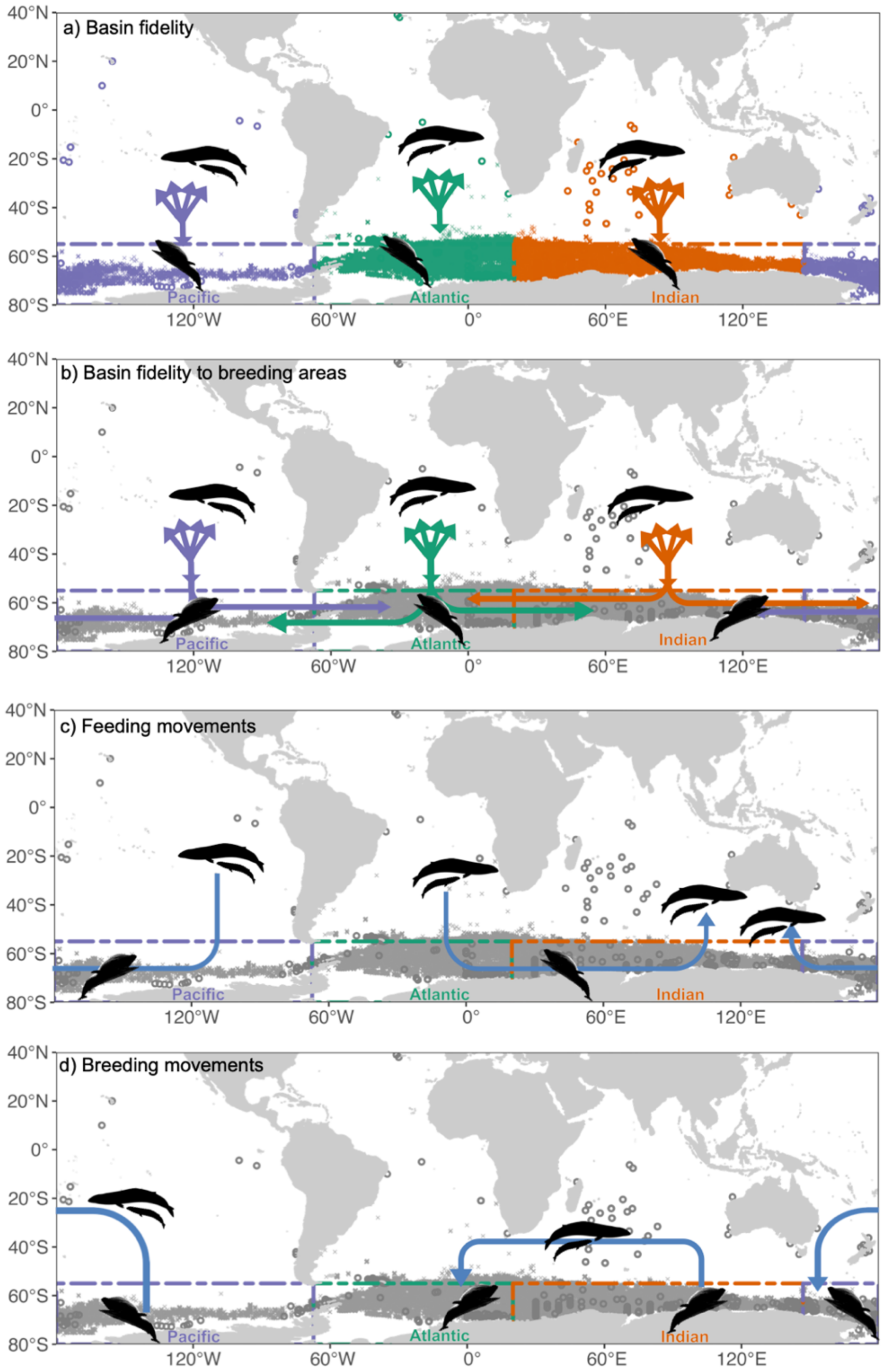

Figure 1.1 Possible scenarios for Antarctic blue whale low-to-high latitude migration including (a) migration routes that are consistently within the same ocean basin, (b) movement among basins during feeding but fidelity to breeding areas within ocean basins, (c) movement among basins during high-latitude feeding and then directed northward migration, and (d) movement among ocean basins at low latitudes and little movement during high-latitude feeding. Acoustic detections (Širović et al. 2018, Branch et al. 2019) of Antarctic blue whales are represented by the circles, and catches (Allison 2020) are represented by the crosses.

Mark-recovery data are often used to understand long distance movements of animals and to differentiate between populations (Schwarz et al. 1993, Nichols & Kendall 1995). During the whaling era, ‘Discovery marks’ were deployed extensively as part of the Discovery Marking project and the International Marking Scheme (e.g., Brown 1954, 1962, 1966). These marks consisted of 23-cm-long metal rods with a unique serial number and directions on where to return them when the whale was harvested. Marks were fired into the dorsal muscles of whales using a modified 12-bore gun (Rayner 1940, Brown 1977). These data have been used to evaluate migratory movements for fin, sperm (*Physeter macrocephalus*), and sei (*Balaenoptera borealis*) whales (e.g., Mizroch et al. 2009, Mizroch & Rice 2013, Mizroch et al. 2016), but analysis of these data for Antarctic blue whales so far has consisted of summarizing time to recapture and straight-line distances between marking and recovery (e.g., Brown 1962, 1966, Branch et al. 2007b, Olson et al. 2022), rather than estimating abundance, survival, and movement rates of Antarctic blue whales. Using these data to estimate movement rates of Antarctic blue whales during the whaling era can provide insight into historical patterns of movement and migration.

Mark-recovery models often use *a priori* designations of locations or strata and estimate movement probabilities between them. One difficulty in estimating population structure in the Southern Ocean only is that we are unable to determine if there is breeding site fidelity as well. Nevertheless, site fidelity to the ocean basins that make up the Southern Ocean (Atlantic, Indian, and Pacific), has been suggested to reflect fidelity to migration routes within these basins for other rorqual species (Pastene et al. 2009, Amaral et al. 2016, Pastene & Goto 2016). As a first step, therefore, we estimate historical interannual movement rates of Antarctic blue whales on the feeding grounds in the main oceanic basins using multistate mark-recovery models implemented in a Bayesian framework. While high probabilities of movement among ocean basins between years cannot rule out breeding site fidelity, low movement probabilities would suggest site fidelity of migrating whales to ocean basins, providing evidence for population structure within Antarctic blue whales.

1.2 Materials and methods

We built a multistate mark-recovery model to estimate interannual movement rates among the three ocean basins. To account for variable harvest rates among regions and over time without creating unwieldy numbers of parameters, we included a theta-logistic population model to estimate harvest rates for each basin and season which were used to predict mark-recoveries. The integrated model is spatially explicit, with model parameters for movement rates between regions, total carrying capacity across all regions, and population-wide intrinsic growth rate and mark loss.

1.2.1 Discovery mark data

Mark-recovery data from the Discovery Marking program and the International Marking Scheme were obtained from the IWC on 1 October 2020. Marking occurred between 1926 and 1963 and recoveries were reported between 1934 and 1962. From the 1960s, when pygmy blue whales (*Balaenoptera musculus brevicauda)* were identified (Ichihara 1961, 1966), researchers separated Antarctic and pygmy blue whales. We excluded identified pygmy blue whales from this study and all marks north of 52°S, where pygmy blue whales occur in summer (Branch et al. 2007a, Branch et al. 2009). There were no mark-recovery pairs with links between the Antarctic and any temperate regions. We grouped the marking and recovery locations into Atlantic, Indian, and Pacific Ocean basins based on the longitudinal boundaries of 20°E, 146.92°E, 67.26°W (Figure 1.2).

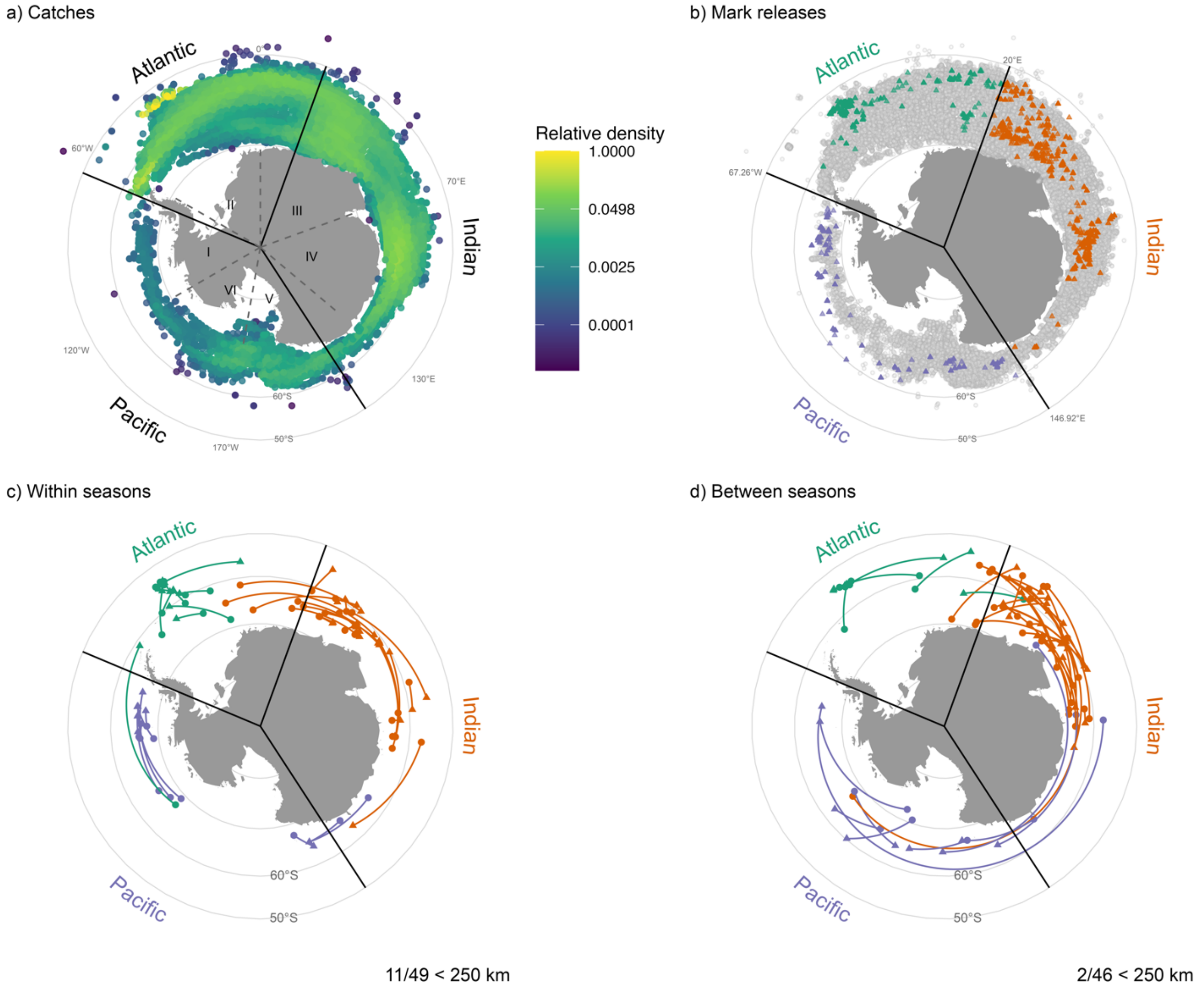

Figure 1.2 Catches and marking locations of Antarctic blue whales in the Southern Ocean, showing same-season mark-recovery pairs and marks recovered in a different season than when they were placed. Mark-recovery pairs are colored based on the basin where they were placed, with a triangles showing mark locations and circles showing recovery locations. Lines connecting marking and recovery locations are approximate and do not represent actual whale movements. For mark-recovery pairs less than 250 km apart, connecting lines are subsumed within the points. This occurred for 11 out of 49 within-season mark-recoveries and 2 out of 46 between-season mark-recoveries. Longitudinal boundaries for IWC management areas are indicated with dashed lines in panel (a) and boundaries for ocean basins by solid black lines.

1.2.2 Catch data

Historical catches of blue whales (not specifically listed as pygmy blue whales) in the Southern Ocean from 1905 to 1973 were obtained from the IWC (Allison 2020). We also included catches from temperate whaling stations, which were considered Antarctic blue whales based on detailed body measurements, including lengths (Mackintosh & Wheeler 1929). Analysis of length frequencies was used to further identify pygmy blue whale catches among the blue whale catches (Branch et al. 2019). Five blue whales coded as pygmy blue whales in the original catch database were recoded as Antarctic blue whales for this analysis, because they were caught south of 60°S and one was longer than maximum pygmy blue whale length of 24.2 m (Omura 1984). We assigned individual catches with location information to the Atlantic, Indian, or Pacific Ocean basins using the same longitudinal divisions used for the mark-recovery data (Figure 1.2). To correct for catches with no location data, total catches in each whaling season (Branch et al. 2004) were assigned to each basin in proportion to the number of catches with location data in each basin during that season. Catches without location data accounted for less than 12% of the total catches used in the model. The Southern Ocean whaling seasons, with peak catches in austral summer that straddled two calendar years, declined in length over time, from year-round in the early years to increasingly restricted to less than two months in the late 1950s. All catches from July 1 to June 30 were considered to be in the same southern whaling season and we use the start year as a shorthand, thus 1924 represents the 1924/25 whaling season. For the temperate whaling stations, peak catches were in winter and calendar years are used.

1.2.3 Modelling mark recoveries

We modelled the mark recoveries with a multistate mark-recovery model (Hilborn 1990) in which marks were grouped based on their original mark location. This model allowed us to estimate the probability that Antarctic blue whales moved among ocean basins from one whaling season to the next. Since marking effort and whaling effort often occurred in the same areas, we excluded all marks that were recovered in the same season. The number of marks applied in basin *g* that could be recovered in basin *i* in each subsequent season is given by:

$$\widehat{M}_{g,i,t+1} = \sum_{j=1}^{n=3} \left(\widehat{M}_{g,j,t} \left(1 - h_{j,t} \right) m_{j,i} s \right) \tag{1}$$

where $\widehat{M}_{g,j,t}$ is the number of marks from each group in each basin at the previous time step, $h_{j,t}$ is the harvest rate, $m_{j,i}$ is the probability of moving from basin *j* to basin *i* between seasons (including the probability of staying in basin *j*), and *s* is the yearly natural survival rate. This formulation assumes that harvest occurs before movement. Additionally, we assumed the probability of moving from basin *i* at time *t* to basin *j* at time *t* + 1 depended only on the location at time *t*.

From the number of marks that are estimated to be in each basin, we calculated the number of marks recovered in each basin and season:

$$\widehat{R}_{g,i,t+1} = \widehat{M}_{g,i,t+1} h_{i,t+1} (1 - l) \tag{2}$$

where $\widehat{R}_{g,i,t+1}$ is the predicted number of marks recovered, and l is the total probability that a mark is lost after being placed, either through falling out after placement, being missed during recapture, or not being reported despite recovery. This assumes that the probability of mark loss does not change with the duration of mark deployment. We also assessed a time-varying mark-loss model that used three mark-loss parameters that corresponded to three time periods which reflected the changes in the composition of whaling nations between the pre-WWII era, during WWII and immediately following it, and Soviet whaling (1930-1943, 1944-1956, and 1957-1972 respectively). However, this version did not improve model fit and therefore we only present the results of the simpler model with a single time-invariant mark-loss parameter. Mark recoveries in each basin were assumed to be independently and negative-binomially distributed, with a single parameter, θ,whose inverse controls the amount of overdispersion in all seasons and regions scaled by the square of the Poisson mean. After marks in year $t+1$ are recovered, the predicted number of available marks in each basin are increased by the new marks that were released in that basin and season ($T_{i,t+1}$):

$$\widehat{M}_{g,i,t+1} = \widehat{M}_{g,i,t+1} + T_{g,\ t+1}\ if\ \ g=i \tag{3}$$

Mark-recovery models assume that 1) the sample is representative of the population, 2) natural survival rates are not affected by marking, and 3) the fate of each marked individual is independent of other marked individuals. All these assumptions were met. Whaling was widespread throughout the Southern Ocean (Figure 1.2), and marking effort occurred on the hunting grounds, therefore marked individuals are representative of the population. Experiments with Discovery marks on Antarctic minke whales (*Balaenoptera bonaerensis*) estimated marking-induced mortality to be 3.8% based on the number of marks found touching bone (Best & Kato 1990). Since Antarctic blue whales are larger than minke whales, it would be harder for marks to fully penetrate to the bone, and therefore marking mortality is likely even smaller.

To test the sensitivity of the model to our selection of the ocean basins as the three states, we also fit the model to three regions based on IWC Management Areas (I+II, III+IV, and V+VI), and estimated movement rates for these regions using the same model outlined above (Supplement S1).

1.2.4 Population model of abundance and harvest rate

The number of marks recovered in each basin and season depends on movement rates and harvest rates (the proportion of whales caught in each region and season). Since catches varied greatly across time and space (Figure 1.3), mark-recovery rates that vary among seasons and basins were required. To incorporate this variation into the mark-recovery model without estimating hundreds of additional parameters, we included a model to estimate harvest rates in each basin and year. Since catch per unit effort (CPUE) for historical catches of whales is not available, we used a population model to estimate these harvest rates starting in 1904. We modelled the population size of Antarctic blue whales in each ocean basin with a theta-logistic model:

$$N_{t+1,\,i} = N_{t,i} + rN_{t,i}\left(1-\left(\frac{N_{t,i}}{K_i}\right)^{\phi}\right) - C_{t,i} \tag{4}$$

where the shape parameter $\phi = 2.39$ is set to ensure that maximum sustainable yield (MSY_i) is obtained at 60% of carrying capacity (K_i), as is common practice for the IWC (Baker & Clapham 2004). We assumed there was a different carrying capacity (K_i) in each ocean basin. To include the same survival parameter (s) in both the mark-recovery and population model, we reparameterized the population model to explicitly incorporate survival, by setting $r = (1-s)\cdot r^*$, where r^* is the limit of the growth rate not accounting for natural survival.

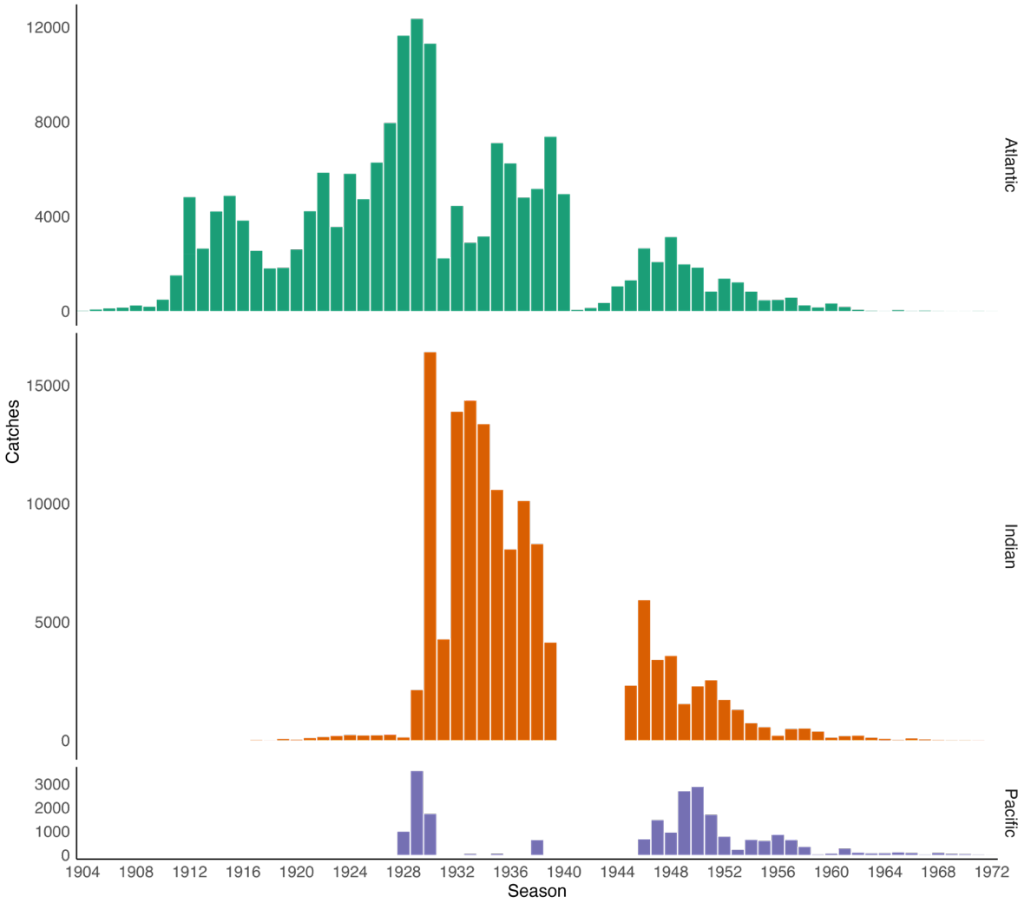

Figure 1.3 Total Antarctic blue whale catches by ocean basin and whaling season.

In the above formulation (Eqn. 4), r and K are highly correlated, and therefore we further reparametrized the model using the fact that $MSY_i = \frac{(1-s)\,r^* K_i \phi}{(\phi+1)^{\frac{1}{\phi}+1}}$ to improve convergence (Monnahan et al. 2015):

$$N_{t+1,\,i} = sN_{t,\,i} + (1-s)\,N_t\left(1+r^*\right)\left(1-\left(\frac{(1-s)\,r^*\phi N_{t,i}}{MSY_i(\phi+1)^{\frac{1}{\phi}+1}}\right)^{\phi}\right) - C_{t,i} \tag{5}$$

The same movement rates used in the mark-recovery model (Eqn. 1) were used for movement between ocean basins in the population model. It was assumed that movement occurred after harvest and natural survival:

$$N_{t+1,\,i} = m_{ii} N_{t+1,\,i} + \sum_{j \in j \neq i} m_{ji} N_{t+1,\,j} \tag{6}$$

Movement rates between basins and the equilibrium population sizes (K_i) in each basin are not independent, therefore we estimated the total carrying capacity of blue whales (*K)* in the Antarctic, then split this into basin-specific carrying capacities (K_i) using the equilibrium distribution of the movement rates. Equilibrium proportions were calculated by multiplying the matrix of movement rates by itself 100 times and then confirming the equilibrium distribution had been reached by checking that all rows of the resulting movement matrix were the same.

The population model was fit to abundance estimates of Antarctic blue whales by ocean basin, but since these were not available for our defined regions, abundance estimates available for each IWC management area (Branch 2007, Hamabe et al. 2023) were assigned to basin-wide abundances according to the proportion of the longitudinal range of each IWC area within each basin (Table 1.1), thus assuming that blue whales are uniformly distributed across each IWC management area.

Table 1.1 Proportion of each IWC management area assigned to each basin

Basin	All	Part
Atlantic	II	7/60 of I 20/70 of III
Indian	IV	50/70 III 17/60 V
Pacific	VI	53/60 I 43/60 of V

We used abundance estimates from circumpolar line-transect surveys conducted between 1978/79 and 2003/04 (Branch 2007) as well as line-transect surveys (JARPA and JARPAII) conducted in IWC areas IV and V (70°E - 170°W) between 1989/90 and 2007/08 (Hamabe et al. 2023). Since the surveys covered different IWC areas in different years, the year of the estimate for each basin was calculated as a weighted average of the years of the corresponding IWC areas. Coefficients of variance (CVs) were calculated by converting the CVs of individual estimates into variances, taking a weighted average of the variances, and then converting the averaged variances back into CVs (Table 1.2). An additional model run was fit to previously published relative abundance estimates from JARPA and JARPAII surveys in IWC areas III-VI (35°E - 145°W (Matsuoka & Hakamada 2014) instead of Hamabe et al. (2023) to test the sensitivity of the model to the differences between these estimates (Supplement S2).

Table 1.2 Abundance estimates, year, and CV for each basin based on abundance estimates, year, and CV from IWC management areas.

Year	Basin	Abundance	CV	Source
1981	Atlantic	91	0.34	Branch (2007)
1986	Atlantic	210	0.4	Branch (2007)
1996	Atlantic	326	0.35	Branch (2007)
1979	Indian	197	0.25	Branch (2007)
1987	Indian	141	0.28	Branch (2007)
1989	Indian	83	0.54	Hamabe (2023)
1991	Indian	78	0.33	Hamabe (2023)
1993	Indian	92	0.26	Hamabe (2023)
1995	Indian	2	0.75	Hamabe (2023)
1996	Indian	754	0.16	Branch (2007)
1997	Indian	174	0.42	Hamabe (2023)
1999	Indian	262	0.39	Hamabe (2023)
2001	Indian	393	0.3	Hamabe (2023)
2003	Indian	45	0.32	Hamabe (2023)
2005	Indian	265	0.36	Hamabe (2023)
2007	Indian	380	0.37	Hamabe (2023)
1982	Pacific	278	0.22	Branch (2007)
1988	Pacific	334	0.23	Branch (2007)
1990	Pacific	81	1.45	Hamabe (2023)
1992	Pacific	150	0.61	Hamabe (2023)
1994	Pacific	107	0.73	Hamabe (2023)
1996	Pacific	4	1.34	Hamabe (2023)
1998	Pacific	128	1.2	Hamabe (2023)
1999	Pacific	1126	0.14	Branch (2007)
2000	Pacific	95	1.21	Hamabe (2023)
2002	Pacific	92	1.09	Hamabe (2023)
2004	Pacific	70	0.61	Hamabe (2023)
2006	Pacific	88	1.21	Hamabe (2023)
2008	Pacific	538	0.95	Hamabe (2023)

Abundance estimates from Branch (2007) cover entire ocean basins, however, the Hamabe et al. (2023) estimates only cover 60% of Indian Ocean longitude and 29% of Pacific Ocean longitude. These were treated as relative indices of abundance ($I_{i,t}$), and two survey coverage parameters, q_i (Indian, Pacific) were calculated to account for the proportion of whales in that basin that were not covered by the Hamabe et al. (2023) estimates, using the maximum likelihood estimate for q_i:

$$\widehat{q}_i = exp\left(\frac{1}{n_{year}} \sum_t \ln\left(\frac{I_{i,t}}{\widehat{N}_{i,t}}\right)\right) \tag{7}$$

where n_{year} is the number of years of abundance estimates in that basin, and $I_{i,t}$ are the abundance estimates from these surveys for each basin and year. All abundance estimates were assumed to be independent and lognormally distributed.

The harvest rates for the mark-recovery model are:

$$\widehat{H}_{i,t} = \frac{C_{i,t}}{\widehat{N_{i,t}}} \tag{8}$$

where $\widehat{N}_{i,t}$ is the estimated abundance in each basin and season from the population model (Eqn. 6) and $C_{i,t}$ is the numbers of whales caught in each basin and season. To avoid numerical issues, if the catch in a basin was greater than the estimated population size in that basin, the harvest rate for that season and basin was set to one (all whales in that basin were harvested) and the population size was set to 0.99 in that basin for that season. Model results were examined to be sure no final fitted population sizes were less than the catch in any season.

1.2.5 Bayesian estimation

Models were fit with Bayesian methods using Stan v2.31 (Stan Development Team 2024) through the CmdStan and cmdstanr interfaces (Gabry & Cesnovar 2022) in R v.4.2.2 (R Core Team 2023). We fixed $s = 0.96$ (Branch et al. 2004). The prior for r was assumed to be $r \sim U[0,0.114]$, with the upper bound based on the biological upper bound for the intrinsic rate of growth for blue whales (IWC 2013). The prior for K was assumed to be $\log(K) \sim U[9, 13]$ with the upper bound above that estimated for Antarctic blue whales based on a previous study (Branch et al. 2004): 239,000 (95% interval 202,000–311,000), and the lower bound lower than the minimum value that would prevent the population from going extinct based on the catch series. The prior on movement between basins ($m_{i,j}$) was assumed to be U[0, 0.50], as a higher probability of movement would suggest that fewer individuals remain than leave between seasons, which is unlikely, as the Southern Ocean is a stable and plentiful food source and whales would be unlikely to preferentially avoid a previous foraging ground. The probability of remaining in each basin between seasons ($m_{j,j}$) was calculated by subtraction, so that movement and staying probabilities for each basin summed to one. A Beta (1,1) prior was used for the mark loss parameter (l), as is common for binomial probabilities. The models were fit with 4 chains, 2,000 iterations and a 50% warm-up. The adapt delta parameter for the No-U-Turn-Sampler, which controls the target acceptance rate, was set to 0.98 and the maximum tree depth was set to 20. All results converged based on trace plots, autocorrelation plots, the Geweke statistic, and $\widehat{R}$ values. For all parameters, convergence values from Bayesian estimation were satisfactory ($0.999 < \widehat{R} < 1.005$ and effective sample size > 881.) Model fit was assessed using posterior predictive checks. Estimates are reported as the posterior medians, and the 2.5% and the 97.5% quantiles as a measure of uncertainty in the estimates. Data and code used for these analyses can be found at: https://github.com/zoer27/MoveABWDiscMarks.

1.2.6 Simulations

We tested the ability of the models to distinguish between low-movement and high-movement scenarios with simulated datasets. For these data sets, we used the mark-recovery and theta-logistic population models described above to create simulated abundance and mark-recovery data sets from the actual number of marks released in each basin and season and the actual catch series, while setting $r = 0.073$, $s = 0.96$, $l = 0.96$, and $K = 200{,}000$. These parameter values were selected based on estimates from Branch et al. (2004). We considered two scenarios for the movement rates, one with high movement among the basins between seasons ($m_{ji} = 0.25, \forall\, i, j \in j \neq i$) and one with low movement ($m_{ji} = 0.01, \forall\, i, j \in j \neq i$) . Simulated marks recovered for each basin and season were drawn randomly from a negative binomial distribution with mean equal to the predicted marks recovered in each basin and season ($\widehat{R}_{g,i,t+1}$) and the overdispersion parameter $\theta = 0.8$. Simulated abundance estimates for the corresponding basin and season included in the actual abundance data were drawn from a lognormal distribution with a mean equal to the log of the predicted population size in that basin and season ($\widehat{N}_{i,t}$) and a CV of 0.2, but assuming that the survey covered the entire ocean basin, thus removing the need to estimate a q_i parameter for partial surveys. Each scenario was simulated 60 times, with different random seeds. The Bayesian estimation model described above was fit to these simulated datasets, each with two chains, 1,600 and 2,500 iterations (high movement and low movement scenarios respectively) and a 50% warm-up, and only simulations which converged based on the diagnostics described above were used.

1.3 Results

1.3.1 Mark recoveries within seasons

A total of 2,159 Antarctic blue whales were marked and 95 marks were recovered. However, 52% (*n* = 49) of the marks were recovered during the same season in which they were marked, and therefore not used to model between-season movements in this study. Most within-season mark recoveries occurred less than 60 days after marking (median duration 43 days, 8–55 days interquartile range), though one mark was recovered 114 days after marking. The median straight-line distance travelled between marking and recovery for same-season recoveries was 669 km (302–1,820 km interquartile range). Ten Antarctic blue whales recovered during the same season had moved to a different ocean basin. Multiple individuals moved between the Atlantic and the Indian ocean basins, and some movement from the Pacific to the Indian was observed. One mark was placed in the Atlantic and recovered in the Pacific, but no individuals marked in the Pacific were recovered in the Atlantic (Table 1.3).

Table 1.3 Number of Antarctic blue whale marks marked and recovered in the same season in each ocean basin. “p(basin)” indicates the proportion marked in each basin (N/Total) and “Prop.” indicates the proportion of marks recovered in each of the three basins.

		Atlantic	Indian	Pacific	Total
Marked	N marked	14	25	10	49
	p(basin)	0.29	0.51	0.20	1
		Prop.	Prop.	Prop.	
Recovered	Atlantic	0.93	0.24	0.00	
	Indian	0.00	0.76	0.23	
	Pacific	0.07	0.00	0.80	

1.3.2 Mark recoveries between seasons

A total of 46 marks were recovered interannually out of the 2,110 marks not recaptured in the same season. Most of these marks (63%) were recovered in the Indian Ocean (the location of 41% of catches); and in all basins, more marks were recovered in the same basin in which they were marked than in another ocean basin. No individuals marked in the Atlantic were recovered in the Pacific or vice versa (Table 1.4).

Table 1.4 Number of Antarctic blue whale marks marked, and number recovered in each ocean basin excluding same season recoveries. “p(basin)” indicates the proportion marked in each basin (N/Total) and “p(recovered)” indicates the proportion of marks in each basin that were recovered. “Prop.” indicates the proportion of recovered marks found in each basin.

		Atlantic	Indian	Pacific	Total
Marked	N marked	772	1012	326	2110
	p(basin)	0.37	0.48	0.15	1
	N recovered	8	29	9	46
	p(recovered)	0.010	0.029	0.028	0.022
		Prop.	Prop.	Prop.	
Recovered	Atlantic	0.87	0.21	0.00	
	Indian	0.13	0.76	0.44	
	Pacific	0.00	0.03	0.56	

Most between-season mark recoveries occurred less than five years after marking (median duration 1.34 years, 0.85–4.15 years IQR). However, one mark was recovered 12 years and 10 months after it was placed. The median straight-line distance for marks that were recovered in the same basin where they were placed was 1,320 km (810–1,868 km IQR). For marks recovered in a different basin than they were marked, the median straight-line distance between marking and recovery was 2,046 km (1,665–4,591 km IQR). The longest distance between marking and recovery was 6,250 km and was from a mark placed in the Pacific basin and recovered in the Indian basin.

1.3.3 Parameter estimates

The total carrying capacity (and assumed pre-whaling abundance) for the Southern Ocean was estimated to be 186,335 (95% BCI: 170,485–204,579; Figure 1.4), with more estimated to be in the Pacific Ocean basin: 83,987 (68,919–101,474), than the Atlantic Ocean: 36,817 (26,057–51,417) or Indian Ocean: 64,654 (52,440–79,403) basins. The intrinsic growth rate (r) was estimated to be 0.086 (0.068–0.104). The probability of mark loss (l) was estimated to be 0.959 (0.928–0.973, Table 1.5, Figure 1.4).

Table 1.5 Median parameter estimates, lower and upper bounds of 95% credible intervals

Parameter	Description	Median	2.5%	97.5%
r	Intrinsic growth	0.086	0.068	0.104
K	Carrying capacity (Total)	186,335	170,485	204,579
K_{Atl}	Carrying capacity (Atlantic)	36,817	26,057	51,417
K_{Ind}	Carrying capacity (Indian)	64,654	52,440	79,403
K_{Pac}	Carrying capacity (Pacific)	83,987	68,919	101,474
$m_{\mathrm{Atl}\rightarrow\mathrm{Atl}}$	Movement	0.558	0.198	0.783
$m_{\mathrm{Ind}\rightarrow\mathrm{Atl}}$	Movement	0.126	0.027	0.339
$m_{\mathrm{Pac}\rightarrow\mathrm{Atl}}$	Movement	0.082	0.009	0.243
$m_{\mathrm{Atl}\rightarrow\mathrm{Ind}}$	Movement	0.145	0.006	0.463
$m_{\mathrm{Ind}\rightarrow\mathrm{Ind}}$	Movement	0.537	0.321	0.736
$m_{\mathrm{Pac}\rightarrow\mathrm{Ind}}$	Movement	0.275	0.133	0.459
$m_{\mathrm{Atl}\rightarrow\mathrm{Pac}}$	Movement	0.287	0.040	0.486
$m_{\mathrm{Ind}\rightarrow\mathrm{Pac}}$	Movement	0.324	0.144	0.484
$m_{\mathrm{Pac}\rightarrow\mathrm{Pac}}$	Movement	0.635	0.444	0.769
l	Mark loss	0.959	0.928	0.973
θ	Overdispersion	0.421	0.192	1.149
q_{Ind}	JARPA coverage (Indian)	0.132	0.101	0.174
q_{Pac}	JARPA coverage (Pacific)	0.080	0.063	0.101

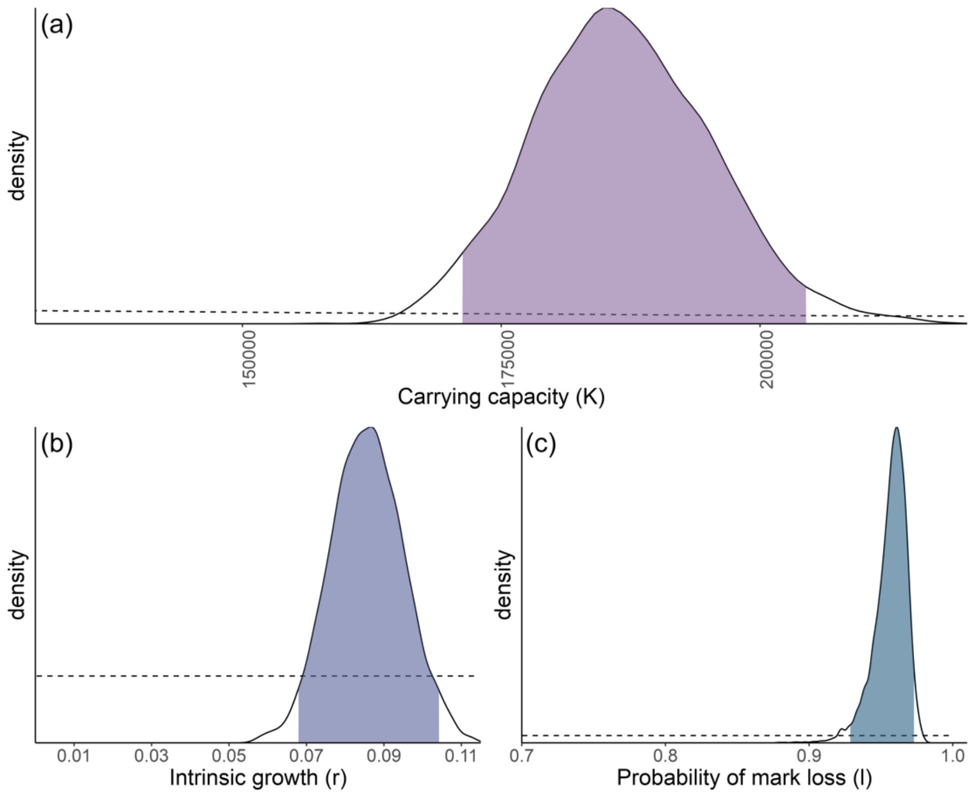

Figure 1.4 Posterior densities of key parameters. Prior (dashed line) and posterior distributions (solid line) with 95% credible interval (shading) for (a) total Antarctic blue whale carrying capacity in the Southern Ocean, (b) intrinsic rate of growth, and (c) mark loss. Parts of the priors for carrying capacity ($\ln K \sim U[9, 13]$) and mark loss ($l \sim \text{Beta}[1,1]$) are beyond the limits of these plots.

The model provided good fits to the abundance estimates, with abundance estimates aligning well with the posterior predictive distributions from the model (Figure 1.5). The model also provided good fits to the mark-recovery data, with most of the data aligning well with the posterior predictive distributions, except in the case of marks placed in the Pacific and recovered in the Indian, where the model predicts recoveries earlier in time than observed, and in the case of marks placed in the Pacific and recovered in the Atlantic, where the model predicts recoveries even though none were observed (Figure 1.6).

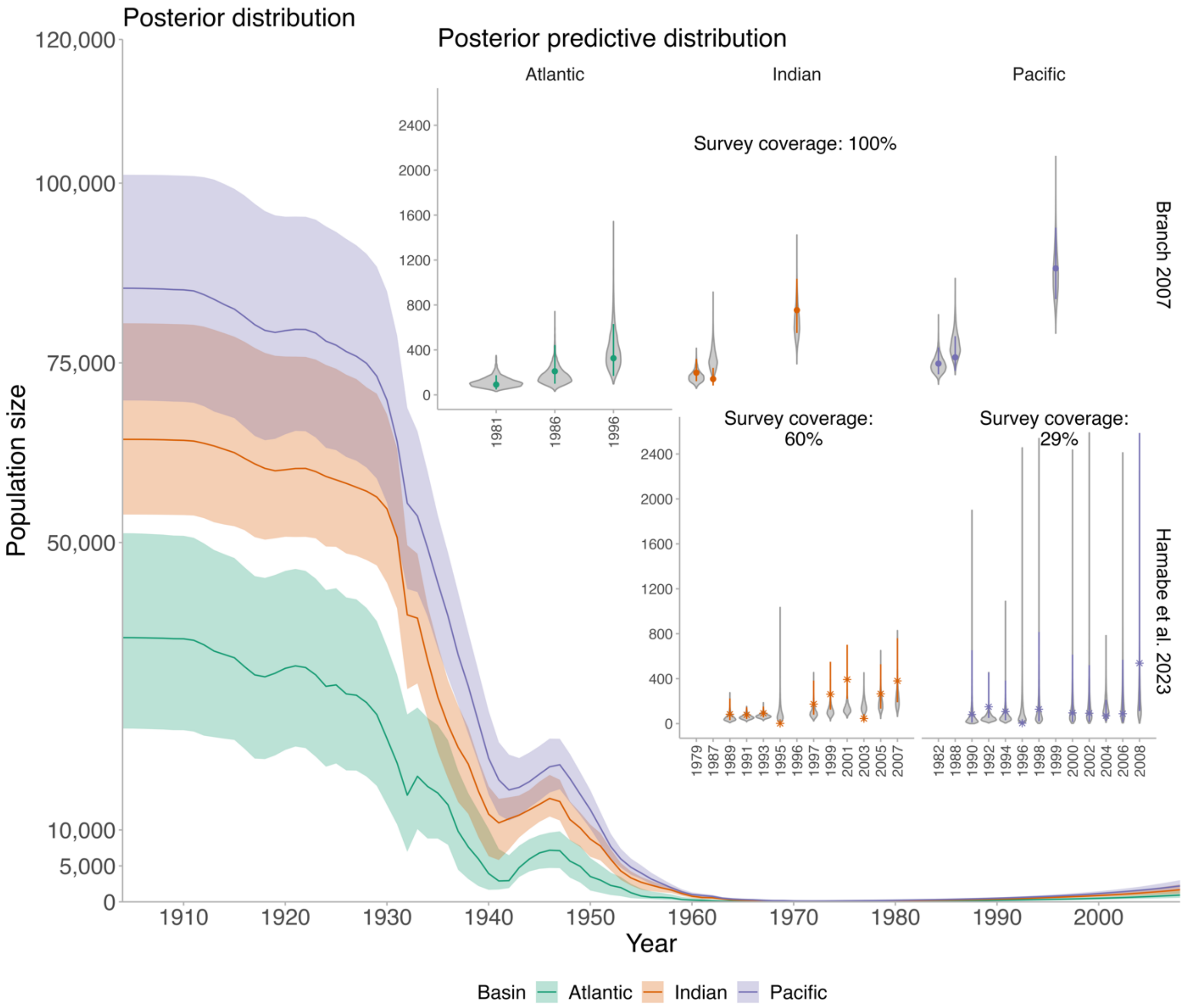

Figure 1.5 Posterior distribution of Antarctic blue whale population size. Posterior medians (solid line) and 95% credible intervals (shading) of Antarctic blue whale population size in each basin (left) and posterior predictive distributions (violins, inset) for each abundance estimate (Table 1.2) with points representing Branch (2007) and stars representing Hamabe et al. (2023). The 95% confidence intervals were calculated from CVs (lines). Survey coverage indicates the proportion of longitude of each basin that was covered by the surveys.

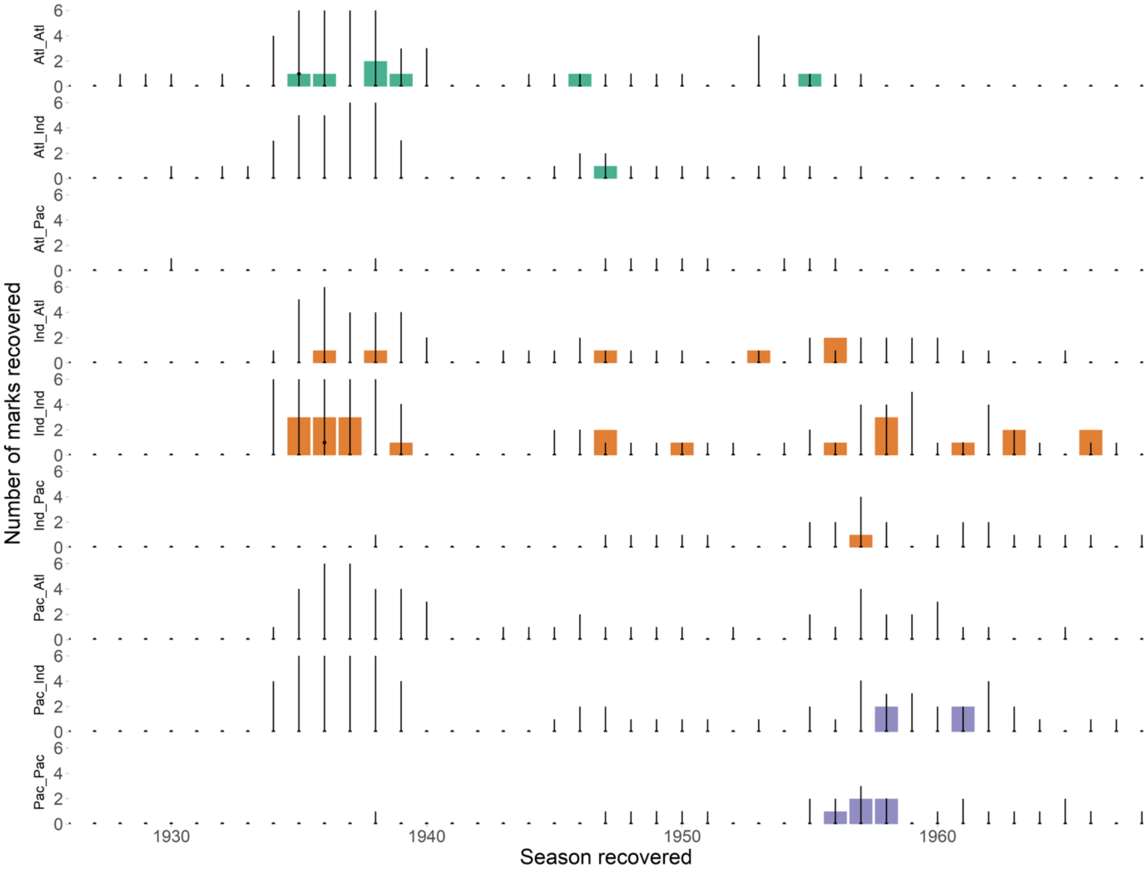

Figure 1.6 Posterior predictive distributions. Posterior predictive medians (points) and 95% intervals (lines) for the number of marks that were originally marked in basin *i* that are recovered in basin *j* (groups are listed as i_j) in each season, as well as actual number of marks recovered for each group in each season (bars). Note that some intervals are subsumed within the points.

Our model estimates that interseason movement between the Indian and Pacific Ocean basins is frequent, with high annual probabilities of moving from the Pacific to the Indian ocean basin and vice versa (0.275 and 0.324 respectively). Similarly, we found relatively frequent interseason movement between the Indian and the Atlantic Ocean basins (0.126 and 0.145). However, while we estimated a high probability of moving from the Atlantic to the Pacific (0.287), the reverse movement was low (0.082) (Table 1.5). Some of these parameter estimates are uncertain and movement between the Atlantic and Pacific may not be fully identifiable given the data as the posterior distributions are very similar to the prior distributions (Figure 1.7).

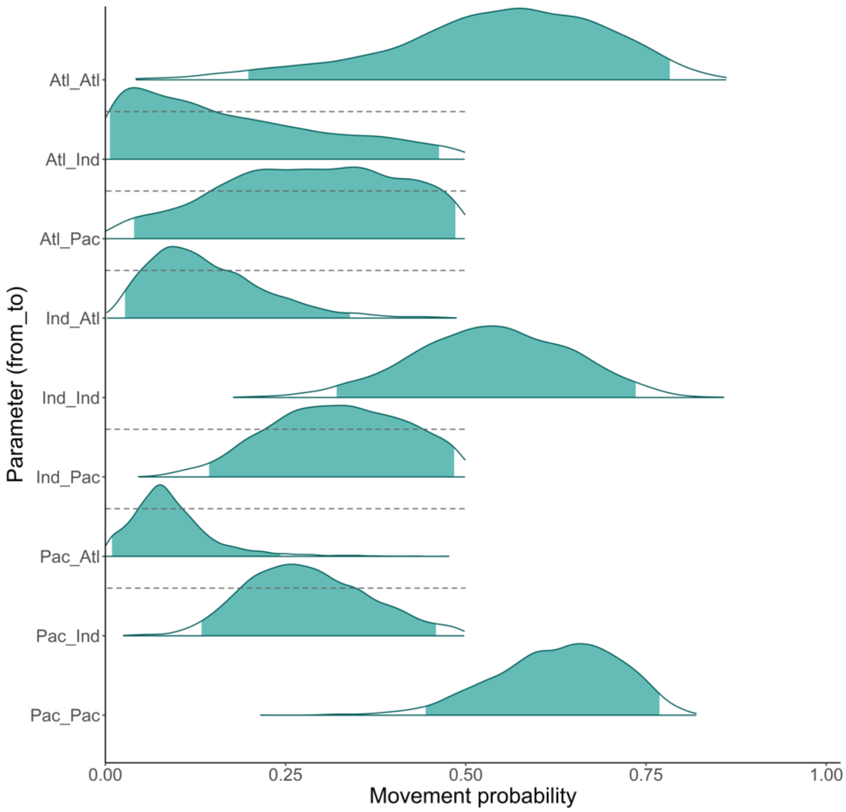

Figure 1.7 Posterior distributions of movement rates. Prior (dashed line) and posterior (solid line) distributions and 95% credible intervals (shaded) for movement probabilities among basins (listed as from_to). The probability of remaining in a basin from season to season was calculated by subtraction.

Based on the estimated movement matrix, the equilibrium distribution of movement rates is reached in less than 10 years, and at this equilibrium, no matter where they start, 20% (14%-27%) of Antarctic blue whales are in the Atlantic basin, 35% (29%-41%) in the Indian basin, and 45% (38%-52%) in the Pacific basin.

We also fit the model to previously published Matsuoka and Hakamada (2014) abundance estimates for the partial surveys instead of Hamabe et al. (2023). Though these abundance estimates are from the same surveys, they were calculated differently and the Matsuoka and Hakamada (2014) estimates cover a larger proportion of the Antarctic (35°E - 145°W). Despite these differences, our median parameter estimates differed by no more than 8% with similar credibility intervals between the two runs, except that the survey coverage parameter (q) for the Matsuoka and Hakamada (2014) abundance estimates were 0.529 and 0.130 (Indian and Pacific, respectively) instead of 0.133 and 0.080 since they covered a greater proportion of these basins (Supplement S2).

1.3.4 Simulation results

For the high-movement scenario, the true values of all parameters fell within the 95% credible intervals of the corresponding posterior distributions in at least 57 of the 60 (95%) simulations for the high-movement scenario. For the low-movement scenario, two simulations were removed because they did not converge. In the converged simulations, the true values of parameters fell within the 95% credible interval in at least 55 of 58 simulations (95%), except the probability of remaining in the Atlantic, which was frequently underestimated (52% of simulations). The probability of remining in the Pacific, and the probability of moving from the Pacific to the Atlantic were also occasionally underestimated (24% of simulations) and the true carrying capacity in the Atlantic fell outside of the 95% credible interval in 22% of simulations but not in a consistent direction (Figure 1.8).

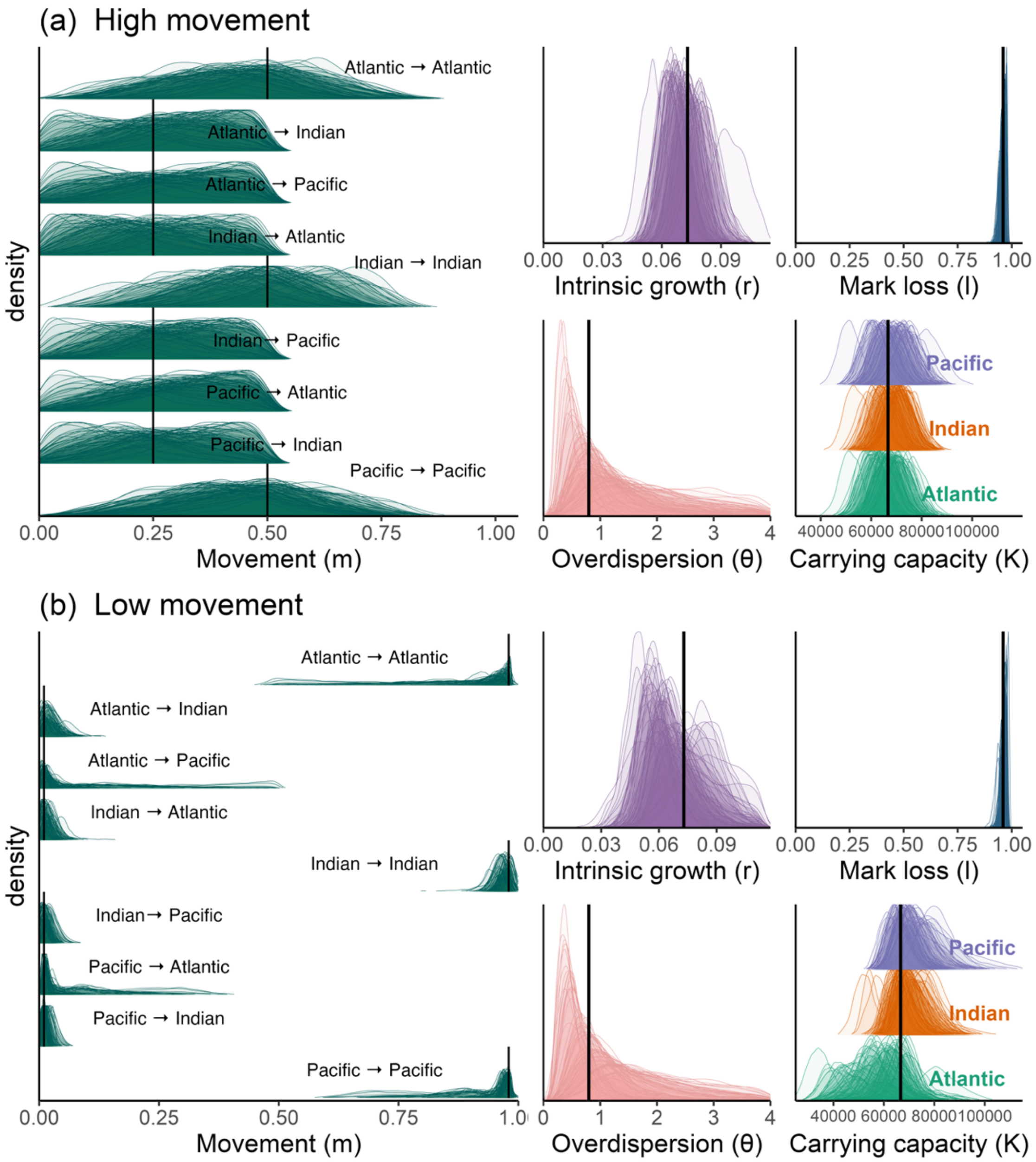

Figure 1.8. Results from simulation experiments. Posterior distributions of parameters from models fit to 60 simulated data sets under high movement (a, 25% move, 50% stay) and low movement (b, 1% move, 98% stay) scenarios. Values used in simulating data are represented by vertical lines.

1.4 Discussion

We outlined four possible scenarios for Antarctic blue whale migration and movement (Figure 1.1), noting that population structure would require breeding ground fidelity. We can eliminate the first scenario: separate populations each breeding and feeding in the same ocean basin, since we found frequent mixing of individuals between the three basins. Even movement at the lowest estimated rate, from the Pacific to the Atlantic (8.2% per year, Table 1.5), is sufficient for complete mixing after only a few years, and blue whales were predicted to move from the Pacific to the Indian and then to the Atlantic at much greater rates. The equilibrium distribution of the movement matrix also suggests that even with low rates of direct movement between the Atlantic and the Pacific, Antarctic blue whales would still be well-mixed throughout the Southern Ocean within ten years.

Our model is unable to distinguish between a scenario where Antarctic blue whales mixed on the feeding grounds but showed fidelity to breeding areas and scenarios where population mixing occurred on either the austral summer feeding grounds or during the austral winter (Figure 1.1, b-d). Same-season mark recoveries indicate that Antarctic blue whales did move widely while in the feeding areas (Figure 1.2), and it is unlikely that movements were restricted to only the feeding grounds. Between-season mark recoveries suggest that Antarctic blue whales moved 2,000–6,000 km between basins in the Southern Ocean. If Antarctic blue whales must travel more than 6,000 km between breeding and feeding areas, and also move 4,000 km on the feeding grounds, an individual would need to travel 10,000 km back to the same breeding area, which, at an average swimming rate of 4.3 km/hr (Calderan et al. 2023) would take more than three months. If whales leave the feeding grounds in April, this would not allow them sufficient time to get to the breeding grounds for calving and conception, which is thought to occur in May–July (Mackintosh & Wheeler 1929, Barlow et al. 2023). Of course, it is conceivable that some Antarctic blue whales may skip one breeding season and remain in the Antarctic, and then return to a particular ocean basin to breed two years later. Data on winter movements of Antarctic blue whales from photo-ID or satellite tagging are needed to differentiate between these possibilities. Given Southern Hemisphere-wide winter acoustic detections of Antarctic blue whales (Širović & Oleson 2022) they may be dispersed widely in the winter months instead of aggregating on discrete calving grounds. Avoiding predation from killer whales has been suggested as a primary motivation for baleen whale migration (Corkeron & Connor 1999). This spatially diffuse approach to breeding, therefore, would be consistent with Antarctic blue whale antipredator strategies, since blue whales flee killer whales at high speeds rather than group together to defend calves like humpback whales (Ford & Reeves 2008).

Information from acoustic song and genetics can be used to further inform Antarctic blue whale population structure. Notably, each blue whale population calls with a distinctive song (McDonald et al. 2006) and the characteristic Z-call in Antarctic blue whale song is heard throughout the Southern Ocean in summer and the Southern Hemisphere in winter (Miller et al. 2014, Shabangu et al. 2024). The most in-depth genetics study of Antarctic blue whales found no evidence of distinct populations within Antarctic blue whales (Attard et al. 2024) and this supersedes earlier studies based on limited haplotypes that returned more ambiguous results (Attard et al. 2016, IWC 2017). A primary challenge for identifying population structure through genetics in Antarctic blue whales is that genetic samples have been collected solely on the feeding grounds. If genetic segregation occurs only during breeding it would be difficult to detect if the populations mix widely on the feeding grounds. For species such as humpback and southern right whales (*Eubalaena australis*) where genetic population differentiation is clear, most of the genetic data were collected on breeding grounds.

Photo-ID matching in the region has shown frequent movement among regions, except between the Pacific and Atlantic basins, however only 16 (of over 500) whales have been resighted between years and most of the effort is concentrated in IWC areas III and IV (Atlantic and Indian basins, (Olson et al. 2020, Olson et al. 2022). Satellite tagging of two individuals also suggests that Antarctic blue whales roam widely in the Southern Ocean, these whales moved 1,433 km (in 14 days) and 6,107 km (in 74 days) respectively (Andrews-Goff et al. 2022, Olson et al. 2022). Both tags demonstrated considerable longitudinal movements, and the whales both crossed the Indian-Pacific dividing line, one from each direction (Olson et al. 2022), but the small sample size and short tagging durations mean that these data provide limited insights into global Antarctic blue whale movement or population structure.

Our estimated carrying capacity for Antarctic blue whales in the Southern Ocean, 170,000–205,000, is smaller and had a narrower credible interval than the 202,000–311,000 estimated in Branch et al. (2004), though the intervals do overlap. This difference is caused by several factors: notably, we estimated the intrinsic rate of increase (*r*) to be 0.086 which is higher than the median in Branch et al. (2004), and a high *r* implies a smaller carrying capacity. Furthermore, our study had a larger number of data points for abundance than Branch et al. (2004), which led to a narrower credibility interval for *r* and *K*. In addition, our model estimated a higher carrying capacity in the Pacific than in the other basins even though only 7% of all catches came from the Pacific (Figure 1.3). This allowed for a smaller pre-exploitation population size without whaling causing the population to go extinct, since the Pacific could function as a partial refuge from whaling and replenish the other basins where catches were higher. The high carrying capacity in the Pacific is a direct result of higher proportions of blue whales remaining in the Pacific (0.444–0.769, Table 1.5) combined with high movement rates from the Atlantic and the Indian into the Pacific. Thus, the model is balancing observed high catches in the other two basins against the movement rates inferred from the Discovery marks. While the Pacific was further from the major modern whaling nations (Norway, Japan, UK), and was closed to whaling in some seasons, we consider this higher population size in the Pacific to be unrealistic for the simple reason that if whales were present in high numbers in the Pacific, more whalers would have focused on this region. Regardless, high movement rates among the ocean basins would lead to similar levels of depletion Antarctic-wide after only a few years, regardless of initial numbers of whales in those basins, and therefore it may not matter what proportion of Antarctic blue whales were in the Pacific Ocean before the start of whaling.

The movement parameters estimated in this study are uncertain because of the small numbers of interseason mark recoveries and variable marking effort among basins. It is worth noting that in the between-season data used to fit the model, no marks that were originally placed in the Atlantic were recovered in the Pacific and no marks placed in the Pacific were recovered in the Atlantic. Therefore, while the model predicts some direct movement between the Atlantic and the Pacific, no movement between these basins has been observed between seasons. In the within-season data, only one whale marked in the Atlantic was recovered in the Pacific (Figure 1.2c). Even in photo-ID studies, only one whale has been observed in both the Atlantic and Pacific basins, and this whale was recaptured very close to the Pacific-Indian boundary (Olson et al. 2022). In addition to a lack of movement between these two regions, these zeros could also be caused by lower marking effort in the Pacific and the Atlantic, lower recovery rates in the Pacific due to fewer catches, and the high rate of mark loss. As a result, the posterior distributions of these parameters are broad. This likely also explains the differences in model estimates between simulations in the low movement scenario. Additionally, the high estimated rate of mark loss (0.959) may be caused, in part, by underreporting of marks by Soviet whalers who were whaling illegally (Ivashchenko & Clapham 2014). Though much of the data from Soviet whaling has been recovered, it is possible that whalers hunting illegally may have discarded any marks that were found. However, this likely only accounted for very few of the lost marks, and the high rate of mark loss may also reflect a large proportion of whales naturally shedding marks over time. Given the small amount of information in the mark-recovery data, model estimates of movement rates between the Atlantic and the Pacific are driven primarily by the prior, the catch series and the abundance estimates.

While our results at a basin scale on the feeding grounds show mixing, there might be finer-scale site fidelity. For example, around South Georgia, and geographic barriers to movement in specific directions might have been obscured by movement in and out of other portions of the basins. Genetic population structure between the Atlantic and Pacific basins in the Southern Hemisphere have been found for both southern right whales and humpback whales (Cypriano-Souza et al. 2017, Carroll et al. 2020), which suggests that an oceanographic barrier, such as the Drake passage, might limit mixing between these two basins for some species. The minimal mark-recoveries between the Atlantic and Pacific basins in both the Discovery marks and photo-ID studies suggest that this may also be a barrier to movement for Antarctic blue whales. Additionally, Antarctic blue whales may favor certain oceanographic features such as the Antarctic Circumpolar Current (Tynan 1998). However, fitting our model at an even finer spatial scale than ocean basins, such as among IWC management areas, with the Discovery mark data would be difficult because of inconsistent marking and whaling effort, and hence little data available to assess interseason recoveries in smaller areas.

Though our model estimates historical movement rates, they may provide insight into contemporary movement patterns as well. Historical and contemporary Antarctic blue whale distributions overlap (Branch et al. 2007b), and whaling data have been shown to provide relevant information about modern distributions and habitat preferences of sperm whales (Letessier et al. 2023). However, caution must be used when interpreting these historical movement rates in terms of current Antarctic blue whale movement. Our model does not account for changes in Antarctic blue whale movement patterns that occurred after whaling. For instance, we assumed time-constant movement rates between ocean basins, but levels of population mixing could have increased over the whaling period as whaling decreased regional population sizes with whales traveling further afield to find conspecifics. Additionally, changing sea ice extent in the Southern Ocean can shift krill abundance and distribution (Braithwaite et al. 2015), which may have caused Antarctic blue whales to modify their movement patterns on the feeding grounds since the end of whaling.

Our model is the first to analyze historical Discovery mark data using an integrated population model (Schaub & Abadi 2010) and provides a framework for integrating these data with contemporary data such as abundance estimates, to account for the variable recovery effort and relatively few mark-recoveries that make these data difficult to analyze quantitatively. Future data collected in the region could be similarly incorporated into a model with these historical data which could allow us to finally put the pieces together and solve the long-standing puzzle of Antarctic blue whale migration patterns.

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Chapter 2. Longer rorqual whale mothers produce more female offspring

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Abstract

Multiple hypotheses have arisen that predict how mammals with the ability to adapt fetal sex ratios should invest in male versus female offspring to maximize inclusive fitness, but large wild-population datasets necessary for testing these hypotheses are challenging to collect. We used whaling data (*n* = 209,254 sexed fetuses from seven rorqual whale species) to test whether mothers with more resources to invest in offspring produce more male or female offspring. We first modeled fetal sex misidentification in the data and estimated that missexing occurred for fetuses under 30-120 cm across five of seven species. Using Bayesian generalized linear mixed models and a size-restricted dataset to account for misidentification, we estimated a 90% posterior probability that longer mothers have more female offspring overall, ranging from 77% for humpback whales to 99% for sei whales. Our results likely reflect both the difficulty of excluding small males from competition in aquatic environments and the exceptionally high costs of gestation and lactation in baleen whales.

2.1 Introduction

Since the 1930s, there have been multiple alternative hypotheses posed to explain how individuals might adapt fetal sex ratios to increase inclusive fitness, including adapting sex ratios based on parental body condition, social hierarchy, or local competition and cooperation [1, 2]. Trivers and Willard [3] developed one of the first hypotheses regarding adaptive fetal sex ratios, which formed the basis for many subsequent hypotheses. Their hypothesis rests on two fundamental postulates: 1) the condition of mature females varies between poor and good, and since a female in good condition has more resources to invest in offspring she will produce a larger, healthier, and stronger offspring that becomes a larger and stronger adult; and 2) resulting differences in body size affect the sexes differently: in particular, female fecundity is similar across large and small females, but larger and stronger males have a substantial advantage and exclude smaller males from reproducing. If these postulates are both true, a female with more resources to invest should prefer to produce a male offspring, which would be larger and have a distinct competitive advantage, resulting in a higher lifetime reproductive success (total number of offspring produced over an individual’s lifetime) for the mother than if she had birthed a female [3].

Leimar [4] extended this hypothesis by recognizing that the reproductive value of the offspring (expected genetic contribution of an individual to future generations) may depend on life history traits other than sex and that it cannot be assumed that males will have a higher reproductive value. Leimar’s [4] argument suggests that even if high quality mothers produce large male offspring that are able to produce a high number of grandoffspring, high quality mothers should prefer to produce daughters if those daughters can pass on this quality, producing high quality grandoffspring. For instance, if high-ranking mothers can pass on this rank to their female offspring, but not their male offspring, then high-ranking mothers should have more female offspring [4, 5]. This is not the only way that mothers may be able to impact the reproductive value of their offspring. Reproductive value is influenced by sex-specific demographic rates, rate of development, and phenotypic inheritance. Mothers with more ability to invest in the maternal care of their offspring should therefore prefer to have the sex whose reproductive value is most strongly influenced by maternal care [4].

Although the Trivers and Willard hypothesis and its extensions depend on the reproductive output of the offspring, the costs to the mother of gestation and lactation for offspring of different sexes must also be considered [6]. This “cost of reproduction” hypothesis suggests that when male offspring are larger than female offspring, the costs of producing a male may be higher, and thus too costly for mothers in poor condition [5, 7, 8], although not all species with sexual dimorphism in body size incur higher costs for producing the offspring of the larger sex [9]. The cost of reproduction hypothesis is difficult to disentangle from the Trivers and Willard hypothesis because it often leads to similar predictions. For example, in ungulates there is male-male competition for mates and adult males are larger than females, therefore both hypotheses would suggest that larger mothers should have more male offspring.

Testing adaptive sex ratio hypotheses is difficult, partly because deviations from an equal sex ratio are likely to be small, but also because there are few non-domesticated mammal species with extensive databases of fetal sex ratios or sex at birth. The Trivers and Willard hypothesis, which predicts that larger mothers will have more male offspring [3], has been widely tested in ungulates and domesticated mammals, though often these studies provide mixed evidence and suffer from small sample sizes [5, 9, 10]. Meta-analyses have found weak but positive support for the Trivers and Willard hypothesis in ungulates and other groups of terrestrial mammals [11, 12].

There have been few evaluations of these hypotheses in marine mammals, though support for a Trivers and Willard-like relationship has been documented in southern elephant seals (*Mirounga leonina*) [8]. However, whaling data provide a uniquely large dataset to test adaptive sex ratio hypotheses. From the 1920s onward, Norwegian—and later international—regulations required whalers to record the sex and length of whales, their pregnancy status, and the sex and length of fetuses. The resulting data include a sample size for fin whales (*Balaenoptera physalus*) alone of over 100,000 sexed fetuses.

For the Trivers and Willard hypothesis and its extensions to hold for baleen whales, differences in maternal body condition, and therefore their ability to invest resources in offspring, must impact the size and health of the calf, and the size of that calf into adulthood [3]. This is likely true, as female baleen whales provide differing levels of parental investment depending on their size and body condition. For instance, maternal body condition and size affect fetal growth rates in common minke whales (*B. acutorostrata*) and southern right whales (*Eubalaena australis*) [13, 14] and calf growth rates in southern right whales and humpback whales (*Megaptera novaeangliae*) [15-17]. Furthermore, baleen whales generally experience a relatively short period

(< 12 months) of rapid growth before weaning that determines overall adult length [18, 19], so that differences in fetal and calf growth impact the size of offspring in adulthood.

Some of the adaptive sex ratio hypotheses above lead to differing predictions for baleen whales. The Trivers and Willard hypothesis [3] leads to the prediction that larger male baleen whales will contribute more to the inclusive fitness of their mothers, if their size provides substantial advantages in mate competition. However, evidence that size confers an advantage to male baleen whales is mixed. Most research on baleen whale mating has been conducted on humpback whales (*Megaptera novaeangliae*), which demonstrate male-male competition for females through song and physical competition [20, 21]. Male blue whales (*Balaenoptera musculus*) appear to occasionally compete for access to females based on observations of vigorous interactions when a second male approaches a male "escort" that is trailing a female [22]. Larger body size is likely an important factor in physical competition, as it allows for endurance and stamina in direct competition, though it may come at a cost of reduced maneuverability underwater [21]. The mating systems of other baleen whales remain largely unknown, though blue and fin whale males produce loud and sustained song that is likely associated with scramble competition [23]. In scramble competition, larger body size likely also provides an advantage, allowing males to remain in the breeding areas (where feeding opportunities are limited) for longer periods of time, increasing their opportunities to mate [21]. Additionally, female humpback whales have shown a preference for larger-sized males [24]. Male right whales (*Eubalaena* spp.) also demonstrate male-male competition for mates, but this primarily occurs through post-copulatory sperm competition [25, 26].

However, despite male-male competition, it cannot be assumed that male offspring have higher reproductive value for baleen whales from their large body size (e.g., Leimar [4]). For baleen whales, large body size is important for a female's ability to reproduce, due to the high costs of gestation and lactation. The reproductive cycle of rorqual whales is closely tied to their migratory cycle, leading to relatively short nursing periods [27, 28]. Additionally, fetal and calf growth is far more rapid in cetaceans than in other mammalian species, which increases the energetic cost to mothers [13, 14, 29], resulting in the body condition of rorqual whale mothers declining by up to 25% during lactation [15, 16, 30]. For most populations, gestation and lactation occur in low-latitude areas, where feeding opportunities are limited, and females must rely on stored fat for most of the energetic demands of these processes. This suggests that larger mothers may have higher probabilities of survival, as they would lose less body volume in relative terms than smaller mothers, and can even occasionally support simultaneous lactation and gestation, as has been observed in humpback whales [31]. Smaller body size is also associated with decreased calving probability for North Atlantic right whales (*E. glacialis*) [32], suggesting that female baleen whales must be above a certain size to reproduce at all. Additionally, females may skip breeding seasons if they are not in sufficient condition to produce a calf [31, 32], and larger females may be able to skip fewer breeding seasons. This suggests that for baleen whales, variation in body size and condition may have a larger impact on female reproductive value than it does on male reproductive value. If so, we would predict that larger mothers should produce more daughters. Similarly, for baleen whales, the cost of reproduction hypothesis [6] suggests that larger mothers will prefer to have more females if females are costlier to produce. Given that adult female baleen whales are larger than males, the costs of rearing a female calf may be proportionally higher for smaller mothers. This has been suggested as the reason that larger southern elephant seal mothers have more male pups (since males are the larger sex in pinnipeds) [8]. If the same logic applies to baleen whales, smaller mothers should have more male offspring.

In this study, we evaluated evidence for adaptive sex ratio hypotheses in rorqual whales (Balaenopteridae). While whaling data provide a uniquely large dataset of fetal sex ratios, measurement and recording biases must be accounted for when using data from historical catches. Notably, it has been hypothesized that sex identification was difficult for small fetuses [33, 34], causing a bias in the fetal sex ratio data, which has subsequently been detected in fetal data for Antarctic blue whales (*B. m. intermedia*) [35]. Therefore, we first assessed fetal sex misidentification in seven species of exploited rorqual whales. After restricting the dataset to eliminate fetuses with potential sex misidentification, we fit generalized linear mixed models to test these hypotheses. If the Trivers and Willard hypothesis holds for rorqual whales, we predict that larger mothers will have relatively more male offspring. However, if larger mothers have relatively more female offspring, this would be consistent with either the Leimar or cost of reproduction hypotheses.

2.2 Materials and methods

We fit two types of Bayesian models to fetal sex ratio data from the International Whaling Commission (IWC). We fit the first type of model to data from each species to estimate the relationship between fetal sex and fetal length and predict the length at which fetuses were correctly sexed based on deviations from this relationship. This allowed us to assess the extent of sex misidentification of small fetuses and create a size-restricted dataset for each species for which sex identification is predicted to be ≥99% accurate. We applied the second type of model to these size-restricted datasets to estimate the relationship between fetal sex and maternal length. In this second model type, we assumed that the length of adult females is a reasonable proxy for ability to invest in fetal growth, since longer mothers have more total body fat, in absolute terms, than shorter mothers. This assumption is required because whaling data do not contain extensive information about blubber thickness or weight.

2.2.1 Available data

Fetal sex data from historical catches were obtained from the IWC individual catch database v.7.1 [36]. Data were collected from 1899 to 2019, although most fetal sex data were collected between 1910 and 1985. Catches after 1985 primarily consisted of Antarctic minke whales (*B. bonaerensis*). Fetuses were sexed visually based on the appearance of external sexual organs [34]. Fetuses that did not have sex information (coded as "unknown") were excluded. Because most fetuses were measured in whole feet, all length measurements were converted to feet and models were fit using lengths measured in feet. Only data for rorqual whales were included: blue whales, fin whales, humpback whales, sei whales (*B. borealis*), Antarctic minke whales, Bryde's whales (*B. edeni*), and common minke whales. Though fetal sex data were available for gray whales (*Eschrichtius robustus*), bowhead whales (*Balaena mysticetus*), and all species of right whales, there were insufficient sample sizes to draw meaningful conclusions (Figure S1, Table S1), and these species were excluded. We also ran models for sperm whales (*Physeter macrocephalus*), but since the focus of this paper is on baleen whales, sperm whale results are relegated to the Appendix. Throughout the paper, sex ratios are reported as the proportion of males.

Species identity was used as indicated in the IWC catch database, except for blue whales, which we split into subspecies and only analyzed for Antarctic (*B. m. intermedia*) and pygmy blue whales (*B. m. brevicauda*). Pygmy blue whales were only identified in the 1960s [37], therefore blue whale catches were separated into Antarctic and pygmy blue whales for this study using length frequencies and catch latitude [38], and we excluded limited data from genetically separate blue whale populations (or subspecies) in the South-East Pacific, North Pacific, and North Atlantic [39]. Catches identified as sei whales may include some Bryde's whales, and catches listed as Bryde's whales may include some Omura's whales (*B. omurai*) [40] and Rice's whales (*B. ricei*) [41], but since it is not possible to separate historical catches further among these species, we used the sei and Bryde's species designations as listed in the IWC database for our analyses.

Fetal data were visually inspected for outliers. Three fetuses recorded as Bryde's whales were larger than 15 ft (4.57 m) and eight fetuses recorded as sei whales were larger than 16.5 ft (5.03 m). These data were removed from the analysis because they were more than 0.5 m longer than published estimates of the length of newborn calves in these species (3.96 m and 4.5 m, respectively [42, 43]) suggesting that these data points arose from measurement errors or species misidentification.

2.2.2 Fetal sex misidentification

The first type of model we built was designed to eliminate bias due to fetal sex misidentification by allowing us to identify the lengths for which we could be confident of fetal sex. We fit three models for each species to predict fetal sex ratio from fetal length: 1) no correction, 2) correction for small female fetuses mistaken for males, and 3) correction for small male fetuses mistaken for females. These models consisted of an assumed linear relationship between fetal sex ratio and fetal length, as well as deviations from this relationship attributed to sex misidentification, which was assumed to follow a logistic selectivity equation where the probability of misidentification was higher at smaller fetal lengths. These models were fit to all rorqual taxa except pygmy blue whales, for which there were insufficient data at small sizes.

Reported fetal sexes were assumed to follow a Bernoulli distribution where 1 = male, and 0 = female:

$$y_i \sim Bernoulli\left(p^*_{male_i}\right) \tag{1}$$

where $p^*_{male_i}$ is the predicted probability that fetus i is reported as male. We then modeled $p^*_{male_i}$ as a function of the estimated true sex ratio, p_{male_i}, and a correction factor, $p_{correct_i}$.

The true (latent) sex ratio, p_{male_i}, was modeled as a function of fetal length, to account for the possibility of differences in sex ratio by fetal size, which could arise either because of differences in birth lengths or in the rate of *in utero* mortality between sexes. This was modeled using logistic regression with a logit link function:

$$logit(p_{male_i}) = a + b \cdot L_i \tag{2}$$

where a is an estimated intercept and b is an estimated coefficient for the effect of fetus length (L_i) on the probability that fetus i is male, both on the logit scale.

Deviations from the estimated logit-linear relationship above were assumed to be a result of sex misidentification. We modeled sex misidentification using a logistic selectivity equation for the probability of correctly identifying the sex of a fetus ($p_{correct_i}$) given its length:

$$p_{correct_i} = \left(1 + e^{\frac{-\ln(19)\cdot(L_i - L_{50})}{\Delta}}\right)^{-1} \tag{3}$$

where L_i is the length of fetus i, L_{50} and Δ are estimated parameters, $\Delta = L_{95} - L_{50}$, and L_{50} and L_{95} represent the length at which 50% and 95% of the fetuses were identified correctly. The fixed value of ln(19) in this equation ensures that Δ estimates the difference between the lengths at which 95% and 50% of fetuses were identified correctly [44]. The correction was applied to all fetal lengths. This model assumes that the probability of correctly identifying the sex of a fetus is a continuously increasing function of length, with a higher probability of correctly identifying larger fetuses.

We fit three alternative forms of $p^*_{male_i}$ (predicted probability that fetus i is reported as male). For the no-correction model,

$$p^*_{male_i} = p_{male_i}\,. \tag{4}$$

For the model in which small female fetuses are mistaken for males,

$$p^*_{male_i} = p_{male_i} + \left(1 - p_{male_i}\right)\cdot\left(1 - p_{correct_i}\right). \tag{5}$$

And for the model in which small male fetuses are mistaken for females,

$$p^*_{male_i} = p_{male_i} \cdot p_{correct_i}. \tag{6}$$

Models were fit using Bayesian methods in Stan v. 2.34 [45] using the CmdStan and CmdStanR interfaces [46]. Each model was fit using four chains, with 1000–5000 iterations as needed for convergence (Table S2). The adapt delta parameter for the No-U-Turn-Sampler, which controls the target acceptance rate, was set to 0.95. A Normal(0, SD = 10) prior was used for the intercept (*a*) and slope (*b)* parameters, as well as the L_{50} and Δ parameters. The normal prior for Δ was truncated at 0 so that only positive values were included. For common minke whales and Bryde's whales, the L_{50} and Δ priors included an upper bound of 2 ft (0.61 m) to improve convergence. Convergence was checked using trace plots and by ensuring that $\hat{R}$ values were < 1.01 (Table S2) [47]. The best model for each species was identified using the Watanabe-Akaike Information Criterion (WAIC) [48] calculated using the *loo* package [49]. WAIC provides an estimate of the expected log pointwise predictive density (elpd), and models were considered strongly preferred if they had a difference in elpd greater than four [50]. To estimate the length at which 99% of fetuses were sexed correctly, the model with the lowest WAIC was used for each species, except for Bryde's whales, where the posterior distributions from the correction models showed no difference between the posterior and prior for the correction parameters, suggesting that those parameters were unidentifiable given the data. In this case, we considered the model without correction the top model for Bryde's whales. We calculated the posterior distribution for the length at which 99% of fetuses were correctly sexed for each species and subsequent analyses only used sex ratio data for fetuses at or above the mode of this posterior distribution.

2.2.3 Relationship between maternal length and fetal sex

Lengths of pregnant whales and the sex of the corresponding fetuses were obtained from the IWC individual catch database v7.1 [36]. Due to the various practices for measuring adult whales (e.g., rounding to the nearest 6 in. or 1 ft, measuring in feet or meters, etc.), maternal lengths were converted to feet and then grouped into 3-inch bins with cutoffs at 1.5, 4.5, 7.5, and 10.5 in. To allow for comparisons across species, these lengths were then centered and scaled by subtracting the mean length for each species and dividing by the standard deviation. To remove obvious issues with measurements (either incorrect species ID or incorrect measurements), only mothers that had scaled and centered lengths between –4 and +4 standard deviations of the species mean were included. We then fit a model to the data for eight taxa of rorqual whales. A model treating sperm whales separately is included in the appendix.

We built a generalized linear mixed model to estimate the relationship between the probability that a fetus is male and maternal length, and we included species-specific random effects on the intercept and coefficient for maternal length. The numbers of male fetuses ($N_{b,s}^{male}$) in each maternal length bin (b) for species (s) were assumed to follow a beta-binomial distribution (to allow for overdispersion relative to the binomial):

$$N_{b,s}^{male} \sim BetaBinomial(n_{b,s}, p_{b,s}, \phi) \tag{7}$$

where $n_{b,s}$ is the total number of fetuses in maternal length bin b for species s; $p_{b,s}$ is the probability of being male for a fetus in maternal length bin b for species s, and ϕ is the estimated overdispersion parameter (a smaller ϕ corresponds with a larger variance). The probability of having a male fetus was modeled as a function of maternal length using a logit link function:

$$\text{logit}(p_{b,s}) = \alpha_s + \beta_s \cdot MaternalLength_b \tag{8}$$

where α_s and β_s are random intercepts and slopes for each species, which are drawn from normal hyper-distributions:

$$\alpha_s \sim Normal(\bar{\alpha}, \sigma_\alpha) \tag{9}$$

$$\beta_s \sim Normal(\bar{\beta}, \sigma_\beta) \tag{10}$$

where $\bar{\alpha}$ and $\bar{\beta}$ are the mean intercept and slope across species, and σ_α and σ_β are standard deviations of the species-specific random effects.

Diffuse Normal(0, SD = 10) priors were used for $\bar{\alpha}$ and $\bar{\beta}$. Exponential(1) priors were used for σ_α and σ_β to avoid floor and ceiling effects caused by the logit link function and to improve convergence [51].

The model was fit using the *brms* package [52] in R v4.3.2 [53], using 4 chains, 6000 iterations, and an 83% warm-up (1000 draws saved after warm-up). The adapt delta parameter for the No-U-Turn-Sampler, which controls the target acceptance rate, was set to 0.95. Convergence was checked using trace plots and $\hat{R}$ values < 1.01 [47]. Results from this model are presented as modes and 95% highest density intervals.

2.3 Results

2.3.1 Fetal sex misidentification

Models to predict fetal sex from fetal length were fit to seven species, but not to pygmy blue whales because almost all pygmy blue whale fetuses were greater than 5 ft (1.5 m), and there were insufficient data to estimate misidentification rates (Figure S1). In four taxa—Antarctic blue, fin, humpback, and sei whales—the models with the most support included a correction factor for small female fetuses that were mistaken for males. In Antarctic minke whales, the opposite pattern was found, and in common minke whales and Bryde's whales there was no bias due to sex misidentification in the models with the most support (Figure 2.1, Table S3). The estimated lengths above which >99% of fetuses were correctly identified (L_{99}) for each species ranged from 0.74–4.07 ft (Table 2.1).

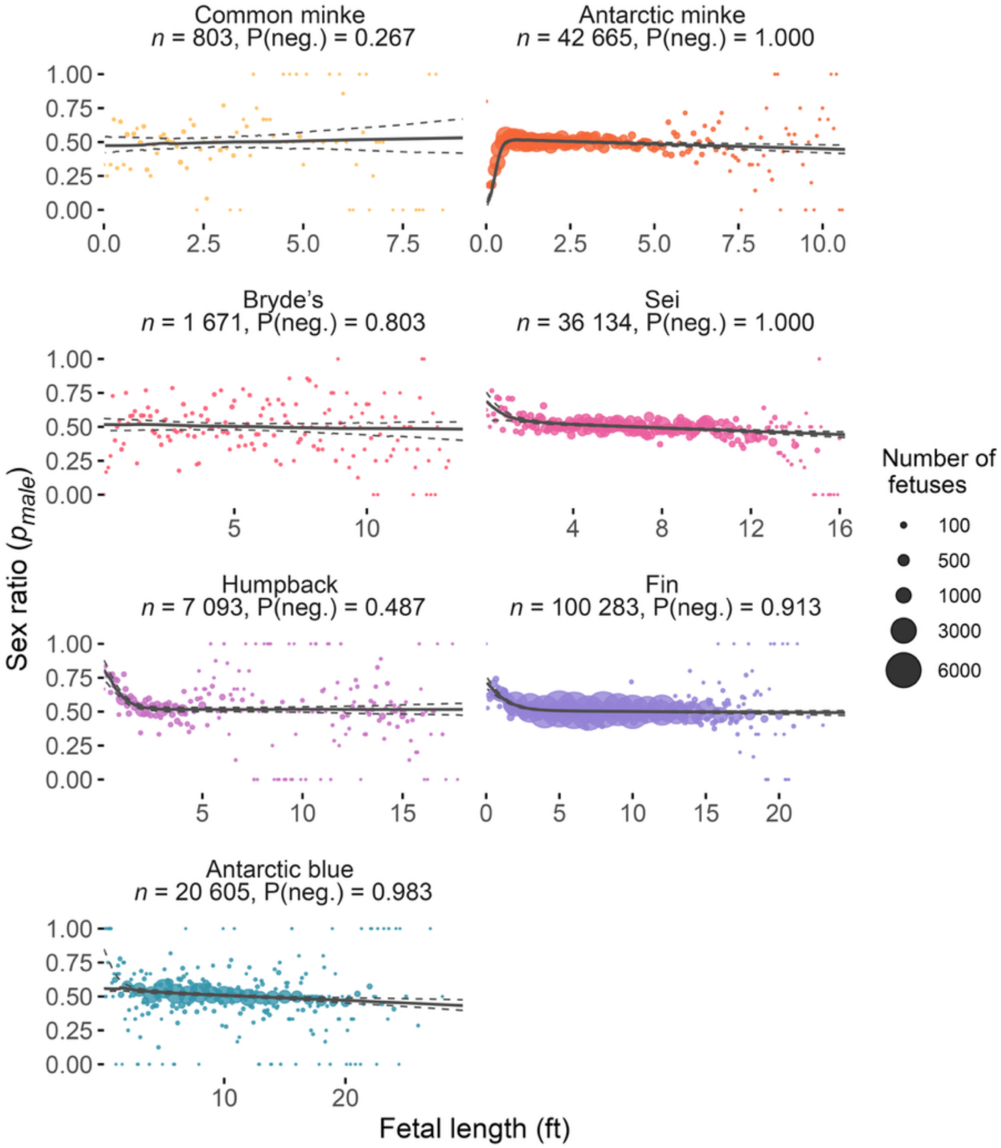

Figure 2.1 Posterior estimates of the fetal sex ratio given fetal length from the models with the most support for each species (Table S3). The points represent the documented proportion male in 1-inch length bins for each species. The size of the points indicates the sample size for each 1-inch bin and darker shading indicates overlapping points. Species are ordered from smallest to largest size. *Pneg.* indicates the posterior probability of a negative effect (*b*; eqn. 2) of fetal length on the probability that a fetus is male, and n indicates the total number of fetuses in each model.

Table 2.1 Posterior estimates (mode) and 95% highest density intervals for the length at which 99% of fetuses were estimated to be correctly identified for each species (L_{99}) based on the best model for each species (Table S3). “Female → Male” indicates small female fetuses were mistaken for males, while “Male → Female” indicates small males were mistaken for females. An asterisk (*) indicates species for which L_{99} was not estimated, either because there were not sufficient data at small fetus lengths to fit models for this species (pygmy blue whales) or because the model with no sex misidentification was the most supported (common minke whales, Bryde’s whales). In these cases, L_{99} estimates from another species or subspecies (Antarctic blue whales, Antarctic minke whales, and sei whales, respectively) were used to remove small fetuses for further analysis.

Species	**Sex misidentified**	**L_{99} (ft)**		
		Mode	**2.5%**	**97.5%**
Antarctic blue whale	Female → Male	3.20	-11.93	14.75
Pygmy blue whale*	No correction	3.20	–	–
Fin whale	Female → Male	4.07	3.32	5.07
Humpback whale	Female → Male	2.57	1.88	3.60
Sei whale	Female → Male	2.58	-0.56	6.27
Bryde’s whale*	No correction	2.58	–	–
Antarctic minke whale	Male → Female	0.74	0.68	0.81
Common minke whale*	No correction	0.74	–	–

Five of the seven species had a high estimated probability that the logit-scale coefficient for fetal length (*b*) is negative, indicating higher proportions of females with increasing fetal length. The probability that the coefficient was negative was highest for sei and Antarctic minke whales (> 0.999). Humpback whales and common minke whales did not have a high probability of a negative coefficient (0.488 and 0.267 respectively; Figure 2.1, Table S4).

2.3.2 Testing the relationship between maternal length and fetal sex

Given the sex misidentification results, for the remaining analysis we removed fetal data below the modal estimate for L_{99}. Although no misidentification models were fit to pygmy blue whales, for consistency in the rest of the analysis only fetuses greater than the estimated L_{99} for Antarctic blue whales (3.20 ft) were included. Similarly, though the best model did not indicate sex misidentification for common minke whales or Bryde’s whales, the estimated L_{99} for Antarctic minke whales (0.74 ft) and sei whales (2.58 ft) were used.

Across all rorqual species, we estimated that the proportion of male fetuses decreased with increasing maternal length (Figure 2.2-2.3). The posterior probability that the mean coefficient for maternal length, $\bar{\beta}$, across species was negative was 0.906. The model estimated little inter-species variability in the coefficient, with the standard deviation between species, σ_β, estimated as 0.0077 (95% interval: 0.00012–0.0410, Table S5). The posterior probability of a species having a negative coefficient was lowest for humpback whales (0.765) and highest for sei whales (0.994) and fin whales (0.940; Figures 2.2-2.3).

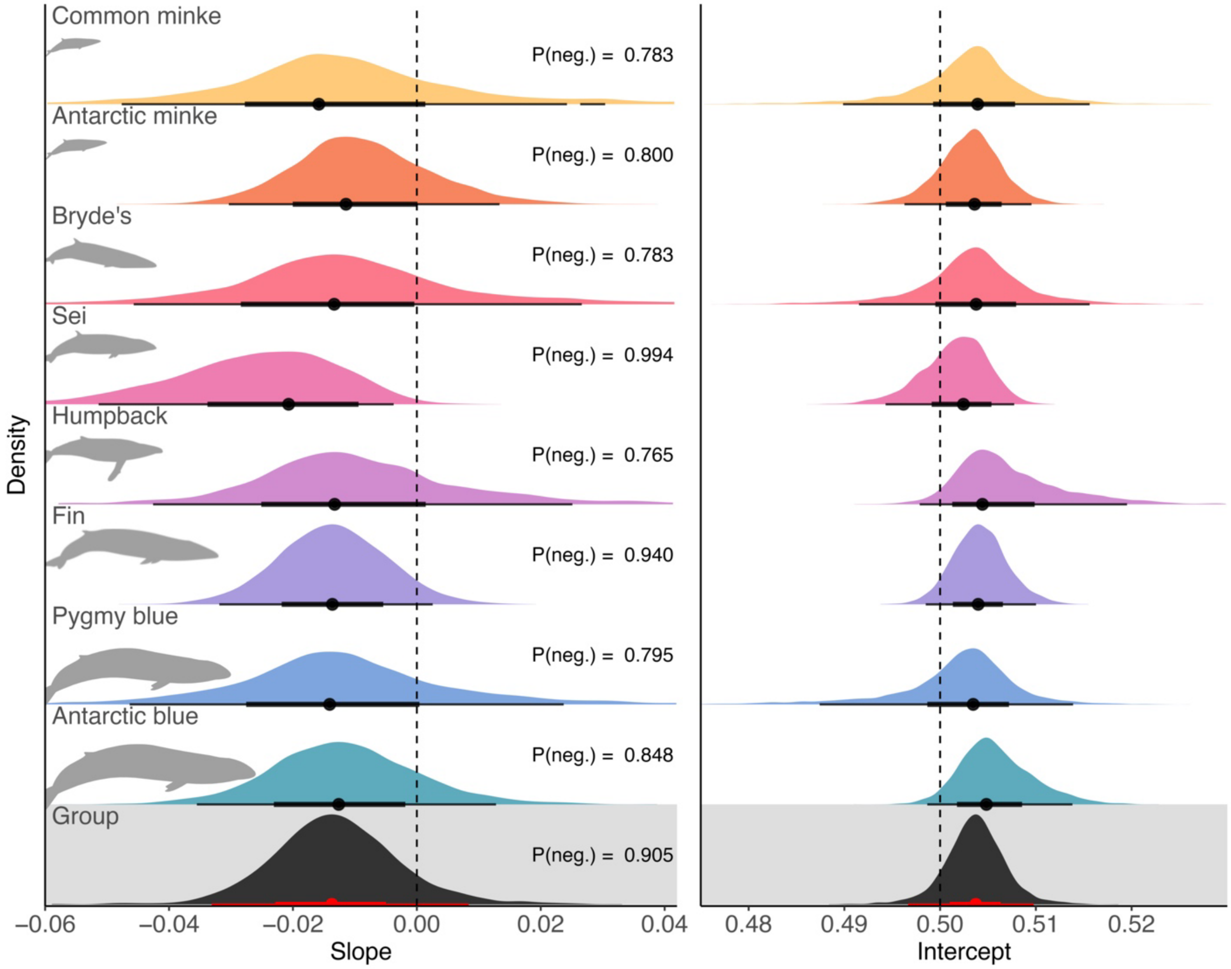

Figure 2.2 Posterior distributions of parameters. Posterior distributions of the estimated slope (left, logit scale) and intercept (right, real scale) parameters, for each rorqual whale species, in a model describing the relationship between having a male fetus (response variable) and maternal length. Also shown is the overall mean across species (gray shaded). The dashed lines represent a slope of 0 (logit scale) indicating no relationship between fetal sex and mother length, and an intercept of 0.5 (real scale) indicating a 50:50 sex ratio at the mean maternal length, with higher values indicating more males than females. The points beneath each distribution represent the posterior mode and the solid lines represent the 66% (thicker) and 95% (thinner) highest density intervals. *Pneg.* describes the posterior probability of a negative slope (β). Species are ordered from smallest to largest.

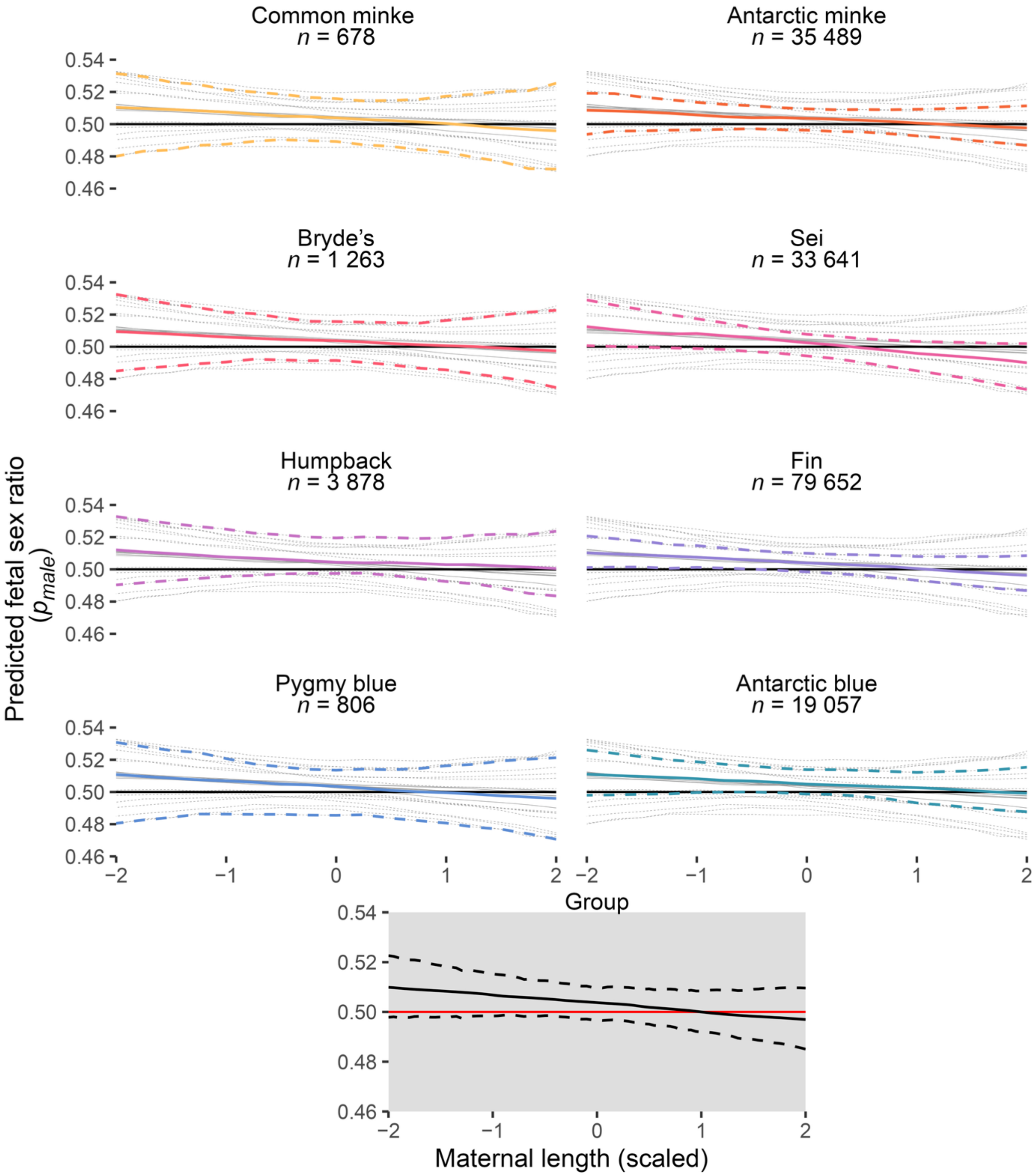

Figure 2.3 Relationship between fetal sex and maternal length. Posterior modes (solid line) and 95% highest density credible intervals (dashed lines) for predicted fetal sex ratio given maternal length for each species (scaled within the species) and the overall trend across species (shaded gray). Solid black horizontal line indicates 50:50 sex ratio and *n* indicates the number of fetuses in each taxon.

The mean intercept parameter across species, $\bar{\alpha}$, which represents the fetal sex ratio at the mean maternal length, when converted to the probability scale, had a mode of 0.504 (95% interval:

0.497–0.510). There was little estimated variation in the species-specific random intercepts, with the posterior mode of the standard deviation, σ_{α}, estimated at <0.0001 (95% interval: 0.000–0.0525, Table S5). This is reflected in the similarity of the species-specific intercept values across species with the mode ranging between 0.502 and 0.505 (on the probability scale) for all species (Figures 2.2-2.3). Finally, the estimated overdispersion parameter was large (1267; 95% interval: 792–1884, Table S5), suggesting that the data were not very overdispersed relative to a binomial distribution.

2.4 Discussion

We evaluated the evidence for adaptive sex ratio strategies in rorqual whales while accounting for biases in fetal sex assignment from whaling data due to sex misidentification of small fetuses. We found evidence that longer mothers have more female calves (Figure 2.2-2.3). For some species, such as sei and fin whales, this pattern was clear, but for others, such as humpback whales, the probability of a negative slope was not as high (77%). This may be a function of data availability, since fin whales have one of the largest sample sizes in the dataset (~79,000 after removing small fetuses) which makes it easier to detect subtle relationships in the data.

Additionally, we found that small female fetuses were recorded as males in four species, while we found the opposite pattern in one species (Antarctic minke whales; Figure 2.1). These results support the pattern found in Antarctic blue whales [35] suggesting that fetal sex misidentification was a widespread problem across species, whaling stations, and fleets. Gambell [33] hypothesized that fetal sex misidentification in sei whales occurred because, at small sizes, non-biologists mistook the relatively large clitoris of the female fetus for a penis, which could explain why we found that small female fetuses were mistaken for males across most species. We found the opposite trend for Antarctic minke whales, confirming previous findings of missing small male fetuses in the whaling data for this species [34]. While it is possible that a difference in the morphology of Antarctic minke whale fetuses might lead to small males being mistaken for females, this seems unlikely given their shared evolutionary history with the other rorqual whales in our study. Instead, this may be an artifact of the timing of Antarctic minke whale catches. Antarctic minke whales are one of the smallest of the exploited whale species and were not caught in large numbers until the 1970s, after the populations of other preferred species had declined. We speculate that it may have been known by inspectors and biologists in Japanese whaling fleets that sex misidentification of small female fetuses was an issue and that the high number of small males recorded as females in these catches resulted from an overcorrection.

We also found evidence that the fetal sex ratio declined with increasing fetal length, suggesting that larger fetuses were more likely to be female in five of the seven species (Figure 2.1). This has been previously observed in Antarctic blue whales and Antarctic minke whales [34, 35] but this work demonstrates that it is a consistent pattern for many exploited cetaceans. This pattern could reflect sexual dimorphism in size at birth, with female calves born at longer lengths than males. Though studies of newborn calves are rare, no differences in the size at birth between sexes has been found for sperm whales [54] or common minke whales [13]. Instead, this decline may reflect higher in-utero mortality for males, with fewer males surviving to birth length than females. This is thought to be a common feature of mammalian reproduction [55, 56] and has been proposed for long-finned pilot whales (*Globicephala melas*) [57]. However, it is not possible to distinguish between these two possibilities from our results alone. Though this negative correlation was not estimated in our model for humpback whales or common minke whales, this may be due to low sample sizes at longer fetal lengths in those species.

In our analysis, we assumed that the length of rorqual whale mothers is a reasonable proxy for their ability to invest in a fetus. We believe that this is a reasonable assumption because offspring size has been shown to be proportional to the body length of mothers in baleen whales, suggesting that longer mothers do produce larger calves [15, 16], and indeed faster calf growth rates have been observed from longer mothers in North Pacific humpback whales [17]. Furthermore, hypotheses about adaptive sex ratio strategies depend on the condition of mothers relative to others in the population, not their absolute size. Therefore, when year-to-year environmental conditions impact the entire population, the Trivers and Willard hypothesis and its extensions would still apply to larger mothers even if they have poorer body condition than in previous breeding seasons [3, 58]. Thus, body length is a reasonable proxy for population-level relative condition, since it is less likely to change with shorter-term environmental change. However, due to this assumption, we are unable to account for variability that may occur when longer whales are in poor condition and shorter whales are in good condition. We believe this effect is likely to be small, since cetaceans may skip a breeding season when in poor condition [31, 32].

Given the estimated sex ratio at the mean maternal length was very close to 50:50 for most species (Figure 2.2) and that we estimated only small departures from a 50:50 sex ratio even at the longest maternal lengths in all species (Figure 2.3), it is likely that rorqual whales have limited control of the sex of their offspring [59]. The actual mechanism for adapting fetal sex ratios in mammals is unclear. It has been hypothesized that mothers may be able to detect differences in X and Y chromosomes, which could lead to adaptive strategies during the process of fertilization, or that sexual dimorphism in embryos could lead to adjustment of sex ratios during the process of implantation [60]. While the exact mechanism remains unknown, there is a general consensus that sex ratio adjustment likely occurs at or near conception [2, 11, 60]. Additionally, small effect sizes could also be explained by a paternity effect in the sex ratios of offspring. For instance, larger, attractive males have been found to produce more male offspring in some species of mammals [58, 61]. Therefore, if larger females mate with “attractive” males, then this could lead to a higher proportion of male offspring despite the larger size of the female.

More female calves produced by longer mothers runs counter to the prediction of the Trivers and Willard hypothesis, which predicts that mothers who are able to invest more in their offspring will have more male offspring because these larger males will be better able to outcompete the smaller males and will increase the inclusive fitness of their mothers [3]. These results are consistent with the hypothesis that physical size is a less important predictor of success in male-male sexual competition for mates in rorqual whales than for terrestrial mammals. Although direct physical competition for mates has been observed in humpback [20] and blue whales [22], it is likely that males are not as easily able to control access to mates in aquatic environments as in terrestrial environments [62]. This is consistent with genetic studies of paternity that have found less variation in male reproductive success in baleen whales compared to polygynous mammals that mate in terrestrial environments [63-66]. For example, humpback whales have been found to have less variation in male reproductive success than southern elephant seals, rhesus macaques (*Macaca mulatta*), red deer (*Cervus elaphus*), vervet monkeys (*Chlorocebus pygerythrus*), and roe deer (*Capreolus capreolus*) [66]. This suggests that males who are less able to compete physically may still find ways to be successful. For instance, smaller males might find mates using what Clapham [20] terms the "roving male" strategy, whereby smaller males look for mates in lower density habitat where they have fewer competitors. Additionally, male humpback, blue, and fin whales all produce songs that are believed to play a role in the attraction of mates [62]. The exact characteristics that make a particular song or singer attractive to females is unknown, but the successful attraction of a mate through song may not be strongly dependent on male body size. This suggests that the presence of male-male competition for mates does not inherently require that size be more important for the reproductive success of male offspring than it is for female offspring and that tests of this assumption are required.

Higher proportions of female calves with increasing female size and body condition have also been found in ungulates such as roe deer [67], reindeer (*Rangifer tarandus*) [68], and elk (*Cervus canadensis*) [69]. The mechanism that is often proposed for this relationship is the local resource competition model for adaptive sex ratios, which suggests that mothers will bias sex ratios towards the sex that competes least for limited resources such as food [59]. For ungulates, where males disperse widely and females remain closer together, this could lead to smaller or poorer condition mothers producing more males because they will compete less for resources [9]. This is unlikely to be true for rorqual whales, where sex ratios are close to equal on the feeding grounds [35].

Instead, our results are consistent with both the idea that larger female calves offer higher reproductive value for their mothers, and the idea that the cost of rearing a female calf is too high for small mothers. Since female baleen whales are larger than males there might be increased costs to rearing a female calf, especially for small mothers. Gestation and lactation are incredibly costly for rorqual whales, but since there are unlikely to be differences in size at birth between sexes [13, 54], any difference in cost between sexes is likely to be incurred during lactation. There are currently no studies on sex-specific milk intake rates for cetaceans. Studies of milk intake rates for pinnipeds show some evidence for sex differences, though there is no consistency across species and there are more studies with no sex differences in milk intake rates than with sex differences [19]. Instead, for pinnipeds, body mass differences between pups of different sexes can largely be attributed to differences in how energy from lactation is converted into growth, with females investing more in lipid-rich tissues while males invest more in lean body mass [19, 70]. Therefore, until it is possible to estimate milk intake rates for cetaceans, we do not have evidence to evaluate whether the costs of lactation are significantly different between sexes.

The high costs of reproduction, regardless of offspring sex, likely increases the reproductive value of larger female offspring relative to the reproductive value of large male offspring. If larger mothers produce larger daughters, these daughters, and therefore also their granddaughters, are more likely to withstand the high costs of gestation and lactation. They are more likely to produce calves without impacting their own survival and may be able to reproduce more often, either by skipping fewer breeding seasons or through simultaneous gestation and lactation [31, 32]. In fact, female offspring below a certain size threshold may not be able to reproduce at all [32]. As we found that larger mothers produce more females, this may suggest that the high reproductive value of large female offspring outweighs the competitive benefit of large body size for male baleen whales.

In conclusion, we found evidence that longer female rorqual whales have more female calves. Though it is difficult to assess how this individual-level strategy impacts population sex ratios [71, 72], it may impact the recovery of these exploited whale species. Our results suggest that a population with most mothers at lengths close to the mean for that species should have a population-level fetal sex ratio close to 50:50. However, whalers preferred to catch larger whales, likely leaving a higher proportion of smaller females in the population, as has been seen in other commercially exploited species [73]. Additionally, the body size of baleen whales, especially females, has been shown to decline in response to changing environmental conditions [74, 75]. If these smaller females have more male offspring, as predicted by our model, then this could lead to a smaller intrinsic rate of increase for the population [76], leading to slower recovery from whaling.

Data accessibility

Data and code used in this analysis are available from: https://doi.org/10.5281/zenodo.16686786

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Chapter 3. Critically endangered Antarctic blue whales are increasing but still far from pre-whaling levels

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Abstract

Antarctic blue whales were a primary target for 20th century commercial whaling, decimating their population and leading to their current listing as Critically Endangered by the IUCN. Here we provide the first population assessment in over 20 years, incorporating new information on Antarctic blue whale catches and recent abundance estimates. We used a Bayesian theta-logistic population model fit to abundance estimates from ship-based line-transect surveys and a mark-recapture abundance estimate from photo-identification data. The estimated intrinsic rate of increase was 4.5% (95% interval 1.6–7.3%), with a carrying capacity (and assumed pre-whaling abundance) of 205,905 (168,473–276,342). Abundance was estimated at just 418 (147–1,099) at the end of whaling in 1973, at just 0.20% (0.08-0.42%) of pre-whaling levels. We estimated that the population has increased to 4,018 (1,874–8,395) in 2024 which is 1.9% (0.7–4.8%) of pre-whaling levels. We conducted sensitivity analyses to test changes in parameter estimates related to model assumptions and data sources and found that model estimates were robust to these changes. These results show that the Antarctic blue whale population has been increasing since the end of whaling, but it will take more than a century before it will return to its pre-whaling abundance.

3.1 Introduction

Antarctic blue whales (*Balaenoptera musculus intermedia)* are the largest and, before whaling, were the most abundant blue whale subspecies globally. They were the primary target of commercial whaling in the 20th century and are currently listed as Critically Endangered by the IUCN due to this exploitation (Cooke 2018). Despite a moratorium on the commercial catch of Antarctic blue whales adopted by the International Whaling Commission (IWC) in 1963 and the end of illegal Soviet whaling by 1973 (Tønnessen & Johnsen 1982, Berzin 2008), Antarctic blue whales still face many threats, including ship strikes, potentially changing krill availability, and anthropogenic noise (Clapham et al. 1999, Castellote et al. 2012, Constable et al. 2014, Blair et al. 2016, Thomas et al. 2016). Accurate estimates of pre-exploitation abundance, population growth rate, and current abundance are essential to assess the recovery of Antarctic blue whales.

The last published assessment of Antarctic blue whales estimated that the population was increasing at 7.3% per year, but that in 1996, Antarctic blue whales were at less than 1% of their pre-exploitation levels (Branch et al. 2004). Since this time, new methods have been developed for distinguishing historical catches of pygmy blue whales from Antarctic blue whale catches (Branch & Mikhalev 2008, Branch et al. 2009, Branch et al. 2025). Additionally, further line-transect surveys now provide more data on current absolute and relative abundance (Branch

2007, Matsuoka & Hakamada 2014, Hamabe et al. 2023). A photo-identification catalogue compiled for Antarctic blue whales, incorporating photographs from scientific surveys and opportunistic sightings, has provided additional estimates of abundance (Olson et al. 2025). These new data on Antarctic blue whale catches and abundance can provide an updated perspective on their current population status.

Conservation of endangered species at the population-level rather than the species level is important to ensure morphological and genetic diversity which allows species to be resilient in the face of environmental change or disturbance (Shaffer & Stein 2000, Smith et al. 2018). While many other species of baleen whales in the Southern Ocean have populations with distinct breeding areas or site fidelity to ocean basins (Pastene et al. 2010, Amaral et al. 2016, Pastene & Goto 2016, Rosenbaum et al. 2017), it is generally assumed that Antarctic blue whales are a single circumpolar population. There are substantial lines of evidence that support this assumption. Notably, Antarctic blue whales share a characteristic song type, the Z-call, which is heard throughout the Southern Ocean (Miller et al. 2024, Shabangu et al. 2024) as well as northward to the equator (and rarely above) in the South Pacific, South Atlantic, and Indian Oceans (e.g., Stafford et al. 2004, Širović et al. 2018, Samaran et al. 2019, Širović & Oleson 2022, Branch et al. 2025). Song types are frequently used to distinguish populations for blue whales because they reflect contemporary movement and association patterns (McDonald et al. 2006, Širović & Oleson 2022) and may correspond to genetic differentiation (Barlow et al. 2018). In addition to song, long-distance movements have been demonstrated from photo-ID recaptures (Olson et al. 2022), analysis of inter-annual movement rates of Antarctic blue whales from historical Discovery mark data suggests that there is frequent mixing among individuals in their Southern Ocean feeding grounds (Rand et al. 2024), and a recent study using a large genetics dataset found no evidence of genetic differentiation in Antarctic blue whales (Attard et al. 2024). These pieces of evidence suggest that it is reasonable to assume a single circumpolar population of Antarctic blue whales.

In this study, we fit an integrated assessment model incorporating historical catch data, line-transect abundance estimates, a photo-ID mark-recapture abundance estimate, and visual sightings to estimate the population size, population growth rate, and level of depletion for Antarctic blue whales. Understanding the status of this population will provide information to more effectively monitor the recovery of Antarctic blue whales in the face of contemporary threats.

3.2 Materials and methods

We built a population model to estimate the pre-whaling abundance and intrinsic population growth rate of Antarctic blue whales. This model used historical catch data and was fit to contemporary abundance estimates from circumpolar line transect surveys from 1978-2004 , regional line-transect surveys from 1989-2008, and a mark-recapture estimate from photo identification data from 2018. Additional model runs were used to explore the sensitivity of the model to the inclusion of each data source as well as to some of the model assumptions. The fitted was used to determine maximum depletion, as well as to estimate the population size and level of depletion in 2024.

3.2.1 Historical catch data

Catch data were provided by the June 2023 release of the IWC's summary database v7.2 (Allison 2023b) and the IWC's individual catch database v7.2 (Allison 2023a). The summary database contains the annual total catches for each species by expedition, region, whaling country, and catch location, while the individual database contains records of individual whales that were caught, including date, catch location, body length, and sex. A total of 386,619 global blue whale catches are included in the summary database, as well as 25,610 catches for which species was unspecified. Of these, 313,965 have individual catch records. The summary database was the starting point for the catch series used in this assessment, with the Antarctic blue whale catches separated from the total blue whale catches and then unspecified whales that were likely Antarctic blue whales added.

3.2.1.1 Distinguishing Antarctic blue whale catches

Since the catch database does not specify population or subspecies, Antarctic blue whale catches need to be separated from catches of other blue whale subspecies in the database. There are currently four recognized subspecies of blue whale (*Balaenoptera musculus*) globally (Committee on Taxonomy 2023), however, these designations are likely to change with recent genomic studies (Attard et al. 2024, Wolf et al. 2025).

For this study, catches were primarily considered Antarctic blue whales based on their distribution (e.g., Branch et al. 2025). We considered all blue whale catches from the North Atlantic and the North Pacific to be from a different subspecies and excluded these from Antarctic blue whale totals. In the South-East Pacific, we considered catches from Chile, Peru, and Ecuador (50°S to 4°S and 180°W to 70°W) to be eastern Pacific blue whales and similarly excluded them. We considered blue whales listed as being caught in the South Shetlands/South Chile area (68°S to 40°S and 76°W to 56°W) to be Antarctic blue whales except for 90 blue whales which were caught in Chile and we considered to be eastern Pacific blue whales. Similarly, we considered all catches taken in the temperate regions of the South Atlantic to be Antarctic blue whales based on morphometrics and song type (Mackintosh & Wheeler 1929, Letsheleha et al. 2022). Almost all these low-latitude catches were taken at Saldanha Bay and Hangklip, South Africa; Walvis Bay, Namibia; and in Angola.

We separated Indian Ocean catches into Antarctic blue whales and pygmy blue whales using their location and length frequencies as described in Branch et al. (2025), although blue whale catches from Durban (n = 3,209) have long been difficult to assign to subspecies (Branch et al. 2007, Branch et al. 2008). Few length measurements are available from Durban for pregnant females and attempts to gather present-day passive acoustic data from Durban are still underway. Given the precipitous decline in blue whale catch rates at Durban before any targeted whaling on pygmy blue whales (Best 2003), we assigned Durban catches to Antarctic blue whales except for four of the catches specifically identified as pygmy blue whales based on their lengths and reported accounts (Branch et al. 2025).

3.2.1.2 Unspecified catches

A total of 25,610 catches in the IWC summary database were not assigned to individual species and came from a variety of whaling expeditions (each expedition is one land station or pelagic fleet in a single Antarctic season). Portions of catches that included unspecified species in Antarctic blue whale areas (e.g., Branch et al. 2025) between 1904 and 1961 were assigned as Antarctic blue whales using the following rules in order depending on what was available in the database: 1) the ratio of the catches in the same expedition with known species, 2) the ratio of known species from a similar expedition (same location, whaling country etc.) in the year before or after, or 3) information from the source of the catch data which was included in the notes of the catch database. We thus assumed that unspecified catches are a consequence of missing data/records, rather than being catches that were difficult to identify to species. This assumption seems reasonable given that there were no unspecified catches for most expeditions and seasons.

3.2.2 Data on recent abundance

Ship-based line-transect abundance estimates are available from three sets of circumpolar surveys conducted between 1978/79 and 2003/04 from the IWC's International Decade of Cetacean Research (IDCR) and Southern Ocean Whale and Ecosystem Research (SOWER) circumpolar programs, south of 60°S (referred to as SOWER estimates) which were calculated using standard distance sampling methods assuming that g(0) = 1 (Branch 2007). Additionally, line-transect abundance estimates from IWC areas IV and V were available from Japan's research program in the Antarctic (JARPA and JARPAII)surveys south of 60°S and between 70°E and 170°W conducted between 1989/90 – 2008/2009 (referred to as JARPA estimates) which were calculated using multiple covariate distance sampling with whether and visibility as covariates on the detection function and assuming that g(0) = 1 (Hamabe et al. 2023). The abundance estimate from the JARPA survey in 1995/1996-1996/1997 was exceptionally low (6) and was considered unreasonable given the estimates in the previous and subsequent surveys, therefore it was removed from the analysis (Table 3.1). Previously published abundance estimates from the JARPA and JARPAII surveys were calculated over a larger spatial area (IWC areas IIE–VIW, 35°E–145°W), but were limited to years after 1995 (Matsuoka & Hakamada 2014). We did not use these estimates in our analysis. We only used the more recently published estimates (Hamabe et al. 2023), which cover the full survey period, in our analysis. However, , these previously published JARPA estimates (Matsuoka & Hakamada 2014) were used in one model run to test the sensitivity of the model to the difference in estimates (Appendix S2).

Table 3.1 Abundance estimates of Antarctic blue whales from IDCR-SOWER, JARPA and JARPA II line-transect surveys. The three SOWER (Branch 2007) surveys were circumpolar (CP) and are treated as absolute estimates of abundance in the model, while the JARPA estimates (Hamabe et al. 2023) are only from IWC areas IV and V and are used as relative abundance estimates. Years are the midpoints of each set of surveys (6-12 yr for IDCR-SOWER and 2 yr for JARPA) that were used in the model.

Area	Year	N	CV	Source
CPI	1980	566	0.40	SOWER (Branch 2007)
CPII	1987	686	0.47	SOWER (Branch 2007)
CPIII	1997	2249	0.36	SOWER (Branch 2007)
IV&V	1989	164	0.780	JARPA (Hamabe et al. 2023)
IV&V	1991	228	0.425	JARPA (Hamabe et al. 2023)
IV&V	1993	199	0.419	JARPA (Hamabe et al. 2023)
IV &V	1995	6	0.964	JARPA (Hamabe et al. 2023)
IV&V	1997	302	0.589	JARPA (Hamabe et al. 2023)
IV&V	1999	357	0.496	JARPA (Hamabe et al. 2023)
IV&V	2001	485	0.388	JARPA (Hamabe et al. 2023)
IV&V	2003	115	0.408	JARPA (Hamabe et al. 2023)
IV&V	2005	353	0.469	JARPA (Hamabe et al. 2023)
IV&V	2007	918	0.577	JARPA (Hamabe et al. 2023)

Additionally, we estimated a circumpolar abundance estimate south of 60°S for 2018/2019 of 2,889 (CV = 0.37) from a mark-recapture analysis of photo-identification data which were collected between 2003 and 2019. This estimate was calculated using a series of POPAN models which had a pre-specified survival parameter (fixed), a constant capture probability, and annually varying probability of entry (Jolly 1965, Seber 1965, Schwarz & Arnason 1996) and were fit using the package *RMark* (Laake & Rexstad 2011). Though abundance was predicted for each year, we used only the estimate from the final year to account for potential non-random population mixing between years. Survival was unidentifiable in the POPAN model; therefore, models were fit with fixed survival values between 0.92 and 1.0. This range of survival values were chosen by calculating survival values that would be consistent with a positive population growth rate, which would be expected from a population that is recovering after being heavily depleted by whaling (Z.R. R. unpubl. analysis). Models were fit separately to photos from left aspects and right aspects of photographed whales. These left and right-side models for each survival probability were averaged using Akaike weights, and the resulting left and right-side estimates were combined using inverse-variance weighting to produce a single estimate. More information about this procedure and data can be found in Olson et al. (2025).

In addition to abundance estimates, visual sightings and effort data were available for Antarctic blue whales south of 60°S from the Japanese scouting vessel (JSV) database (Miyashita et al. 1995) from 1965/1966–1987/1988 (Table 3.2, Branch 2008). Because the method of recording search effort changed after 1977, the JSV data were split into “early” and “late” time series.

Table 3.2 Sightings (number of blue whales) from the Japanese scouting vessel (JSV) databasetogether with total search effort (km) , reprinted from Branch (2008). Only search effort and sightings recorded south of 60°S and between November and February were included in this dataset. No effort matching these criteria was recorded in 1970/71. Sightings before 1978 were considered part of the early time series, and sightings from 1978 and on were considered part of the late time series.

Year	Sightings	Effort (km)
1967	8	15,898
1968	5	8,182
1969	0	2,847
1970	-	0
1971	0	3,219
1972	0	47,889
1973	1	32,936
1974	0	15,642
1975	0	51,767
1976	31	30,017
1977	3	12,707
1978	0	5,124
1979	1	10,975
1980	15	15,179
1981	0	5,136
1982	0	5,836
1983	9	18,527
1984	22	32,908
1985	6	18,101
1986	10	22,791
1987	0	863

3.2.3 Assessment model

3.2.3.1 Model structure

We predicted abundance using a theta-logistic population model:

$$\widehat{N}_{t+1} = \widehat{N}_t + r_{max}\widehat{N}_t\left(1 - \left(\frac{\widehat{N}_t}{K}\right)^{\theta}\right) - C_t \tag{1}$$

where $\widehat{N}$ is the predicted population size at time t, r_{max} is the maximum intrinsic growth rate, K is the carrying capacity (and assumed pre-whaling abundance), θ is the shape parameter, and C_t are the catches in each year. It is common practice for the IWC to set $\theta = 2.39$ to ensure that population size at maximum sustainable yield is 60% of carrying capacity (Baker & Clapham 2004). However, more recent work by Kanaji et al. (2024) estimates that maximum productivity occurs at 69 – 87% of carrying capacity for baleen whales. Given the lack of data at high abundance, it is not possible to estimate θ for Antarctic blue whales, therefore, we fit models using $\theta = 11.2$, resulting in maximum productivity at 80% of carrying capacity which is the mean value in Kanaji et al. (2024) (though sensitivity to this assumption was tested and is discussed below).

The model begins at carrying capacity in the 1904/1905 season and is projected forward given the parameter values and catches to 2024/2025. Hereafter, all seasons are referred to by the first year in the season (e.g., 1904/1905 will be referred to as 1904). To improve convergence, we fit the model using the "backwards" procedure (e.g., Branch et al. 2004) so that the model estimates r_{max} and the population size in 1973 (N_{1973}), at the end of whaling for Antarctic blue whales; and then the corresponding value of K is calculated using Brent's algorithm (Brent 1973) in the *Optim* package (K Mogensen & N Riseth 2018) in Julia v.1.10.2 (Bezanson et al. 2017). We constrained the search for K between 100,000 and 400,000.

Line-transect survey abundance estimates (A) were assumed to be lognormally distributed. In addition to the CV estimated by distance sampling methods we estimated additional coefficients of variation for SOWER (CV_{add_S}) and JARPA (CV_{add_J}) to account for process error which were converted to variances given $\sigma^2 = \log(CV^2 + 1)$:

$$A_{SOWER,t} \sim Lognormal(\ln(\hat{N}_t), \ln(\mathrm{CV}_{SOWER,t}{}^2 + CV_{add\_S}{}^2 + 1)) \qquad (2)$$

Estimates from JARPA are relative indices of abundance, since they only cover part of the Southern Ocean, and therefore a survey-coverage parameter (q) was estimated to scale these estimates to circumpolar abundance:

$$A_{JARPA,t} \sim Lognormal(\ln(q\hat{N}_t), \ln(\mathrm{CV}_{JARPA,t}{}^2 + CV_{add\_J}{}^2 + 1)) \qquad (3)$$

The photo-ID abundance estimate was also assumed to be lognormally distributed, but no additional coefficient of variation was estimated:

$$A_{Photo,t} \sim Lognormal(\ln(\hat{N}_t), \ln(\mathrm{CV}_{Photo,t}{}^2 + 1)) \qquad (4)$$

3.2.3.2 Bayesian estimation

The prior for the maximum intrinsic rate of increase (r_{max})was Uniform(0, 0.114) with the upper bound based on the maximum biologically plausible increase rate for baleen whales (IWC 2013). The prior for the natural log of the population size in 1973 was Uniform(ln(106), ln(2000)). The lower bound for this prior was based on Sremba et al. (2018) who found 53 mitochondrial DNA haplotypes in 73 samples of Antarctic blue whales, which suggests that when the population was at its minimum it contained at least 53 mature females. Doubling this number (to account for males, assuming a 50:50 sex ratio) provides a conservative number for the minimum population size. The upper bound on this prior was set close to the highest IDCR/SOWER abundance estimates (Table 3.1). Weakly informative priors were used for all other parameters (Table 3.3).

Table 3.3 Priors used for parameters in Bayesian assessment model.

Model	Parameter	Description	Prior
Base	r_{max}	Intrinsic growth rate	Uniform(0, 0.114)
	$ln(N_{1973})$	Natural log of the population size in 1973	Uniform(1.8, 7.6)
	q_{JARPA}	Coverage parameter for JARPA	Uniform(0,1)
	CV_{add_S}	Additional CV for SOWER	Exponential(1)
	CV_{add_J}	Additional CV for JARPA	Exponential(1)
JSV	q_{early}	Coverage parameter for early JSV	Uniform(0,1)
	q_{late}	Coverage parameter for late JSV	Uniform(0,1)
	ϕ_{early}	Overdispersion for early JSV	Gamma(0.1, 0.1)
	ϕ_{late}	Overdispersion for late JSV	Gamma(0.1, 0.1)
Song intensity r	r_{max}	Intrinsic growth rate	Normal(0.0373, 0.015^2)

Bayesian convergence was difficult to obtain even with the highly efficient no-U-turn sampler (e.g., Monnahan et al. 2019). The best solution was to fit models in the Turing package (Ge et al. 2018) in Julia v.1.10 (Bezanson et al. 2017), using a random permutation Gibbs sampler (Geman & Geman 1984) with univariate slice sampling (Neal 2003). The initial step size was set to 2.0, and the model was fit using 4 chains, 2000 saved iterations (after a thinning rate of 50) and a 50% burn-in. Convergence was checked using traceplots, autocorrelation plots, and by assuring that $\hat{R}$ values were less than 1.01 (Vehtari et al. 2021). Posterior predictive distributions were drawn for each abundance estimate from the fitted model and used to evaluate model fit. Post-processing of results and the creation of figures were done using R v.4.5.1 (R Core Team 2025). Data and code used for these analyses can be found at: https://github.com/zoer27/ABWPopulationAssessment

3.2.3.3 Sensitivity analyses

In addition to a base model, sensitivities to the different data sources, the priors, and fixed parameter values were explored. The "base" model outlined above included abundance estimates from SOWER and JARPA surveys and the photo-ID mark-recapture analysis incorporating survival rates from 0.92-1. For the base model, we also assumed $\theta = 11.2$, and used a prior for r_{max} of Uniform(0, 0.114). In addition to the base model, 8 additional models were run, which are outlined below (Table 3.4).

Table 3.4 Model descriptions for sensitivity analyses. Text indicates changes from the base model in the first row. "–" indicates that there was no change from the base model. Parameters are described above (Table 3.3).

Model name	Estimated parameters	Fixed parameters	Data sources	Prior for r
Base	r_{max}, $ln(N_{1973})$, q_{JARPA}, CV_{add_S}, CV_{add_J}	$\theta = 11.2$	SOWER abundance estimates, JARPA abundance estimates, photo-ID abundance estimate	Uniform(0, 0.114)
JSV	Add q_{early}, q_{late}, ϕ_{early}, ϕ_{late}	–	Add JSV sightings	–
Song intensity r	–	–	–	Normal(0.0373, 0.015^2)
Adjusted θ	–	$\theta = 2.39$	–	–
Fixed survival	–	$s = 0.96$	Used alternate photo-ID abundance estimate created with s = 0.96	–
No Photo ID	–	–	Remove photo-ID abundance estimate	–
No JARPA	Remove CV_{add_J}, q_{JARPA}	–	Remove JARPA abundance estimates	–
No SOWER	Remove CV_{add_S}	–	Remove SOWER abundance estimates	–
Just SOWER	Remove CV_{add_J}, q_{JARPA}	–	Remove JARPA and photo-ID abundance estimates	–

JSV: one model included sightings data from the Japanese scouting vessel database. In addition to the parameters outlined above, this model estimated a conversion parameter between model-estimated abundance and number of whales sighted for both the "early" and "late" time series (q_{early}, q_{late}). The model predicted the number of sightings for a given amount of effort using the predicted abundance, effort data, and estimated q, and was fit to the actual sightings using a negative-binomial likelihood. Separate overdispersion parameters (ϕ_{early}, ϕ_{late}, where smaller ϕ indicates greater variance than would be accounted for in a Poisson distribution) were estimated for the early and late time series. We divided the nominal effort by 100,000 to improve convergence. Weakly informative priors were used for these additional parameters (Table 3.3).

Seasonal song intensity prior for r_{max}: to explore the sensitivity of our model results to priors on r_{max}, we fit an additional model with a prior of Normal(0.0373, 0.015^2) which was built based on the annual mean and standard deviation of the increase in Antarctic blue whale chorus intensity (measured as the mean spectrum density at a +-0.25-Hz frequency band around the mean value of unit 1 of the Z call in each year) at the Cape Leeuwin hydrophone from 2002–2020. To correct for background noise, including individual calls or call chorus from fin whales *(Balaenoptera physalus*), the mean value of noise intensity in the two adjacent bands of 0.5-Hz width were subtracted (Gavrilov et al. 2012); and A. N. Gavrilov & R. D. McCauley pers. comm., Z. R.

Rand unpubl. analysis). This assumes that acoustic energy at the frequency of Antarctic blue whale increases in proportion to their population size, and that increasing song intensity is not the result of changes in acoustic distribution or behavior (e..g, Gavrilov et al. 2012, Širović & Oleson 2022). Finally, we assumed that seasonal song intensity was neither directly nor indirectly affected by trends in the environmental and anthropogenic sources that have been observed from the Cape Leeuwin hydrophone (Park et al. 2023).

Adjusted θ*:* in addition to the fixed value of the theta-logistic shape parameter of $\theta = 11.2$, we fit a model with a $\theta = 2.39$ as is common practice for the IWC.

Fixed survival: Since the photo-ID abundance estimate in the base model was averaged across survival rates, we also used a photo-ID abundance estimate calculated for a single value of survival ($s = 0.96$); (e.g., Branch et al. 2004): 2,846 (CV: 0.30), using the POPAN model and the left-and-right side model averaging methods described in Olson et al. (2025). We fit the model to this abundance estimate and explicitly incorporated the fixed survival value into the population dynamics equation, rather than implicitly included in the r_{max} parameter (e.g., Rand et al. 2024). The value of $s = 0.96$ has been assumed the most likely value in previous Antarctic blue whale studies (e.g., Branch et al. 2004).

Excluding data components: we also fit models excluding each of the data sources (SOWER estimates, JARPA estimates, and photo-ID estimate) to explore their influence on the model results (Table 3.4).

3.3 Results

The total catch of Antarctic blue whales was 347,662 including 746 of the 25,610 unspecified catches in the database. Unspecified catches account for only 0.21% of the total Antarctic blue whale catches. Antarctic blue whale catches increased from a low of 11 in 1904 to a high of 30,405 in 1930, decreasing afterwards, with periods of few catches during World War I and World War II, until the final Antarctic blue whale catch in 1973 (Figure 3.1, Appendix S1).

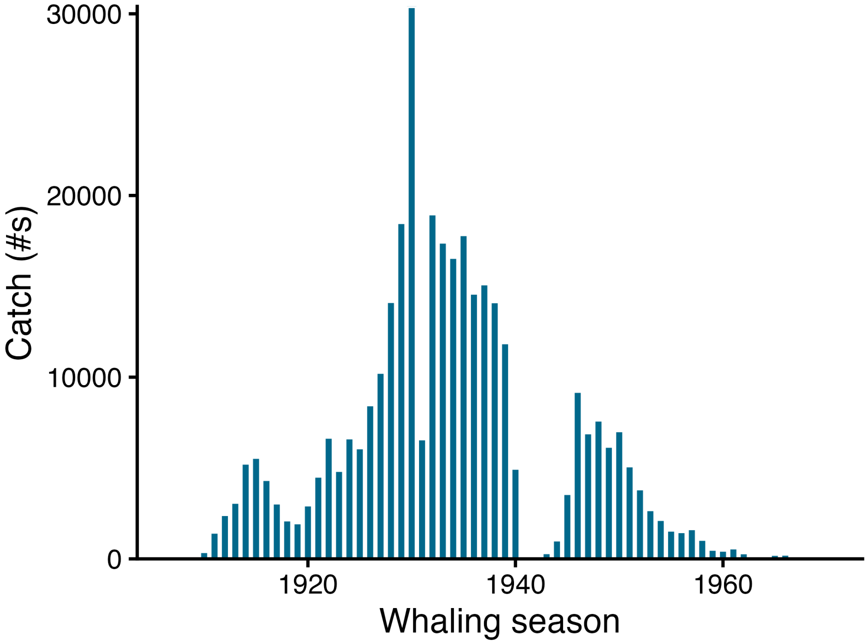

Figure 3.1 Annual catches of Antarctic blue whales from 1904-1973 from commercial whaling in the Southern Ocean.

3.3.1 Base model

Our base model estimated a maximum intrinsic growth rate (r_{max}) for Antarctic blue whales of 0.045 (0.016–0.073; Figure 3.2a). Their estimated pre-whaling abundance was 205,905 (168,473–276,342; Figure 3.2b). We estimated that the population size in 1973 was 418 (147–1,099; Figure 3.2c), which was 0.20% (0.008–0.42%) of their estimated pre-whaling abundance (Figure 3.2d; Table 3.5).

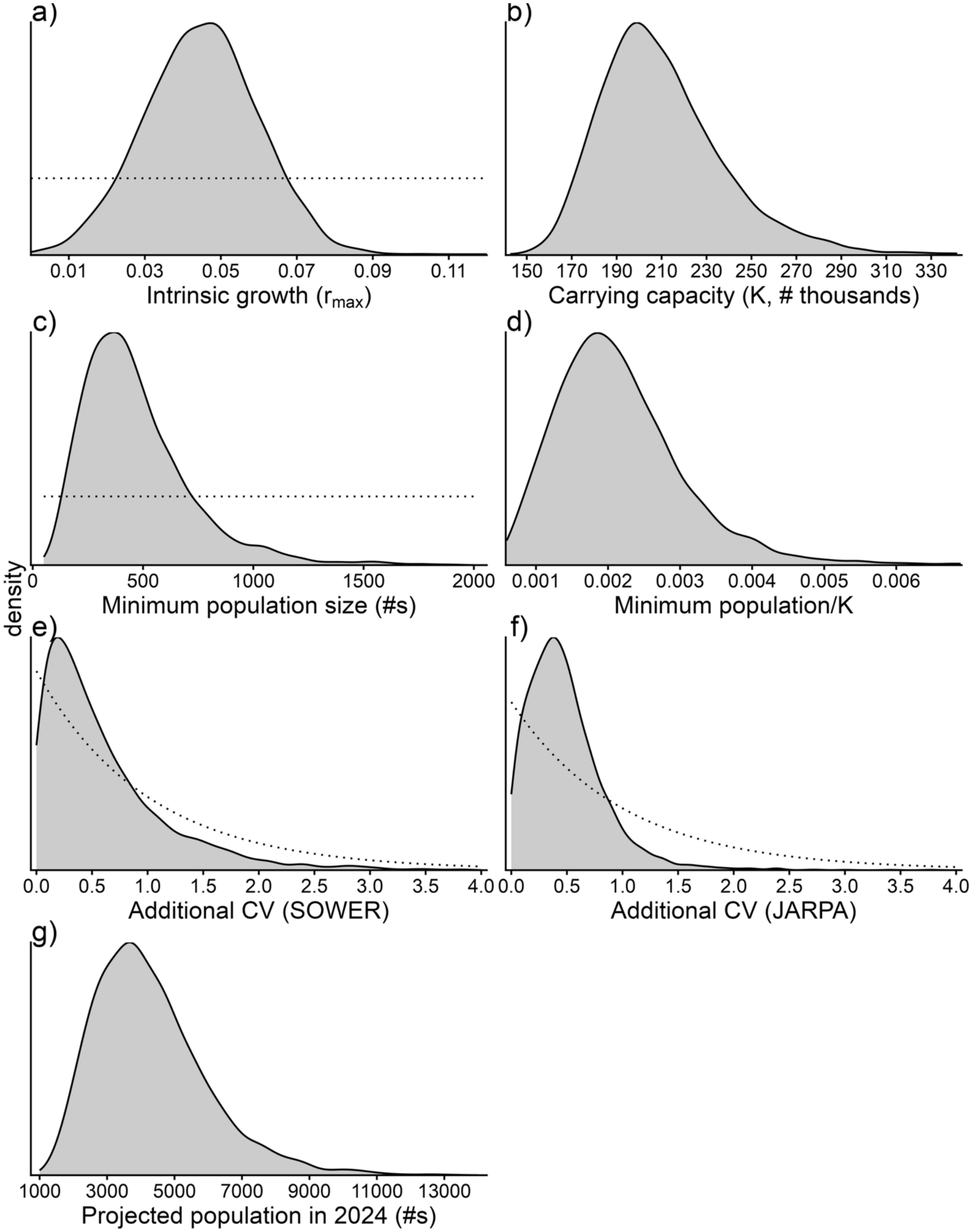

Figure 3.2 Posterior densities (solid lines) of estimated parameters and derived quantities from the base population assessment model fit to abundance estimates from line-transect surveys and a mark-recapture photo-ID estimate. For parameters that were directly estimated in the model, priors are included as dotted lines.

Table 3.5 Medians (50%) and 95% credible intervals (2.5%-97.5%) of key parameters from the base model as well as models run as part of sensitivity analysis (Table 3.4).

Model		r_{max}	K	N_{1973}	N_{2024}	N_{1973}/K	N_{2024}/K
Base	50%	0.045	205,905	418	4,018	0.0020	0.019
	2.5%	0.016	168,473	147	1,874	0.0008	0.007
	97.5%	0.073	276,342	1,099	8,395	0.0042	0.048
JSV	50%	0.055	191,184	279	4,265	0.0015	0.022
	2.5%	0.026	160,111	110	1,957	0.0007	0.008
	97.5%	0.082	245,183	742	9,270	0.0031	0.057
Song intensity r	50%	0.041	213,040	465	3,710	0.0022	0.017
	2.5%	0.021	182,066	207	1,911	0.0011	0.008
	97.5%	0.062	260,088	1,020	7,046	0.0041	0.038
Adjusted θ	50%	0.044	247,246	425	4,010	0.0017	0.016
	2.5%	0.015	206,764	148	1,882	0.0007	0.007
	97.5%	0.075	305,671	1,128	8,902	0.0038	0.042
Fixed survival	50%	0.044	207,183	421	3,896	0.0020	0.019
	2.5%	0.017	169,613	135	2,010	0.0008	0.008
	97.5%	0.072	274,315	1,122	7,460	0.0043	0.042
No photo ID	50%	0.057	187,597	361	6,523	0.0019	0.035
	2.5%	0.0085	140,823	135	880	0.0008	0.003
	97.5%	0.105	305,860	960	36,698	0.0039	0.255
No JARPA	50%	0.046	204,969	410	4,056	0.0020	0.020
	2.5%	0.016	166,255	138	1,826	0.0008	0.007
	97.5%	0.075	277,474	1,123	9,186	0.0042	0.053
No SOWER	50%	0.050	197,573	277	3,585	0.0014	0.018
	2.5%	0.011	161,449	107	1,666	0.0006	0.007
	97.5%	0.080	296,713	1,556	8,010	0.0055	0.047
Just SOWER	50%	0.073	168,750	322	12,303	0.0019	0.073
	2.5%	0.0087	136,290	132	1,194	0.0009	0.004
	97.5%	0.111	304,827	1,079	54,431	0.0044	0.388

This depletion was caused by harvest rates between 10–40% in many years, well above sustainable levels (Figure 3.3).

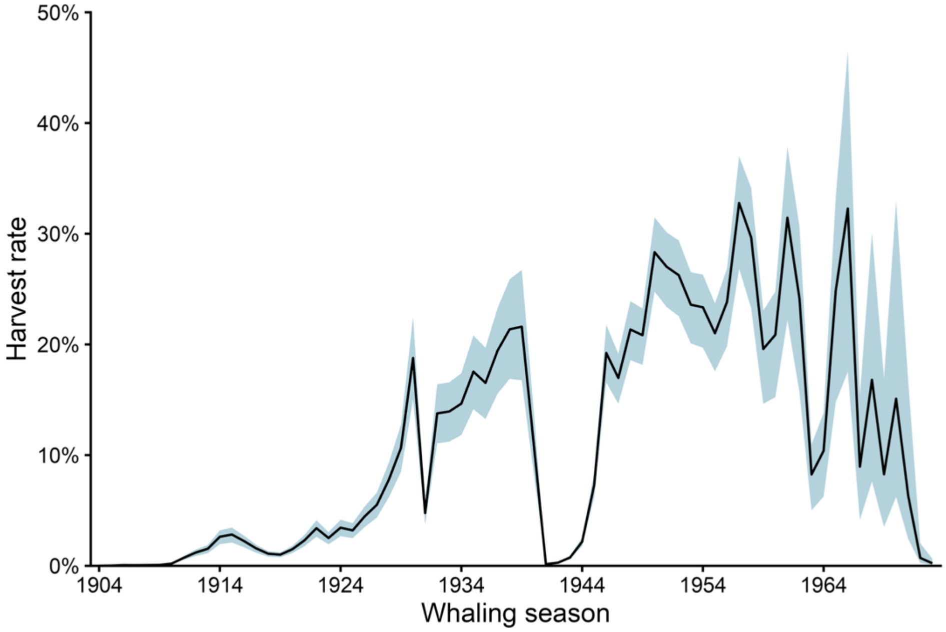

Figure 3.3 Antarctic blue whale harvest rates. Median (line) and 95% credible interval (shading) of the proportion of total Antarctic blue whale population caught in each whaling season estimated from the base population assessment model.

Despite their near extinction from whaling, the current population is estimated to be increasing (Figures 3.4-3.5). Our base model estimated the population to be 4,018 (1,874 –8,395) in 2024 (Figure 3.2g), which is 1.9% (0.7–4.8%) of their estimated pre-whaling abundance. The base model fits well to the abundance estimates, with abundance estimates near the 95% credible intervals of the population size predicted by the model and contained within the posterior predictive distributions (Figure 3.5).

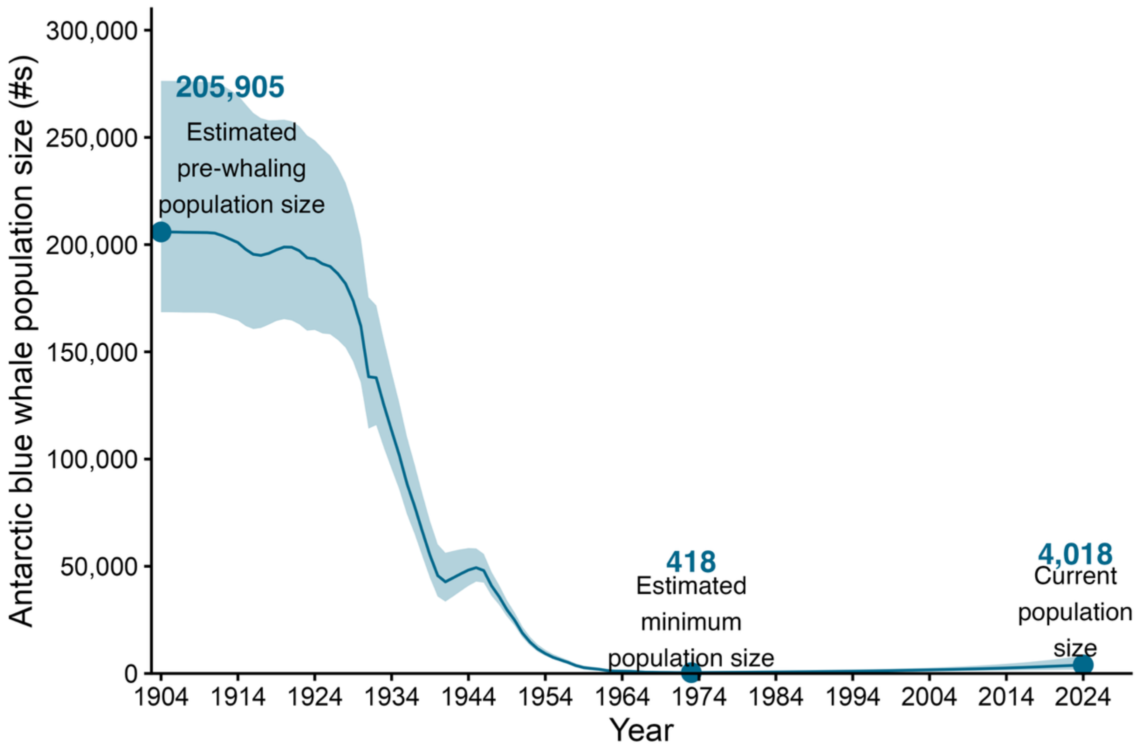

Figure 3.4 Antarctic blue whale population size over time. Posterior median (solid line) and 95% credible intervals (shading) of modeled Antarctic blue whale population size over full period of the study from the base population assessment model fit to line-transect and mark-recapture abundance estimates.

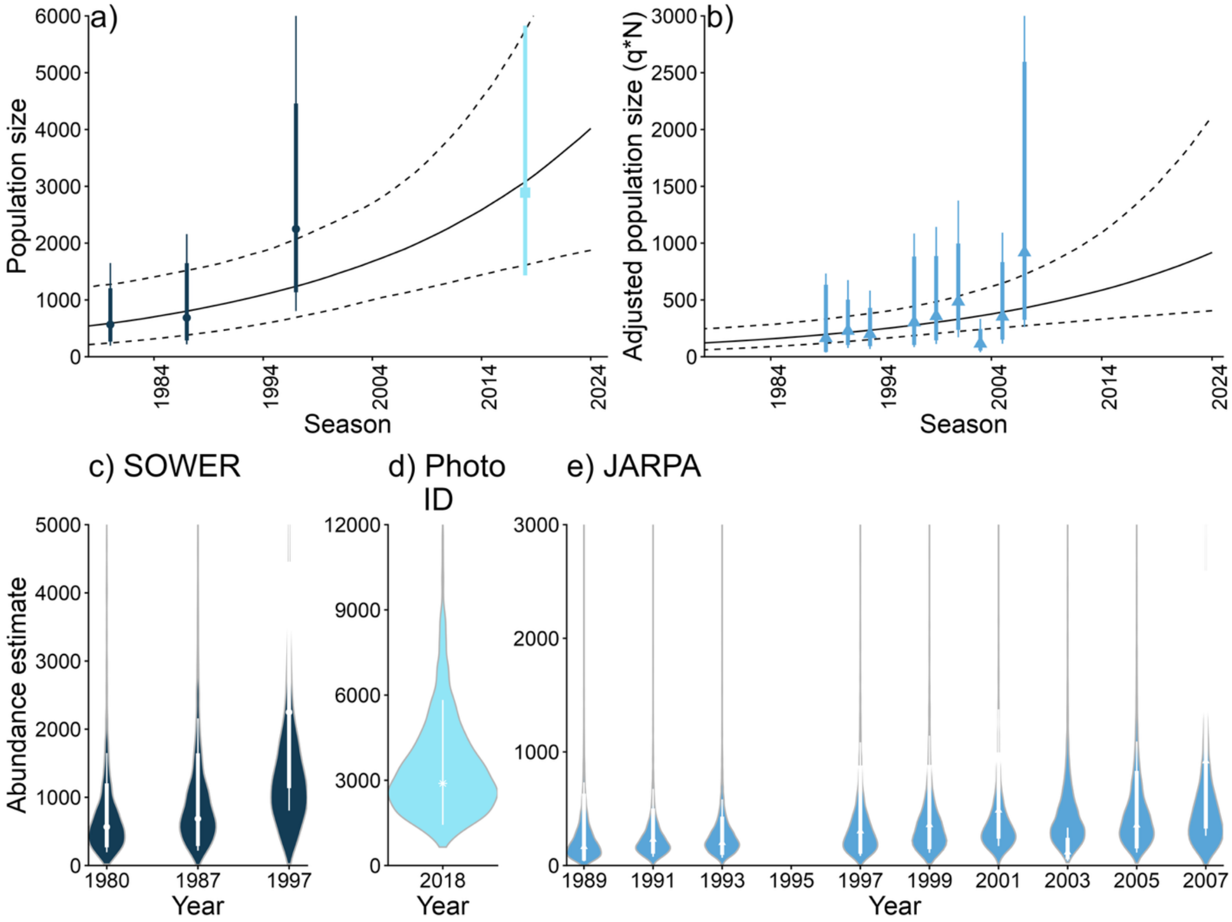

Figure 3.5 Posterior and posterior predictive distributions from the base model. (a) Abundance estimates from SOWER surveys (circles) and photo-ID data (square) and 95% confidence intervals built from estimated CVs (thick colored lines) and model-estimated additional CV (thin colored line) included with the median posterior population size from 1978-2024 (line) and 95% credible interval (dashed line) (b) as well as JARPA abundance estimates (triangles) with adjusted population size (estimated q_{JARPA}*N) from 1978-2024. (c-e) Posterior predictive distributions (violins) for each abundance estimate (points) included in the base model. 95% confidence intervals built from the abundance estimate CV are indicated by thicker lines, and thinner lines indicate 95% confidence intervals built including estimated additional CV.

3.3.2 Sensitivities

Estimates of r_{max} were generally robust to changes in the data sources, the value of θ, and the priors, and the inclusion of a fixed survival parameter. Median estimates ranged from 0.041–0.057 for all models except for the model which only included abundance estimates from the SOWER surveys, which had a median estimate of 0.073 (Table 3.5). The informative prior for $r_{max},$ predictably led to a more precise estimate, while excluding data sources led to less precise estimates (Figure 3.6a).

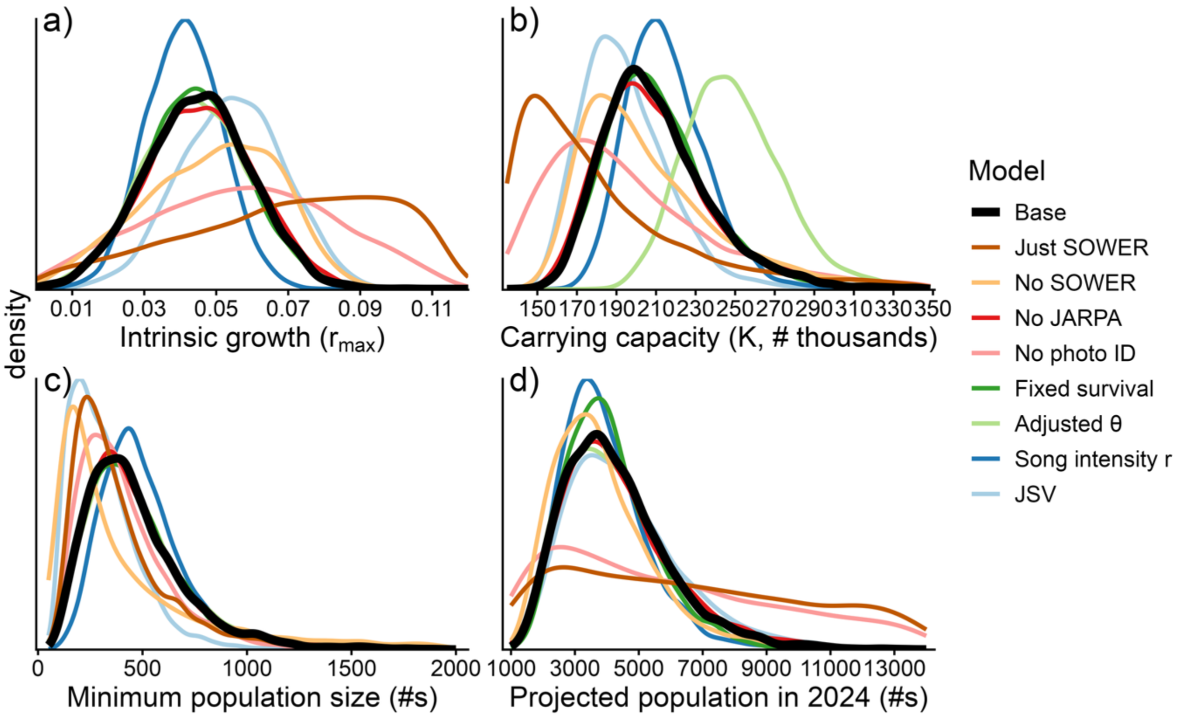

Figure 3.6 Posterior distributions from the sensitivity tests. Posterior densities of key parameters and derived quantities for the base model (black) as well as sensitivity model runs (colored lines, see Table 3.4 for descriptions of each model).

Estimates of carrying capacity were also largely robust to changes in the data sources, priors and the inclusion of fixed survival, with median estimates ranging from 168,000–213, 000 for all models except for $\theta = 2.39$ where carrying capacity was estimated to be 247,246 (206,764–305,671; Table 3.5, Figure 3.6b).

Estimates of the population size in 1973 ranged from 277–465, with the lowest estimate in the model that did not include the SOWER data, and the highest in the model with the song intensity prior for r_{max} (Table 3.5). The song intensity prior for r_{max} removed the possibility of some higher values of r_{max}, requiring a higher minimum population size to reach similar abundance estimates.

Finally, estimates of the population size in 2024 were largely driven by the photo-ID abundance estimate. In models where the photo-ID abundance estimate was included, estimates of the population size in 2024 ranged from 3,710–4,265 (Table 3.5), but in the models without this estimate, N_{2024} was estimated to be substantially higher, for example 6,523 (880–36,698) for the “No photo ID “ model and 12,303 (1,194–54,431) for the “just SOWER” model (Table 3.5). N_{2024} also had much broader posterior distributions in the non-photo-ID models (Figure 3.6d). This is the only source of information for recent global abundance, and the model was forced to fit to it more precisely than the survey abundance estimates since no additional variance was estimable for this estimate.

3.4 Discussion

We estimated that Antarctic blue whales declined from a high of 206,000 to a low of 418 in less than 70 years of commercial whaling. Since the end of whaling in 1973, the Antarctic blue whale population has increased. Branch et al. (2004) found that Antarctic blue whales were increasing but had reached less than 1% of their pre-whaling levels in 1997. Our projections estimate the abundance to be 1.9% of pre-whaling levels in 2024 (Figure 3.4). If Antarctic blue whales continue to increase following the estimated theta-logistic model, they are expected to reach 60% of pre-whaling abundance only by 2102.

Our estimated annual rate of increase (0.045) from the base model is lower than the 0.073 (0.014–0.116) estimated by Branch et al. (2004). This difference is due to the inclusion of revised JARPA estimates and the new photo-ID abundance estimate, since the model with just the SOWER estimates resulted in a higher rate of increase (0.073, Table 3.6, Figure 3.6).

Our estimated pre-whaling abundance (206,000; 168,000–276,000) is also lower than the 239,000 (202,000–311,000) in Branch et al. (2004) though the credible intervals overlap. This likely reflects the use of $\theta = 11.2$ in our model, instead of $\theta = 1$ (simple logistic growth model) in Branch et al. (2004). Increasing the value of θ leads to a slower decline of the per capita growth rate as the population size increases, resulting in a lower pre-whaling abundance (K) for a given value of r. This effect can be seen in the results of our adjusted θ model, which assumed $\theta = 2.39$ and had a higher estimated carrying capacity (247,000; Table 3.5, Figure 3.6) than the base model.

One source of uncertainty in these results stems from the catch data. There are no indications in the catch data of the number of whales that were struck and killed by whalers but not caught and processed ("struck-and-lost"). It is sometimes assumed that before 1916 the number of struck-and-lost whales was 30% of the annual catch total (e.g., International Whaling Commisson 2017, Cooke 2018). However, since relatively few Antarctic blue whales were caught before 1916, this is unlikely to have a substantial impact on our results and therefore we did not adjust the catch values in our study.

The abundance estimates used in these models only included Antarctic blue whales south of 60°S (Branch et al. 2004, Hamabe et al. 2023, Olson et al. 2025). This ensures that these estimates exclude pygmy blue whales which range north of this region (Branch et al. 2007, Branch et al. 2009, Branch et al. 2025). However, it is possible that these estimates are negatively biased, due to missing some Antarctic blue whales that may have remained north of this latitude. It is not currently possible to estimate the extent of this bias, but it is likely to be small (Branch et al. 2004). The abundance estimates used in this study also do not account for blue whales that may have been missed because they were inside of the pack ice and inaccessible to vessels. The proportion of Antarctic blue whales missed due to being inside the pack ice is also likely to be small because Antarctic blue whales are less likely to be within the pack ice than other species, notably Antarctic minke whales (*Balaenoptera bonaerensis;* Kasamatsu et al. 2000).

Another potential form of negative bias in the estimates from line-transect surveys stems from the $g(0) = 1$ assumption which describes the proportion of whales sighted on the track line. In both survey estimates (SOWER and JARPA) it is assumed that all Antarctic blue whales on the track line can be seen. Blue whales are large and have highly visible blows, and the sightings surveys were undertaken by trained and experienced observers, therefore it is likely that $g(0)$ is high, though it is unlikely that *all* whales on the track line are seen since blue whales are frequently underwater and seas are not always calm (e.g., Barlow 2015). For North-east Pacific blue whales, $g(0)$ has been estimated to be 0.90 (Calambokidis & Barlow 2004) and for North Atlantic blue whales it has been estimated to be 0.83 (Pike et al. 2019). A simulation study based on blue whale diving behavior found that $g(0)$ ranged from 0.80–0.96 depending on sighting conditions, vessel speed, whale swim speed, and the duration of the whale's dive (Leaper et al. 2015). Since $g(0)$ is a scaling factor, if these lower values of $g(0)$ were used this would lead to survey-based abundance estimates 4–25% higher than used in this study. The use of independent observer platforms on the IDCR-SOWER surveys affords the opportunity to estimate g(0) for Antarctic blue whales, especially in combination with Calderan et al. (2023) estimates of Antarctic blue whale surfacing rates and dive times. However, to date no such analysis has been conducted.

These negative biases in the survey estimates suggests there is likely a negative bias in our estimates of the minimum population size and pre-whaling abundance. The estimate of the population size in 2024 was largely driven by the photo-ID abundance estimate (Figure 3.6d) so the negative bias from the $g(0)$ assumption likely has less of an impact on that estimate. However, the photo-ID abundance estimate may also be negatively biased due to unequal sampling effort in different IWC management areas (Olson et al. 2025). Additionally, the photo-ID estimate assumes that the Antarctic blue whale population is randomly mixing every year. This assumption is likely to be violated for Antarctic blue whales, as the probability of returning to the same ocean basin from one year to the next has been estimated to be between 54-64% and if the population was completely randomly mixed every year, we would expect this number to be closer to 33% (Rand et al. 2024). These negative biases suggest that our estimates of the current population size as well as the rate of increase may be an underestimate of the true values. However, while these are conservative estimates, this would not change the overall conclusion that Antarctic blue whales were heavily depleted by commercial whaling, their population is increasing, and that they are still far from their pre-whaling levels.

While Antarctic blue whales are increasing, it will take over a century for them to approach pre-whaling levels. Many exploited cetacean populations have returned to or exceeded their pre-whaling levels in the past decade including eastern North Pacific blue whales (Monnahan et al. 2015), eastern North Pacific gray whales (*Eschrichtius robustus*) (Stewart et al. 2023), North Pacific humpback whales (*Megaptera novaeangliae*) (Cheeseman et al. 2024), and some populations of Southern Hemisphere humpback whales (Seyboth et al. 2023). Most of these populations, however, were not as heavily depleted as Antarctic blue whales.

The carrying capacity for Antarctic blue whales may have shifted since pre-whaling times, suggesting that a return to pre-whaling levels may not be possible for this species. Southern right whales, for example, have shown a decline in recent years even though their current population size is not near their estimated pre-whaling abundance and despite increasing exponentially in the years immediately after whaling protection (Grundlehner et al. 2025). The availability of Antarctic krill (*Euphausia superba*), the main Antarctic blue whale prey, is a key factor that could limit Antarctic blue whale population growth and ultimate carrying capacity in the

Southern Ocean, though the complexities of interspecific competition, anthropogenic disturbance, and climate change make it difficult to predict exactly how krill availability will change and how this will impact blue whale recovery.

Baleen whales can act as a “whale pump”, diving to deep depths to consume several tons of krill each day and then excreting fecal matter at the surface that contains nutrients and trace metals that are important for primary productivity within the photic zone (Roman & McCarthy 2010). Through this mechanism, baleen whales are hypothesized to be a key component of a positive feedback loop, adding iron-rich fecal matter to areas of high primary productivity, sustaining the phytoplankton blooms that support krill populations (Savoca et al. 2021, Monreal et al. 2025). Therefore, the loss of millions of baleen whales, and especially the loss of Antarctic blue whales which were the largest krill consumer (Savoca et al. 2021), may have drastically changed the structure of this ecosystem and led to declining krill populations.

Even if Antarctic blue whales can fully resume their function as a whale pump as their populations recover, they will likely still face increased competition for krill, which will impact their ability to return to pre-whaling abundance. Humpback, Antarctic minke, and fin whales all feed primarily on krill in the Southern Ocean and may be returning to pre-whaling levels faster than Antarctic blue whales (Herr et al. 2022, Moosa & Butterworth 2024). However, interspecific competition for krill may be somewhat mitigated through niche-partitioning, for example, by targeting krill at different depths (Friedlaender et al. 2009), or preferring krill of different sizes, life-stages, or swarm properties (Santora et al. 2010, Friedlaender et al. 2014, Miller et al. 2019). Human harvest of krill can be equivalent to or higher than the demands of other krill-consuming predators, and krill fisheries are projected to increase in the future (Trathan et al. 2022). Climate change may also impact krill availability, as krill density has been shown to decline with decreasing sea ice cover and ocean warming (Atkinson et al. 2004, Tulloch et al. 2019, Kawaguchi et al. 2023).

As other species of baleen whales have returned to their pre-whaling population sizes they have been subject to increasing effects from changing environmental conditions (Stewart et al. 2025). For example, eastern North Pacific gray whales have experienced large fluctuations in population size in response to changes in sea ice cover in their Arctic feeding areas (Stewart et al. 2023). In addition, North Pacific humpback whales have declined in response to marine heatwaves (Cheeseman et al. 2024). Therefore, as the Antarctic blue whale population continues to increase, they may be increasingly affected by a changing environment. If their carrying capacity has declined since pre-whaling times, then we may see these effects long before Antarctic blue whales reach pre-whaling levels.

As a critically endangered species, it will be important to monitor the population size of Antarctic blue whales to understand the impacts that future ecosystem-level changes will have on their recovery. Data on the current population size of Antarctic blue whales remains limited. Line-transect surveys for Antarctic blue whales have largely ceased or are limited to small regions of the Antarctic (e.g., Paarman et al. 2021). While photo-identification effort is ongoing, including from platforms of opportunity (e.g., Calderan et al. 2020), there has not been consistent coverage throughout the Southern Ocean, and resighting rates are low (Olson et al. 2025). Mark-recapture studies require effort over more than 12 years to produce a reliable estimate of abundance for Antarctic blue whales (Peel et al. 2015), suggesting that long-term photo-identification studies are critical to estimating current abundance. Passive acoustic monitoring has proven a reliable method for producing encounters with Antarctic blue whales (Miller et al. 2015). When coupled with line-transect surveys and photo-identification sampling, passive acoustic monitoring can improve encounter rates and reduce encounter rate variance, especially when animal densities are low (Peel et al. 2014). Furthermore, improved methods for analysis of passive acoustic recordings (e.g., de Castro et al. 2024, Harris et al. 2025) have helped standardize outputs and have paved the way for passive acoustic density estimation, though abundance estimates based on passive acoustic monitoring remain contingent on establishment of a relationship between call density and abundance. Whether or not Antarctic blue whales continue to increase, additional line-transect surveys, passive acoustic monitoring, and increased photo-ID effort are needed to provide abundance estimates that can be used to monitor the Antarctic blue whale population into the future and provide the fine-scale data that is needed to assess the impacts of prey-availability and environmental changes and stochasticity on their recovery.

Integrated assessment models, such as the one we present here, provide the opportunity to bring together abundance and trend information from line-transect surveys, passive acoustic monitoring, photo-identification mark-recapture studies, and sightings from platforms of opportunity. As more of these data become available, this assessment provides a framework that can be used to monitor the Antarctic blue whale population into the future and assess the impacts of prey-availability and environmental changes and stochasticity on their recovery.

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Chapter 4. Estimates of blue whale growth and reproduction parameters from historical data

Publication history: This study was co-authored with Trevor A. Branch, André E. Punt, Hikari Maeda and Sally Mizroch. At the time this dissertation was submitted, a version of this chapter was in preparation to be submitted to *Marine Mammal Science*.

Abstract

Blue whales (*Balaenoptera musculus*) were exploited during whaling in the 20th century, bringing many of their populations near to extinction. During whaling, biological data, such as earplugs and ovarian corpora, were collected that can provide information about key demographic parameters that can provide information about population status and recovery from whaling. We compiled earplug age data (*n* = 2,037), and fit models to estimate age-length relationships for Antarctic, eastern North Pacific (ENP), and pygmy blue whales. We estimated the asymptotic length for females to be 21.8 m (95% interval: 21.6–22.0 m) for pygmy, 23.7 m (22.8–24.5 m) for ENP, and 26.7 m (26.2–27.0 m) for Antarctic blue whales; while males were shorter with asymptotic lengths of 21.2 m (21.0–21.3 m) for pygmy, 22.7 m (21.4–23.8 m) for ENP, and 24.2 m (23.5–24.8 m) for Antarctic blue whales. Additionally, we modelled relationships between age and number of ovarian corpora (*n* = 50) for pygmy and ENP blue whales, estimating that corpora are added every 2.8 yr for pygmy and 2.5 yr for ENP blue whales. We also estimated that female pygmy blue whales are sexually mature at 9.5 (6.3–10.8) years and female ENP blue whales at 8.9 (4.4–10.5) years. These estimates provide a historical baseline to assess population recovery and changes in growth or reproduction for blue whales.

4.1 Introduction

Baleen whales were heavily exploited in the 20th century due to commercial whaling (Clapham et al. 1999) and blue whales were no exception, with multiple populations whaled to near extinction, resulting in their current listing globally as Endangered by the IUCN (Cooke 2019, Thomas et al. 2016). Whaling proceeded sequentially from one region to the next as each population was depleted. In the North Atlantic, whaling of blue whales began in 1864 and it is likely that between 15,000 and 20,000 blue whales were caught, though catch records are incomplete (Aguilar & Borrell 2022, Cooke 2019). However, by the early 20th century blue whales had been largely depleted in the North Atlantic and fin whales (*Balaenoptera physalus*) had become the primary target of whaling (Aguilar & Borrell 2022). At least 10,000 blue whales were caught in the North Pacific between 1905 and 1971, affecting the eastern North Pacific and the central and western North Pacific populations of blue whales (Monnahan et al. 2015). In the Southern Hemisphere, Antarctic blue whales (*B. m. intermedia*) were the most valuable target of whaling, which started in 1904, and by 1950, more than 300,000 Antarctic blue whales had been caught, exceeding the entire population abundance before the start of whaling (Chapter 3). Pygmy blue whales (*B. m. brevicauda*) are found in the Indian Ocean and were not heavily pursued by whalers until the late 1950s. However, between 1959 and 1972 almost 12,000 pygmy blue whales were caught, spanning multiple populations (Branch et al. 2025). In addition, more than 2,000 Southeast Pacific (Chilean) blue whales were caught between 1908 and 1972 (Williams et al. 2011).

Despite their extensive exploitation, there is still much that is unknown about blue whale biology. For instance, while the differences in mean lengths among blue whale populations have been explored (e.g., Barlow et al. 2023, Branch et al. 2007a, Ichihara 1966), how length changes with age as blue whales grow has yet to be quantified. Whalers collected extensive biological data throughout the 20th century, including length, stomach contents, and sex; as well as the presence, sex, and length of fetuses from pregnant whales. However, the best way to age baleen whales was not discovered until the mid-1950s. Alternating light and dark layers of wax in the ear canal, known as an earplug, can be used to estimate age (Laws & Purves 1956, Purves 1955). Since most blue whale populations had been depleted by this time, the only previously published aging data for blue whales from earplugs are for pygmy blue whales (Branch & Mikhalev 2008, Ichihara 1966, Ichihara & Doi 1964). However, earplug data were also collected from eastern North Pacific blue whales (Rice 1963), western North Pacific blue whales, and Antarctic blue whales, which we collate for the first time in a single compilation in this paper. Age-length models can be used to predict lengths for a given age and can be used to understand patterns in physical growth as well as differences in mean lengths among age classes. While ages from earplug data and corresponding whale lengths have been plotted for pygmy blue whales (Ichihara 1966), no published age-length models currently exist for blue whales.

In addition to growth, reproductive rates are also unquantified for blue whales. Unlike some other well-studied baleen whales, blue whales do not aggregate close to shore during breeding and calving seasons, making it difficult to estimate pregnancy rates for this species, except through occasional hormone assays from biopsy data (Atkinson et al. 2019). Consequently, reasonable estimates of age at sexual maturity and pregnancy rates have long been of interest for blue whales. Before reliable aging methods were available, early researchers thought that the age at sexual maturity was 2-3 years (Laurie 1937, Mackintosh & Wheeler 1929). However, ovarian corpora data and earplug ages have challenged this for pygmy blue whales and for other species of baleen whales (Branch & Mikhalev 2008).

Ovarian corpora data can provide information about the age of sexual maturity for females and pregnancy rates. During mammalian ovulation, ova are produced inside the follicles and then are released when the follicles rupture. These follicles then transform into a corpus luteum, which, if a pregnancy occurs, secretes hormones such as progesterone that maintain the pregnancy. After pregnancy, or if the pregnancy fails, the corpus luteum regresses into a corpus albicans which is formed of fibrous scar tissue and, in cetaceans, remains macroscopically visible on the ovary (Robeck & O'Brien 2018). This was known by biologists working on large cetaceans and counts of corpora lutea and corpora albicans (referred to collectively as ovarian corpora) were collected starting in the 1930s (Laurie 1937). Since ovarian corpora are only present in sexually mature females (produced during ovulation), when combined with age data from earplugs, the age at which these begin to form can provide information on the age of sexual maturity. Limited ovarian corpora data were used to estimate an age of sexual maturity for female pygmy blue whales of 9-11 years from Soviet data (Sazhinov 1970) and ~10 years from Japanese data (Ichihara 1966). For Antarctic blue whales, ovarian corpora data from Japanese expeditions were used to estimate an age of sexual maturity of 10 years for females (Ohsumi 1979), though the data and methods used were not outlined.

Using ovarian corpora data to infer pregnancy rates is more complex. There is some debate as to how long corpora albicans remain visible on the ovaries of cetaceans. For baleen whales, it is often assumed that corpora albicans from all ovulations remain visible indefinitely and therefore counts of ovarian corpora represent a whale's lifetime history of ovulation (e.g., Best 2011, Laws 1961, Tarpley et al. 2016). However, for bottlenose dolphins this was found to only be true for corpora lutea that persisted through pregnancy, which would suggest that these counts represent the number of pregnancies (both successful and unsuccessful) and not the number of ovulations (Brook et al. 2002). For blue whales, it is currently unknown whether these counts represent a history of ovulation or pregnancy. Ohsumi (1979) stated that ovarian corpora are produced every 2.5 years for Antarctic blue whales. Catch records of pregnant Antarctic blue whales suggest that whales become pregnant every 2.3 years on average (Branch et al. 2004), which suggests that ovarian corpora likely represent a history of pregnancy for blue whales. Pregnancy rates from ovarian corpora data are an overestimation of calving rates, since at least some proportion of pregnancies are unsuccessful (Ichihara 1962), but would represent an upper bound that could be refined with future research.

In this study, we aggregated all available earplug data for blue whales, including Antarctic blue whales, pygmy blue whales (from Japanese and Soviet whaling data), and North Pacific blue whales (from both the eastern North Pacific and western North Pacific). When available, we also compiled ovarian corpora data collected from the same individuals as the earplugs. Using these data, we modelled age-length relationships for blue whales and estimated their age of sexual maturity and pregnancy rates.

4.2 Methods

4.2.1 Data

4.2.1.1 Pygmy blue whales (Soviet data)

Pygmy blue whale earplugs were collected during Soviet whaling operations from 1961 to 1973 and were provided by Y. Mikhalev from work completed by E. Sazhinov in 1980 (Mikhalev 2019). Soviet earplug data contained ages and lengths (in m) for 351 females and 445 males (Figures 4.1-4.2). No information on location, aging accuracy, year, expedition, or sexual maturity was available for these data. There are at least five populations of pygmy blue whales in both the northern and southern Indian Ocean, which were all targeted by Soviet whalers (Branch et al. 2025). Since location data were not available, we treated these data only at a subspecies level (pygmy blue whales) rather than the population level. (We note that the SMM Committee on Taxonomy treats northern Indian Ocean blue whales as a separate subspecies, *B. m. indica*, but here include these within pygmy blue, *B. m. brevicauda*, whales following the reasoning in Branch et al. (2025).) Only whole earplugs were used for aging in the Soviet data (Mikhalev 2019), therefore all ages were treated as exact. However, in the data provided, Soviet analysts assumed that two pairs of dark-light earplug laminae represented one year of life. For these data, and all earplug data used in this study, we followed the accepted convention of assuming that one pair of earplug laminae was added per year of life for baleen whales, as convincingly argued by Lockyer (1984) and Best (2011). After correcting for this, odd-numbered ages are underrepresented in the data, perhaps because analysts occasionally rounded up to a whole-numbered age instead of listing half-year ages. For example, whales with 5 pairs of earplug laminae would have resulted in an age of 2.5 years based on Soviet analysis methods, however, this was likely rounded up to an age estimate of 3 years, resulting in an age estimate of 6 years in the corrected data, rather than 5 years. In the original data there are 175 half-year ages and 621 listed as whole-year ages, resulting in higher numbers of even-numbered ages than odd-numbered ones in our data. However, given the long lifespans of whales and the wide range of ages, we did not expect this possible rounding error to impact our results.

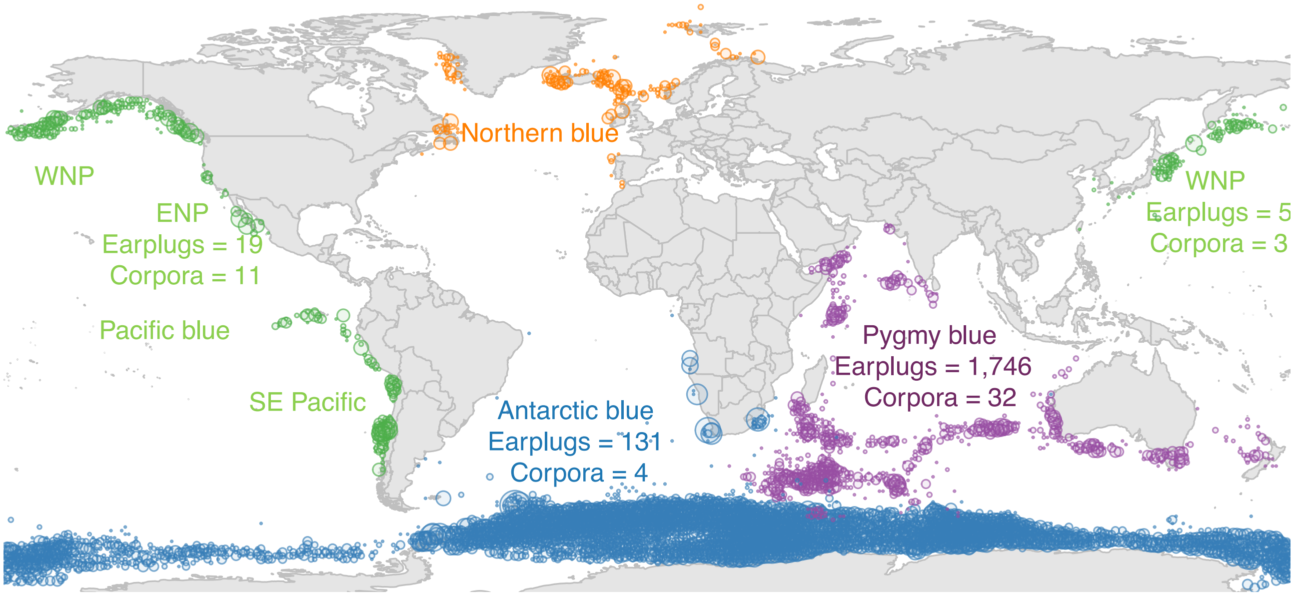

Figure 4.1 Map of global blue whale catches (circles), separated by subspecies/population (following conventions of Branch et al. (2025)). Larger circles represent more catches in that location. Numbers indicate the sample sizes of earplug and ovarian corpora data that are available for each subspecies/population.

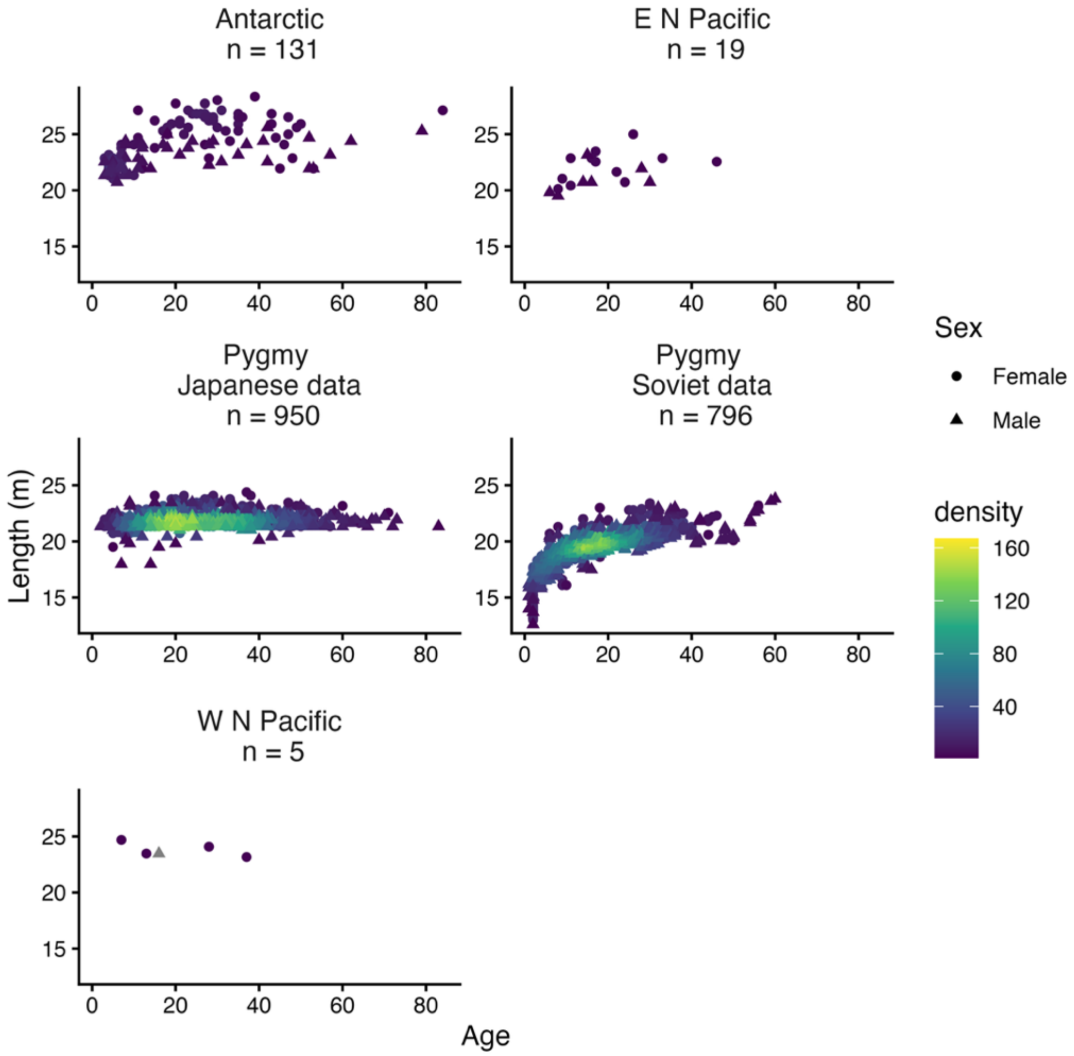

Figure 4.2 Ages of blue whales from earplugs collected during whaling by subspecies and population and corresponding length of the whale. Almost all whales under 21.3 m (70 ft, the minimum legal landing size) were reported as exactly 21.3 m by the Japanese whalers. Brighter colors represent higher densities of overlapping points.

4.2.1.2 Pygmy blue whales (Japanese data)

Pygmy blue whale earplugs were also collected on Japanese expeditions to the south-western Indian Ocean during 1960–1964; the samples and associated data were provided by Fisheries Resources Institute, Japan Fisheries Research and Education Agency, and the original age estimates from these earplugs were made at the former Whale Research Institute (Tokyo). Earplug data from Japanese expeditions contain ages and lengths (in whole ft) for 513 female and 533 male pygmy blue whales. In addition to age and length information, the location of catch, expedition, date of catch, as well as sexual maturity are available. For consistency with the Soviet data, pygmy blue whales were not separated by population or subspecies, but based on catch locations were primarily from the Southwest Indian Ocean (SWIO) population (Branch et al. 2025). Partial earplugs were aged, resulting in some minimum ages and underestimated ages in these data. Any partial earplugs were removed for the purposes of this study (~10% of Japanese data, randomly distributed across lengths). However, there is still some uncertainty in these data with regards to the length measurements. While Soviet whalers were whaling illegally and therefore did not adhere to any regulations (Ivashchenko & Clapham 2014), Japanese whales adhered to the "minimum length" regulations, where blue whales could only be caught if they were longer than 70 ft (21.3 m). This resulted in some length values being "stretched", where whales that were less than 70 ft were reported as being 70 ft (Branch & Mikhalev 2008).

During Japanese whaling expeditions, counts of ovarian corpora were also available for some catches. Pygmy blue whale corpora counts (*n* = 32) and corresponding ages from earplugs are available from Ichihara (1966) (Figures 4.1, 4.3).

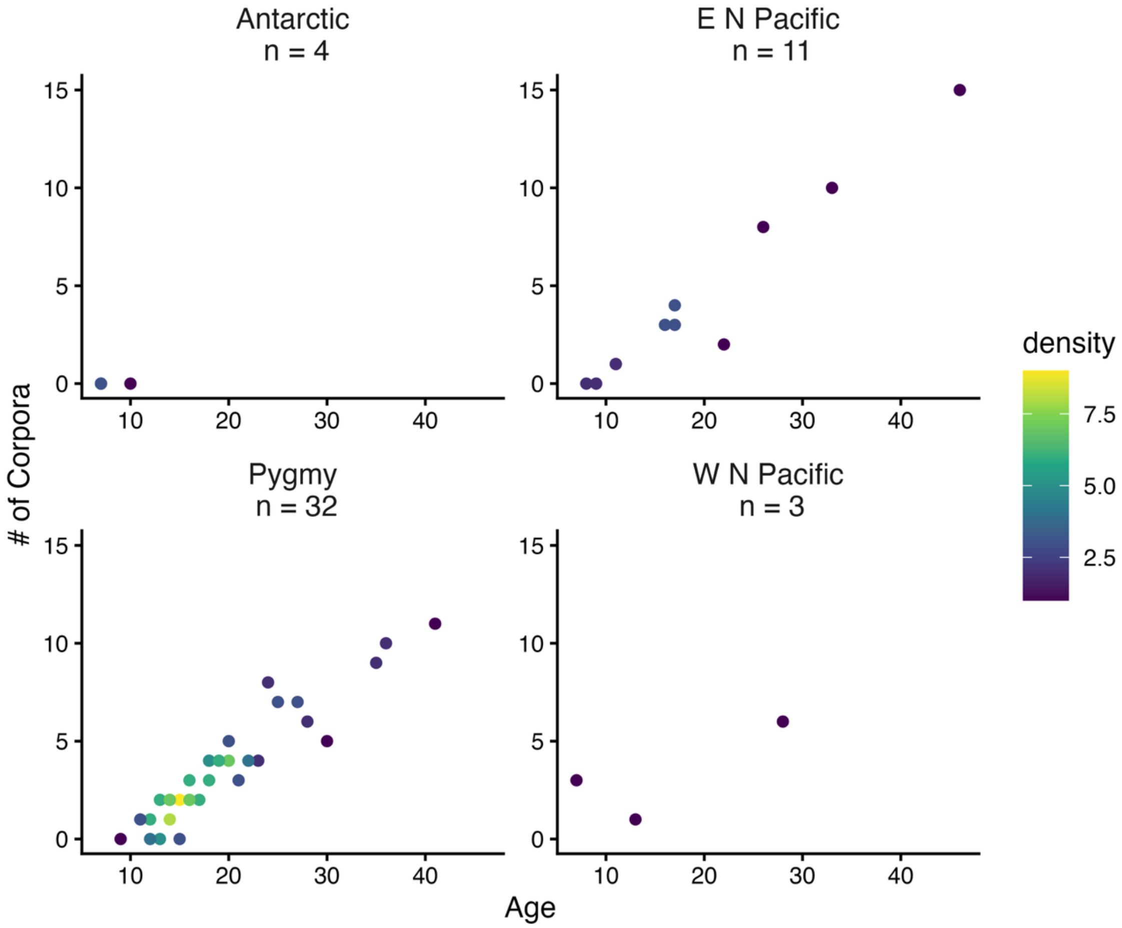

Figure 4.3 Ages of blue whales from earplugs and corresponding number of ovarian corpora from the same caught whales. Brighter (more yellow) colors represent higher densities of overlapping points.

4.2.1.3 Antarctic blue whales

Earplug data from Japanese expeditions also contain ages and lengths (in whole ft) for Antarctic (80 females, 45 males) blue whales. While minimum length regulations also applied to Antarctic blue whales, most caught Antarctic blue whales were larger than 70ft (Branch et al. 2007a), so "whale-stretching" for this subspecies is less likely to impact the results. Similarly to the data for pygmy blue whales, the location of catch, expedition, date of catch, and sexual maturity are available. Additional earplugs for Antarctic blue whales (4 females, 2 males) were collected during the Discovery Marking program (Allison 2020, Brown 1977), and corpora counts are available for these females (Figures 4.1-4.3).

4.2.1.4 Eastern North Pacific blue whales

The Japanese data from the Institute of Cetacean Research contains corpora counts and corresponding ages for one eastern North Pacific blue whale. Earplugs were additionally collected from eastern North Pacific blue whales (12 females, 7 males) during whaling operations off the coast of California between 1959 and 1965 (Figure 4.1-4.2; Rice 1963). These whales were all measured by a trained biologist and were recorded exactly (no whale stretching). Corpora counts were recorded for 10 of these females (Figure 4.3).

4.2.1.5 Other blue whales

Japanese data contain earplugs from a few western North Pacific blue whales (4 females, 1 male), and corpora counts for three of these individuals (Figures 4.1-4.3). As far as we know, no earplug data exists for North Atlantic blue whales or Southeast Pacific blue whales (Figure 4.1). All earplug and ovarian corpora data used in this analysis are available in Appendix S1.

4.2.2 Model of age-length relationships

Age-length relationships were modelled using the generalized Richards growth curve (Richards 1959) as parametrized by Schnute (1981). The length at each age ($\widehat{L_a}$) was predicted given the age *a,* the estimated length (L_1) at a first reference age (A_1), the estimated length (L_2)at a second reference age (A_2)*,* an estimated growth rate (k) and an estimated shape parameter (*b):*

$$\widehat{L_a} = (L_1^b + \left(L_2^b - L_1^b\right)\frac{1-e^{-k(a-A_1)}}{1-e^{-k(A_2-A_1)}})^{1/b} \tag{1}$$

For this work, we set A_1 to the youngest age available in the data and A_2 is to the oldest age available in the eastern North Pacific data (the population with the fewest old ages in our data) such that $A_1 = 1$ and $A_2 = 46$. The parameter *b* can be freely estimated to capture various possible relationships between age and length (Schnute 1981). When *b = 1*, this curve is equivalent to the Von Bertalanffy growth equation (von Bertalanffy 1957) and in the limit as *b* approaches 0 it is equivalent to the Gompertz growth equation (Gompertz 1825).

Equation 1 is fit to three blue whale groupings: the pygmy and Antarctic subspecies, and the eastern North Pacific population. Western North Pacific blue whales were excluded due to their small sample size (Figure 4.2). Based on the lengths in the whaling records, we expected whales of each population to have a different asymptotic length and for males to be smaller than females. Therefore, we modelled fixed effects of population and sex on L_1 and L_2 (e.g..,

$L_{1,Pygmy,Female}$, $L_{1,Pygmy,Male}$, $L_{1,Antarctic\,,Female}$), such that the length at each age for each sex (s) and population (p) was predicted from:

$$\widehat{L_{a,s,p}} = (L_{1,s,p}^{b} + \left(L_{2,s.,p}^{b} - L_{1,s,p}^{b}\right)\frac{1-e^{-k(a-A_1)}}{1-e^{-k(A_2-A_1)}})^{\frac{1}{b}} \tag{2}$$

The growth rate parameter, *k,* and the shape parameter, *b*, were shared across populations and between sexes. Additional model formulations were also considered and are presented in Appendix S2.

Asymptotic length ($\widehat{L_\infty}$) for each sex and population was calculated from the estimated parameters:

$$\widehat{L_{\infty,s,p}} = (L_{1,s,p}^{b} + \frac{L_{2,s,p}^{b} - L_{1,s,p}^{b}}{1-e^{-k(A_2-A_1)}})^{1/b} \tag{3}$$

4.2.2.1 Parameter estimation and alternative models

The observed length at each age was assumed to be normally distributed around the predicted length-at-age ($\widehat{L_{a,s,p}}$) with a population-specific standard deviation parameter, σ, and subject to the possibility of censoring at 70 ft (21.336 m) for the Japanese data for pygmy blue whales. We assumed all data listed as 70 ft in the Japanese data for pygmy blue whales was censored, meaning that the true value could be any length up to and including 70 ft. For these censored data, the likelihood component came from the cumulative distribution function (CDF) of the normal distribution, given the minimum length (21.3 m), the predicted lengths ($\widehat{L_{a,s,p}}$), and the estimated standard deviation parameter for pygmy blue whales, σ_{Pygmy}:

$$L\left(L_i, \hat{L}_{a[i],s[i],p[i],}\sigma_{p[i]}\right) = \prod\nolimits_i \begin{cases} P\left(L_i,\ \hat{L}_{a[i],s[i],p[i],}, \sigma_{p[i]}\right) & if\ \ L_i < or > 21.336\,m \\ D\left(21.336\,,\ \hat{L}_{a[i],s[i],p[i],}, \sigma_{Pygmy}\right) & if\ L_i = \ 21.336\,m \end{cases} \tag{4}$$

where L_i is the observed length for observation *i,* $\hat{L}_{a[i],s[i],p[i],}$is the predicted length given the age, sex, and population of observation *i* following equation 2, and $\sigma_{P[i]}$ is the estimated standard deviation for the population of observation *i,* and *P(x)* represents the PDF of the normal distribution, and *D(x)* represents the CDF of the normal distribution.

For pygmy blue whales, model diagnostics revealed that Japanese and Soviet data could not be reliably combined in a single model (Appendix S3). Since the Japanese data include few data points for lengths under 70 ft, our model with data from only Soviet expeditions is presented as our base case. Additional model runs including both the Japanese and Soviet data and only the Japanese data are included as sensitivities (Table 4.1). In addition to the base model, fitting generalized (Richards) model (with freely estimated shape parameter), we also added sensitivities for the von Bertalanffy (b = 1) and Gompertz models (b=0.0001*)* with the data from Soviet expeditions for pygmy blue whales (Table 4.1).

Table 4.1 Models considered for age-length relationships.

Model	**Growth curve**	**Data sources for pygmy blue whales**	**Likelihood**	**Model fitting**
Soviet only (base case)	Richards	Soviet data	Uncensored	6,000 iterations, 83% warmup 4 chains
Von Bertalanffy	Von Bertalanffy	Soviet data	Uncensored	2,000 iterations 50% warmup 4 chains
Gompertz	Gompertz	Soviet data	Uncensored	3,000 iterations 66% warmup a 4 chains
Japanese only	Richards	Japanese data	Censored for pygmy blue whales	9,000 iterations 89% warmup 4 chains
All data	Richards	Soviet and Japanese data	Censored for Japanese data of pygmy blue whales	20,000 iterations 75% warmup 4 chains thinning rate of 10

All models were built using RTMB v1.8 (Kristensen 2024) in R v.4.5.1 (R Core Team 2025). They were fit using Bayesian methods with the NUTS algorithm using the package *tmbstan* (Monnahan & Kristensen 2018). Weakly-informative priors were used with bounds chosen to improve convergence (Table 4.2). Iterations and warmups were set for each model as needed for convergence (Table 4.1). For all models, the adapt-delta parameter was set to 0.97 and the maximum tree depth was set to 17. Convergence was checked by checking that $\hat{R}$ values were less than 1.01 (Vehtari et al. 2021) as well as visually assessing traceplots and autocorrelation plots. Model adequacy was assessed using posterior predictive checks. For data points that were censored, posterior predictions were drawn from the uncensored posterior, and then, if they were below the minimum length (21.3) they were set to equal the minimum length. The Richards, Gompertz, and Von Bertalanffy models were compared using the expected log pointwise density (*elpd)* calculated using the *loo* package (Vehtari et al. 2022). Models with an absolute value of the difference in *elpd* of > 4 were considered worse models (Sivula et al. 2023). Results are reported as medians and 95% credible intervals.

Table 4.2. Parameter descriptions and priors for Bayesian model of age-length relationships. All parameters except b were logged during estimation so that only values ≥ 0 were considered.

Parameter	Description	Prior
$L_{1,Pop,Sex}$	Length at age 1 for each population and sex	Uniform(5,25)
$L_{2,Pop,Sex}$	Length at age 46 for each population and sex	Uniform $(0, 10{,}000)$
k	Growth rate	Uniform(0.05, 0.3)
b	Shape parameter (only estimated in Richards model)	Uniform(0, 15)
σ_{Pop}	Standard deviation for each population	Uniform $(0, 10{,}000)$

4.2.2.2 Simulation study

Simulated datasets were used to evaluate the ability of the model and its associated estimation method to estimate the parameters of interest given the censored likelihood used for Japanese pygmy blue whale data. This simulation study used only pygmy blue whale data and only estimated parameters for pygmy blue whales. Further information about this simulation study can be found in Appendix S4.

4.2.3 Estimating reproductive parameters

A model of the relationship between ovarian corpora counts and age was fit for pygmy blue whales and eastern North Pacific blue whales. The data for Antarctic and western North Pacific blue whales were excluded from these analyses because of small sample sizes (Figure 4.3). The model-predicted number of corpora ($\widehat{C_{a,p}}$)for a given age (a) and population (p), is based on a population-specific intercept parameter (α_p) which represents the theoretical number of corpora at $a = 0$, and a population-specific slope parameter (β) which represents the number of corpora formed per year:

$$\widehat{C_{a,p}} = \alpha_p + \beta_p * a \tag{5}$$

Models without population effects on the intercept or slope were also considered. However, since the purpose of this model is to understand biologically meaningful rates (age at sexual maturity and rate of ovarian corpora accumulation) we present the most flexible model here (population effects on both slope and intercept).

The observed corpora counts were assumed to be negative binomially distributed to allow for overdispersion, with the predicted number of corpora at each age as the mean and an estimated overdispersion parameter, ϕ, where a larger value leads to a variance closer to the Poisson mean. Predicted corpora counts below 0 were constrained to be 0 using a smooth max function. The number of years between corpora formation was calculated as $1/\beta_p$, and the age at sexual maturity for each population was estimated by the x-intercept (when corpora count = 0), i.e. $\widehat{Age}_{mat,p} = -\frac{\alpha_p}{\beta_p}$.

The model was built using RTMB v1.8 (Kristensen 2024) in R v.4.5.1 (R Core Team 2025). It was fit using Bayesian methods with the NUTS algorithm using the package *tmbstan* (Monnahan & Kristensen 2018). An Inverse Gamma(0.4,0.3) prior was assigned to the overdispersion parameter (ϕ) since this is an accepted approximation of the penalised complexity prior, which places a lower prior likelihood on the data being highly overdispersed (Simpson et al. 2017). Since little additional information about age at sexual maturity or the rate of corpora formation, a prior of Uniform(0, $10{,}000$) was used for the slope parameters (β_p) and a prior of Uniform(-1000, 1000) was used for the intercept parameters (α_p). The model was fit with 10,000 iterations, a thinning rate of 10, a 50% warmup, and four chains. The adapt-delta parameter was set to 0.98 and the maximum tree depth was set to 15. Convergence was checked by visually assessing traceplots and autocorrelation plots and checking that $\hat{R}$ values were less than 1.01 (Vehtari et al. 2021). Model adequacy was assessed using posterior predictive checks. Results are reported as medians and 95% credible intervals.

4.3 Results

4.3.1 Predicting length from age

The Richards model was the model with the best predictive power (Table 4.3), and therefore we primarily present estimates from this model. At age 46, female Antarctic blue whales were estimated to be the at 26.4 m (25.9–26.7 m), while male pygmy blue whales were estimated to be the shortest at 21.0 m (20.8–21.1 m). The length at age one (L_1) was only well-estimated for pygmy blue whale males (14.9 m, 14.4–15.4 m; Figure 4.4). There was very little data at young ages for Antarctic or eastern North Pacific blue whales of either sex, resulting in wide posterior distributions for L_1 similar to their prior (Figure 4.4). In addition, while there are data for female pygmy blue whale at young ages, most of these data are for individuals >2 years old, leading to a wide posterior distribution for L_1 (Figures 4.4-4.5).

Table 4.3. Parameter estimates (medians) and 95% credible intervals for Richards, Von Bertalanffy and Gompertz age-length models. Models are ordered based on the difference in their expected log pointwise densities ("elpd diff.") The model with an elpd difference of 0.0 is considered the model with the best predictive power. L_1 is the estimated length in meters at age 1, L_2 is the estimated length in meters at age 46. "Py" represents pygmy blue whales, "ENP" represents eastern North Pacific blue whales, and "Ant" represents Antarctic blue whales.

Model			**Richards**			**Von Bertalanffy**			**Gompertz**		
***elpd* diff.**			**0.0**			**-21.0 (SE = 7.3)**			**-24.0 (SE = 8.0)**		
Parameter			**50%**	**2.5%**	**97.5%**	**50%**	**2.5%**	**97.5%**	**50%**	**2.5%**	**97.5%**
L_1	**Ant**	**F**	11.5	5.2	20.0	20.0	19.1	20.8	20.0	19.2	20.8
		M	21.2	19.7	22.3	20.9	19.7	22.1	20.8	19.7	22.0
	ENP	**F**	8.2	5.1	19.4	17.4	12.8	21.8	17.7	13.9	22.0
		M	8.5	5.1	20.1	17.6	12.9	22.0	17.7	14.1	21.8
	Py	**F**	7.1	5.1	12.2	15.1	14.7	15.4	15.2	14.9	15.5
		M	14.9	14.4	15.4	15.8	15.5	16.1	15.9	15.6	16.2
L_2	**Ant**	**F**	26.4	25.9	26.7	26.0	25.7	26.4	26.0	25.6	26.4
		M	24.0	23.4	24.5	23.8	23.3	24.3	23.8	23.3	24.3
	ENP	**F**	23.5	22.6	24.2	23.2	22.0	24.4	23.1	21.9	24.3
		M	22.5	21.1	23.5	21.9	20.3	23.5	21.8	20.3	23.4
	Py	**F**	21.6	21.4	21.7	21.5	21.3	21.7	21.5	21.3	21.7
		M	21.0	20.8	21.1	20.7	20.6	20.9	20.7	20.5	20.9
k			0.052	0.050	0.061	0.117	0.104	0.131	0.127	0.113	0.142
σ	**Ant**		1.27	1.13	1.44	1.22	1.09	1.38	1.22	1.08	1.39
	ENP		1.20	0.887	1.72	1.24	0.890	1.88	1.22	0.889	1.86
	Py		0.883	0.841	0.929	0.909	0.865	0.957	0.913	0.871	0.959
b			8.45	7.86	8.94	1 (fixed)	–	–	0.0001 (fixed)	–	–

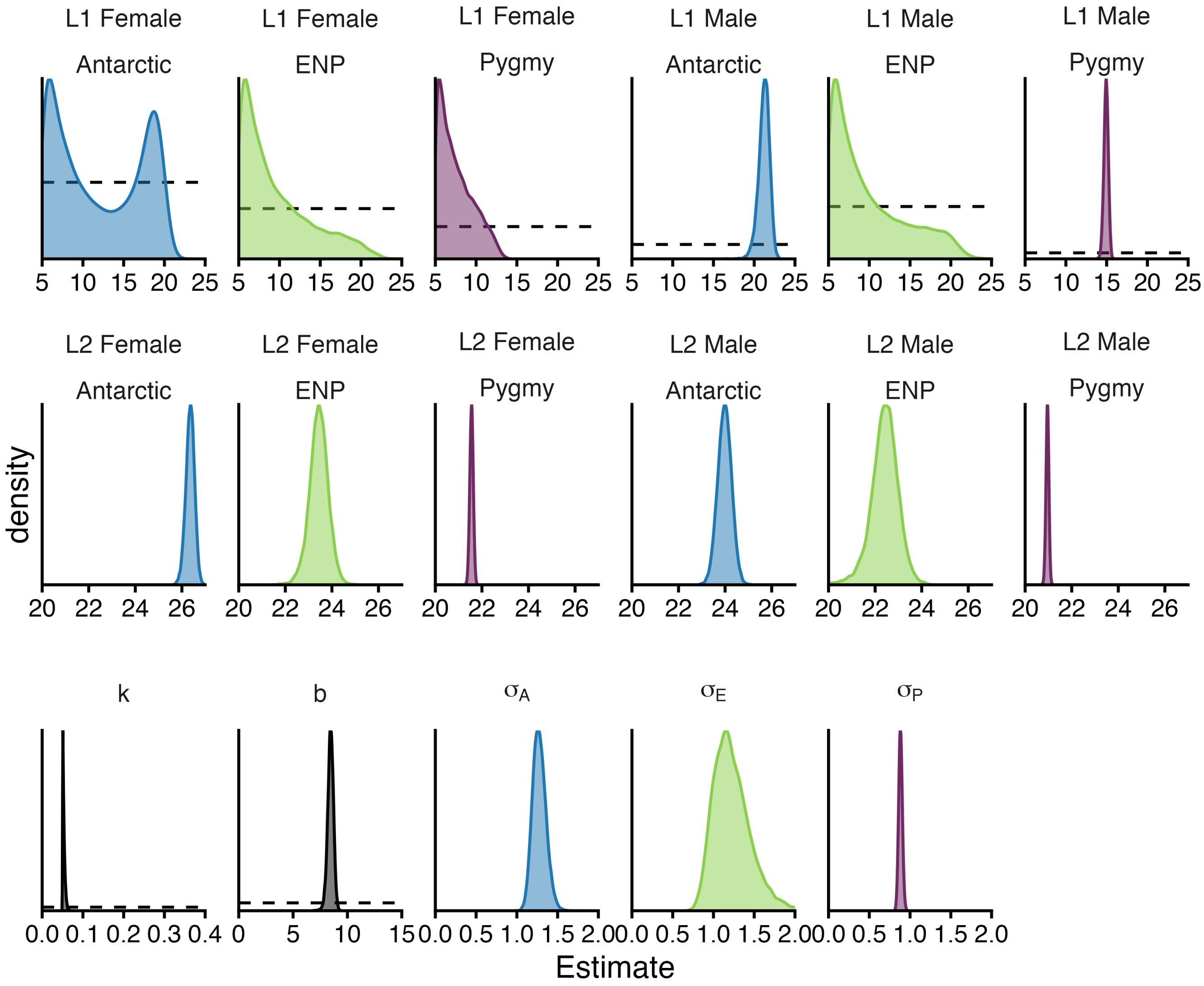

Figure 4.4 Posterior distributions (solid line) for estimated parameters from the base case Richards model. For parameters that had informative priors (Table 4.2), the priors are shown as dashed lines. Lengths (e.g., L_1 and L_2) are estimated in meters.

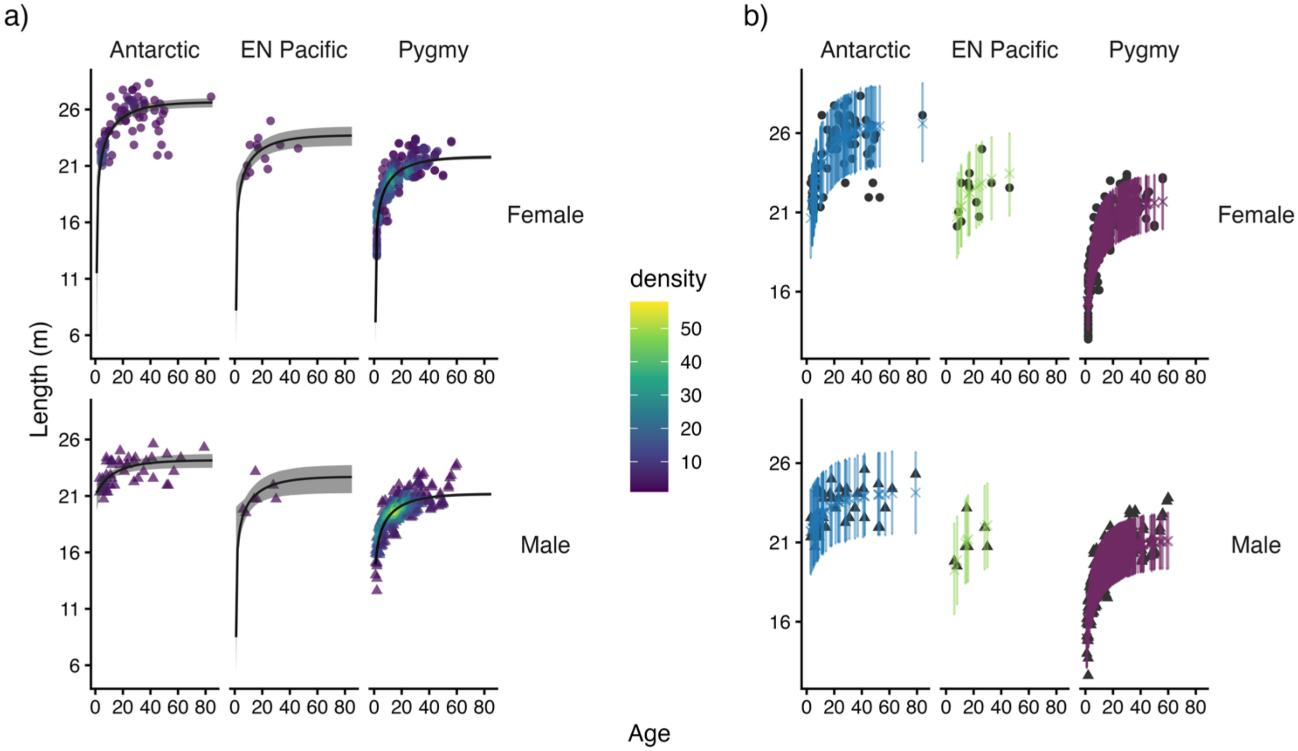

Figure 4.5 Posterior distribution and posterior predictive distributions. a) Posterior median (line) and 95% credible intervals (shading) of the posterior distribution of for the predicted relationship between age and length from the Richards model for each blue whale population/subspecies by sex, and the data used to fit the model (points) where brighter colors represent higher densities of overlapping points. b) Posterior predictive medians (x's) and 95% intervals (error bars) from the Richards model, and the data used to fit the model (points), where colors represent the different populations.

The growth rate parameter (*k*) was estimated to be 0.052 yr^{-1} (0.050–0.061) and the shape parameter (*b*) was estimated to be 8.45 (7.86–8.94; Table 4.3, Figure 4.4). This results in a steeper shape (faster growth) at young ages than the Von Bertalanffy and Gompertz growth curves. Posterior predictive checks suggest that this model fits the data adequately (Figure 4.5).

For all populations, females had longer estimated asymptotic lengths ($\hat{L}_\infty$) than males (Figure 4.6). Asymptotic lengths were greatest for Antarctic blue whales, with female asymptotic lengths estimated to be 26.7 m (26.2–27.0 m) and male asymptotic lengths estimated to be 24.2 m (23.5–24.7 m). Pygmy blue whales were estimated to have the smallest asymptotic lengths, with females estimated to have asymptotic lengths of 21.8 m (21.6–22.0 m) and males of 21.2 m (21.0–21.3 m). Eastern North Pacific blue whales had estimated asymptotic lengths of 23.7 m (22.8–24.5 m) for females and 22.7 m (21.3–23.8 m) for males (Figure 4.6).

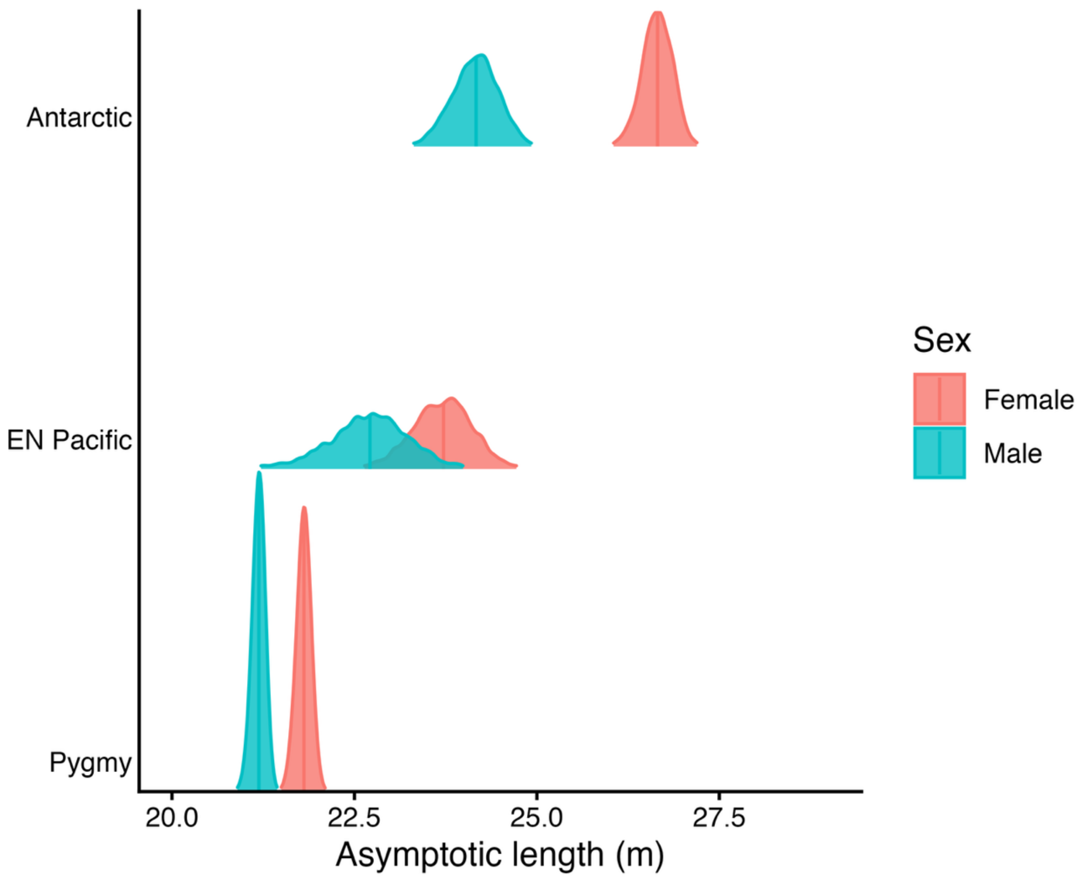

Figure 4.6 Posterior distribution of derived asymptotic length ($\hat{L}_\infty$) for males (blue) and females (red) of each blue whale population/subspecies.

When the Japanese data for pygmy blue whales are included in the age-length models, the posterior distributions for eastern North Pacific and Antarctic blue whales are unchanged. The posterior distributions for the growth rate (k) and shape parameter (b) were similar to the base case though they were less precise (Figure 4.7). The posterior median estimates of the length at age one for pygmy blue whales (L_1) increased from the base model values of 7.03 and 14.9 m (Table 4.3), to 20.03 and 21.0 m (Figure 4.7), for females and males, respectively, when the Soviet data were excluded since there is very little information about the lengths at young ages for pygmy blue whales in the Japanese data (due to censoring). The inclusion of Japanese data also resulted in higher posterior median estimates of the length at age 46 (L_2) for pygmy blue whales. When only the Japanese data were included, the length at age 46 was estimated to be 22.2 m (22.0–22.3 m) for females and 21.6 m (21.5–21.7 m) for males, which was higher than in the base model. When both datasets were included, the model split the difference between these two estimates, leading to estimates of 22 m (21.9–22.2 m) for females and 21.3 m (21.2–21.5 m) for males. In addition, the use of both datasets led to a higher estimated standard deviation of length-at-age, reflecting the conflict between these two data sources (Figure 4.7).

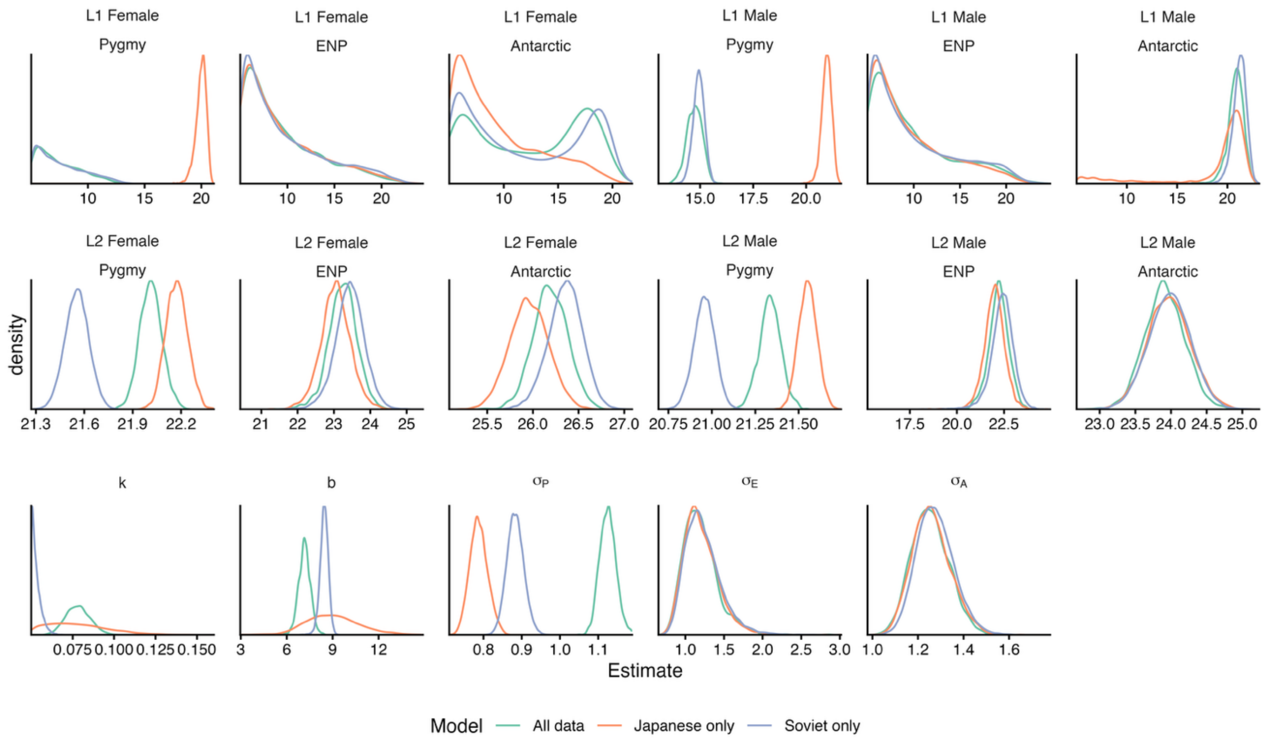

Figure 4.7 Posterior distributions of parameters from sensitivity tests. Posterior distributions of parameters from Richards growth models fit to the base model which only included Soviet data for pygmy blue whales, as well as models fit to only Japanese data, and the Soviet and Japanese data for pygmy blue whales combined. Data included for Antarctic and eastern North Pacific blue whales did not change between model fits.

4.3.2 Estimates of reproductive parameters

The number of corpora formed per year (β_p) was estimated to be 0.344 (0.236–0.465) for pygmy blue whales and 0.372 (0.215–0.590) for eastern North Pacific blue whales. This suggests that corpora are added every 2.90 years (2.15–4.23 years) for pygmy blue whales and every 2.68 years (1.70–4.63 years) for eastern North Pacific blue whales (Figure 4.8). The estimated age of sexual maturity is 9.33(5.63–10.7) years for pygmy blue whales and 8.62 (3.41–10.4) years for eastern North Pacific blue whales. Posterior predictive checks suggest that this model fits the data adequately (Figure 4.8).

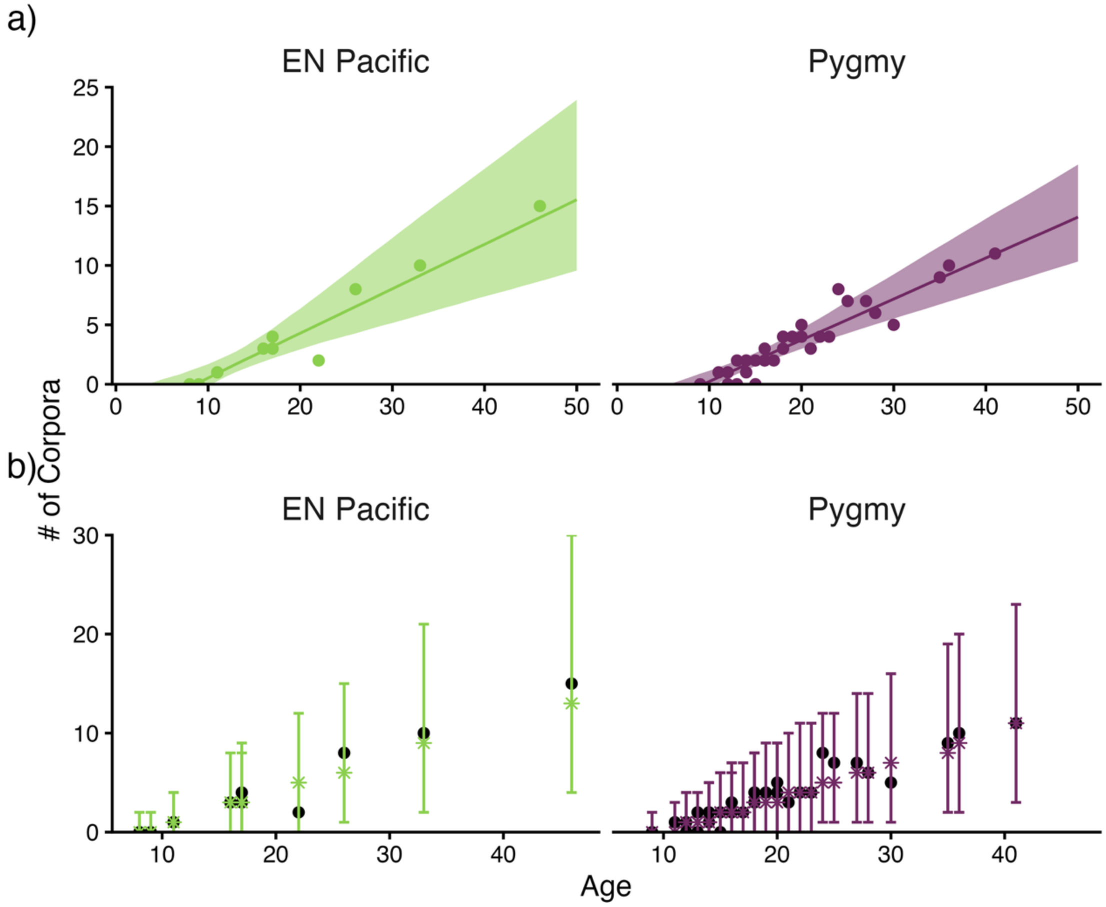

Figure 4.8 Posterior distributions and posterior predictive distributions. a) Posterior medians (lines) and 95% credible intervals (shading) for estimated relationship between age and number of ovarian corpora, with points representing the data used to fit the model. b) Posterior predictive medians (stars) and 95% intervals (error bars) for each data point used to fit the model.

4.4 Discussion

We present the first global compilation of earplug and ovarian corpora data for blue whales. By combining data across whaling countries, expeditions, and fleets, we were able to obtain more precise estimates of key demographic parameters for blue whales and to make comparisons among populations and subspecies.

In terms of asymptotic length, we found that Antarctic blue whales were the largest and had the greatest difference in asymptotic length between the sexes. Pygmy blue whales and eastern North Pacific blue whales had less sexual dimorphism and were closer in asymptotic size to each other, though pygmy blue whales were about 1-2 m shorter than eastern North Pacific blue whales (Figure 4.6). These differences in asymptotic size are likely due to genetic differences between these subspecies of blue whales (Attard et al. 2024) and may be a result of different habitats and migration strategies on an evolutionary timescale.

Differences in migration strategies may have led to different evolutionary pressures in terms of body size for the blue whale subspecies in our study. The stereotypical baleen whale migration pattern of annual long-distance movement between low-latitude breeding grounds and high latitude feeding grounds does not hold for all blue whale populations. For instance, New Zealand blue whales are present in the South Taranaki Bight region of Aotearoa New Zealand year-round, relying on pulsed upwelling plumes that support aggregations of krill all year (Barlow et al. 2023). Antarctic blue whales, on the other hand, generally appear to undergo low-to-high latitude migrations, based on annual fluctuations in the population size in the Southern Ocean and the lack of historical catches in temperate waters during the austral winter (Branch et al. 2007b). In addition, Antarctic blue whales have been shown to move widely throughout the Southern Ocean (Andrews-Goff et al. 2022, Olson et al. 2022, Rand et al. 2024), covering distances of more than 6000 km (Rand et al. 2024). Finally, eastern North Pacific blue whales feed seasonally off the coast of California, USA (though they have been found to travel as far north as the Gulf of Alaska), and then migrate to lower-latitude wintering areas near Baja California and the Costa Rica Dome (Bailey et al. 2010). Larger marine mammals swim faster and therefore can cover longer distances more quickly (Watanabe et al. 2011). Amongst migrating cetaceans, the largest species with the most energy reserves tend to migrate the longest distances (Adamczak et al. 2023).

Larger body size may also reflect polar proximity. Marine mammal taxa at higher latitudes tend to be larger than those at lower latitudes (Adamczak et al. 2023). Thermoregulation is likely easier for larger organisms, because a lower surface-to-volume ratio decreases heat loss (Mayr 1956). This has been shown for pilot whales (*Globicephala* spp.) where larger and better insulated individuals are located in colder northern climates (Adamczak et al. 2020). This may also be explained by prey availability, as higher latitudes tend to have higher productivity and larger prey (McNab 1971, McNab 2010). This mechanism has been suggested to explain variation in female sperm whale (*Physeter macrocephalus*) body size across latitudinal gradients (Best et al. 2017). Latitudinal gradients could also explain differences in the asymptotic body size in blue whale subspecies, since Antarctic blue whales are found at high latitudes in summer, while pygmy blue whales rarely venture south of 52°S (Branch et al. 2007b), and eastern North Pacific blue whales are rarely north of 45°N (Hamilton et al. 2009).

We found that length at age one was difficult to estimate, given the lack of data at young ages (Figure 4.4). Our estimates of length at age one (L_1) likely stem from the shape of the curve (*k,* and *b* parameters) which is primarily driven by data from pygmy blue whales due to pygmy blue whales contributing the most data (Figure 4.5).

Additionally, we found that lengths collected by Soviet and Japanese expeditions were not fit well with a single joint model (Appendix S3). This can be seen particularly well in the estimates of length at age 46 from the two data sources (Figure 4.7). Soviet vessels ignored the minimum length regulation (70 ft) and caught blue whales of all ages and lengths, while Japanese vessels reported few catches under the minimum length but the data include evidence of "whale stretching" where those under the minimum length were reported as being exactly equal to 70 ft. In addition, there may be different practices for measuring whales between the Soviet and Japanese fleets. While IWC regulations specified procedures for measuring the lengths of whales in 1949 (before the data in this study were collected), there is evidence that, in practice, these procedures differed greatly on different whaling vessels (Best 1989), and hence fleets. However, the difference in these estimates may also reflect a true difference in the sizes of different populations of pygmy blue whales. Japanese whalers were following area-based regulations and only taking pygmy blue whales between 20º–80ºE and 40º–52ºS, which meant they primarily targeted the Southwest Indian Ocean (SWIO) population (Branch et al. 2025). Soviet catches, however, were widespread through the Indian Ocean and targeted all populations of pygmy blue whales (Branch et al. 2025). Based on Soviet whaling data, at sexual maturity, female pygmy blue whales in the SWIO are estimated to be 19.5 m (19.3–19.6 m) but 18.8 m (18.6–19.0 m) in the northern Indian Ocean and 19.4 m (19.2–19.6 m) off Australia and New Zealand (Branch & Mikhalev 2008). This suggests that the populations targeted by Japanese whalers may have had longer body lengths than some of those targeted by Soviet whalers.

We estimated that the mean age at sexual maturity for females was 9.5 yr for pygmy blue whales and 8.9 yr for eastern North Pacific blue whales. Although the point estimates are different for these two subspecies, the credible intervals overlap, suggesting that there may not be a true difference in the age of sexual maturity among these subspecies. This may also be true for Antarctic blue whales, where the age of sexual maturity for females was stated to be 10 yr (Ohsumi 1979). Our estimate for pygmy blue whales is consistent with previous estimates of 9-11 yr from Soviet data (Sazhinov 1970) and 10 yr from Japanese data (Ichihara 1966), and sightings histories of eastern North Pacific females with the youngest age with calves being 11 yr and 13 yr (Sears et al. 2013).

We estimated that ovarian corpora are added every 2.8 yrs for pygmy and 2.5 yrs for eastern North Pacific blue whales. As with the age at sexual maturity, the credible intervals of these rates overlap. These rates are also consistent with a rate of 2.5 yrs for Antarctic blue whales (Ohsumi 1979), and 2.57 yrs from sightings data for eastern North Pacific blue whales (Sears et al. 2013). Assuming that each ovarian corpus is added only when blue whales become pregnant, these can be considered a baseline estimate of pregnancy rates. The similarity in these estimates among populations suggests that reproductive parameters may not be strongly influenced by environmental drivers and are more fundamentally related to blue whale biology. While it is likely that environmental drivers would impact calving rates (e.g., Seyboth et al. 2016, Williams et al. 2013), the pregnancy rates we present here do not reflect birth rates, since occasional failed pregnancies may also result in the addition of ovarian corpora (Ichihara 1962). Therefore, changing environmental conditions may affect birth rates by changing the rate of failed pregnancies rather than the actual pregnancy rate.

While we account for “whale stretching” by treating Japanese data at the minimum length as censored, we assumed all other length measurements were accurate. However, it is possible that larger whales may also have been reported as shorter than they were. For sperm and fin whales, there is evidence from the Durban whaling station that whale stretching may have also led to “whale shrinking”, where larger whales were reported as shorter than they were to account for the lower-than-expected oil yields when catching whales below the minimum length (Best 1989). If this was the case for Japanese expeditions catching blue whales, then the true asymptotic lengths for pygmy blue whales may be slightly higher than those we estimated with Japanese data. However, since our estimates represent population means, if whale shrinking only affected the longest whales and did not dramatically shorten these longer whales, this effect is likely to be small.

There is evidence that other species of baleen whales are decreasing in size in recent years. The asymptotic length of gray whales (*Eschrichtius robustus*) on the northeast Pacific coast, for instance, has been declining by 0.05-0.12 m/year since 2000 (Pirotta et al. 2024a). Additionally, North Atlantic right whales (*Eubalaena glacialis*) have shown a 7.3% decline in maximum body length from 1981-2019 (Stewart et al. 2021). These declines have been attributed to oceanographic changes, such as the Pacific Decadal Oscillation index and seasonal upwelling patterns, as well as to anthropogenic stressors such as entanglements in fishing gear, vessel strikes, and interference in foraging activity (Pirotta et al. 2024a, Stewart et al. 2021). Declining body size may have population effects as body size has been shown to be positively associated with calving probability for North Atlantic right whales (Pirotta et al. 2024b, Stewart et al. 2022). These trends were detectable for these species because of long-term monitoring of body size and reproductive rates. These types of long-term data are difficult to collect for blue whales, as they do not aggregate near coasts during their breeding season. However, as contemporary data on blue whale body size and reproductive parameters become available, our study provides a historical baseline to compare with contemporary data. The results we present here will allow future work to detect changes in body size and reproductive rates for blue whales and better monitor the effects of a changing environment for this endangered species.

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Chapter 5. Estimates of annual survival for pygmy blue whales using historical data

Publication history: This study was co-authored with Trevor A. Branch, Andre E. Punt, and Hikari Maeda. At the time this dissertation was submitted, a version of this chapter was in preparation to be submitted to *Marine Mammal Science*.

Abstract

Pygmy blue whales (*Balaenoptera musculus brevicauda*) were targeted between 1959-1973 by commercial whaling. Estimates of key demographic parameters, such as survival, are needed to better assess their recovery from whaling. We collated biological information from caught whales, including age data from extracted earplugs, and used these catch-at-age data and generalized linear mixed-effects models to estimate natural survival for pygmy blue whales. Their annual survival was estimated to be 0.923 (95% credible interval: 0.916–0.930) across sexes. Annual survival for females (0.917; 95%: 0.905–0.928) was less than annual that for males (0.931; 95%: 0.924–0.938). To ground truth the model we used the estimated rate at which ovarian corpora accumulate in ovaries to estimate survival from the frequency of corpora in catches. The resulting ovarian corpora estimate of female survival (0.915; 0.88x–0.94x) was consistent with the estimate from the earplug data, although less certain. These estimates of survival provide a baseline estimate of pygmy blue whale survival that can be used in future age-based population assessment models to assess the recovery of pygmy blue whale populations after whaling.

5.1 Introduction

The pygmy blue whale (*Balaenoptera musculus brevicauda*) is a subspecies of blue whale primarily found in the Indian Ocean (Branch et al. 2025, Ichihara 1966). This subspecies, along with another subspecies, Antarctic blue whales (*B. m. intermedia*), were the primary targets of Southern Ocean whaling during the 20th century. The impacts of whaling on Antarctic blue whales and their subsequent population recovery has been a subject of much analysis (e.g., Branch et al. 2004, Chapter 3), but little analysis has been conducted on the effects of whaling on pygmy blue whales. Pygmy blue whales were described after other subspecies, during the late 1950s and were subsequently exploited by Japanese and Soviet whalers (Ichihara 1961, Ichihara 1966, Mikhalev 2000). More than 12,000 pygmy blue whales were caught, almost all between 1959 and 1973 (Branch et al. 2025). No published quantitative assessments for any populations of this subspecies currently exist. Information about the demography of this subspecies could lead to a better understanding of their current population status and recovery from whaling.

Annual survival probability is an important parameter in population assessments and abundance estimation. Assessments for exploited baleen whales are often based on age-structured population dynamics (Punt 2017), and age-structured models are necessary to define the age-at-maturity and hence generation times and the mature population size for use in IUCN assessments (Cooke 2019). Age-structured population dynamics models explicitly include an annual survival term, which, for Southern Hemisphere blue whales, is often assumed to be equal to 0.96, which is the value used for fin whales (*Balaenoptera physalus;* e.g., Branch et al. 2004), or is based on limited information from Northwest Atlantic blue whales (e.g., Cooke 2019). Even when survival is not explicitly incorporated into a population assessment, it can be used to construct informative priors for the rate of population increase (e.g., Branch et al. 2004, Monnahan et al. 2015). Photo-identification data are often used to estimate the abundance of blue whales using mark-recapture methods (e.g., Barlow et al. 2018, Calambokidis et al. 2007, Olson et al. 2025, Whittome et al. 2024). While it is possible to estimate survival from mark-recapture methods, the small sample sizes of photographs for blue whales can make this parameter difficult to estimate (e.g., Olson et al. 2025). In addition, mark recapture methods estimate “apparent” survival (the probability of surviving and remaining available for recapture). If individuals can leave the sampling area, apparent survival estimates can deviate meaningfully from true survival.

Catch-curve analysis has traditionally been used in fisheries to estimate total mortality from age-frequency data (e.g., Ricker 1975). Moreover, it can be used to estimate natural mortality for populations where fishing mortality is known to be negligible in the years immediately before age data were collected (Dunn et al. 2002, Maunder et al. 2023, Ricker 1975, Smith et al. 2012). Similarly, age-at-harvest data are also frequently used in wildlife populations to monitor trends in abundance and estimate survival (Allen et al. 2018, Conn et al. 2008, Gamelon et al. 2021, Skelly et al. 2023). Using this approach, biological data that were collected during whaling can be leveraged to estimate survival for pygmy blue whales.

The best way to age whales remained a mystery until the mid-1950s when it was discovered that the alternating layers of light and dark ear wax that forms in the ear canal, known as an earplug, can be used to estimate age (Laws & Purves 1956, Purves 1955). Another potential source of aging data for females comes from ovarian corpora data. Soft bodies form periodically on the ovaries of mammals which produce the hormones necessary to sustain a pregnancy and then after pregnancy these form scars. These soft bodies and scars are collectively known as ovarian corpora (Branch & Mikhalev 2008). When combined with earplug data, these data have been used to challenge previously held beliefs about the age at sexual maturity for pygmy blue whales, revising the previously held estimate of 2-3 years old (Laurie 1937, Mackintosh & Wheeler 1929), to 10 years old (Branch & Mikhalev 2008, Ichihara 1966). Earplug and ovarian corpora data have also been used to estimate age-length relationships and reproductive parameters for Antarctic, pygmy, and eastern North Pacific blue blue whales (Chapter 4). If the rate at which ovarian corpora are formed is known, these data can provide a proxy of age (age since sexual maturity) for female baleen whales that is independent of the earplug data.

Few published estimates of natural survival exist for Southern Hemisphere blue whales. An early attempt at estimating mortality for pygmy blue whales used earplug data from Japanese whaling expeditions (Ichihara & Doi 1964). However, they had limited sample sizes and used catch-curve analysis methods that may have led to biased estimates of annual survival (Mainguy et al. 2024). In this study, we estimate natural survival for pygmy blue whales using an aggregation of earplug data across Soviet and Japanese whaling expeditions. We use these combined data sources and contemporary Bayesian models to produce an improved estimate of pygmy blue whale survival. Additionally, we ground-truth this estimate using implied age-frequencies from ovarian corpora data.

5.2 Methods

We used age-frequency data from pygmy blue whale earplugs collected on Japanese and Soviet whaling expeditions to estimate natural survival using a Bayesian model that predicts the catch at each age given estimated intercept and instantaneous mortality parameters. We convert the resulting instantaneous mortality rate to an annual survival estimate. The base model was fit to all earplug data, but separate models by sex and data source are also presented as sensitivity analyses. We compared this estimate to one for females obtained by fitting the same model to age frequencies from implied age since sexual maturity from ovarian corpora data.

5.2.1 Data

Pygmy blue whale earplug data from Soviet expeditions were provided by Y. Mikhalev (National Academy of Sciences of Ukraine) from work in E. Sazhinov's 1980 PhD dissertation. These data were collected during the 1960s and early 1970s throughout the Indian Ocean. The Soviet data grouped all earplugs together as pygmy blue whales, whether caught off New Zealand, Australia, or in the southern and northern Indian Ocean, thus including the putative northern Indian Ocean subspecies (*B. m. indica*). In our analysis, following Branch et al. (2025), we consider data from all these regions to be from pygmy blue whales. Pygmy blue whale earplugs were also collected on Japanese expeditions to the south-western Indian Ocean during 1960–1964; the samples and associated data were provided by Fisheries Resources Institute, Japan Fisheries Research and Education Agency, and the original age estimates from these earplugs were made at the former Whale Research Institute (Tokyo). The Japanese data contain estimates of ages from earplugs that were not recovered in full. Partial earplugs only provide an estimate of minimum age and were excluded for the purposes of this study (about 10% of Japanese data, randomly distributed across lengths). Counts of ovarian corpora come from Table S1 of Branch et al. (2009). Only data from whales caught north of 52°S and east of 35°E were used, to ensure that these were restricted to pygmy blue whales, since only 0.5% of catches in this region were estimated to be Antarctic blue whales (Branch et al. 2009).

5.2.2 Survival model

Natural survival was modeled using a Poisson generalized linear mixed model with age as the predictor and the frequency at each age as the response (e.g., Millar & Wilberg 2015). This model is based on the idea that survival can be expressed as the number of whales at age a (N_a) that survive to age $a+1$. This is ideally estimated by following individual cohorts of animals over time. However, when longitudinal data for cohorts is not available, this can be approximated by using a sample from many cohorts. This approximation rests on the assumptions that there is constant mortality across time and age class, that the population is closed (no emigration), that ages are accurate, and that the data are an unbiased sample of age classes (no age class is over- or underrepresented). Following these assumptions, the expected number of age-a whales in a population is a product of the survival rate and the number of whales that are in the first age class (0):

$$N_a = N_0 s^a \tag{1}$$

The catch of whales at age a (C_a) is proportional to the number of whales at age a assuming that all whales are equally available to be caught. However, this assumption is only true for whales above a certain age (a_0), since whalers selected for larger whales while hunting. Therefore, the survival of whales above the age of full selection by whaling becomes:

$$N_a = N_{a_0} s^{a - a_0} \text{ for } a \geq a_0 \tag{2}$$

where N_{a_0} is the number of whales newly available to be caught, and the number of whales caught at age *a* becomes:

$$C_a = qN_{a_0} s^{a - a_0} \text{ for } a \geq a_0 \tag{3}$$

where *q* represents the proportion of the population whaled under the assumption of uniform selectivity harvesting above age a_0. Given that instantaneous mortality (*z*) is equivalent to $z = -\log(s)$, taking the natural logarithm, this then becomes:

$$\log(C_a) = \log\left(qN_{a_0}\right) - a_0 z - z * a,\ for\ a \geq a_0 \tag{4}$$

Since the age of full selection (a_0) is pre-specified, $\log\left(qN_{a_0}\right) - a_0 z$ is a constant and can be estimated as the intercept parameter. The model therefore becomes:

$$\log(C_a) = \alpha - za,\ for\ a \geq a_0 \tag{5}$$

which forms the basis of a generalized linear model with a log-link function, an estimated intercept parameter (α) and the parameter *z* (negative slope) being the instantaneous mortality rate. To account for annual variability in recruitment, we added a random effect of age to the intercept parameter (e.g., Millar & Wilberg 2015) such that:

$$\log(C_a) = \alpha_a - za,\ for\ a \geq a_0 \tag{6}$$

$$\alpha_a \sim N(\bar{\alpha}, \sigma_\alpha)$$

where $\bar{\alpha}$ is the estimated mean intercept parameter, and σ_α is an estimated standard deviation parameter that describes the among-age variation in the intercept parameter.

Survival rate (*s*, per year) was calculated as:

$$s = \exp(-z) \tag{7}$$

which assumes that the only contribution to mortality in this population is natural mortality. This assumption is reasonable since pygmy blue whales were only exploited in high numbers after their discovery in 1959 (Ichihara 1961, Ichihara 1966, Rand & Branch 2024) and were only caught until 1973 (Branch et al. 2025). Additionally, 70% of these catches were taken within an 8-year time span from 1959-1966 (Figure 5.1). Therefore, the relative proportions of whales above age a_0 should be unaffected by whaling (Ricker 1975). We conducted a simulation study that validated this assumption (see Appendix S1 for details).

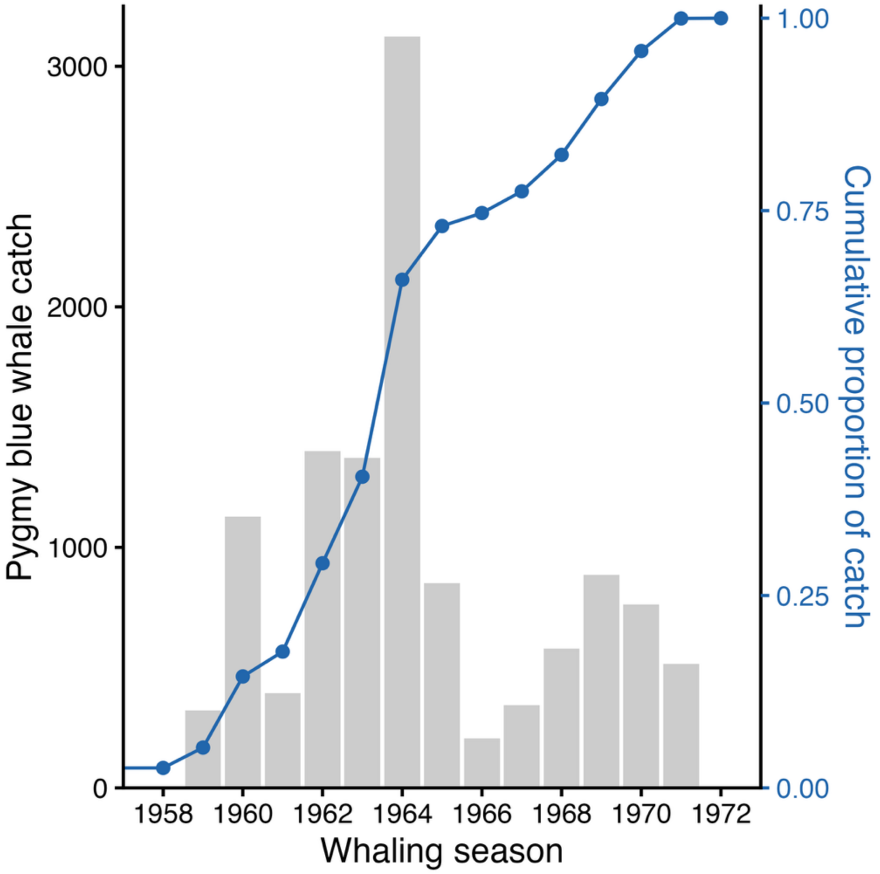

Figure 5.1 Pygmy blue whale catch totals in each whaling season after 1957 (bars; Branch et al. 2025), and the cumulative proportion of the total pygmy blue whale catches taken in each whaling season (points and line). The catch numbers during 1958 and 1972 were so low (< 5) that they are not visible on the plot.

The model above (Eqn. 6) was fit to age frequencies from pygmy blue whale earplug data. Separate models were run using all the earplug data (base model), as well as individually for each sex. Additionally, as a sensitivity, models were run separately for Japanese and Soviet data. The age of full selection, a_0, was fixed at the age of maximum frequency + 1, as is common in this type of analysis (Mainguy et al. 2024), except for the model using only Soviet data, where the third highest age frequency was used because there were anomalously high catches at young ages (ages 2 and 5). As a sensitivity, models were also run for the base model starting at ages -3, -2, -1, +1, +2, and +3 years from the best value for a_0.

A separate model was run for the ovarian corpora data, assuming a constant rate of corpora accumulation after sexual maturity. Counts of ovarian corpora were converted to ages (a_s) by multiplying the number of ovarian corpora (N_o) by the expected number of years to produce an ovarian corpus (k) :

$$a_s = N_o * k \tag{8}$$

This results in ages (a_s) that represent the number of years since the age of sexual maturity (9-10 years old, Chapter 4) The number of years between the formation of an ovarian corpus (k) was based on the estimate from Chapter 4 and included as a parameter in the model with a prior distribution of SkewNormal (2.899, 0.548, 2) to account for the uncertainty in this estimate (Appendix S2). Since no data was included to estimate *k* in this model, the resulting posterior distribution of *k* is the same as the prior distribution. However, this allows the resulting ages, and therefore the resulting instantaneous mortality estimate, to incorporate the uncertainty from this parameter. The number of catches at each of the resulting ages were used were fit with the model above. Since ovarian corpora are only present in females, this survival estimate is only applicable to females.

All models were fit using Bayesian methods using Stan v. 2.36 (Stan Development Team 2025b)in R v. 4.51 (R Core Team 2025). The earplug models were fit using *brms* package (Bürkner 2017) while the corpora model was fit using the *rstan* package (Stan Development Team 2025a). All age-frequencies were assumed to be Poisson-distributed (since the random intercept accounts for overdispersion in the data). Flat priors were used for $\bar{\alpha}$ and z, and a Student-t distribution (3, 0, 2.5) was used as a prior for σ_α. Earplug models were fit with 2,000 iterations, a 50% warm-up, and 4 chains. Corpora models were fit with 6,000 iterations, a 50% warm-up, and 4 chains. Convergence was checked using $\hat{R}$, effective sample sizes, traceplots and autocorrelation plots. Model adequacy was assessed using posterior predictive checks. All estimates are reported as medians and 95% credible intervals.

5.2.3 Rate of increase

We calculated a distribution for plausible rates of increase for pygmy blue whales using the Euler-Lotka equation (e.g., Branch et al. 2004, Monnahan et al. 2015, Zerbini et al. 2010):

$$e^{t_m\delta} = e^{(t_m-1)\delta}S + pqs_js^{t_m-1} \quad (9)$$

where t_m is the age at first parturition, s is annual survival for adults, p is the annual pregnancy rate, q is the proportion of births that are female, s_j is the first-year (calf) survival rate, and δ is the rate of increase of the population.

The survival (*s*) value was obtained from the posterior distribution of survival from the base model. For the age of first parturition (t_m), we used the posterior distribution of the estimated age of sexual maturity for female pygmy blue whales from Chapter 4 and then added a year to account for mating and gestation. Additionally, we calculated a distribution for the annual pregnancy rates by using the posterior distribution of the annual rate of ovarian corpora formation (1/*k*; Chapter 4). We calculated a distribution of calf survival from our posterior distribution of adult survival by assuming that the difference between calf and adult survival was uniformly distributed between 0.02 and 0.12 (e.g., Branch et al. 2004). We assumed that the proportion of births that were female (*q)* was 0.473 (Branch et al. 2004).

5.3 Results

5.3.1 Model of survival from earplug data

The age of full selection (a_0) was assumed to be the age at highest catch frequency + 1, which resulted in a starting age of 17 for the model including all of the earplug data. This model estimated an instantaneous mortality rate (*z*) of 0.08 (0.073–0.088) which resulted in an estimate for annual survival of 0.923 (0.916–0.930). The median of the posterior for the intercept parameter (on the log scale), α, was estimated to be 5.82 (5.55–6.12) and the among-age variability (σ_α) was estimated to be 0.27 (0.19– 0.38; Figure 5.2a). The posterior predictive checks suggest that the model fits the data well (Figure 5.2b).

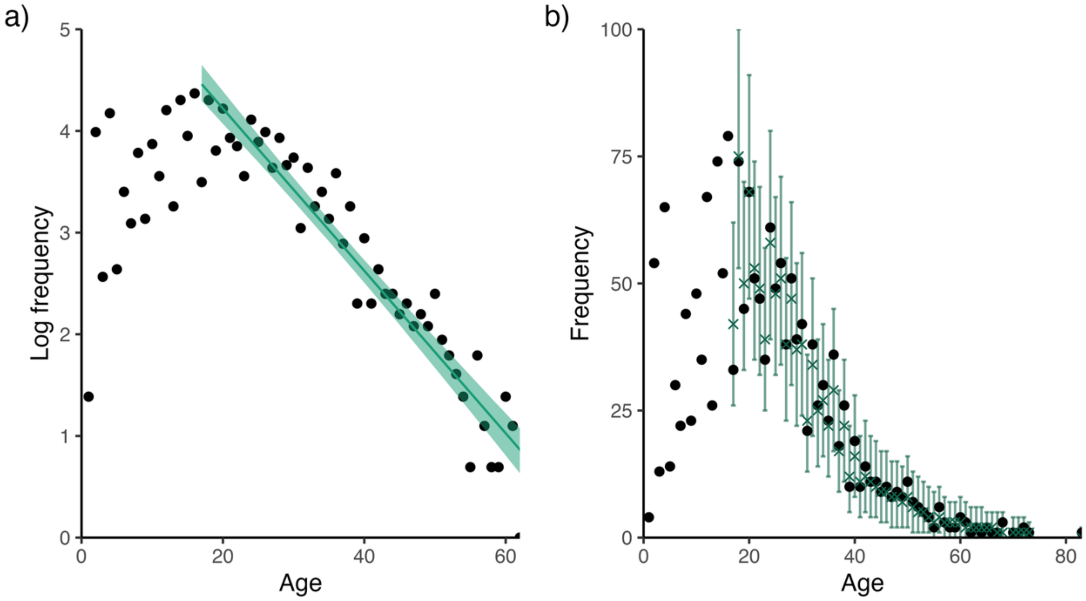

Figure 5.2. Posterior model fit and posterior predictive distributions. a) Posterior median (line) and 95% credible interval (shading) of the estimate Poisson generalized linear model (plotted without random effects) that included all earplug data (points), and b) the median (x) and 95% credible intervals (error bars) of the posterior predictive distribution for each data point used to fit the model (points).

The survival estimate was robust to the choice of starting age: models using starting ages (a_0) of 14-20 resulted in survival estimates between 0.925 and 0.920 (Figure 5.3).

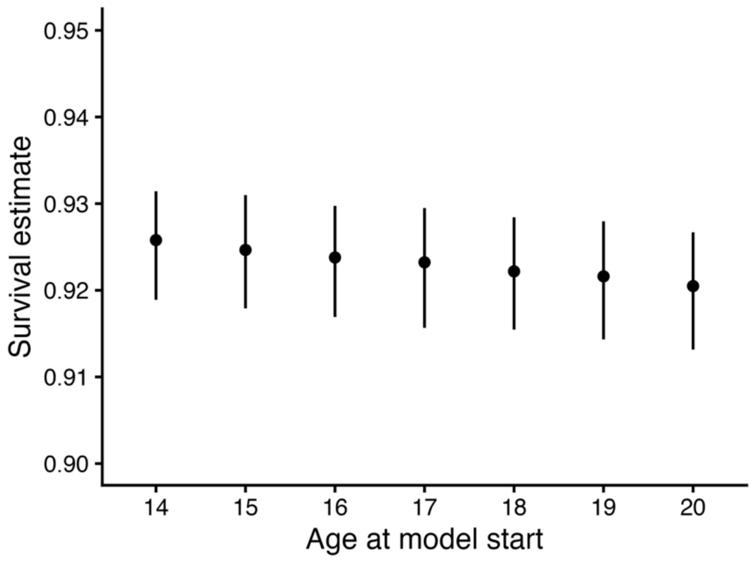

Figure 5.3. Sensitivity to age at model start.Estimated survival (points) and 95% credible intervals (lines) from additional runs of the model assuming different ages for the age of full selectivity by whaling (age at model start). The base model assumed an age of full selectivity of 17.

Models were also fit separately to each data source (Japanese, Soviet), and to each sex. The age of full selection, $a_{0,}$ was assumed to be the age at highest catch frequency + 1, resulting in a starting age of 22 for the Japanese data, 15 for the female earplugs and 17 for the male earplugs. For the model with only Soviet data, there were anomalously high frequencies at age 2 and age 5, and therefore the age of third highest frequency was used, resulting in a starting age of 15.

The model using only Japanese data resulted in the highest annual survival estimate of 0.928 (0.920–0.934), while the model using the Soviet data resulted in a lower and less precise estimate of 0.905 (0.888–0.920). Annual survival was estimated to be higher for males 0.931 (0.924–0.938) than for females 0.917 (0.905–0.928), though the credible intervals overlap (Figure 5.4).

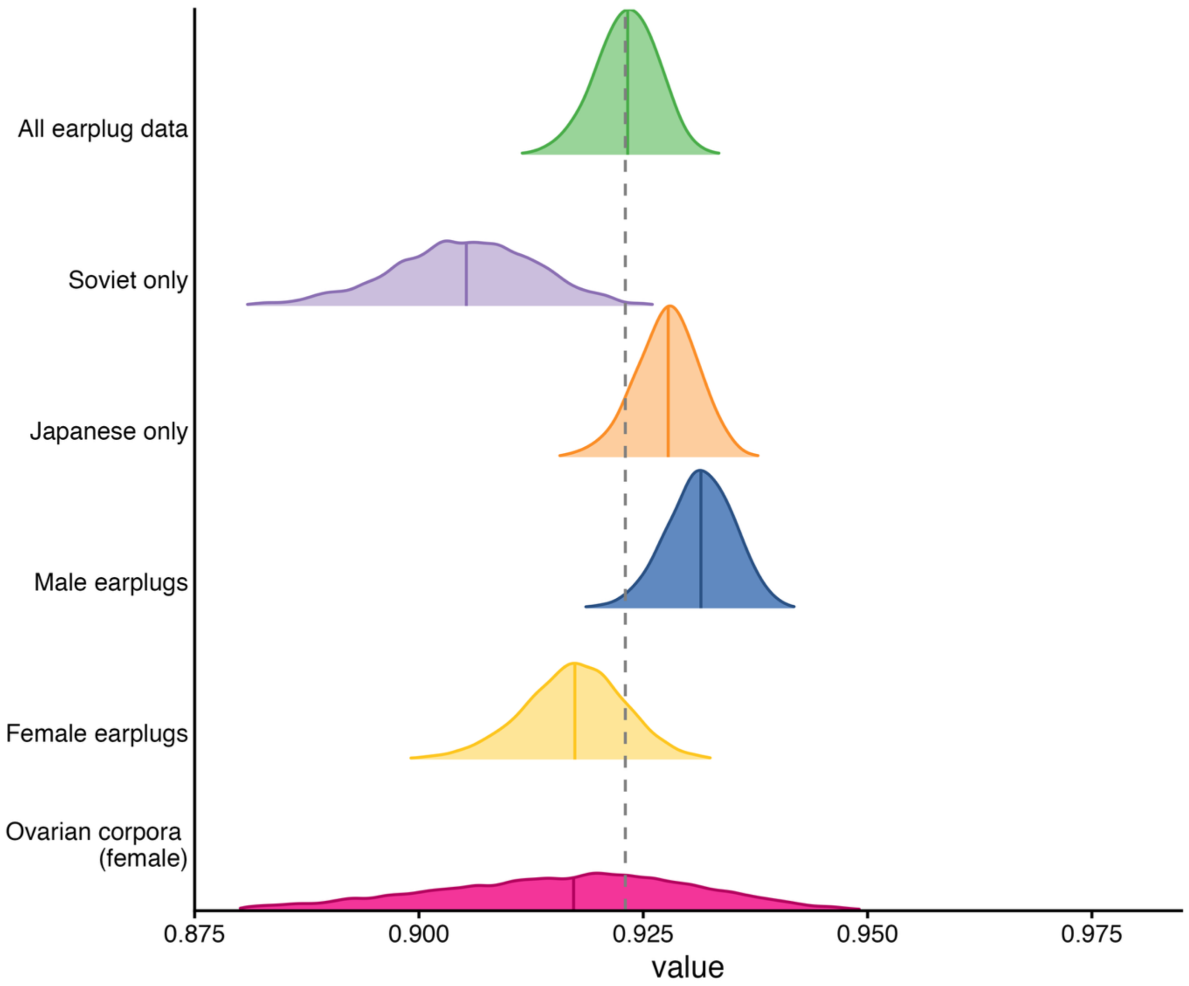

Figure 5.4 Posterior distributions for natural survival with median estimate indicated by lines for models using earplug data separated by data source and sex; and the model using ovarian corpora data. The dashed line represents the median estimate based on all earplug data.

5.3.2 Model of survival from ovarian corpora data

The age of full selection, a_0, was assumed to be the corpora count that had the highest frequency + 1, which was a corpora count of 3 (c. age 18). The model fit to ovarian corpora data estimated an instantaneous mortality rate (z) of 0.087 (0.060–0.13), which is equivalent to an annual survival (for females) of 0.917 (0.877–0.942). This overlaps with the estimated survival rate for females from the earplug data but has a wider posterior interval (Figure 5.4). The median of the distribution for the intercept parameter (on the log scale), α , was estimated to be 5.70 (5.38–6.03) and the among-age variability (σ_α) was estimated to be 0.23 (0.11 –0.43; Figure 5.5a). The posterior predictive distribution suggests that the model fits the data well (Figure 5.5b).

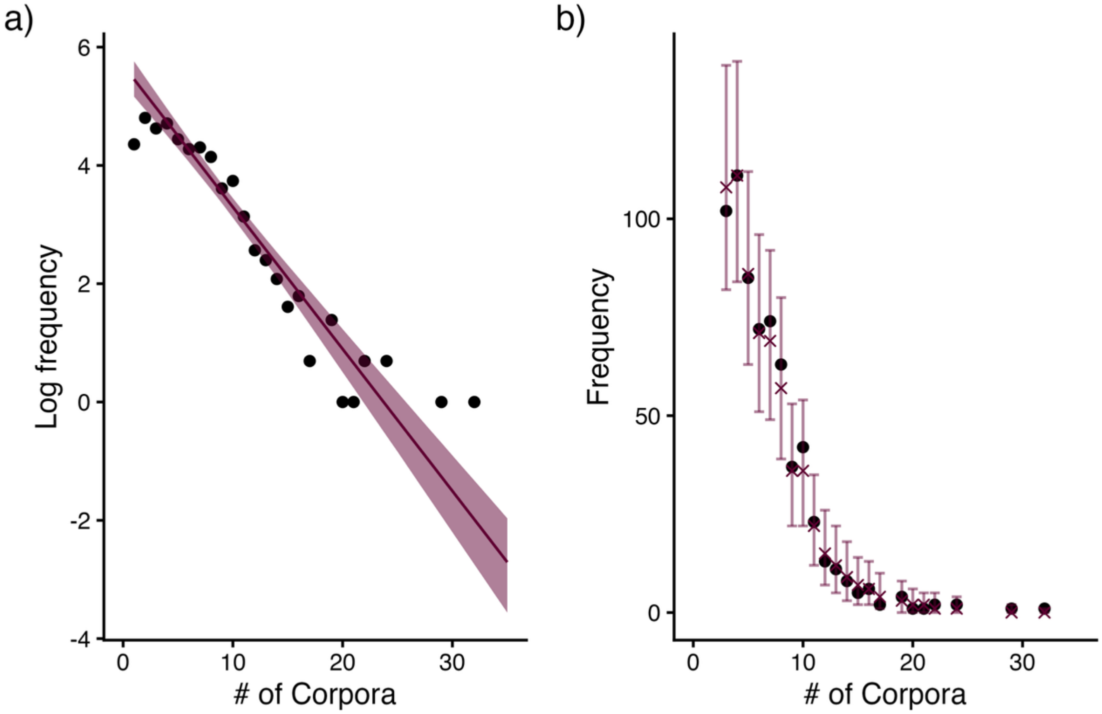

Figure 5.5 Posterior model fit and posterior predictive distributions. a) Posterior median (line) and 95% credible interval (shading) of the Poisson generalized linear model (plotted without random effects) that included ovarian corpora data and b) the median (x) and 95% credible intervals (error bars) of the posterior predictive distributions for each data point used to fit the model (points).

5.3.3 Population rate of increase

Based on the estimated survival rates from the base model, the population rate of increase from the Euler-Lotka equation is estimated to be -0.0062 (-0.023–+0.014). The probability of the rate of increase being negative was 0.763.

5.4 Discussion

Here we provide the first estimate of the annual survival rate for a Southern Hemisphere blue whale using modern quantitative techniques. We estimated pygmy blue whale survival to be 0.923 (0.916–0.930) across sexes (Figure 5.4). Our estimate is lower than the only existing pygmy blue whale estimate of 0.95 from Ichihara and Doi (1964). However, their estimate was based solely on Japanese earplug data and included two fewer years of data. Our estimate is similar to that for North Pacific blue whales, where survival was estimated to be 0.929–0.952 using earplug data (Ohsumi 1979). Blue whales in the Gulf of St. Lawrence had a much higher estimated survival rate (0.975), but this estimate was based on visual sightings and is likely positively biased due to very long-term sightings records for some individuals (Ramp et al. 2006). Additional survival estimates for North Pacific blue whales of 0.99 – 0.89 were estimated from mark-recapture methods (Calambokidis et al. 2007, Whittome et al. 2024) but represent "apparent" survival (including permanent emigration) in a study area that does not include the full range of the species, so cannot be directly compared with our estimate.

We estimated that female survival (posterior median 0.917) was lower than male survival (posterior median 0.931; Figure 5.4) though their credible intervals overlapped. While this suggests that survival may not be different for male and female blue whales, this is likely because we did not have high enough sample sizes to distinguish survival between the two sexes. It is expected that female survival would be lower than male survival for baleen whales, since gestation and lactation are extremely energetically costly for baleen whale mothers. Reproductive cycles are tied closely to migration, leading to rapid fetal and calf growth in very short periods of time (Branch 2025, Kato 1995). These high growth rates are costly to maintain (Christiansen et al. 2022, Christiansen et al. 2014, Christiansen et al. 2018, Wachtendonk et al. 2022) and mothers have to support these rapid growth rates while in low-latitude breeding and calving areas, where there are limited prey. This likely reduces the overall survival of females.

We found that the model that only used Japanese data estimated a higher survival rate (0.928) than that which used only Soviet data (0.905), though their 95% credible intervals overlapped somewhat (Figure 5.4). This may be because Japanese catches were concentrated between 20°–80°E and 40°–52°S from February to April while Soviet whalers caught pygmy blue whales throughout their range (Branch et al. 2025). The Japanese catches come primarily from a single population (the Southwest Indian Ocean population) while the Soviet catches likely span five different populations (Branch et al. 2025). If these different populations experience different environmental conditions leading to differing prey environments or exposure to killer whales, this could explain the difference in survival estimates between these two data sources. In addition, Japanese commercial catches largely ended in 1964 with the moratorium on catching blue whales, while Soviet catches continued through 1973, therefore the expected survival for the latter data may also be slightly negatively biased relative to unexploited survival because it includes some of the effects of whaling mortality (Appendix S1).

True pygmy blue whale natural survival may be slightly underestimated by our model. While a few pygmy blue whales were caught before 1959, 97% of pygmy blue whale catches occurred in the 14 years between 1959 and 1973 (Figure 5.1; Branch et al. 2025). With a survival rate of 0.93 it would take approximately 5-10 years of whaling for the estimated survival rate from the catch curve to be negatively influenced by whaling mortality (Appendix S1). Therefore, there is likely some effect of whaling in our results. However, this effect is likely to be small since 70% of catches were taken within 8 years (Figure 5.1) and our simulation study demonstrated that this effect would decrease our estimate of survival by less than 0.01 (Appendix S1).

These survival estimates for pygmy blue whales in the 1960s reflect a population before the start of whaling. Using the estimated survival rates, we estimated a population growth rate indistinguishable from 0 (76% probability of being negative), which is consistent with a population at carrying capacity. This supports the common assumption that blue whale populations were near carrying capacity before the start of whaling (e.g., Branch et al. 2004, Chapter 3). However, this survival estimate and resulting low population growth rate, could also be reflective of other environmental conditions at the time unrelated to density dependence, such as low prey availability or increased predation.

This estimate provides a good baseline for pygmy blue whale survival based on their historical population size, however, contemporary pygmy blue whale survival may be higher due to density-dependent factors. The primary limiting resource for baleen whales is likely prey availability (Stewart et al. 2025). Since whaling decreased the population size, lessening intraspecific competition for prey, the end of whaling could lead to higher survival rates and birth rates, resulting in an increasing population size. Regional estimates of acoustic intensity of pygmy blue whale song in the Eastern Indian Ocean suggest that the population size of pygmy blue whales may be increasing at 4.3% per year (McCauley et al. 2018). Future data on survival, such as through range-wide photo-ID mark-recapture studies, could provide a better insight into current pygmy blue whale survival and trends in abundance.

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Discussion

Baleen whales were heavily exploited by commercial whaling and still face many anthropogenic threats, so it is essential to assess their population status and recovery. This dissertation applies contemporary quantitative methods to the extensive database of biological data from historical whaling to answer long-standing questions about baleen whale demography and population status—centering on blue whales that were brought near to extinction by commercial whaling. I applied innovative Bayesian modeling techniques to combine historical and contemporary datasets and account for some of the inherent biases in whaling data. The results from this dissertation can be used to manage current threats to blue whale populations, as well as provide a methodological framework for incorporating historical whaling data into population models for other species.

Antarctic blue whales were a primary target of commercial whaling in the Southern Ocean and are currently listed as Critically Endangered due to this exploitation (Cooke 2018). The most recent published assessment for this subspecies was completed over 20 years ago and assumed Antarctic blue whales were a single circumpolar population although there was little evidence to support this assumption (Branch et al. 2004). In Chapter 1 of this dissertation, I investigated this assumption using a historical mark-recovery dataset collected during the whaling era. I found high interannual movement rates, suggesting that Antarctic blue whales mix freely on the feeding grounds and may be comprised of a single circumpolar population. These results are consistent with the most recent and comprehensive genetic study of Antarctic blue whale population structure (Attard et al. 2024). Given these results, in Chapter 3, I used additional line-transect abundance estimates, as well as a new abundance estimate from photo-identification data, to assess the population status and recovery of Antarctic blue whales. I found that while they are currently estimated to be increasing at about 4.5% per year, they are still at less than 2% of their pre-whaling levels and will take more than 70 years to reach 60% of carrying capacity.

Assessments for exploited baleen whales are often based on age-structured population dynamics (Punt 2017). However, age-structured assessments require parameters that are difficult to estimate for blue whales. Whaling data provide some of the largest sample sizes of biological data for baleen whales, providing a unique opportunity to understand biological processes and estimate demographic rates. In this dissertation, I use the first global compilation of earplug and ovarian corpora data across blue whale subspecies to estimate age of sexual maturity and pregnancy rates for eastern North Pacific and pygmy blue whales (Chapter 4), and natural survival rates for pygmy blue whales (Chapter 5). These results provide a historical baseline for these parameters that can be used in age-structured assessments.

In this dissertation I also use whaling data to address long-standing biological and ecological questions for baleen whales. For instance, the relationship between age and length for blue whales has long been a mystery, and in this dissertation I compile all available age data for blue whales and estimate these relationships for Antarctic, eastern North Pacific, and pygmy blue whales, providing new insights into differences in asymptotic lengths between subspecies as well as patterns of blue whale growth (Chapter 4).

Mammalian fetal sex ratios have also been an area of active research since the 19th century, when Charles Darwin was intrigued by how parents seemed to produce equal numbers of males and females, although he did not understand the underlying mechanism (Darwin 1874). Many hypotheses exist to predict how mammals should invest in male versus female offspring to maximize their inclusive fitness, known as adaptive sex ratio behavior (Leimar 1996, Myers 1978, Trivers & Willard 1973). However, testing these hypotheses can be challenging because deviations from an equal sex ratio are likely to be small and difficult to detect without an extensive database of sex ratios from fetuses or recent births, and there are few wild populations for which such a database exists. Whaling data provide a uniquely large database to examine these hypotheses, with a sample size for fin whales alone of over 100,000 sexed fetuses. In Chapter 2, I evaluate the evidence for adaptive sex ratio behavior in rorqual whales, finding that longer mothers tend to have more female offspring. This differs from what would be expected in terrestrial ungulates where males compete for access to females (Trivers & Willard 1973), which suggests that since reproduction is so costly for baleen whale females, there is an advantage to being large that larger mothers pass on their daughters. This chapter provides the first evidence of adaptive sex ratio behavior in cetacean populations and contributes to a growing body of evidence that mammals may adapt the sex ratio of their offspring in response to their own body condition, social structure and competition for resources (Clutton-Brock & Iason 1986, Hardy 1997, Hardy & Boulton 2019).

Throughout this dissertation I adapted statistical modelling approaches to address some of the challenges of working with historical data, and to discover new insights into cetacean ecology, conservation, and evolution. Discovery mark data were collected extensively throughout whaling (Brown 1966), however, one of the key challenges that has so far prevented quantitative analysis of this data is that no data on whaling effort was collected, and to estimate mark-recovery rates, harvest rates are needed. I solved this challenge with an original use of integrated population models (Schaub & Abadi 2011) to estimate whaling effort and enable the estimation of population size from this data for the first time. This allowed us to better understand the population structure of Antarctic blue whales and will lead to a more precise estimate of their recovery from whaling. Furthermore, this project produced the first integrated population model to incorporate historical mark-recovery data from whaling and can be used as a blueprint for other similar analyses for other whale species (Chapter 1). Similarly, combining multiple data sources (Japanese and Soviet earplug data) allowed me to estimate age-length relationships despite "whale-stretching" by the Japanese fleets (Chapter 4). Additionally, in Chapter 2, I developed new statistical approaches to account for the biases in the data from sex misidentification by adapting models originally developed for estimating gear-selectivity in fisheries (Punt & Kennedy 1997). I used this model to correct for fetal sex misidentification, and I was then able to use the fetal data to examine questions about adaptive sex ratios in baleen whales.

In this dissertation, I also used innovative Bayesian modeling techniques to improve model-fitting efficiency and convergence. Models were primarily fit using Stan (Stan Development Team 2025), which has been shown to be one of the most efficient software programs for Bayesian inference (Monnahan et al. 2017). In Chapters 4 and 5, the use of RTMB (Kristensen 2024) brings the ease of coding in R to the efficiency of fitting models with TMB and Stan (Monnahan et al. 2019, Monnahan et al. 2017). The Antarctic blue whale assessment model was fit using the programming language Julia (Bezanson et al. 2017). Julia uses "just-in-time" compilation, which similarly to the use of RTMB, allows for faster computation time while maintaining flexible and readable code (Aycock 2003). However, the added benefit of Julia is that all underlying packages and code are also written in Julia*,* allowing me to use an optimization algorithm to find the carrying capacity from the estimated minimum population size (the "backwards" procedure) inside a Bayesian model. This also allows for Bayesian models written in Julia to be flexibly fit with different MCMC algorithms, which facilitated the selection of the most efficient algorithm (slice sampling) for the Antarctic blue whale assessment model (Chapter 3).

While this dissertation demonstrates the usefulness of historical whaling data, especially when analyzed with contemporary quantitative techniques, it also highlights the need for more data on blue whale abundance, distribution, and behavior. Although there is some information on current abundance for Antarctic blue whales from photo-identification, there has not been consistent coverage throughout the Southern Ocean, and resighting rates are low (Olson et al. 2025). Additionally, line-transect surveys for Antarctic blue whales have largely ceased or are limited to small regions of the Antarctic. Furthermore, of the blue whale populations in the Southern Hemisphere, Antarctic blue whales are relatively well-studied. Catch data and some abundance estimates exist for pygmy blue whales (Barlow et al. 2018, Branch et al. 2025), although no comprehensive population assessment has been completed for populations of this subspecies. There are additionally many populations of blue whales for which there are few abundance estimates and no completed population assessments. Furthermore, while the insights into reproductive parameters, growth rates, and natural survival in this dissertation provide a historical baseline for some of these populations, contemporary data on calving rates and changes in body size are needed to monitor the effects of climate change and its impact on population recovery.

Although this dissertation focuses on single-species models without environmental covariates, understanding ecosystem processes is increasingly important given climate change. Results from this dissertation, especially the time series of Antarctic blue whale population size in Chapter 3 and baseline survival and reproductive rates from Chapters 4 and 5, could be incorporated into ecosystem-level models that link baleen whale abundance, krill availability, and climate drivers to understand the impacts of climate change on the Southern Ocean ecosystem (e.g., Tulloch et al. 2019, Tulloch et al. 2017). Additionally, while this dissertation treats demographic parameters such as carrying capacity, intrinsic growth, and natural survival as static, future work could examine changes in these parameters over time related to environmental changes. Models incorporating environmental changes and anthropogenic threats have been used to demonstrate that major gray whale (*Eschrichtius robustus*) mortality events were linked to low prey biomass and high levels of ice cover (Stewart et al. 2023). While Antarctic blue whales are currently far from recovery and therefore unlikely to be affected by density-dependent factors such as environmental variability or climate impacts (Stewart et al. 2025), this will become increasingly necessary in the future as the climate continues to change and the Antarctic blue whale population continues to grow. However, for blue whale populations such as the eastern North Pacific, which may be recovered from whaling (Monnahan et al. 2015), models that can include effects of a changing environment and anthropogenic stressors are needed to understand current population status and manage threats to their population.

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List of Publications

The following publications were written by Zoe Rand during her PhD:

Rand, Z. R., Branch, T. A. , Punt, A. E., Maeda, H. *In prep.* Estimates of annual survival for pygmy blue whales using historical data. *Marine Mammal Science*

Rand, Z. R., Branch, T. A., Punt, A. E., Maeda, H., Mizroch, S. *In prep.* Estimates of blue whale growth and reproduction parameters from historical data. *Marine Mammal Science*

Rand Z. R., Olson, P.A., Kinzey, D., Double, M. C., Miller B. S., Matsuoka, K. Findlay K. and Branch, T.A. *In review.* Critically endangered blue whales are increasing but still far from pre-whaling levels. *Endangered Species Research.*

Rand Z. R., Koehn L. E., Morrigan, A. and Hanson, B. M. *In review.* Increasing presence of Bigg's killer whales and changing seasonality of Southern Resident killer whales in Washington waters. *PLOS One.*

Rand Z. R., Branch, T. A. and Converse, S. J. (2025) Battle of the sexes: longer rorqual whale mothers have more female offspring. *Proceedings of the Royal Society B.* Accepted.

Branch, T.A., Monnahan, C.C., Leroy, E.C., …, **Rand Z. R.,** *et al.* (2025). Separating historical catches among pygmy blue whale populations with the aid of recent song detections. *Marine Mammal Science.* e70003.

Rand Z.R., Branch, T. A. and Jackson J. A. (2024). High historical movement rates of Antarctic blue whales (*Balaenoptera musculus intermedia*) on Southern Ocean feeding grounds estimated from Discovery marks. *Endangered Species Research.* 55: 109-128.

Rand, Z. R., Ward, E. J., Zamon, J. E., Good, T. P., and Harvey, C. J. (2024). Using hidden Markov models to develop ecosystem indicators from non-stationary time series. *Ecological Modelling*, 495:110800. 10.1016/j.ecolmodel.2024.110800

Battle L., Patil A., Branch T.A., **Rand Z. R.** (2023) Visualizing historical whaling voyages over time. *Interactions* 30:22-23

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Appendix 1: Supplemental Material for Chapter 1

S1: Testing model with alternative boundaries between states

To test the sensitivity of our results to the use of ocean basins as the states of our model, we tested an alternative form of the model with different boundaries between states based on the IWC management areas (Figure S1.1). In this model, IWC areas II&III were one state, areas IV&V were another, and areas VI&I were the third. The catch and mark recovery data, as well as the abundance estimates were assigned to these states following a similar process for the ocean basins outlined in the main text. Catches before 1913 (which do not have location data) were assumed to be in areas I II&III, since most of the early catches occurred in these areas. In this model, the abundance estimates from the JARPA and JARPAII surveys were in a single state (areas IV&V) and therefore only a single q parameter was calculated.

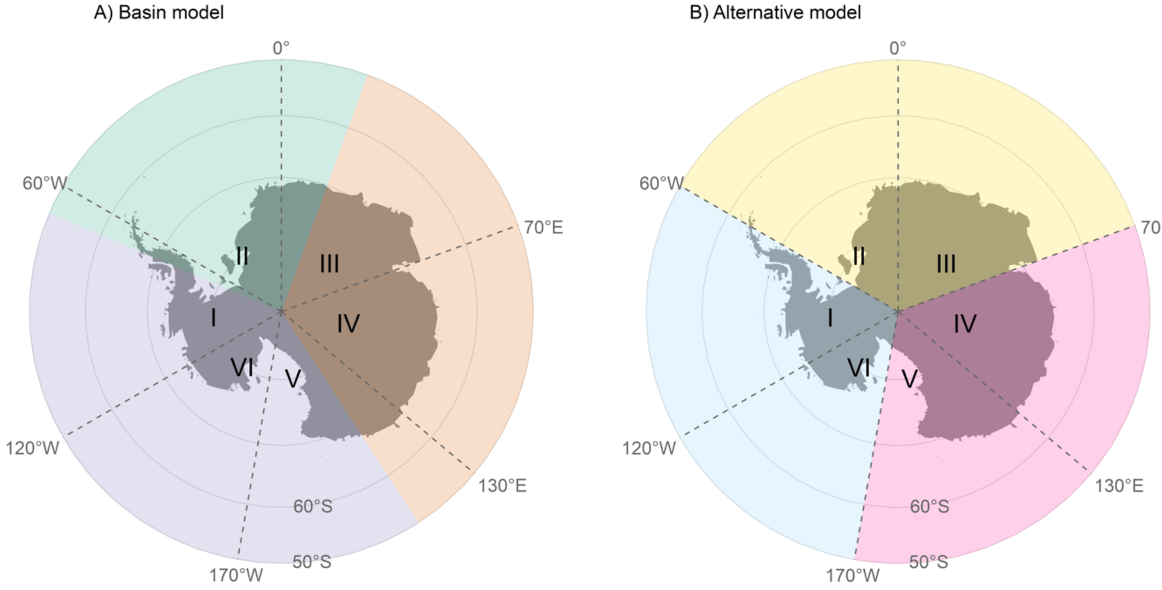

Figure S1.1. State designations used in multi-state mark recovery model for the model using ocean basins (A) and the alternative model (B) as well as the included IWC management areas.

We estimated high rates of movement between the three states used in this model, with the lowest estimated rate of movement of 0.107 (0.005–0.390) from areas II&III to areas VI&I. Estimated movement in the other direction, however, was high (0.382, 95% CI: 0.167–0.432). Annual movement rates among the other states were high, with medians greater than 0.14 (Figure S1.2).

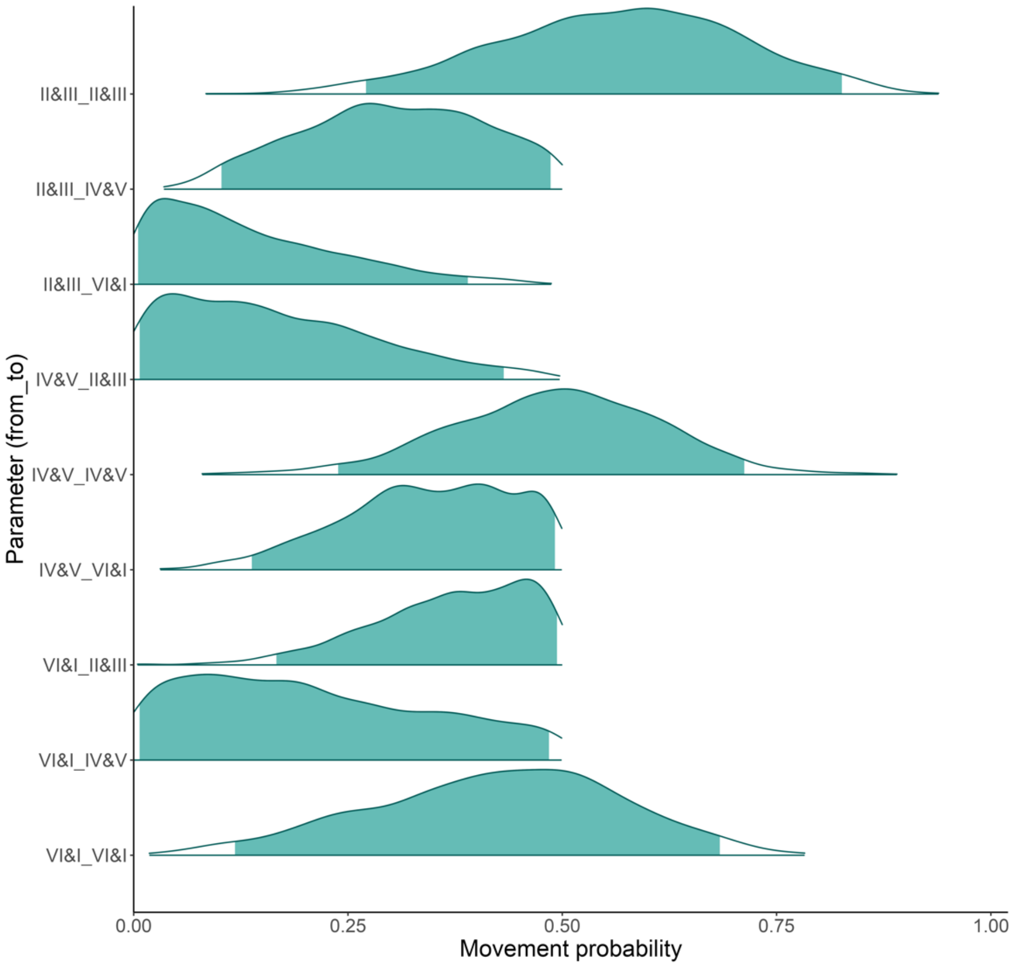

Figure S1.2. Posterior distributions and 95% credible intervals (shading) for the movement probabilities among the three states in the alternative model. The probability of remaining in each state was calculated by subtraction.

The estimate of carrying capacity (*K*) was 13% larger in this model than in the basin model, and the estimate of *r* was 34% smaller, but the credible intervals of these parameters overlap in both models (Table S1.1). The differences in these estimated are likely explained by the wider posteriors in this model compared to the basin model, indicating the parameter estimates from this model are more uncertain. The wide posteriors are likely a result very little information in the data for areas VI&I, since there are no JARPA abundance estimates for these areas, and the number of annual Antarctic blue whale catches in these areas were generally less than 2000 per year.

Table S1.1. Parameter estimates (median and 95% credible intervals) from the alternative model. In this model, state A was IWC management areas II&III, state B was areas IV&V, and state C was areas VI&I.

Parameter	Description	Median	2.5%	97.5%

r	Intrinsic growth	0.061	0.031	0.096
K	Carrying capacity (Total)	212862	178402	257974
K_{A}	Carrying capacity (A)	81278	56119	114535
K_{B}	Carrying capacity (B)	70875	40240	104692
K_{C}	Carrying capacity (C)	59317	33924	96787
$m_{\mathrm{A}\to\mathrm{A}}$	Movement	0.574	0.271	0.826
$m_{\mathrm{B}\to\mathrm{A}}$	Movement	0.145	0.007	0.432
$m_{\mathrm{C}\to\mathrm{A}}$	Movement	0.382	0.167	0.494
$m_{\mathrm{A}\to\mathrm{B}}$	Movement	0.305	0.102	0.486
$m_{\mathrm{B}\to\mathrm{B}}$	Movement	0.496	0.239	0.712
$m_{\mathrm{C}\to\mathrm{B}}$	Movement	0.188	0.007	0.485
$m_{\mathrm{A}\to\mathrm{C}}$	Movement	0.107	0.005	0.390
$m_{\mathrm{B}\to\mathrm{C}}$	Movement	0.352	0.138	0.491
$m_{\mathrm{C}\to\mathrm{C}}$	Movement	0.433	0.118	0.684
l	Mark loss	0.962	0.943	0.975
θ	Overdispersion	0.820	0.268	270.301
q_B	JARPA coverage (B)	0.286	0.170	0.466

S2: Model results with Matsuoka and Hakamada (2014) abundance estimates

In an additional model run, the model was fit to previously published abundance estimates for the JARPA and JARPAII surveys (Matsuoka & Hakamada 2014) instead of those published by Hamabe et al. (2023) to test the sensitivity of our results to the differences in these estimates. Matsuoka & Hakamada (2014) provide estimates for IWC areas IIIE-VIW (35°E - 145°W) though only areas IV and V were surveyed in all years. Therefore, for this sensitivity test, we used estimates from years where all areas were surveyed (1995/96–2008/09). Since the surveys covered different IWC areas in different years, the year of the estimate for each basin was calculated as a weighted average of the years of the corresponding IWC areas. Coefficients of variation (CVs) were calculated by converting the CVs of individual estimates into variances, taking a weighted average of the variances, and then converting the averaged variances back into CVs (Table S2.1).

Table S2.1. Abundance estimates, year, and CV for each basin based on abundance estimates, year, and CV from IWC management areas.

Year	Basin	Abundance	CV	Source
1981	Atlantic	91	0.34	Branch (2007)
1986	Atlantic	210	0.40	Branch (2007)
1996	Atlantic	326	0.35	Branch (2007)
1979	Indian	197	0.25	Branch (2007)
1987	Indian	141	0.28	Branch (2007)
1995	Indian	203	0.18	Matsuoka & Hakamada (2014)
1996	Indian	754	0.16	Branch (2007)

1997	Indian	437	0.19	Matsuoka & Hakamada (2014)
1999	Indian	861	0.17	Matsuoka & Hakamada (2014)
2001	Indian	421	0.15	Matsuoka & Hakamada (2014)
2003	Indian	763	0.13	Matsuoka & Hakamada (2014)
2005	Indian	558	0.16	Matsuoka & Hakamada (2014)
2007	Indian	904	0.17	Matsuoka & Hakamada (2014)
1982	Pacific	278	0.22	Branch (2007)
1988	Pacific	334	0.23	Branch (2007)
1996	Pacific	97	0.24	Matsuoka & Hakamada (2014)
1998	Pacific	148	1.25	Matsuoka & Hakamada (2014)
1999	Pacific	1126	0.14	Branch (2007)
2000	Pacific	227	0.29	Matsuoka & Hakamada (2014)
2002	Pacific	130	0.27	Matsuoka & Hakamada (2014)
2004	Pacific	502	0.31	Matsuoka & Hakamada (2014)
2006	Pacific	106	0.69	Matsuoka & Hakamada (2014)
2008	Pacific	319	0.26	Matsuoka & Hakamada (2014)

Median parameter estimates from the model fit to these data differed by no more than 8% from those from the model fit to the Hamabe et al. (2023) estimates, except the survey coverage parameter (q) which reflect the difference in surveyed area for the two sets of estimates (Table S2.2).

Table S2.2. Median parameter estimates, lower and upper bounds of 95% credible intervals.

Parameter	*Description*	**Matsuoka & Hakamada (2014)**			**Hamabe et al. (2023)**		
		Median	*2.5%*	*97.5%*	*Median*	*2.5%*	*97.5%*
r	Intrinsic growth	0.091	0.074	0.107	0.086	0.068	0.104
K	Carrying capacity (Total)	181752	168180	197600	186335	170485	204579
K_{Atl}	Carrying capacity (Atlantic)	36481	25539	49824	36817	26057	51417
K_{Ind}	Carrying capacity (Indian)	63302	51472	76804	64654	52440	79403
K_{Pac}	Carrying capacity (Pacific)	81579	67437	97655	83987	68919	101474
$m_{\mathrm{Atl}\to\mathrm{Atl}}$	Movement	0.560	0.208	0.778	0.558	0.198	0.783
$m_{\mathrm{Ind}\to\mathrm{Atl}}$	Movement	0.132	0.029	0.330	0.126	0.027	0.339
$m_{\mathrm{Pac}\to\mathrm{Atl}}$	Movement	0.082	0.010	0.236	0.082	0.009	0.243
$m_{\mathrm{Atl}\to\mathrm{Ind}}$	Movement	0.157	0.006	0.459	0.145	0.006	0.463
$m_{\mathrm{Ind}\to\mathrm{Ind}}$	Movement	0.534	0.328	0.738	0.537	0.321	0.736
$m_{\mathrm{Pac}\to\mathrm{Ind}}$	Movement	0.278	0.141	0.449	0.275	0.133	0.459
$m_{\mathrm{Atl}\to\mathrm{Pac}}$	Movement	0.278	0.053	0.481	0.287	0.040	0.486
$m_{\mathrm{Ind}\to\mathrm{Pac}}$	Movement	0.321	0.145	0.483	0.324	0.144	0.484
$m_{\mathrm{Pac}\to\mathrm{Pac}}$	Movement	0.635	0.446	0.771	0.635	0.444	0.769
l	Mark loss	0.958	0.927	0.974	0.959	0.928	0.973
θ	Overdispersion	0.411	0.196	1.116	0.421	0.192	1.149
q_{Ind}	Survey coverage (Indian)	0.529	0.394	0.709	0.132	0.101	0.174

q_{Pac}	Survey coverage (Pacific)	0.130	0.101	0.168	0.080	0.063	0.101

Appendix 2: Supplemental Material for Chapter 2

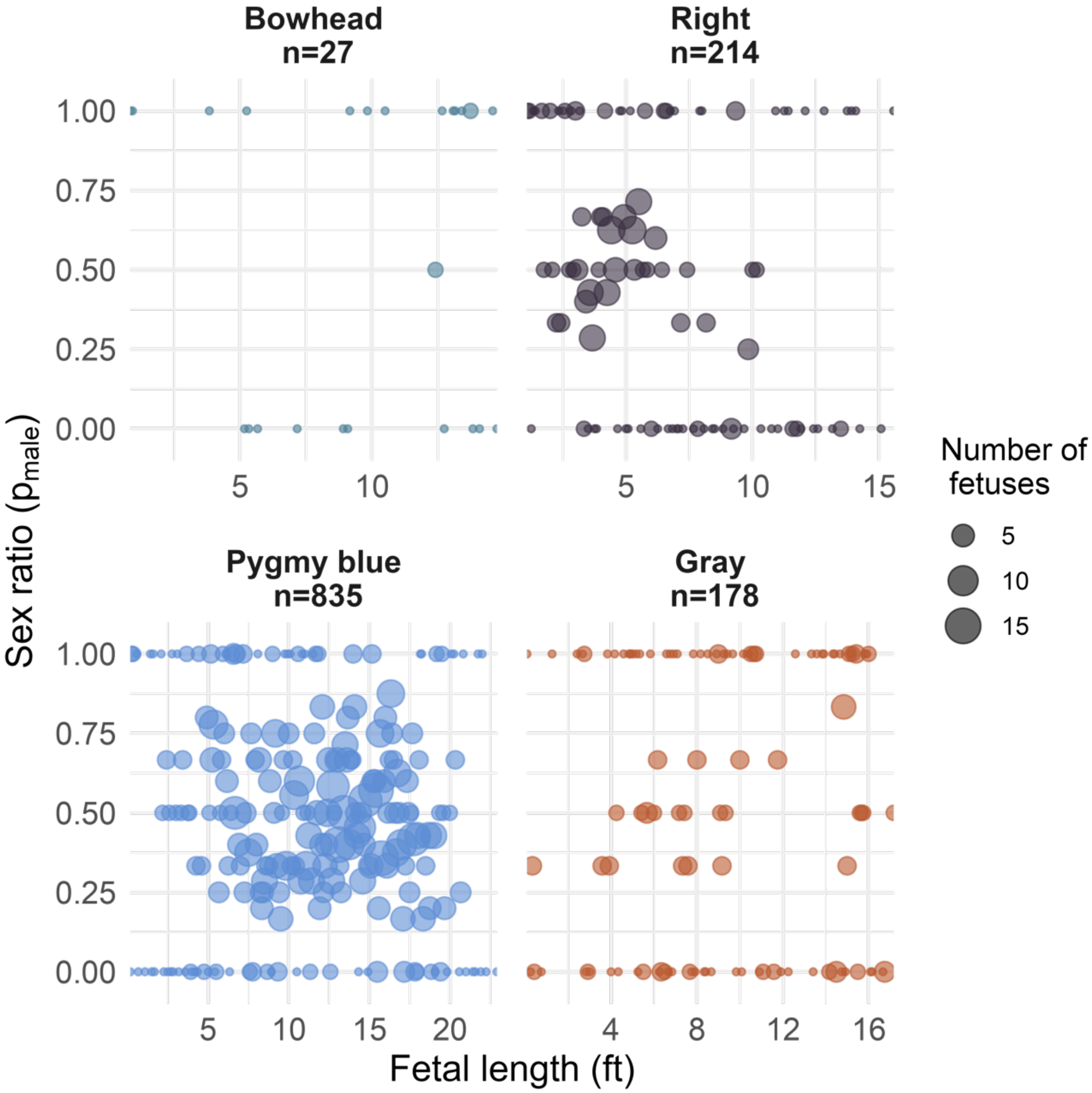

Figure S1. The proportion of male fetuses (points) in 1-inch length bins for species not included in fetal mis-identification models because of insufficient data. The size of the points indicates the sample size for each 1-inch bin and darker shading indicates overlapping points. “n” indicates total number of fetuses for each species.

Table S1. Number of fetuses in 1 ft fetal length bins for each sex by species and total number of fetuses of each sex by species. Species are ordered from highest to lowest total fetus sample sizes. Only a subset of these species were used for modeling.

Length (in 1ft bins)	**Fin**		**Antarctic minke**		**Sei**		**Antarctic blue**		**Sperm**		**Humpback**		**Bryde's**		**Pygmy blue**	
	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
1	1,120	635	5,558	6,145	345	212	72	36	891	641	562	319	51	70	5	2
2	2,491	1,945	7,035	6,993	596	484	294	210	990	989	979	803	113	83	2	3
3	3,289	2,998	4,261	4,143	1,055	951	484	414	967	1,028	768	721	81	98	6	7
4	4,053	4,011	2,241	2,206	1,711	1,682	670	650	781	779	532	519	94	88	9	9
5	5,103	4,838	1,184	1,234	2,397	2,249	1,019	859	566	618	234	215	114	92	8	10
6	5,117	4,917	476	515	2,416	2,332	1,038	924	424	366	117	75	86	90	21	14
7	4,591	4,752	202	207	2,226	2,192	890	861	307	294	62	42	71	67	26	16
8	4,895	4,810	50	66	2,069	2,116	1,001	894	400	357	28	20	76	68	15	20
9	4,092	3,945	32	39	1,792	1,796	764	699	389	399	19	19	54	48	17	28
10	4,085	4,051	28	34	1,527	1,502	840	814	447	522	21	24	33	41	22	27
11	2,810	2,742	9	7	1,019	1,077	558	531	555	649	28	18	27	40	25	21
12	3,083	3,013	0	0	612	784	675	705	572	719	49	50	23	29	24	27
13	1,852	1,880	0	0	250	340	411	417	527	604	100	82	12	16	32	34
14	1,691	1,722	0	0	120	170	448	487	387	382	159	141	3	3	40	35
15	1,240	1,233	0	0	28	57	403	389	109	94	128	129	0	0	30	31
16	689	756	0	0	9	15	295	297	33	19	44	58	0	0	35	37
17	404	429	0	0	2	8	195	206	7	8	9	14	0	0	34	26
18	293	302	0	0	0	0	214	255	0	2	3	2	0	1	20	36
19	97	109	0	0	0	0	80	95	1	0	0	0	1	0	15	23
20	66	73	0	0	1	0	107	129	0	0	0	0	0	1	8	13
21	15	24	0	0	0	0	47	53	0	0	0	0	0	0	7	7
22	7	7	0	0	0	0	40	32	0	0	0	0	0	0	2	3
23	3	4	0	0	0	0	22	24	0	0	0	0	0	0	0	2

25	0	1	0	0	0	0	7	6	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	15	18	0	0	0	0	0	0	1	0
26	0	0	0	0	0	0	2	5	0	0	0	0	0	0	0	0
27	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0
30	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Total	**51,086**	**49,197**	**21,076**	**21,589**	**18,175**	**17,967**	**10,594**	**10,011**	**8,353**	**8,470**	**3,842**	**3,251**	**839**	**835**	**404**	**431**

Length (in 1ft bins)	**Common minke**		**Right**		**Gray**		**Bowhead**	
	Male	Female	Male	Female	Male	Female	Male	Female
1	111	105	0	0	2	6	2	0
2	100	124	9	2	1	0	0	0
3	61	72	12	7	4	4	0	0
4	49	41	16	21	3	4	1	0
5	40	31	23	16	6	3	0	0
6	14	9	17	11	7	6	1	3
7	18	16	10	8	5	10	0	0
8	1	6	3	9	7	10	0	1
9	2	3	2	6	4	4	0	1
10	0	0	4	9	9	5	2	1
11	0	0	3	5	10	3	1	0
12	0	0	2	5	2	6	0	0
13	0	0	2	2	1	1	2	2
14	0	0	2	3	4	1	5	1
15	0	0	1	1	8	9	1	3
16	0	0	1	1	15	7	0	0
17	0	0	0	0	1	7	0	0
18	0	0	1	0	2	1	0	0
Total	**396**	**407**	**108**	**106**	**91**	**87**	**15**	**12**

Table S2**.** Number of iterations, the proportion of chains used as warm-up, the minimum and maximum $\hat{R}$ and ratio of effective sample sizes (ESS) to total sample size for across parameters in each Bayesian fetal sex mis-identification model. Models listed as “female” indicate the correction assumed that small females were mistaken for males, and models listed as “male” indicate the opposite.

Species	**Model**	**# of iterations**	**% warmup**	$\hat{R}$		**ESS ratio**	
				Min	**Max**	**Min**	**Max**
Antarctic blue	No correction	2000	50	1.001	1.009	0.175	0.844
Antarctic blue	Female	3000	67	1.001	1.018	0.065	0.783
Antarctic blue	Male	3000	67	1.000	1.007	0.160	1.091
Fin	No correction	1000	50	1.001	1.021	0.219	0.732
Fin	Female	2000	50	0.999	1.006	0.160	1.004
Fin	Male	2000	50	1.000	1.004	0.207	1.042
Sperm	No correction	2000	50	1.000	1.007	0.224	0.833
Sperm	Female	3000	67	1.000	1.018	0.047	0.816
Sperm	Male	3000	67	1.000	1.005	0.143	0.905
Humpback	No correction	1000	50	1.002	1.009	0.216	0.659
Humpback	Female	5000	80	1.000	1.005	0.302	1.079
Humpback	Male	5000	80	1.000	1.011	0.280	0.837
Sei	No correction	1000	50	1.001	1.004	0.195	0.745
Sei	Female	3000	67	1.001	1.009	0.060	0.919
Sei	Male	3000	67	1.000	1.005	0.152	1.072
Common minke	No correction	1000	50	1.000	1.007	0.246	0.577
Common minke	Female	2000	50	1.000	1.006	0.389	1.137
Common minke	Male	2000	50	1.000	1.003	0.368	1.351
Antarctic minke	No correction	1000	50	1.001	1.010	0.239	0.804
Antarctic minke	Female	2000	50	1.001	1.004	0.183	1.004
Antarctic minke	Male	2000	50	1.000	1.003	0.405	1.137
Brydes	No correction	2000	50	1.000	1.004	0.225	0.721
Brydes	Female	3000	67	1.000	1.010	0.079	0.814
Brydes	Male	3000	67	1.000	1.030	0.056	0.744

Table S3. Watanabe-Akaike Information Criterion (WAIC) and difference in the value and standard error of the expected log pointwise predictive density (elpd), and the standard error of the elpd (se_elpd) for each fetal mis-identification model. The model with the lowest WAIC for each species is indicated in italics and (*) indicates models that are strongly preferred based on having an absolute value of the difference in expected log pointwise density (elpd_diff) of > 4 [54]. [#]For Bryde’s whales, the posterior distributions indicated that the correction terms were not identifiable given the data, therefore, though the male correction had the lowest WAIC, the model without correction was used as the best model for the rest of the analysis.

Species	**Model**	**WAIC**	**elpd_diff**	**se_diff**
Antarctic blue	*Female*	*28517.0*	*0.00*	*0.00*
Antarctic blue	No correction	28519.0	-1.01	1.66
Antarctic blue	Male	28519.5	-1.27	1.73
Fin	*Female**	*138805.4*	*0.00*	*0.00*
Fin	No correction	138923.4	-59.01	10.88

Fin	Male	138923.7	-59.13	10.89
Sperm	*Female**	*23277.3*	*0.00*	*0.00*
Sperm	No correction	23299.9	-11.31	4.80
Sperm	Male	23300.1	-11.36	4.84
Humpback	*Female**	*9723.4*	*0.00*	*0.00*
Humpback	No correction	9776.3	-26.42	7.17
Humpback	Male	9776.4	-26.49	7.20
Sei	*Female**	*50015.8*	*0.00*	*0.00*
Sei	No correction	50025.8	-5.01	3.23
Sei	Male	50026.6	-5.41	3.37
Common minke	*No correction*	*1116.6*	*0.00*	*0.00*
Common minke	Male	1116.7	-0.05	0.08
Common minke	Female	1116.7	-0.05	0.09
Antarctic minke	*Male**	*58760.4*	*0.00*	*0.00*
Antarctic minke	No correction	59137.2	-188.41	19.74
Antarctic minke	Female	59137.6	-188.63	19.75
Bryde’s	*Male*	*2315.2*	*0.00*	*0.00*
Bryde’s	Female	2319.5	-2.19	1.98
Bryde’s	No correction[#]	2319.6	-2.24	1.96

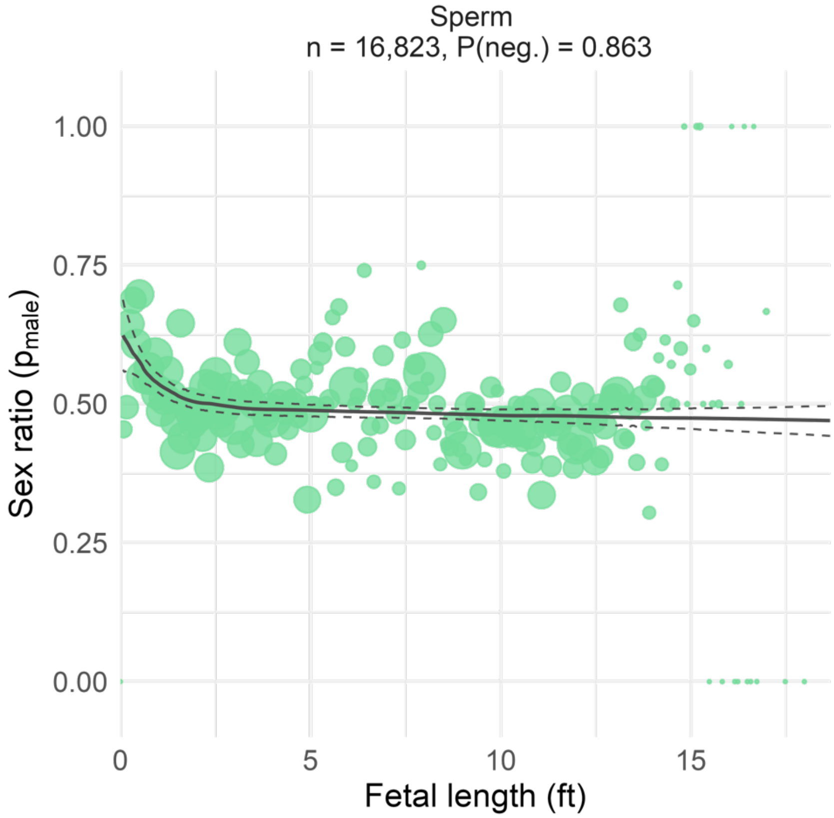

Figure S2. Mode (solid line) and 95% highest-density credible intervals (dashed lines) of the posterior distribution for fetal sex ratio given fetal length from the best model for sperm whales (Table S3). The points represent the proportion male in 1-inch length bins for each species. The size of the points indicates the relative sample size for each 1-inch bin and darker shading indicates overlapping points. $P_{neg.}$ indicates the posterior probability of a negative slope (*b* (eqn. 5), on logit scale) and *n* indicates the total number of fetuses in the model.

Table S4. Parameter estimates (median and lower 2.5% and upper 97.5% credible intervals) from Bayesian fetal mis-identification models for each species. Models indicated in italics indicate the model use as the best model in the rest of the analysis (Table S2).

Species	**Model**	**Intercept *(a)***			**Slope (*b*)**			**L_{50}**			**Δ**		
		Med.	**2.5%**	**97.5%**	**Med.**	**2.5%**	**97.5%**	**Med.**	**2.5%**	**97.5%**	**Med.**	**2.5%**	**97.5%**
Antarctic blue	*Female*	*0.184*	*-0.013*	*0.259*	*-0.015*	*-0.022*	*-0.002*	*-1.79*	*-17.77*	*0.535*	*3.28*	*0.861*	*18.29*
Antarctic blue	No correction	0.216	0.153	0.276	-0.017	-0.023	-0.011	-	-	-	-	-	-
Antarctic blue	Male	0.220	0.157	0.286	-0.018	-0.024	-0.011	-10.54	-25.10	-1.46	3.26	0.160	13.62
Fin	*Female*	*0.035*	*-0.011*	*0.075*	*-0.003*	*-0.007*	*0.001*	*-0.288*	*-0.789*	*0.033*	*2.81*	*2.17*	*3.75*
Fin	No correction	0.142	0.111	0.168	-0.014	-0.017	-0.010	-	-	-	-	-	-
Fin	Male	0.142	0.116	0.169	-0.014	-0.017	-0.010	-11.24	-25.80	-1.59	1.92	0.119	9.43
Sperm	*Female*	*-0.020*	*-0.151*	*0.057*	*-0.006*	*-0.015*	*0.006*	*-0.678*	*-3.26*	*-0.151*	*2.12*	*1.21*	*6.65*
Sperm	No correction	0.098	0.040	0.154	-0.018	-0.025	-0.011	-	-	-	-	-	-
Sperm	Male	0.102	0.045	0.160	-0.018	-0.025	-0.011	-11.23	-25.65	-1.48	2.79	0.111	12.62
Humpback	*Female*	*0.061*	*-0.061*	*0.157*	*0.000*	*-0.013*	*0.015*	*0.310*	*-0.025*	*0.497*	*1.50*	*1.01*	*2.33*
Humpback	No correction	0.250	0.184	0.323	-0.020	-0.032	-0.008	-	-	-	-	-	-
Humpback	Male	0.256	0.186	0.329	-0.020	-0.032	-0.009	-11.02	-25.32	-1.90	2.86	0.116	12.88
Sei	*Female*	*0.164*	*0.084*	*0.233*	*-0.024*	*-0.033*	*-0.015*	*-0.579*	*-10.02*	*0.067*	*2.14*	*1.11*	*7.59*
Sei	No correction	0.216	0.162	0.267	-0.031	-0.038	-0.023	-	-	-	-	-	-
Sei	Male	0.222	0.165	0.422	-0.031	-0.048	-0.024	-10.96	-24.98	-1.77	3.44	0.176	19.02
Common minke	*No correction*	*-0.083*	*-0.311*	*0.156*	*0.023*	*-0.048*	*0.102*	-	-	-	-	-	-

Common minke	Male	-0.087	-0.332	0.138	0.024	-0.056	0.105	-6.96	-22.57	-0.482	0.999	0.062	1.95
Common minke	Female	-0.075	-0.301	0.163	0.022	-0.059	0.099	-7.18	-22.72	-0.528	0.981	0.049	1.94
Antarctic minke	*Male*	*0.092*	*0.054*	*0.133*	*-0.029*	*-0.045*	*-0.015*	*0.263*	*0.242*	*0.281*	*0.309*	*0.268*	*0.356*
Antarctic minke	No correction	-0.059	-0.091	-0.027	0.018	0.005	0.030	-	-	-	-	-	-
Antarctic minke	Female	-0.061	-0.104	-0.028	0.018	0.005	0.031	-11.81	-26.45	-2.42	2.45	0.106	13.55
Bryde's	Male	0.177	-0.037	0.405	-0.028	-0.063	0.006	0.109	-8.08	0.402	0.777	0.129	1.92
Bryde's	Female	0.076	-0.103	0.260	-0.014	-0.044	0.016	-4.97	-9.65	-0.738	0.934	0.050	1.95
Bryde's	*No correction*	*0.074*	*-0.110*	*0.262*	*-0.014*	*-0.046*	*0.016*	-	-	-	-	-	-

Table S5. Parameter estimates (mode and 95% highest density intervals) for Bayesian generalized linear mixed model of fetal sex given maternal length with random effects on the slope and intercept for each species, as well as $\hat{R}$ and the tail effective sample size for each parameter.

Parameter	**Description**	**Mode**	**2.5%**	**97.5%**	$\hat{R}$	**ESS**
$\bar{\alpha}$	Across species intercept (real scale)	0.504	0.497	0.510	1.001	2118
$\bar{\beta}$	Across species slope (logit scale)	-0.014	-0.033	0.008	1.002	2399
σ_{α}	Standard deviation of intercept random effect	0.0000	0.0000	0.0525	1.003	1515
σ_{β}	Standard deviation of slope random effect	0.0077	0.0001	0.0410	1.002	1981
ϕ	Overdispersion parameter	1238	792	1884	1.000	3140

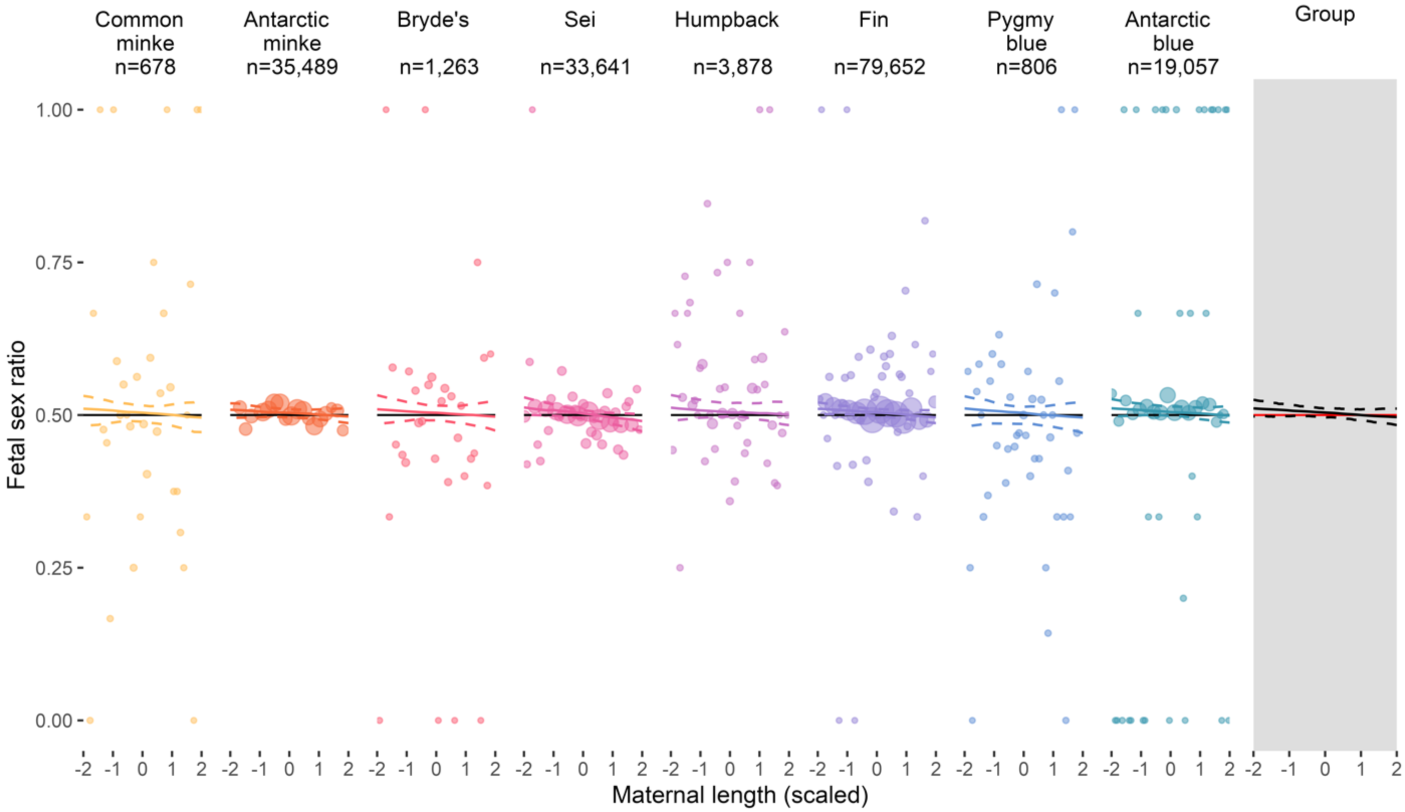

Figure S3. Posterior modes (solid colored line) and 95% highest density credible intervals (dashed lines) for predicted fetal sex ratio given maternal length for each species of rorqual whale in the analysis, and the overall trend across species (shaded gray). Solid black horizontal line indicates 50:50 sex ratio and *n* indicates the number of fetuses in each taxon. Points represent the observed fetal sex ratio in each length bin, with size of the point indicating the relative number of observations (across species) in that length bin.

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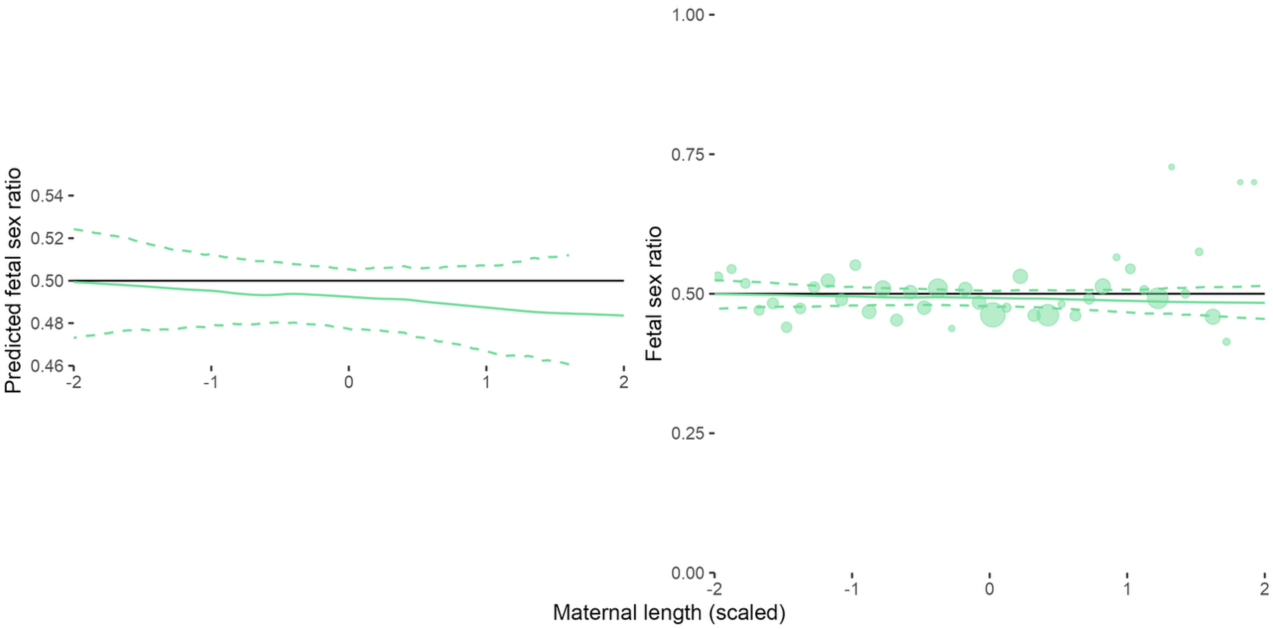

Figure S4. Posterior modes (colored solid line) and 95% highest density credible intervals (dashed lines) for predicted fetal sex ratio given maternal length for sperm whales from single species beta-binomial GLM. Solid black line indicates 50:50 sex ratio. Observed fetal sex ratio given maternal length is represented by the points, with size representing relative total number of observations in each bin. The probability that the slope parameter (*beta*) is negative on the logit scale is 0.78.

Appendix 3: Supplemental Material for Chapter 3

S1: Antarctic blue whale annual catch totals

Year	Catch
1904	11
1905	51
1906	139
1907	121
1908	148
1909	176
1910	409
1911	1,476
1912	2,448
1913	3,121
1914	5,276
1915	5,595
1916	4,377
1917	3,083
1918	2,151
1919	1,992
1920	2,976
1921	4,559
1922	6,702
1923	4,876
1924	6,666
1925	6,120
1926	8,488
1927	10,275
1928	14,172
1929	18,518
1930	30,405
1931	6,614
1932	18,994
1933	17,441
1934	16,601
1935	17,853
1936	14,631
1937	15,143
1938	14,159

1939	11,902
1940	4,994
1941	65
1942	127
1943	349
1944	1,048
1945	3,605
1946	9,227
1947	6,945
1948	7,647
1949	6,204
1950	7,061
1951	5,127
1952	3,862
1953	2,716
1954	2,177
1955	1,589
1956	1,506
1957	1,669
1958	1,083
1959	535
1960	484
1961	610
1962	342
1963	94
1964	114
1965	256
1966	265
1967	53
1968	95
1969	41
1970	72
1971	27
1972	3
1973	1
Total	347,662

S2: Model using Matsuoka and Hakamada 2014 abundance estimates

As a sensitivity, we also fit the base model (Table 4) to alternate abundance estimates from the JARPA and JARPA II surveys. Matsuoka and Hakamada (2014) provide estimates for a larger area of the Southern Ocean (IWC management areas IIIE-VIW; 35°E - 145°W) though only areas IV and V were surveyed in all years. Therefore, for this sensitivity test, we used estimates from years where all areas were surveyed (1995/96–2007/08; Table S2. 1).

Table S2.1. Abundance estimates from JARPA and JARPAII from 35°E–145°W (Matsuoka and Hakamada 2014). These estimates were used as relative indices of abundance one run of the model instead of the Hamabe et al. (2023) estimates from Table 1.

Area	**Year**	**N**	**CV**
IIE–VIW	1995	300	0.32
IIE–VIW	1997	585	0.80
IIE–VIW	1999	1088	0.35
IIE–VIW	2001	551	0.32
IIE–VIW	2003	1265	0.35
IIE–VIW	2005	664	0.38
IIE–VIW	2007	1223	0.34

Median parameter estimates fit to these data differed by no more than 11% from those from the base model in the paper, except the survey coverage parameter and the additional variance which reflect the difference in the amount of surveyed area and the number of years surveyed in the two sets of estimates (Table S2.2).

Table S2.2. Median parameter estimates and lower and upper bounds of 95% credible intervals for base model fit to both data sources.

Parameter	*Description*	**Hamabe et al. (2023)**			**Matsuoka and Hakamada (2014)**		
		Median	*2.5%*	*97.5%*	*Median*	*2.5%*	*97.5%*
r	Intrinsic growth	0.045	0.016	0.073	0.049	0.019	0.080
K	Carrying capacity	205,905	168,473	276,342	200,176	162,088	267,803
q_{JARPA}	Survey coverage	0.23	0.12	0.47	0.51	0.27	0.92
$CV_{add,\_J}$	Additional variance for JARPA estimates	0.43	0.03	1.34	0.34	0.02	1.27
N_{1973}	Population size in 1973	418	147	1,099	378	130	1,018

N_{2024}	Projected population size in 2024	4,018	1,874	8,395	4,389	1,979	9,609
N_{1973}/K	Maximum depletion	0.0020	0.0008	0.0042	0.0019	0.0008	0.0039
N_{2024}/K	Depletion in 2024	0.019	0.0072	0.048	0.022	0.008	0.057

S3: Posterior credible intervals of predicted population size from 1904-2100 (only in publication)

S4: All posterior draws of predicted population size from 1904-2100 (only in publication)

Appendix 4: Supplemental material for Chapter 4

S1: Table of earplug and corpora data (in publication only)

S2: Age-length model selection

Fixed effects of population and sex were considered for the growth rate parameter (*k*) and the shape parameter (*b*) in the Richards age-length model (Eq. 1). The model comparisons were conducted using all available data (including both Japanese and Soviet data). For both parameters, we considered just sex effects, just population effects, an interaction between the population and sex effect (each population and sex has its own parameter), and a shared parameter for all populations and sexes, and we tested all possible combinations of these (Table S2.1). The models were all fit with 20,000 iterations, a 75% warmup, four chains and a thinning rate of 10, except for models 1, 6, 7, 9 and 10 which were fit with 25,000 iterations and an 80% warm-up in order to improve convergence. Models 1 and 9 did not converge so were removed from further comparison.

Table S2.1. Models for age-length relationships. Each column corresponds to a parameter from the model in the main text, and the text describes the fixed effects on that parameter. "–" indicates that fixed effects are the same as in the row previous. "Single value" indicates models where there was only a single estimated parameter for both sexes and all populations.

Model	L_1	L_2	k	b	σ
1	Population and sex	Population and sex	Population and sex	Population and sex	Population
2	–	–	–	Population	–
3	–	–	–	Sex	–
4	–	–	–	Single value	–
5	–	–	Population	Population and sex	–
6	–	–	–	Population	–
7	–	–	–	Sex	–
8	–	–	–	Single value	–
9	–	–	Sex	Population and sex	–
10	–	–	–	Population	–

11	–	–	–	Sex	–
12	–	–	–	Single value	–
13	–	–	Single value	Population and sex	–
14	–	–	–	Population	–
15	–	–	–	Sex	–
16	–	–	–	Single value	–

The posterior distributions of *k* and *b* were wide and not very different from the prior, when there was an interaction effect between sex and population as well as the population only effect, suggesting that there was insufficient data to obtain a reliable estimates for these parameters (Figure S2.1). In the other models, estimates of *k* and *b* were similar and the credible intervals of the posteriors of these parameters overlapped (Figure S2.1). Additionally, comparison using leave-one-out cross validation (*loo* package; Vehaari et al. 2022) suggested that there was very little difference in the predictive ability of these models (the absolute value of all *elpd diff.* estimates were less than 4; Sivula et al. 2023). Therefore, to simplify future predictions, the model with the shared *k* and shared *b* parameter across populations and sexes (Model 16) was used.

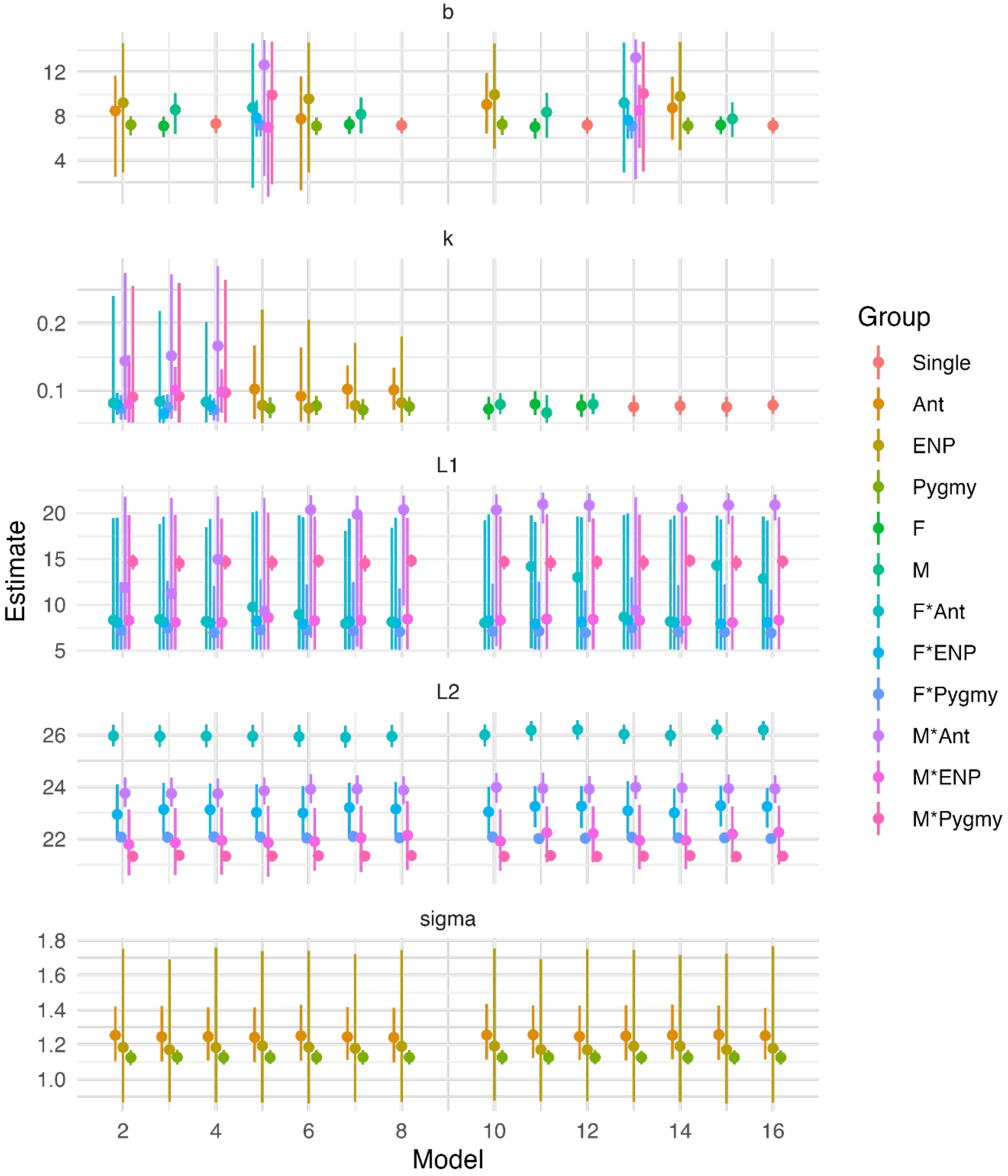

Figure S2.1. Posterior medians (points) and 95% credible intervals (lines) for growth rate, k, and shape parameter, b, for all age-length models tested. Model numbers (x-axis) correspond to the descriptions in Table S2.1. Colors represent the parameter for the specified group (either sex, population, or combined population and sex). “Single” indicates models where there was only a single estimated parameter for both sexes and all populations.

S3: Posterior predictive checks for models with different data sources

Posterior predictive distributions were constructed for three models to examine model adequacy: one with only the Soviet data for pygmy blue whales, one with only the Japanese data for pygmy blue whales, and one with both datasets. Posterior predictive distributions for the fits to simulated data (Figure S4.1) were examined to understand the expected shape when the same model was used to both fit and generate the data. Posterior predictive distributions were estimated for each data point. For censored data (Japanese data only), posterior predictions were drawn from the uncensored posterior, and then, if they were below the minimum length (21.336) they were set to equal the minimum length.

Posterior predictive p-values were derived by calculating the proportion of the posterior predictive distribution that was below the actual data point, giving an indication of the percentile that the actual data point is of the posterior predictive distribution. When the simulated data were fit to the same model it was generated by, these p-values were uniformly distributed for both data sources and across all ages, except for the censored data points which always had a posterior predictive p-value of 0 (Figure S3.1).

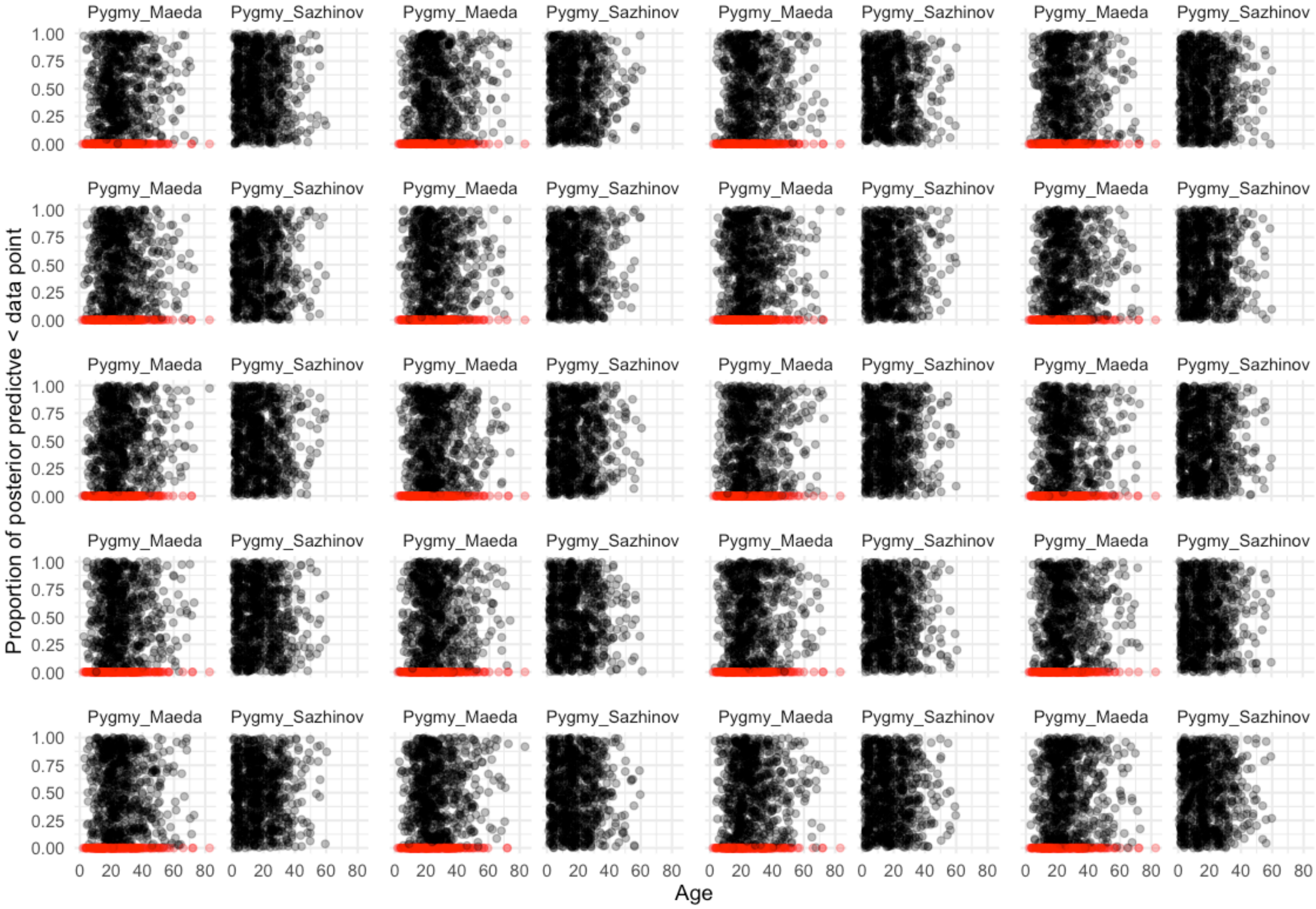

Figure S3.1. Posterior predictive p-values for each data source for pygmy blue whales and age for models fit to a random selection of 20 out of the 1,000 simulated datasets. Red points indicate data points that were censored.

However, when the model was fit to the true data including both data sources, the posterior predictive p-values for pygmy blue whales clustered near 1 for the Japanese data and 0 for the Soviet data (Figure S3.2). This suggests that the model was overestimating the Soviet observations and underestimating the Japanese observations.

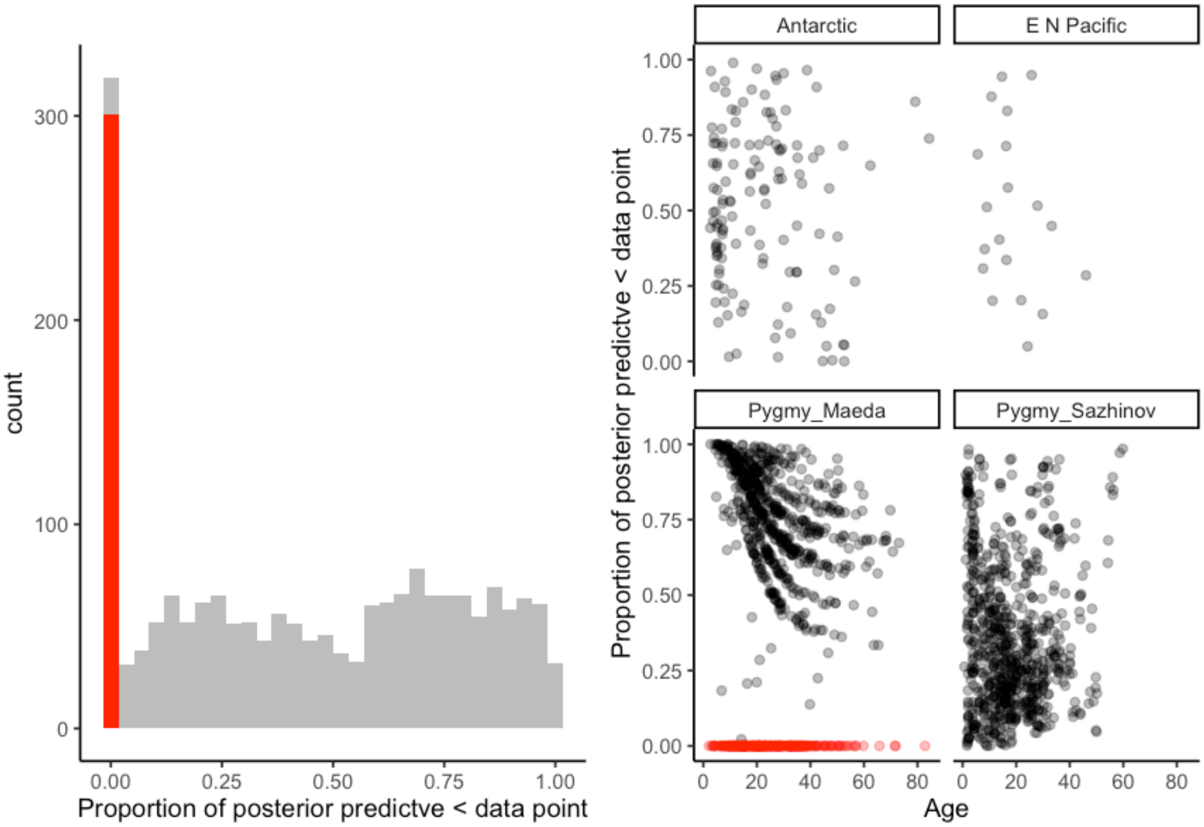

Figure S3.2. Posterior predictive p-values for the entire dataset including all populations (left) and for each population and age (right) for model fit to both the Japanese and Soviet data for pygmy blue whales. Red indicates data points that were censored. The appearance of lines in the scatterplot is because Japanese data were rounded to whole feet.

The distribution of the posterior predictive p-values were closer to those expected based on the simulations when models were fit separately to only the Soviet observations or only the Japanese observations, suggesting that have separate models for each data type was better as the Soviet and Japanese data were in conflict (Figures S3.3-S3.4).

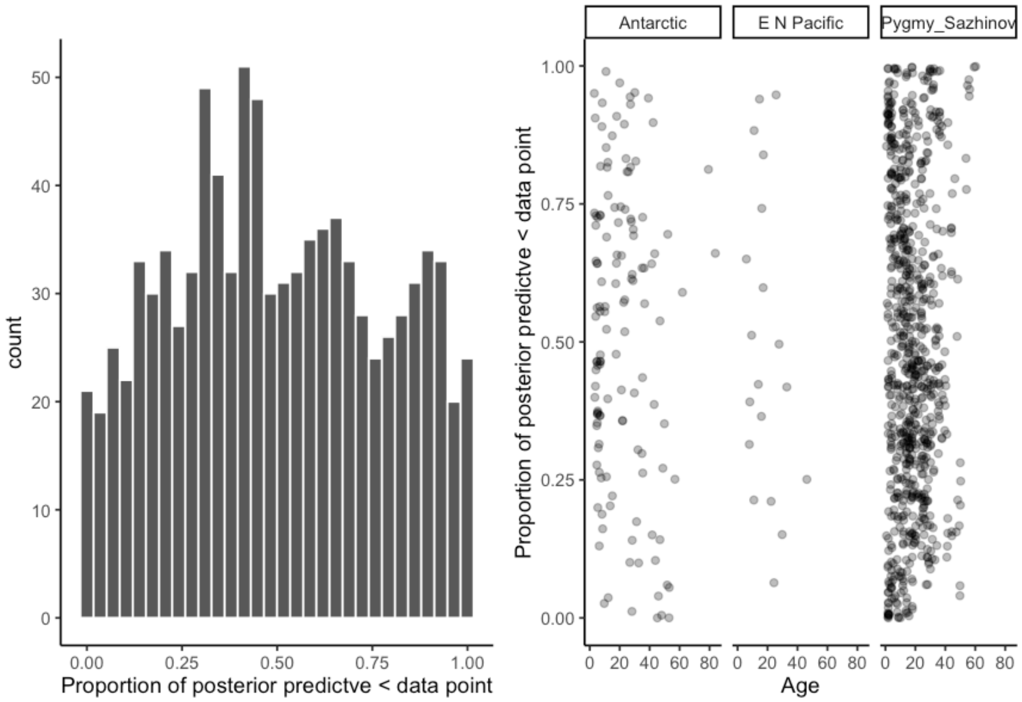

Figure S3.3. Posterior predictive p-values for the entire dataset including all populations (left) and for each population and age (right) for model fit to only the Soviet data for pygmy blue whales.

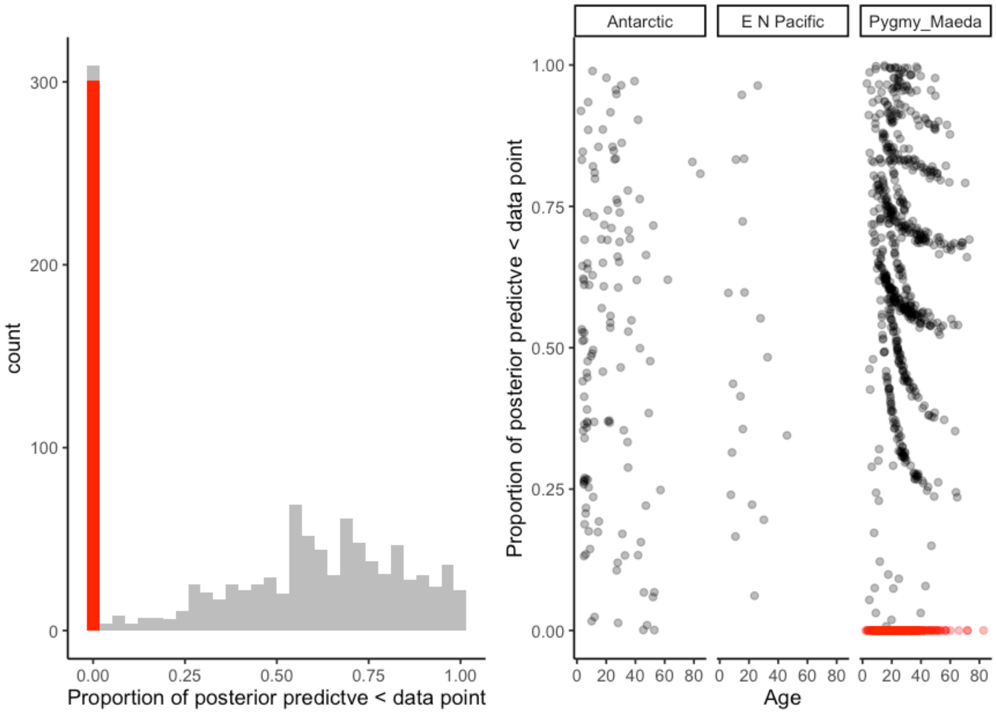

Figure S3.4. Posterior predictive p-values for the entire dataset including all populations (left) and for each population and age (right) for model fit to only the Japanese data for pygmy blue whales. Red indicates data points that were censored. The appearance of lines in the scatterplot is because the Japanese data were rounded to whole feet.

S4: Simulations to test censored likelihood approach

Simulated data were used to test the censored likelihood approach for estimating age-length relationships for pygmy blue whales. Only data from Pygmy blue whales was simulated, using a Von Bertalanffy growth equation. The data were simulated assuming that the length at age 46 for females was 21 m and that for males was 20 m. We assumed that the length at age 1 was 16 m for both males and females, and that the growth rate (*k*) was 0.17 yr^{-1}. A total of 1,000 datasets were drawn from a normal distribution with mean equal to the predicted length at each age included in the original data, and a standard deviation of 1.1. Each of these datasets were fit to the Von Bertlanffy model described in the main text, except that the esimation model also included sex-specific effects of *k.* These models were fit with four chains, 4,000 iterations and an 75% warmup (1,000 draws saved after warmup). Convergence was checked using R-hat values and visual inspections of the posteriors. The simulated value of the parameters was contained in at least 94% of the resulting 95% credible intervals (Figure S4.1).

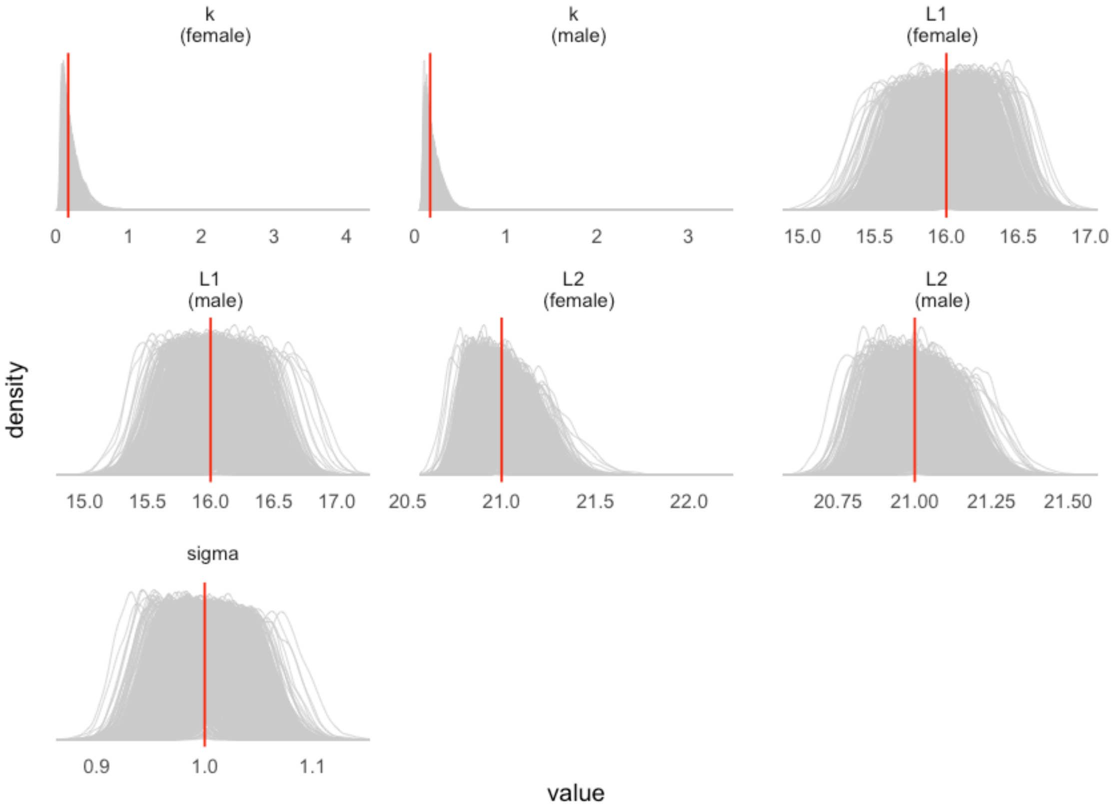

Figure S4.1. Posterior densities for models fit to simulated dataset (gray lines) and value of parameter used to create simulated datasets (red line).

Appendix 5: Supplemental Material for Chapter 5

S1: Catch curve simulation

We built an age-structured model to simulate catches at each age to test the ability of the model to estimate natural survival and to see the effects of whaling mortality on this estimate. This model assumed that the carrying capacity for the 1+ population was 50,000 whales and started the 1+ population at this number. Population dynamics (survival and fecundity) were simulated over a 500-year time span without catches, to ensure that the population was at equilibrium. We assumed that calf survival was 0.85 (Branch et al. 2004), and the maximum fecundity rate was 0.38. Theta-logistic density dependence was assumed for fecundity, with $\theta = 2.39$ which is common practice for the International Whaling Commission (Baker & Clapham 2004). Then, catches were simulated for 100 years, assuming 10% of whales were harvested each year. This harvest rate was chosen based on Antarctic blue whale harvest rates in the late 1950s (Rand et al. submitted). We assumed that whaling selectivity was logistic with a relative probability of being caught of 50% at age 15 and 95% at age 20 so that the age with the highest catch frequency was similar to what we were seeing in our data (ages 15-20). We ran two sets of simulations, with (true) adult survival at 0.93 and at 0.98. No recruitment variability was included in the simulations.

Annual simulated earplug data were drawn from the predicted catches at each age using multinomial distribution based on the proportion of catches at each age with a total sample size of 1,745 (the total number of earplugs in the original data). We simulated datasets for data collected 2-40 years after the start of whaling. A total of 100 datasets were simulated for each of these, with different random seeds. The age of full selection (age of highest frequency of earplug data + 1) was calculated for each dataset and ages less than this value were removed. Each simulated dataset was fit with the catch curve estimator described in the main text. Each model was fit with 4000 iterations, a 50% warmup and 4 chains.

The age at highest frequency ranged from 16-20 for all datasets, regardless of survival rate. We found that for an true survival rate of 0.93, the estimated survival rate was within the credible interval in at least 90% of 95% posterior credible intervals when data included the first five years of whaling. After 10 years, the true survival rate was within the 95% credible interval in only in 12% of the posteriors, and after 12 years the true survival rate was no longer in the credible intervals (the estimated rate was always slightly lower). Even when not perfectly estimated, the lower limit of the credible interval (2.5%) was within 0.01 of the true survival rate in at least 71% of posteriors even after 27 years. For a true survival rate of 0.98, the true survival rate was within the 95% credible interval in at least 90% of posteriors when data included the first eight years of whaling. After 10 years, this dropped to only 26% of posteriors. The lower limit of the credible interval was within 0.01 of the true survival rate in at least all of posteriors up to 28 years after the start of whaling. (Figure S1.1).

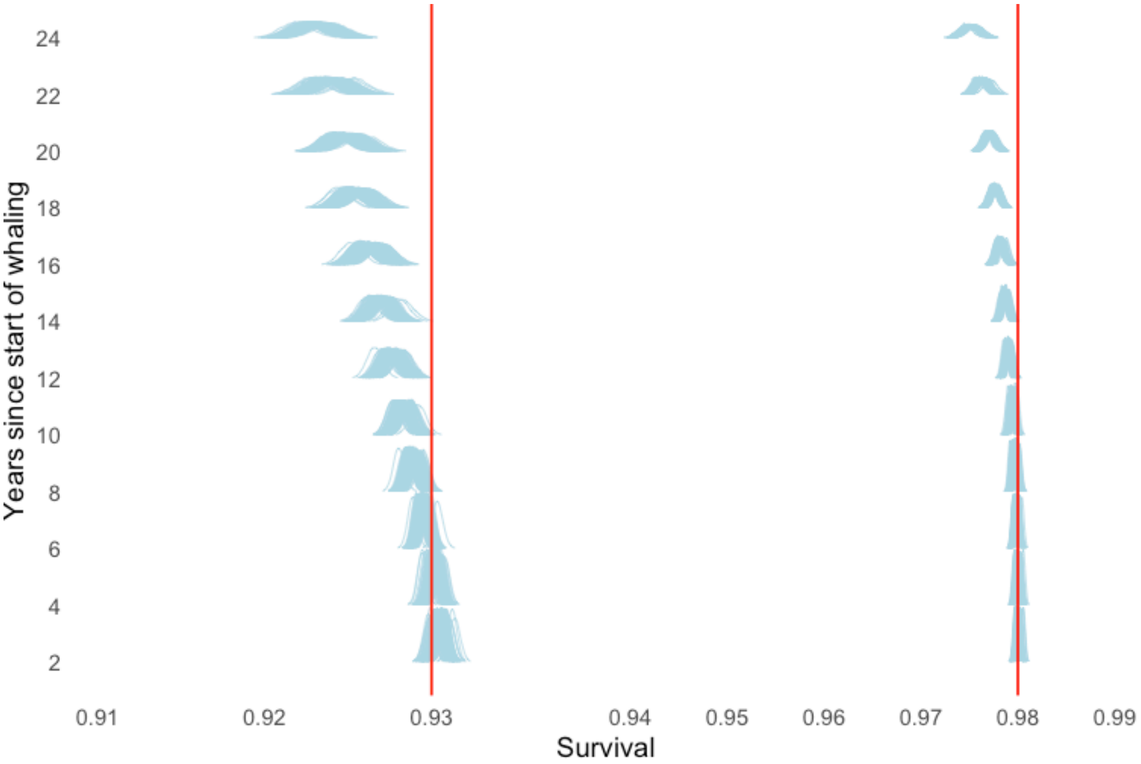

Figure S1.1. Posterior distributions of survival rate for simulated datasets given the number of years (2-24) of data collected after the start of whaling. Red lines indicate values of survival used to simulate data.

References

Baker, C. S. and P. J. Clapham. (2004). Modelling the past and future of whales and whaling. *Trends in Ecology and Evolution, 19*,365-371. 10.1016/j.tree.2004.05.005

Rand, Z. R., P. A. Olson, D. Kinzey, M. C. Double, K. Matsuoka, K. Findlay and T. Branch. (submitted). Endangered Antarctic blue whales are increasing but still far from pre-whaling levels. *Endangered Species Research*.

S2: Distribution of rate of corpora formation

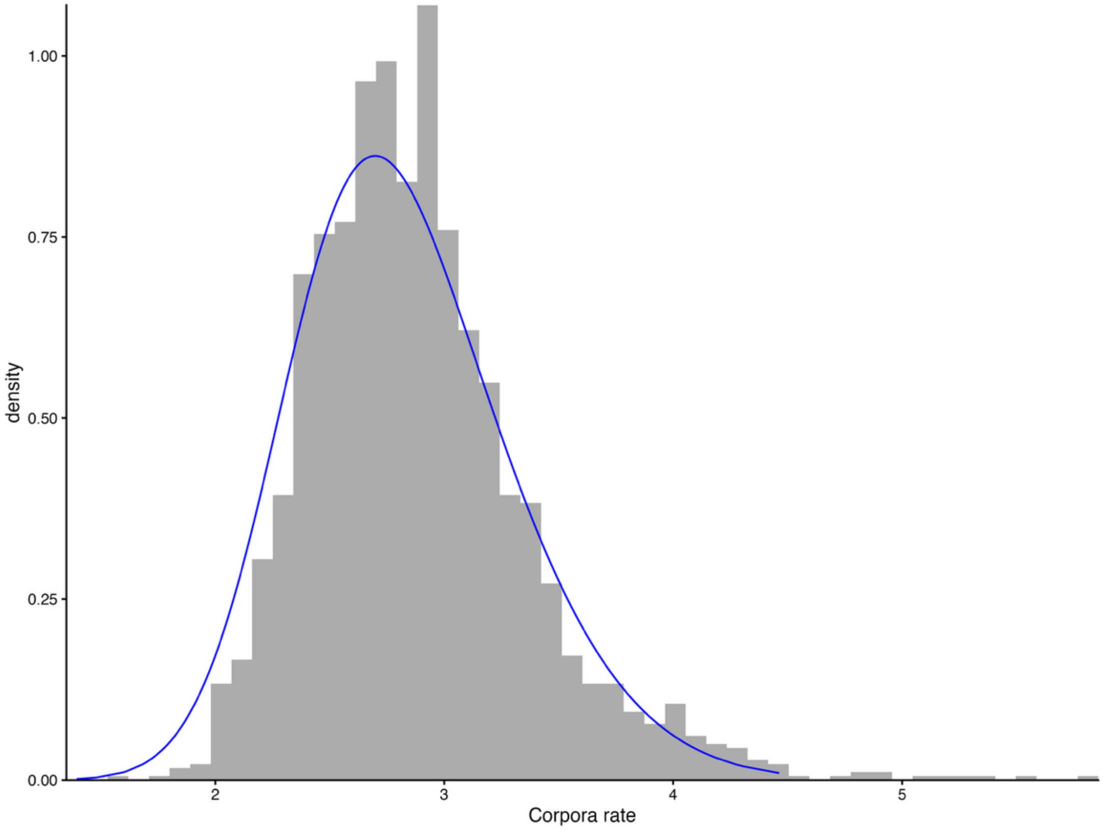

Figure S2.1. Posterior distribution of the rate of corpora formation (k, in main text; gray histogram) from Rand et al. in prep, as well as SkewNormal(2.824, 0.482, 2) prior distribution used for this parameter in the analyses.