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 whales, 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 historical Discovery mark—recovery data with a multistate model to estimate historical interyear movement rates among the 3 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% (0.9—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.

KEY WORDS: Discovery marks · Mark—recovery · Migration · Movement models · Population structure · Southern Ocean · Whaling · Baleen whales

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 8400 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

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waters, including fin whales *Balaenoptera physalus* in the Mediterranean (Bérubé 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, 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 2 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 preexploitation 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 2 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 (>8000) 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 (Fig. 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 broadly distributed 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 (Fig. 1b), as has been seen for humpback and fin whales (Bérubé et al. 1998, Schall et al. 2021); conversely, gray whales mix on the breeding grounds but have feeding grounds spread more than 5000 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 (Fig. 1c,d).

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 *B. borealis* whales (e.g. Mizroch et al. 2009, 2016, Mizroch & Rice 2013), 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 breeding grounds 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. 2010, Amaral et al. 2016, Pastene & Goto 2016). As a first step, therefore, we estimate historical interannual movement rates of Antarctic blue whales among 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.

2. MATERIALS AND METHODS

We built a multistate mark—recovery model to estimate interannual movement rates among the 3 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—
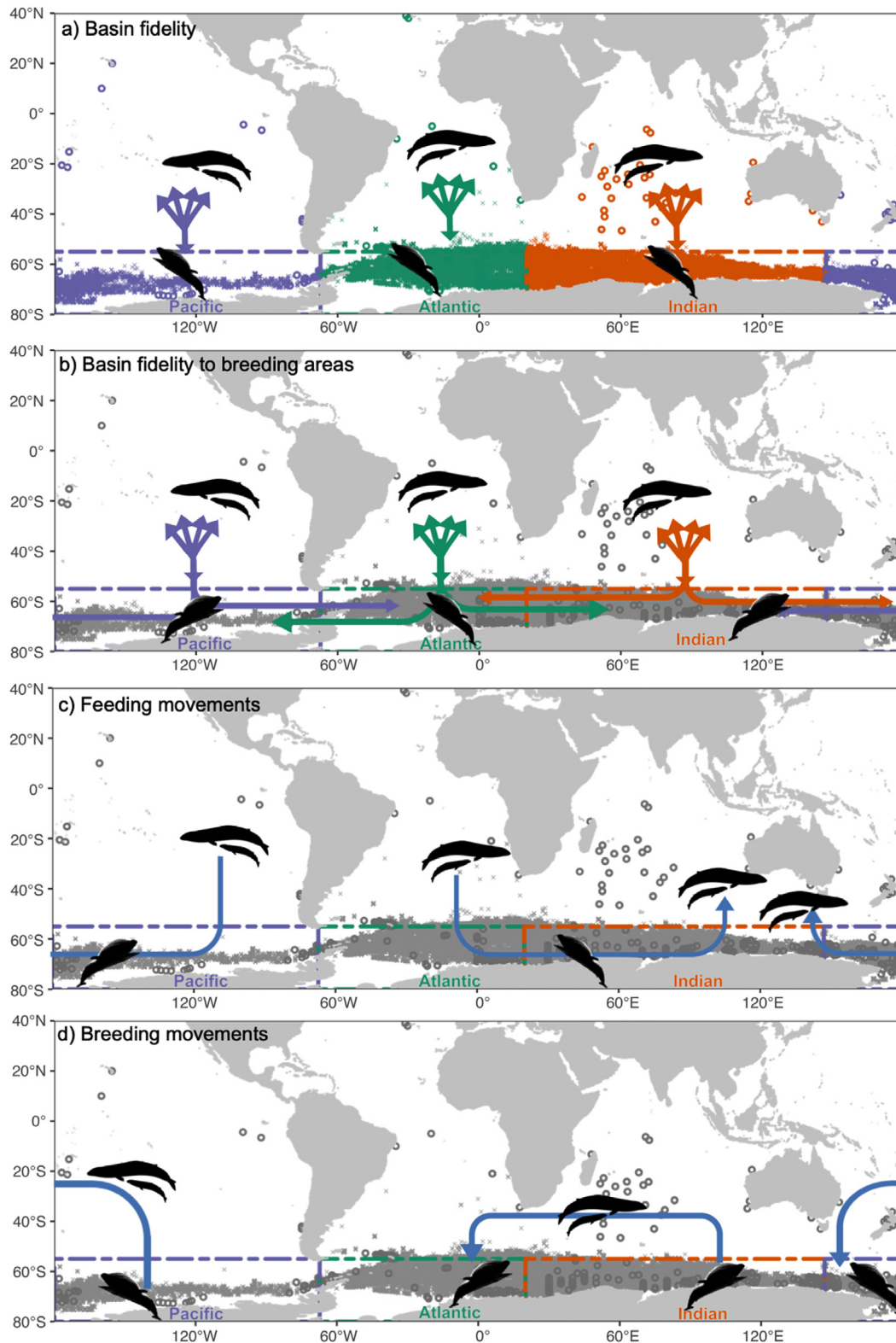
Fig. 1. Possible scenarios for Antarctic blue whale low-to-high latitude migration, including (a) migration routes that are consistently within the same ocean basin, (b) movement among basins during feeding but fidelity to breeding areas within ocean basins, (c) movement among basins during high-latitude 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 2020b) are represented by the crosses

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.

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 (Allison 2020a). 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, 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, and 67.26° W (Fig. 2).

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 2020b). 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 (Fig. 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 2 calendar years, declined in length over time, from year-round in the early years to increasingly restricted to less than 2 mo 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.

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 (M) applied in basin g that could be recovered in basin i in each subsequent season ($t + 1$) is given by:

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

where $\hat{M}_{g,j,t}$ 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 (R) in each basin and season:

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

where $\hat{R}_{g,i,t+1}$ 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 3 mark—loss parameters that corresponded to 3 time
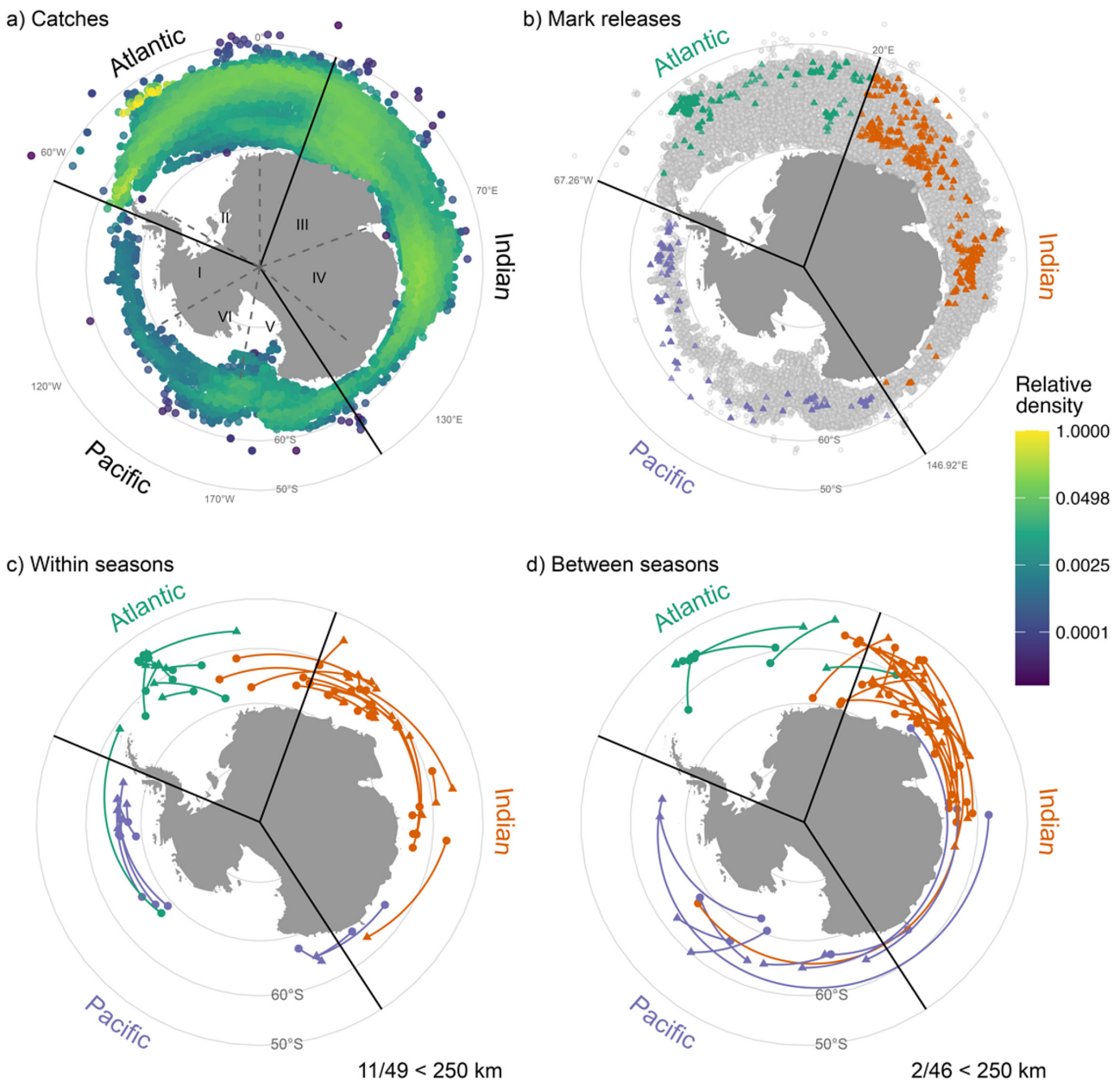
Fig. 2. (a) Catches and (b) mark releases of Antarctic blue whales in the Southern Ocean, showing (c) same-season mark—recovery pairs and (d) marks recovered in a different season than when they were placed. Mark—recovery pairs are colored based on the basin where they were placed, with triangles showing 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

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 ($T_{i,t+1}$):

$$\hat{M}_{g,i,t+1} = \hat{M}_{g,i,t+1} + T_{g,t+1} \text{ if } g = i \qquad (3)$$

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 (Fig. 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 *B. 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 3 states, we also fit the model to 3 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 1 at www.int-res.com/articles/suppl/n055p109_supp.pdf; for both supplements).

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 (Fig. 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 (N) of Antarctic blue whales in each ocean basin with a theta-logistic model:

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

where r is the intrinsic growth rate and 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 $r = (1 - s) \cdot r^{\star}$, where $r^{\star}$ is the limit of the growth rate not accounting for natural survival.

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

$$N_{t+1,i} = sN_{t,i} + (1-s)N_t(1+r^{\star})\left\{1 - \left[\frac{(1-s)r^{\star}\phi N_{t,i}}{(\phi+1)^{\frac{1}{\phi}+1}}\right]^{\phi}\right\} - C_{t,i} \qquad (5)$$

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

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

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), thus assuming that blue whales are uniformly distributed across each IWC management area.

We used abundance estimates from circumpolar line-transect surveys conducted between 1978/1979 and 2003/2004 (Branch 2007) as well as line-transect surveys (JARPA and JARPAII) conducted in IWC areas IV and V (70° E−170° W) between 1989/1990
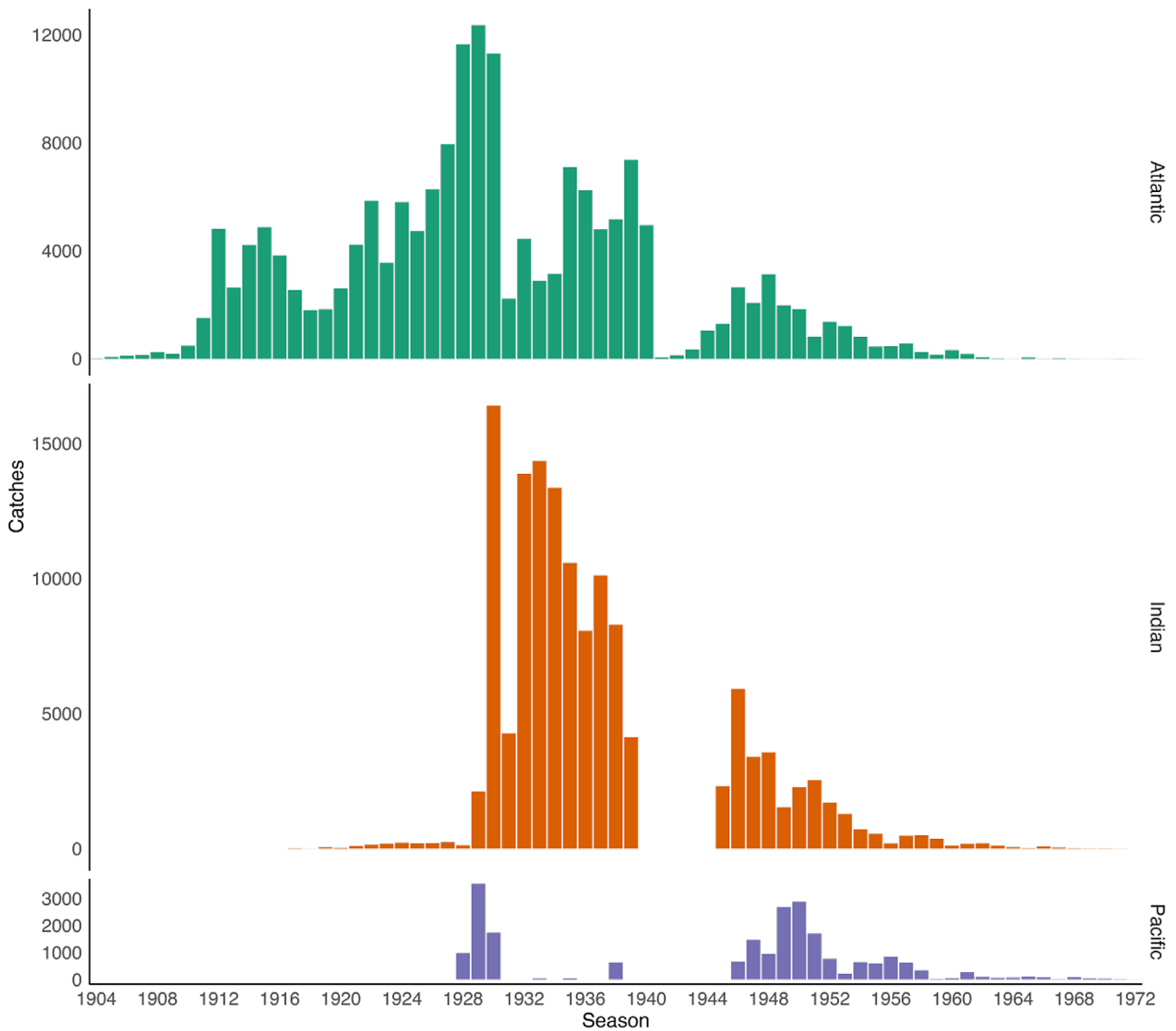
Fig. 3. Total Antarctic blue whale catches by ocean basin and whaling season

Table 1. Proportion of each IWC management area assigned
to each basin (Donovan 1991)

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

and 2007/2008 (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 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 2).

Abundance estimates from Branch (2007) cover entire ocean basins, however, the Hamabe et al. (2023) estimates only cover 60% of Indian Ocean lon-

Table 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 et al. (2023)
1991	Indian	78	0.33	Hamabe et al. (2023)
1993	Indian	92	0.26	Hamabe et al. (2023)
1995	Indian	2	0.75	Hamabe et al. (2023)
1996	Indian	754	0.16	Branch (2007)
1997	Indian	174	0.42	Hamabe et al. (2023)
1999	Indian	262	0.39	Hamabe et al. (2023)
2001	Indian	393	0.3	Hamabe et al. (2023)
2003	Indian	45	0.32	Hamabe et al. (2023)
2005	Indian	265	0.36	Hamabe et al. (2023)
2007	Indian	380	0.37	Hamabe et al. (2023)
1982	Pacific	278	0.22	Branch (2007)
1988	Pacific	334	0.23	Branch (2007)
1990	Pacific	81	1.45	Hamabe et al. (2023)
1992	Pacific	150	0.61	Hamabe et al. (2023)
1994	Pacific	107	0.73	Hamabe et al. (2023)
1996	Pacific	4	1.34	Hamabe et al. (2023)
1998	Pacific	128	1.2	Hamabe et al. (2023)
1999	Pacific	1126	0.14	Branch (2007)
2000	Pacific	95	1.21	Hamabe et al. (2023)
2002	Pacific	92	1.09	Hamabe et al. (2023)
2004	Pacific	70	0.61	Hamabe et al. (2023)
2006	Pacific	88	1.21	Hamabe et al. (2023)
2008	Pacific	538	0.95	Hamabe et al. (2023)

gitude and 29% of Pacific Ocean longitude. These were treated as relative indices of abundance ($I_{i,t}$), and 2 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:

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

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 (h) for the mark−recovery model are:

$$\hat{h}_{i,t} = \frac{C_{i,t}}{\hat{N}_{i,t}} \tag{8}$$

where $C_{i,t}$ 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 1 (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.

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, 2000 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 $\hat{R}$ values. For all parameters, convergence values from Bayesian estimation were satisfactory ($0.999 < \hat{R} < 1.005$ 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.

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 2 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 ($\hat{R}_{g,i,t+1}$) 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 ($\hat{N}_{i,t}$) 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 2 chains, 1600 and 2500 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.

3. RESULTS

3.1. Mark recoveries within seasons

A total of 2159 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 d after marking (median duration 43 d, 8—55 d interquartile range [IQR]), though 1 mark was recovered 114 d after marking. The median straight-line distance travelled between marking and recovery for same-season recoveries was 669 km (302—1820 km

IQR). 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 3).

3.2. Mark recoveries between seasons

A total of 46 marks were recovered interannually out of the 2110 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 4).

Most between-season mark recoveries occurred less than 5 yr after marking (median duration 1.34 yr,

Table 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 basin

		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	

Table 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	

0.85−4.15 yr IQR). However, 1 mark was recovered 12 yr and 10 mo after it was placed. The median straight-line distance for marks that were recovered in the same basin where they were placed was 1320 km (810−1868 km IQR). For marks recovered in a different basin than they were marked, the median straight-line distance between marking and recovery was 2046 km (1665−4591 km IQR). The longest distance between marking and recovery was 6250 km and was from a mark placed in the Pacific basin and recovered in the Indian basin.

3.3. Parameter estimates

The total carrying capacity (and assumed prewhaling abundance) for the Southern Ocean was estimated to be 186 335 (95% Bayesian credible interval [BCI]: 170 485−204 579; Fig. 4), with more estimated to be in the Pacific Ocean basin: 83 987 (68 919−101 474) than in 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 5, Fig. 4).

The model provided good fits to the abundance estimates, with abundance estimates aligning well with the posterior predictive distributions from the model (Fig. 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 (Fig. 6).

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 5). Some of these
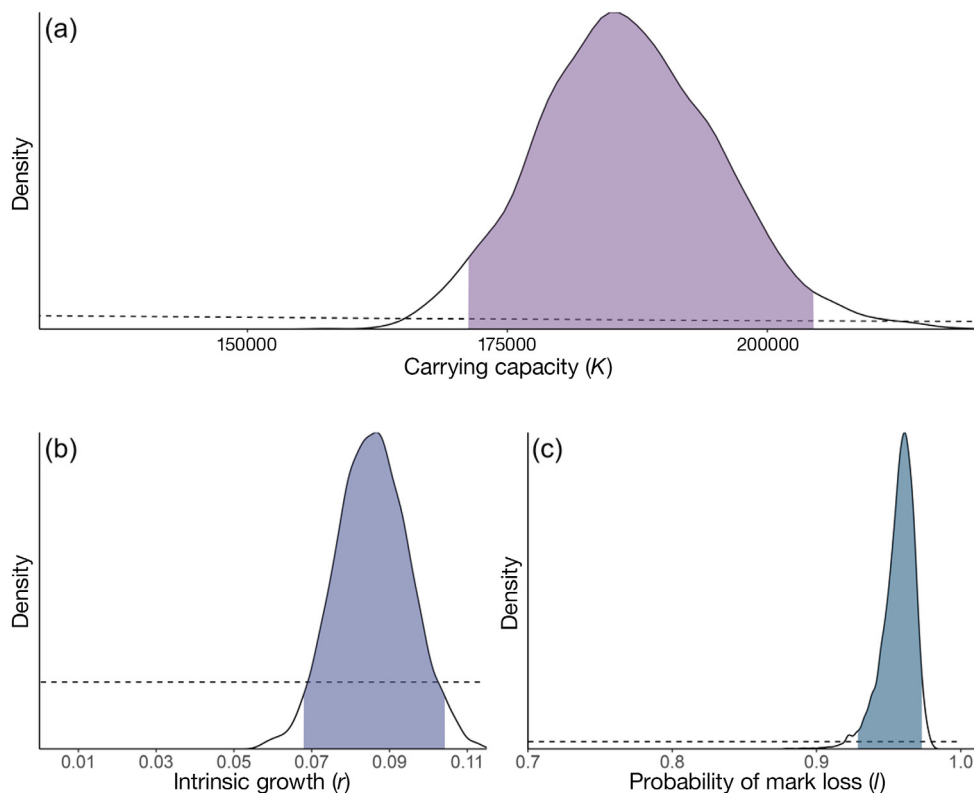

Fig. 4. Prior (dashed line) and posterior distributions (solid line) with 95% credible interval (shading) for (a) total Antarctic blue whale carrying capacity in the Southern Ocean, (b) intrinsic rate of growth, and (c) mark loss. Parts of the priors for carrying capacity ($\ln K \sim U[9, 13]$) and mark loss ($l \sim$ Beta[1, 1]) are beyond the limits of these plots

Table 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)	186335	170485	204579
K_{Atl}	Carrying capacity (Atlantic)	36817	26057	51417
K_{Ind}	Carrying capacity (Indian)	64654	52440	79403
K_{Pac}	Carrying capacity (Pacific)	83987	68919	101474
$m_{Atl \to Atl}$	Movement	0.558	0.198	0.783
$m_{Ind \to Atl}$	Movement	0.126	0.027	0.339
$m_{Pac \to Atl}$	Movement	0.082	0.009	0.243
$m_{Atl \to Ind}$	Movement	0.145	0.006	0.463
$m_{Ind \to Ind}$	Movement	0.537	0.321	0.736
$m_{Pac \to Ind}$	Movement	0.275	0.133	0.459
$m_{Atl \to Pac}$	Movement	0.287	0.040	0.486
$m_{Ind \to Pac}$	Movement	0.324	0.144	0.484
$m_{Pac \to Pac}$	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

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 (Fig. 7).

Based on the estimated movement matrix, the equilibrium distribution of movement rates is reached in less than 10 yr, 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 & 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 & 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 credible intervals between the 2 runs, except that the survey coverage parameter (q) for the Matsuoka & 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 2).

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, 2 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 remaining 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 (Fig. 8).

4. DISCUSSION

We outlined 4 possible scenarios for Antarctic blue whale migration and movement (Fig. 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 3 basins. Even movement at the lowest estimated rate, from the Pacific to the Atlantic (8.2% per year; Table 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 10 yr.

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 (Fig. 1b—d). Same-season mark recoveries indicate that Antarctic blue whales did move widely while in the feeding areas (Fig. 2), and it is unlikely that movements were restricted to only the feeding grounds. Between-season mark recoveries suggest that Antarctic blue whales moved 2000—6000 km between basins in the Southern Ocean. If
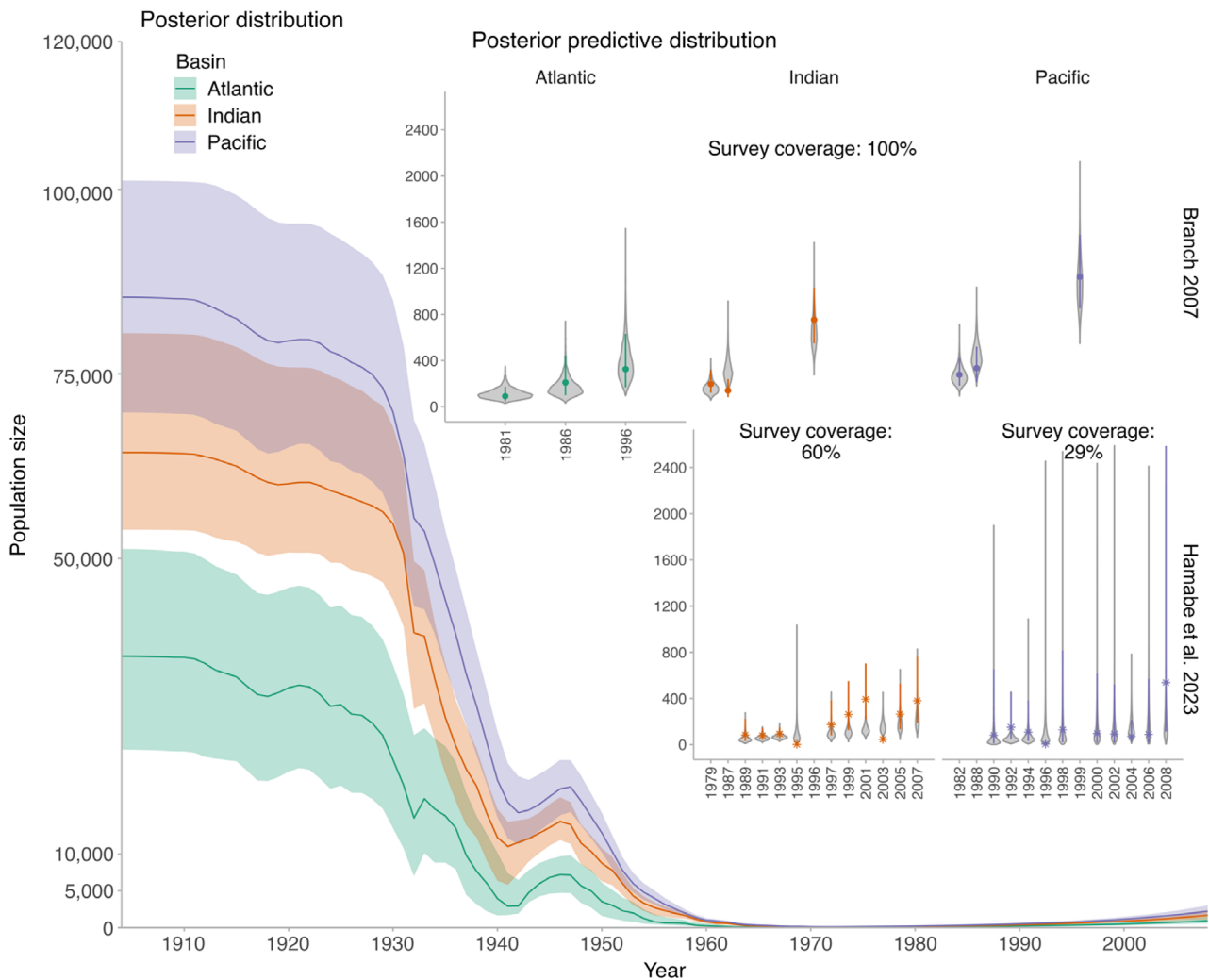
Fig. 5. Posterior medians (solid line) and 95% credible intervals (shading) of Antarctic blue whale population size in each basin (left) and posterior predictive distributions (violins, inset) for each abundance estimate (Table 2) with points representing Branch (2007) and stars representing Hamabe et 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

Antarctic blue whales must travel more than 6000 km between breeding and feeding areas, and also move 4000 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 h^{-1} (Calderan et al. 2023) would take more than 3 mo. 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 2 yr 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 anti-predator strategies, since blue whales flee killer whales at high speeds rather than group together to defend calves like humpback whales (Ford & Reeves 2008).
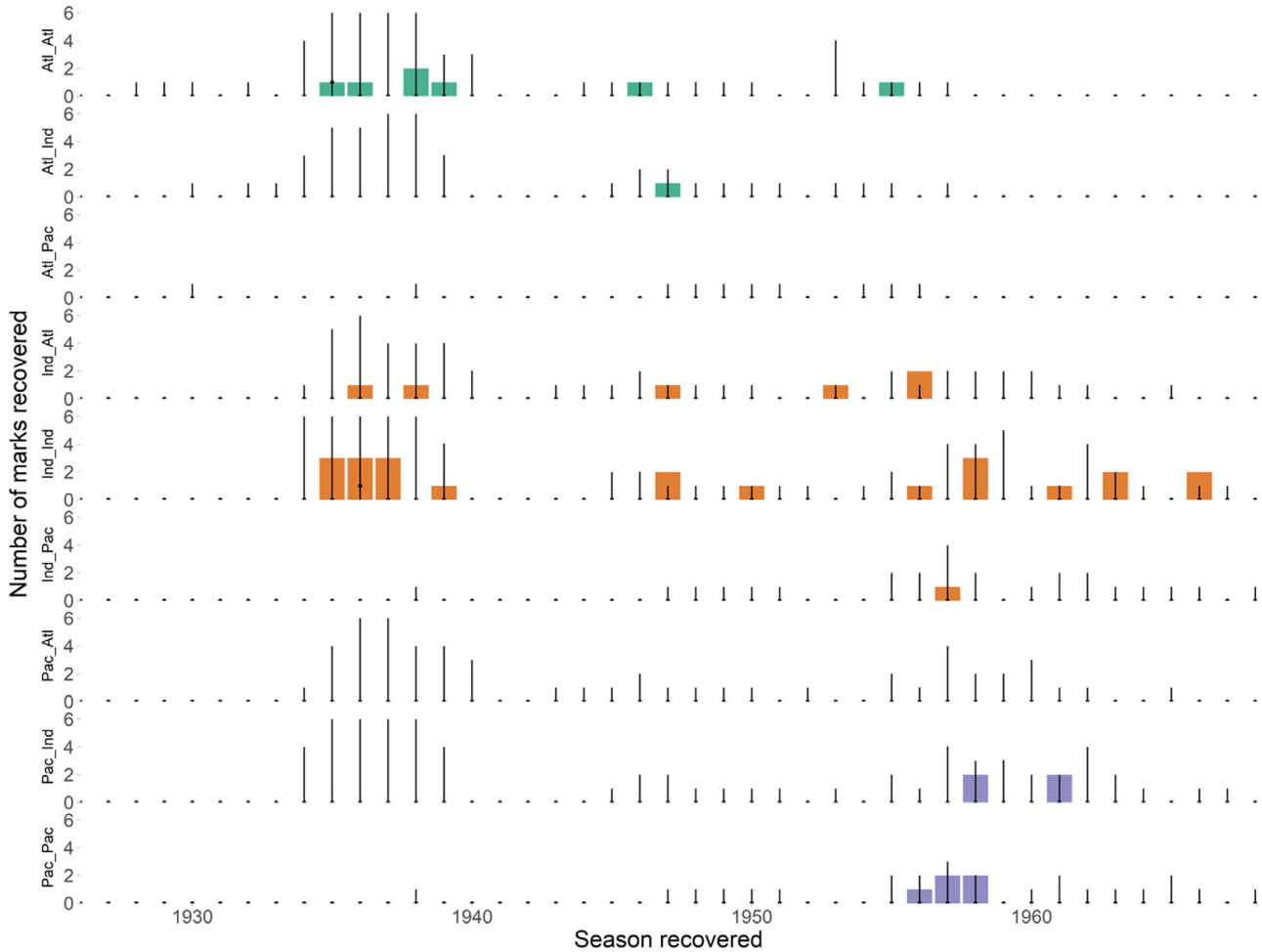
Fig. 6. Posterior predictive medians (points) and 95% credible intervals (lines) for the number of marks that were originally marked in basin *i* that are recovered in basin *j* (groups are listed as *i_j*) in each season, as well as actual number of marks recovered for each group in each season (bars; colors as in Fig. 5). Note that some intervals are subsumed within the points

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, 2022). Satellite tagging of 2 individuals also suggests that Antarctic blue whales roam widely in the Southern Ocean, these whales moved 1433 km (in 14 d) and 6107 km (in 74 d) 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
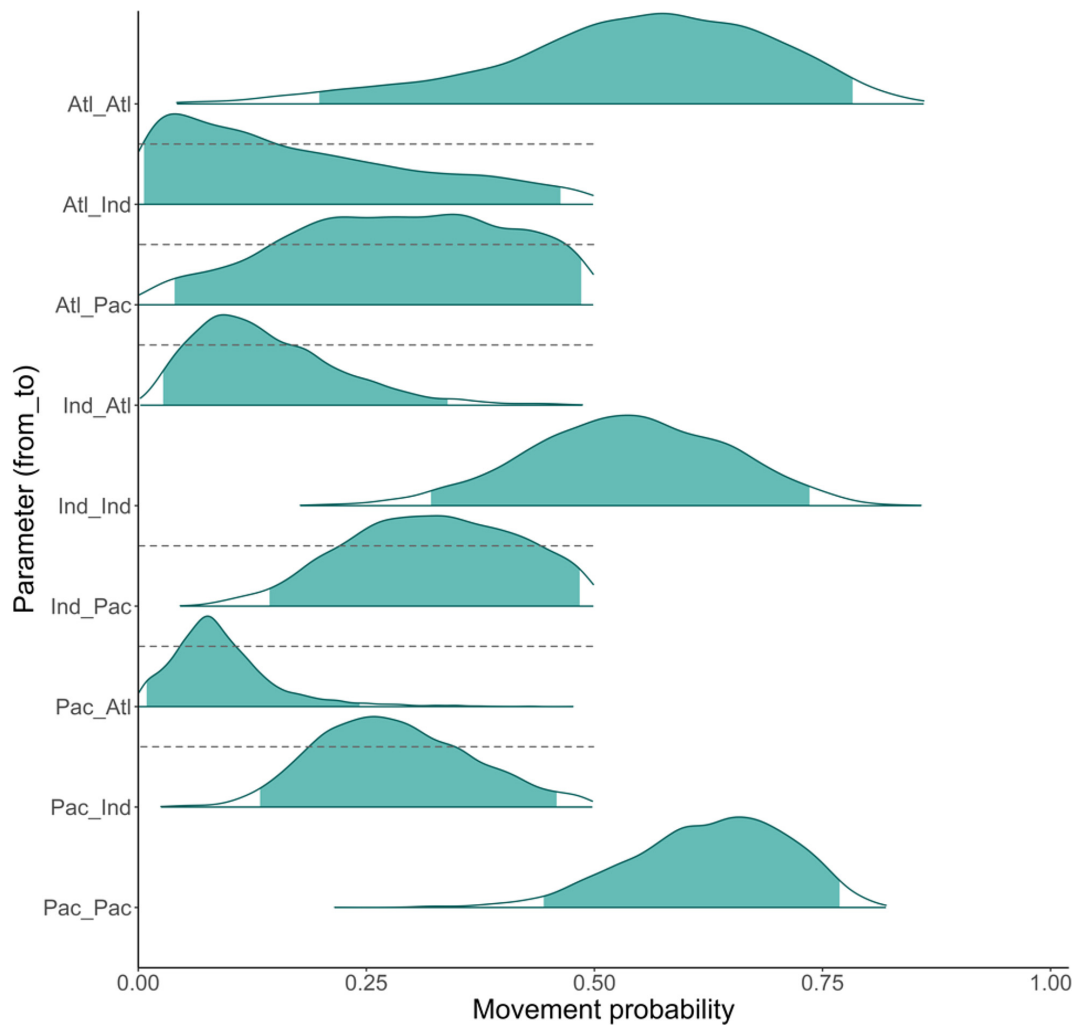
Fig. 7. Prior (dashed line) and posterior (solid line) distributions and 95% credible intervals (shaded) for movement probabilities among basins (listed as from_to). The probability of remaining in a basin from season to season was calculated by subtraction

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 (Fig. 3). This allowed for a smaller preexploitation 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 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 2 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
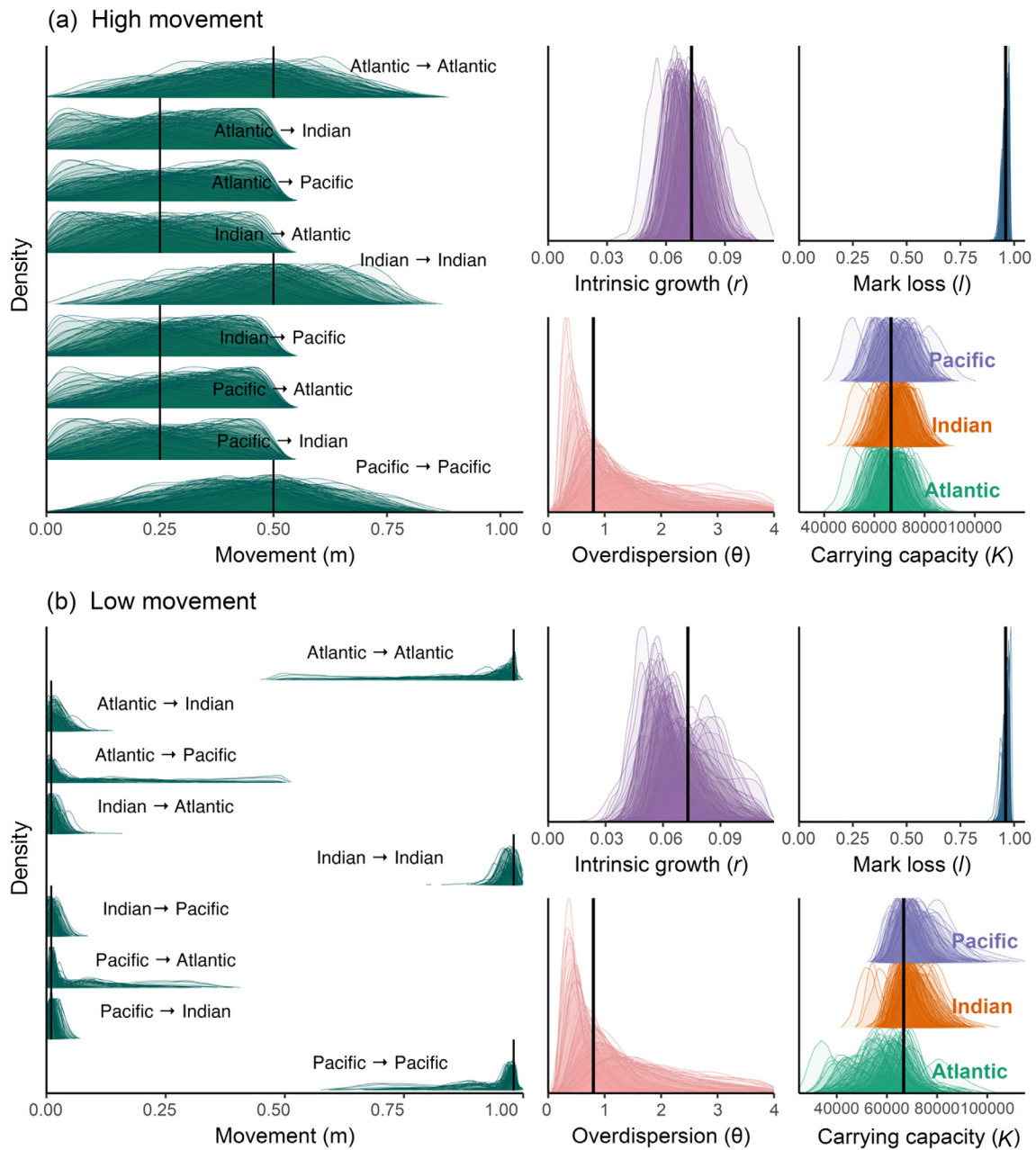
Fig. 8. Posterior distributions of parameters from models fit to 60 simulated data sets under (a) high movement (25% move, 50% stay) and (b) low movement (1% move, 98% stay) scenarios. Values used in simulating data are represented by vertical lines

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 inter-season 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 (Fig. 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 2 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 e.g. 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 2 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 2011) 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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