

Southern elephant seal population breeding probability declines with increased sea-ice cover in a key foraging region

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ABSTRACT

Regional differences in southern elephant seal (*Mirounga leonina*) population trends have long been hypothesised to reflect environmental variation affecting prey availability. By combining census counts, demographic data, and locally relevant winter sea-ice conditions, we provide new evidence quantifying the suspected link between seal numbers in the Macquarie Island population and regional sea-ice cover in the Southern Ocean. We developed an integrated population model using annual abundance and capture–mark–recapture data from 1980–2023, accounting for observation error and temporal random effects. Population breeding probability varied annually (50–65% on average). To assess how environmental conditions influence reproductive dynamics, we tested the effect of winter sea-ice cover within the known foraging range of adult females. We compared two covariate structures and a null model, incorporating one-year-lagged (B-COV1) and same-year (C-COV0) sea-ice conditions. Covariate models confirmed a negative relationship ($\beta_{B-COV1} = -0.0103 [-0.025; 0.0037]$ to $\beta_{C-COV0} = -0.0345 [-0.049; -0.021]$), indicating that reduced population breeding probability was associated with higher-than-average sea-ice cover. Estimates of the total population size (N) mirrored the observed decrease in seal numbers from annual abundance counts. N was used to project historical scenarios representing persistently ‘best’, ‘neutral’, and ‘worst’ case sea-ice cover conditions over the full timeseries. The scenario-specific intrinsic growth rates ranged from a slow decrease under the best-case scenario ($r = -0.495\%$) to a substantially stronger decline under the worst-case scenario ($r = -3.126\%$), with the neutral scenario closely matching the observed population trend ($r \approx -2\%$). These comparisons emphasise how local-regional scale habitat conditions can alter long-term population trajectories at magnitudes relevant to species recovery.

1. Introduction

Many marine mammals remain either threatened or protected as they recover from 19th and 20th century commercial harvesting (Koss et al. 2023). Current anthropogenic pressures can have interacting or compounding effects, including fishing, pollution, climate-related changes and habitat loss (Clapham 2016; Sequeira et al. 2025; Von Schuckmann et al. 2026). Depending on the animal’s habitat and life history, many species may be moving towards a new equilibrium state, (Bestley et al. 2020). In the southern hemisphere, many marine predators depend on the Southern Ocean as their primary foraging ground

(Murphy et al. 2021), from whales seeking krill in the austral summer, seabirds foraging in upwelling systems and pinnipeds exploiting mesopelagic fish and squid. Land-breeding pinnipeds and seabirds, which return to Sub-Antarctic Islands to breed and raise their young, are tied to regional habitat conditions with evidence that poor foraging conditions can affect breeding success and population dynamics (Croxall, Reid, & Prince 1999; Weimerskirch et al. 2003). For these species, the conditions within their foraging range can directly influence reproductive success and population viability. This is especially true for southern elephant seals (*Mirounga leonina*) where there are known links between foraging success and population growth rates (e.g. van den Hoff et al.,

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2014). The elephant seal population at Macquarie Island is particularly interesting because it continues to decrease post an initial recovery after 19th and 20th century sealing ended (Hindell et al., 2025).

Southern elephant seals are long-lived marine predators with a circumpolar distribution (Hindell et al. 2016). Since the mid-20th century the four major populations have showed differing population trends (McMahon et al. 2005a). Until recently, the genetically distinct populations at South Georgia, Îles Kerguelen and Península Valdés were considered stable or increasing (Beltran, Hindell, & McMahon 2022), while Macquarie Island exhibited a slow but steady population decrease throughout the last 70 years (Hindell et al. 2025). Environmental influences on prey availability have frequently been proposed as causes for this sustained decline (Hindell et al. 2025, McMahon et al. 2005a, van den Hoff et al. 2014), although this link has been difficult to quantify. The potential mechanism linking environmental variability to population change lies in the species' life-history strategy. As capital breeders, adult southern elephant seals rely on stored energy acquired during foraging trips to support reproduction (Boyd 1991, Laws 1953), making breeding participation particularly sensitive to foraging success in preceding seasons.

Adult southern elephant seals return annually to their natal breeding grounds (Hindell et al. 2016), with females arriving in September to give birth and nurse their pups while fasting on land (Carrick et al., 1962). During the short (23 day) lactation period (McMahon et al. 1997), substantial energy reserves are transferred to their young (Beltran, Hindell, & McMahon 2022); pups gain around 100kg while mothers lose up to 35% of their body mass (Carrick, Csordas, & Ingham 1962; Fedak, Arnborn, & Boyd 1996, Hindell & Slip 1997). Maternal condition is an important determinant of pup weaning mass, which can affect both early juvenile survival and recruitment (McMahon & Burton 2005; Oosthuizen et al. 2018). Weaning mass itself has been used as a proxy of maternal foraging success in relation to habitat conditions (Clausius et al., 2017; Oosthuizen et al., 2015) and indeed, adult females can skip a breeding season to preserve their body condition and prioritise

long-term survival (Desprez et al. 2018). This strategy for maximising individual lifetime reproductive output may play a role in linking habitat conditions and foraging success directly with reproduction, and recruitment into the breeding population, on an annual basis.

Adult female elephant seal survival rates decrease in years with strong negative anomalies in the Southern Oscillation Index (i.e., La Niña years) (Volzke et al. 2021), while adult male survival is less influenced by external habitat conditions (Volzke et al. 2024). In the East Antarctic sector, La Niña years are typically associated with increased sea-ice extent and concentration in the Southern Ocean adjacent to the Ross Sea (Kwok & Comiso 2002). Tracking studies have shown that a subset of adult females from the Macquarie Island population forage along the Antarctic continental shelf within this region (Figure 1) during winter (Pascoe et al. 2016; Hindell et al. 2017). Focusing specifically on the Macquarie Island population, Clausius et al. (2017) reported that years with increased pup weaning masses were also characterised by greater numbers of breeding females ashore, and that both measures were negatively correlated with maximum sea-ice extent in the Ross Sea. This finding underpins the hypothesis that sea-ice mediated changes in maternal foraging success may be a contributing factor in the long-term population decline at Macquarie Island (Clausius et al. 2017). Hindell et al. (2017) confirmed that the overall population size is negatively correlated with sea-ice concentration, with some regions showing a stronger response than others. Therefore, considering the spatial relevance of the covariate is paramount, as only a portion of adult females departing from Macquarie Island forage in the southernmost regions of their range along the Antarctic continental shelf. Annual population growth rate also increased with decreased sea-ice duration, after a time lag of three years was incorporated (van den Hoff et al. 2014). Since females of the species can mature as early as age three (McMahon et al. 2005b; Desprez et al. 2018), this may be a contributing factor in recruitment or breeding dynamics.

Here, we tested the hypothesis that regional sea-ice extent may influence the proportion of female southern elephant seals that return

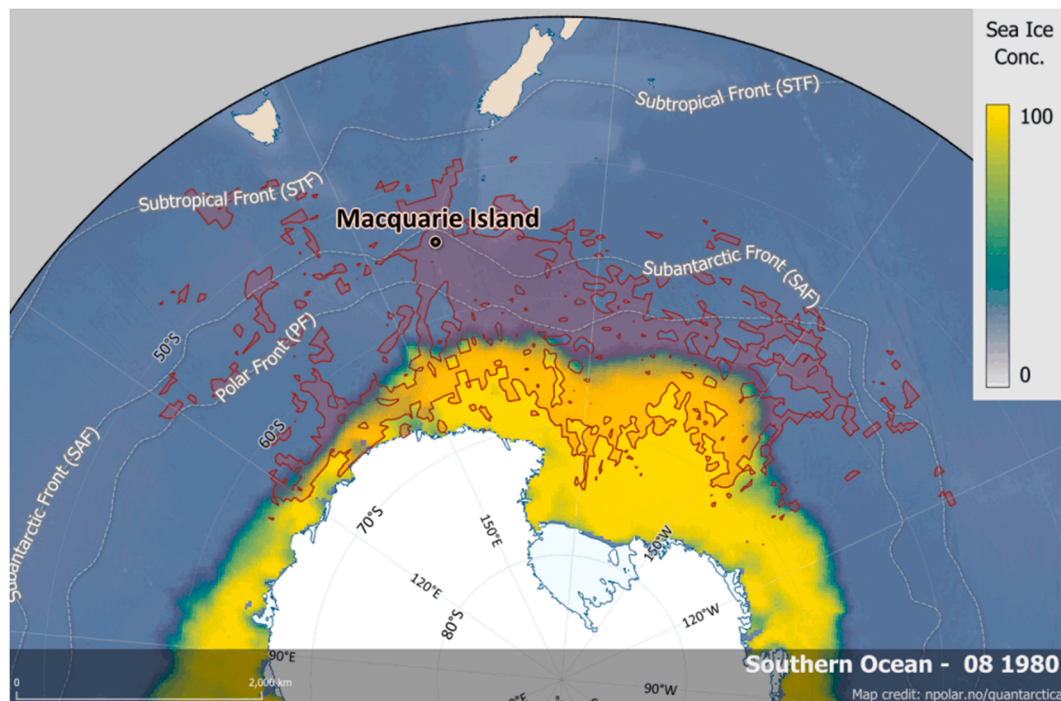


Figure 1. The overlap of Southern Ocean sea ice expanding into the key foraging area (red) of adult female southern elephant seals tracked from Macquarie Island. Tracking data from their post-moult foraging trip (March – October) were summarised into a spatial polygon based on the number of seal days spent per 50 × 50 km grid cell, published by Hindell et al. (2025). Winter (August) average 25km NSIDC Sea-Ice Concentration extracted from Niles Software at the Australian Antarctic Data Centre (Steketee, Chua, & Commonwealth of Australia 2023). Digital version rotates sea-ice conditions from 1980 – 2023 to visualise annual variability in coverage.

annually to Macquarie Island to breed. Specifically, we asked whether variation in sea-ice conditions would be reflected in annual variation of population-level breeding probability, such that years with higher sea-ice extent would correspond to fewer females returning to breed. To test this, we developed an Integrated Population Model (IPM) that combines capture-mark-recapture data with annual census counts of adult females and pups to model the demographic structure of the female population between 1980 and 2023. This framework estimates the total number of adult females, including those not observed in a given year, and predicts how many of these individuals are expected to breed annually. Breeding probability is then allowed to vary among years and is modelled as a function of sea-ice conditions, enabling us to evaluate whether interannual environmental variability is associated with systematic changes in breeding participation across the population. We tested temporally lagged and unlagged terms to evaluate whether sea-ice conditions in the same or previous year were most strongly associated with population breeding probability.

2. Methods

2.1. Data sources

Elephant seals have high site fidelity, returning to their natal islands to breed and to moult. Macquarie Island (54° 30' S, 158° 56' E) is one of four major breeding sites of the species, located midway between Australia and the Antarctic continent in the Southern Ocean (Figure 1). The major populations are considered closed for demographic analysis, due to the geographic isolation of the breeding islands resulting in very limited genetic exchange (Corrigan et al. 2016; Slade et al. 1998). Adults arrive to breed in the austral spring, between August and November (Carrick et al., 1962). Females give birth and spend three weeks nursing their pups before mating and returning to sea to replenish their energy stores (Carrick et al., 1962). Weaned pups are independent of their mothers and embark on their first trip out to sea shortly afterwards (Le Boeuf & Laws 1994). Juvenile development is a time when much of the energy gained from food is allocated to rapid growth. Meanwhile, the first year foraging at sea is associated with high mortality (Hindell 1991; McMahon, Burton, & Bester 1999; McMahon, Burton, & Bester 2000; Volzke et al. 2023). The 'Yearlings', i.e. seal that survive their first year of life, expand their foraging range, venturing further away from their natal island every year as they age (Field et al. 2005). Females can mature as early as age three (Carrick et al. 1962), however, most are seen with their first pup at age four, and some as late as age seven, noting the energetic consequences of breeding while still needing to acquire energy for growth (Desprez et al. 2014).

Counts of breeding females and pups at Macquarie Island were made from 1949 with variable effort. By 1985, these counts were largely standardised and undertaken annually during or close to the peak of the breeding season in mid-October. Organised searches recorded the total number of females within each breeding aggregation. Hindell et al. (2025) provided a detailed breakdown of the methodology and published updated count data for adult females and derived number of pups, as well as number of counts undertaken as an indicator of effort (Appendix A). These numbers were used as confirmed abundance estimate for adult females (y_t) and pups (z_t). A few years with missing count data were estimated by the model using realistic count data means and variances (Appendix A). Surveys were standardised to be conducted during the peak of the breeding season (15 October) and most years, multiple surveys were done to control for observer error (Hindell et al. 2025). However, a few years were missing counts and some only had less than five counts available. These years were included as data input with a more flexible variability term.

A capture-mark-recapture project was conducted at Macquarie Island from 1993 to monitor individuals and gain important insights on age-dependent survival (McMahon, Burton, & Bester 2000), breeding dynamics (Desprez et al. 2013), and maternal investment (Clausius,

McMahon, & Hindell 2017). A total of 2000 (male and female) pups were sexed and hot iron branded at weaning over each of seven annual cohorts from 1993 – 1999 (McMahon et al. 2006). This equated to an average of 1000 female pups per cohort released for long-term monitoring (Appendix A). Recapture data were collected through strategic resight surveys annually during the breeding season. Where possible, life-history status was noted by the observer, which included notes on age class and breeding status (yearling, juvenile, breeding adult with pup, etc). This enabled the distinction between known-age female juveniles and first-time breeders observed actively reproducing in the breeding season. Each individual female seal entered the capture history record as a juvenile of known age 0. This information was then collated to create capture histories (h_i) for all individuals and their assigned age class (1 = juvenile, 2 = adult, 0 = not seen) summarised for each year of the whole timeseries of the IPM: 1980 – 2023, corresponding with seal season 1981 – 2024. These capture histories were collapsed into a multistate m-array (M) for analysis (Browne et al. 1993).

The spatial extent of at-sea foraging habitat was derived from tracking data of 70 female southern elephant seals during their post-moult foraging trip (March – October) from Macquarie Island (Hindell et al. 2025). Tracking data were collected between 2000 and 2010 (Hindell et al. 2017), with two additional individuals included from recent tracking work in 2023. A utilisation distribution based on the number of seal days spent per 50 × 50 km grid cell was used to generate the spatial polygon plotted in Figure 1, following the methodology by Harcourt et al. (2021). For the purpose of this analysis, we chose a broadly restrictive area (50% polygon) enclosing the most used cells which together accounted for 50% of the total time spent at sea. This ensured the area captured a regionally relevant spatial extent, defining this as our 'key foraging habitat' of adult female elephant seals from Macquarie Island.

Monthly average sea-ice concentrations (SIC) were extracted from satellite-derived National Snow and Ice Data Centre (NSIDC) oceanographic records extracted using Nilas Software (Steketee, Chua, & Commonwealth of Australia 2023) at a 25km spatial scale and cropped to the key foraging area spatial polygon. We considered only the months relevant for the seals' post-moult trip (March – October) and aggregated these to give an annual average percent ice cover (percentage of foraging polygon covered by more than 15% SIC) per year from 1980 until 2023 (Figure 3a). These percentages were then converted to annual anomalies (x_t) by subtracting the mean of the complete timeseries (37.47% cover) from each estimate, so a year of high percent ice cover has a positive anomaly, and negative percent ice cover was represented by a negative anomaly value.

2.2. Demographic analysis

We developed a Bayesian IPM to estimate demographic rates and population size of southern elephant seals at Macquarie Island by combining multiple data sources within a single hierarchical framework (Schaub and Abadi 2011). The analysis was coded in R Studio ((R Studio Team. 2025) with R version 4.4.3. (R Core Team 2025) using *jagsUI* (ver. 1.6.2) package (Kellner 2024). The model integrates inputs from annual observation abundance data (z_t : pup counts and y_t : adult female counts during the breeding season) and capture-mark-recapture data (h_i : capture-histories). Each data source is linked to the underlying, unobserved population states through an observation model, allowing all datasets to contribute jointly to parameter estimation via a shared likelihood framework. Population dynamics were described using a two-stage matrix population model with juvenile and adult states, in which individuals could either survive within a stage or transition from juvenile to adult through maturation (Figure 2). Annual demographic rates (e.g. survival and maturation probability) were modelled on the logit scale with temporal random effects, allowing covariance among these processes. These rates informed a state-space model describing temporal changes in the latent population, divided into groupings

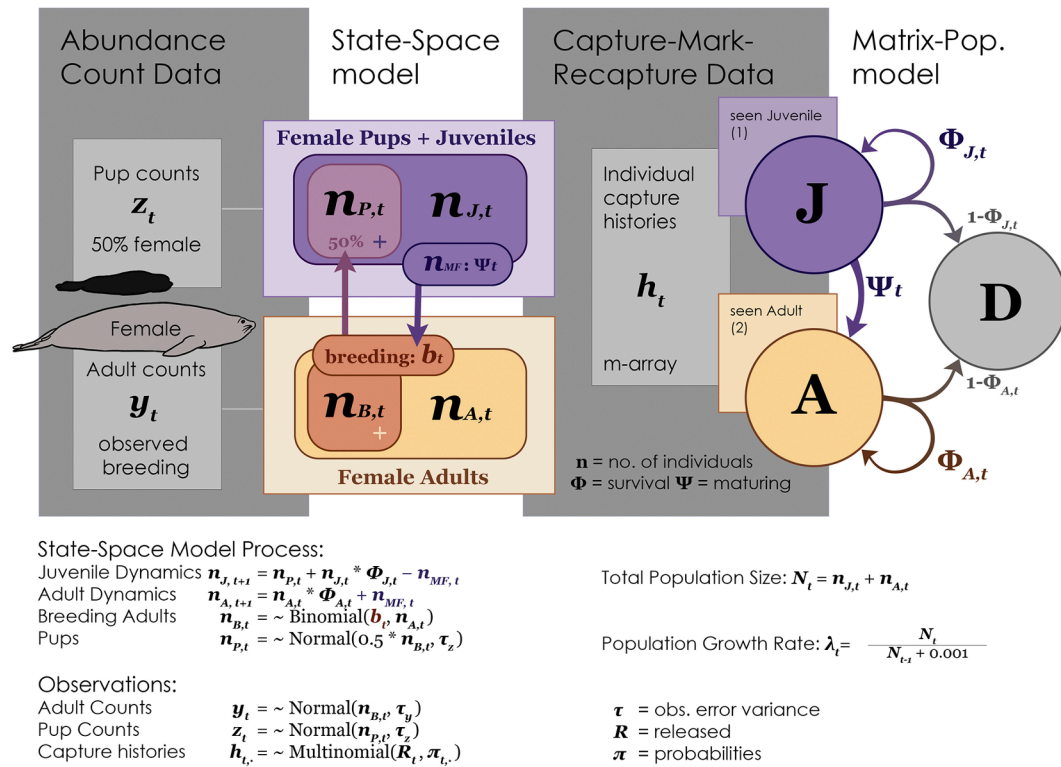


Figure 2. Graphical illustration of an Integrated Population Model using multiple data inputs to estimate the number of female individuals in a population of southern elephant seals using a state-space-model (SSM). Data inputs are defined in the ‘Observations’ section and include the counts of female adults (y_t), derived number of pups (z_t) and capture-mark-recapture data of both (h_t). The number of Juveniles ($n_{J,t}$) includes the number of pups ($n_{P,t}$) in a given year t . n_P is informed by a 50% sex ratio of pups produced by female adults observed in the breeding season ($n_{B,t}$). n_B are a part of the adult population as a whole ($n_{A,t}$), which includes non-breeding and unobserved individuals. The model progresses through time by including state-dependent survival ($\Phi_{J,t}$, $\Phi_{A,t}$) computed by a two-state matrix population model (MPM) of known individuals. In both SSM and MPM, juveniles can mature to enter the adult population at a probability (Ψ_t), closing the loop and allowing for age progression of individuals over time.

(number of pups, juveniles, adults). Breeding status was modelled as a binomial process, so the number of breeding females each year depended on the total adult population and an annual population breeding probability.

To investigate environmental effects, breeding probability was modelled on the logit scale with a temporal random effect and evaluated under three alternative formulations: a null model with no covariates, a lagged sea-ice model incorporating conditions in the previous year, and an unlagged model including same-year sea-ice extent. Priors were specified using a combination of diffuse and informed distributions, with informed priors applied to parameters with existing empirical support from previous studies, and all model components were jointly estimated within the Bayesian framework to produce coherent estimates of demographic rates, population size, and derived quantities such as population growth.

2.3. Matrix Population Model

The Matrix Population Model (MPM) describing the female population was structured with two observed states (Juvenile and Adult). Annual progression either described maturing (transitioning from J to A) or survival (remaining in each state, not transitioning to a dead state D) (Figure 2). Detection probabilities were state- and time-dependent and were used to construct a multistate m-array. The m-array summarised capture histories across all occasions and states, which was modelled using a multinomial likelihood (Gimenez 2020). Temporal variation in demographic rates was incorporated through random effects. Annual survival probabilities for juveniles ($\Phi_{J,t}$) and adults ($\Phi_{A,t}$), as well as the maturation (Ψ_t) transition probability were modelled with a multivariate normal distribution on the logit scale. This allowed for

correlation between all three demographic transition processes (Appendix A). Bayesian priors were set either as uninformed (uniform) distributions of mean survival and variance estimates, and informed (beta distribution) for mean detection and transition probability. Informed priors were based on previous demographic research revealing insights on realistic expected values of mean rate of juveniles maturing (Desprez et al. 2014), as well as important findings on sampling effort and detection variability over time (Desprez et al. 2013). Two discrete states (seen Juvenile, seen Adult) were assigned based on observed traits and formatted into an m-array across 44 annual capture occasions (1980 – 2023). The number of columns in the m-array is calculated as: $K = n_{occasions} * n_{states} - (n_{states} - 1)$ so $K = 43 * 2 - 1 = 83$. Each row of the m-array is modelled using a multinomial distribution: $M_{t,1:K} \sim \text{Multinomial}(R_t, \pi_t)$ and associated log-likelihood: $\log \mathcal{L}_M = \sum_{t=1}^{T-1} \log \Pr(M_{t,1:K} | R_t, \pi_t)$.

Here, π_t is the vector of predicted transition probabilities between states and occasions at time t , and R_t is the total number of individuals released at time t . This efficient formulation captures the probability of individuals transitioning between states and being recaptured across subsequent occasions.

The parameter Φ_A of the MPM is also used to propagate adults surviving within the adult population modelled by a state-space process. It is a known limitation of this study that these data were collected from females returning in the breeding season. Therefore, these individuals are part of the breeding population n_B . However, there was no data available on ‘non-breeding’ individuals, as they can remain at-sea without being captured. We therefore assumed that adult survival is consistent between breeding and non-breeding female adults.

2.4. State-Space Model

We assumed pups were born with a 50% sex ratio (Carrick, Csordas, & Ingham 1962; Laws 1953), so the number of counted pups was halved to represent female pups (z_t) as productivity input. We modelled observed counts of pups z at time t as normally distributed around the predicted pup count $n_{p,t}$ with observation precision τ_z : $z_t \sim \text{Normal}(n_{p,t}, \tau_z^{-1})$, corresponding with the log-likelihood: $\log \mathcal{L}_z = \sum_{t=1}^T \log f_{\text{Norm}}(z_t | n_{p,t}, \tau_z)$. Similarly, the observed breeding female adult counts y at time t were modelled as normally distributed around the predicted number of breeding females $n_{B,t}$ with observation precision τ_y : $y_t \sim \text{Normal}(n_{B,t}, \tau_y^{-1})$ with a corresponding log-likelihood: $\log \mathcal{L}_y = \sum_{t=1}^T \left[\frac{1}{2} \log(\tau_{y,t}) - \frac{1}{2} \log(2\pi) - \frac{\tau_{y,t}}{2} (y_t - n_{B,t})^2 \right]$.

And the overall log-likelihood for model ranking was defined as: $\log \mathcal{L} = \log \mathcal{L}_y + \log \mathcal{L}_z + \log \mathcal{L}_M$.

The estimated number of pups $n_{p,t}$, juveniles $n_{J,t}$, breeding female adults $n_{B,t}$, and all female adults $n_{A,t}$ (accounting for breeding and non-breeding) were estimated annually and propagated through time (1980–2023) by a state-space model (SSM) process (Figure 2). The estimated number of juveniles and adults at time $t+1$ was defined as the previous estimate at time t multiplied by state-dependent survival ($\phi_{s,t}$) accounting for the proportion of juveniles that matured at probability ψ_t ($n_{M,t}$). A maturing juvenile was observed breeding for the first time and therefore entered the breeding adult population of that timestep. $\phi_{s,t}$ and ψ_t were computed by a two-state MPM of known individuals from the capture history data. The breeding parameter was defined as the differentiating characteristic between $n_{B,t}$ and $n_{A,t}$. Therefore, b_t described the probability of any individual in the adult population being observed during the breeding season of a given year.

$$n_{B,t} \sim \text{Binomial}(b_t, n_{A,t})$$

Breeding probability was considered a population-level effect, as this parameter does not capture individual-level data directly. This simplification enabled the estimation of a key parameter that has been notoriously difficult to capture as it describes the difference between observed (counted) individuals and unobserved (hidden) individuals that are alive in the population but not observed and therefore missing from the dataset for that year.

The model included some useful derived parameters to visualise and check on the validity of overall estimates. The total number of individuals in the population (N_t), was simply calculated as the sum of $n_{J,t}$ and $n_{A,t}$ each year, which informs the population rate of change from year to year (λ), commonly calculated as $\lambda = N_{t+1}/N_t$, which is converted to the continuous exponential rate of growth $r = \ln(\lambda)$. It should be noted that this analysis combined all relevant demographic data from the major breeding site on the northern isthmus of Macquarie Island (the estimated ‘population’). This is representative of around 13% of the whole island population size (McMahon et al. 2005b), as recently confirmed by a strong positive correlation between isthmus counts and whole island counts (Hindell et al. 2025).

2.5. Covariate structure

To assess the influence of sea-ice cover on population breeding probability, three different Generalised Linear Models were constructed within the IPM. For all three models, breeding probability was modelled on the logit scale and included a temporal random effect (ε_t) to account for unexplained interannual variation.

- **Model A (Null Model, NULL):** Breeding probability varied over time with a random effect and no covariate influence:

$$\text{logit}(b_t) = \alpha_{\text{cov}} + \varepsilon_t$$

- **Model B (Lagged Covariate Model, COV1):** Breeding probability was influenced by the covariate in the previous year (x_{t-1}):

$$\text{logit}(b_t) = \alpha_{\text{cov}} + \beta_{\text{ice}} * x_{t-1} + \varepsilon_t$$

- **Model C (Unlagged Covariate Model, COV0):** Breeding probability was influenced by sea-ice extent in the same year:

$$\text{logit}(b_t) = \alpha_{\text{cov}} + \beta_{\text{ice}} * x_t + \varepsilon_t$$

In all models, the first year ($t = 1$) was assigned a separate intercept (α_{pre}) due to the absence of covariate data in the first year when including a time lag model. The covariate intercept best converged with an informative prior ($\alpha_{\text{cov}} \sim \text{dbeta}(13, 7)$), to avoid unrealistically low (0–0.25) and extremely high (0.95–1) estimates in population breeding probability.

2.6. Model testing

Model fit and predictive performance was assessed using several complementary Bayesian diagnostics. Posterior estimates for key latent states and demographic rates (e.g., $n_{B,t}$, b_t) were compared directly with the raw data informing those components to verify that the fitted model reproduced observed patterns. For covariate effects, we examined posterior density plots to assess prior influence and data-dominance. Observation-model adequacy was evaluated using posterior predictive checks. For each posterior draw, we generated replicated breeding and pup counts from the fitted likelihoods and compared predictive intervals with the observed data, reporting coverage and standardized p-values (Appendix B). Additionally, prior predictive checks were used to ensure that chosen priors produced biologically reasonable data before conditioning on observations. For model selection, we computed two information criteria for each model: the Widely Applicable Information Criterion (WAIC), and Leave-One-Out cross-validation (LOO). The WAIC and LOO were calculated from the three input data (z_t , y_t , h_t) log-likelihood functions (Appendix B). These metrics allowed model comparison based on both goodness-of-fit and complexity and assessed the relative support of the sea-ice covariate effect on breeding probability. Additionally, all parameter estimates were checked for convergence and overall model deviance was checked and recorded alongside the potential scale reduction factor ($\hat{R}$) (Appendix C). Some deterministic or data-absent nodes displayed $\hat{R} = 0$, as expected for parameters without posterior variance, and several latent state variables with weak data-support showed slightly elevated $\hat{R}$ values without affecting inference on key demographic parameters.

2.7. Historical projections

We generated posterior predictive population trajectories by forward-simulating the model C-COV0 under four persistent sea-ice anomaly scenarios (best, worst, neutral, and observed). For each posterior draw, we extracted juvenile survival ($\phi_{J,t}$), adult survival ($\phi_{A,t}$), maturation probability (ψ_t), and the breeding probability (α , β). Breeding probability for each year was computed using a logistic link, $b_t = \text{logit}^{-1}(\alpha + \beta * x_t)$, where x_t was replaced by the scenario-specific anomaly series. Population dynamics were projected using a 2-stage Leslie matrix incorporating stage-specific survival, maturation, and fecundity ($F_t = 0.5 b_t$). Juvenile and adult abundances were propagated forward for each posterior draw, generating posterior predictive distributions of total population size (N_t) through time. For each scenario, we summarised trajectories using the median and 95% credible intervals. To estimate intrinsic population growth rate (r), we computed $\ln(N_t)$ and fitted a linear regression of $\ln(N_t)$ against time; these r estimates are reported in Table 2, while the full posterior predictive trajectories are shown in Figure 6.

3. Results

3.1. Population Breeding Probability

We estimated annual variation in population breeding probability; a latent variable plotted in Figure 3 (b). Estimates mostly oscillated between 55–60% but notably spiked up above 65% in years when sea-ice cover was especially low (e.g. 1980, 1993). The opposite effect is most notable during the period 1996–2001, which featured increased sea-ice cover while population breeding probability dropped to a minimum ~45% in 2001 (Figure 3 b). This is followed by a decade of estimates oscillating between ~50–60%, before increased sea-ice cover once again correlated with a reduction in population breeding probability below the 50% mark in 2013. The periods up to 1993, and from 2013 onwards were most pronounced in model C-COV0 deviating from the other two models, with a stronger negative linear relationship amplifying the effect on the estimates.

3.2. Population estimates

IPM estimates of total (female) population size at Macquarie Island N (i.e., juvenile plus adult) are plotted alongside the contributions of the different latent states in Figure 4. From 1980 until 2023 the total number of females varied temporally but never reached levels higher than the starting population. Notably, N peaked twice in the timeseries, once in the years just prior to 1990 and then a second time around 2001, after which estimates rapidly declined to settle at a population size of approximately 7000 females. Time-specific estimates of population growth rate (λ_t) reflect the population rate of change (growth or decline), with the overall rate of decline estimated at 0.992 ± 0.033 for the full 1980–2023 timeseries. While the confidence interval is wide, this supports a small population decline or may hint at a ‘levelling off’ of the growth rate being near a 1:1 ratio. Notably, λ is based on the total population estimates, including hidden states of unobserved individuals.

In contrast to N_t , the number of breeding adults ($n_{B,t}$) in the

population revealed a different trend with a steep initial decrease, before stabilising to a slow decline over the remainder of the study period (Figure 4). Notably, $n_{B,t}$ did not increase during the rises in N_t evident over the late 1980s and early 2000s, indicating that more individuals were alive within the hidden states of $n_{A,t}$ that did not return to breed in those years. Estimates of juvenile maturation (ψ_t) from the capture-mark-recapture data reveal this parameter increased during 1995–2000, suggesting juveniles matured at earlier ages to replace a portion of breeding adult females. This result is supported by a negative correlation between adult survival ($\Phi_{A,t}$) and juvenile maturation (ψ_t) in the MPM output (Appendix B).

Annual estimates of survival and detection probabilities were generated within the MPM framework. Overall juvenile survival ($\Phi_{J,t}$) was 81% (95% CI: 0.61–0.92) while mean adult survival ($\Phi_{A,t}$) was estimated at 82.2% (95% CI: 0.63–0.94). Detection varied significantly over the timeseries, which is a known limitation that needed to be accounted for before computing vital rates (Appendix B). Maturation probability (ψ_t) also varied over time with posterior estimates falling back on a vague prior between 10–50 % unless data was available during the time of active individual observations during the MPM capture-mark-recapture project (1993–2005). While this places some limitations on the model, this structure was tested through multiple iterations of IPM configurations. Both represent necessary assumptions to achieve model convergence and ensure a useful model structure that can generate predictions.

3.3. Covariate Effects on Breeding Probability

Figure 5 illustrates the outcomes of modelling population breeding probability in relation to annual changes in percent sea-ice cover within the foraging area of adult female southern elephant seals. Both sea-ice covariate models (lagged and unlagged) estimated a negative relationship, indicating population breeding probability declined with increasing sea-ice cover (Figure 5). Both covariate models were preferred over the no-covariate model on the basis of WAIC and LOO,

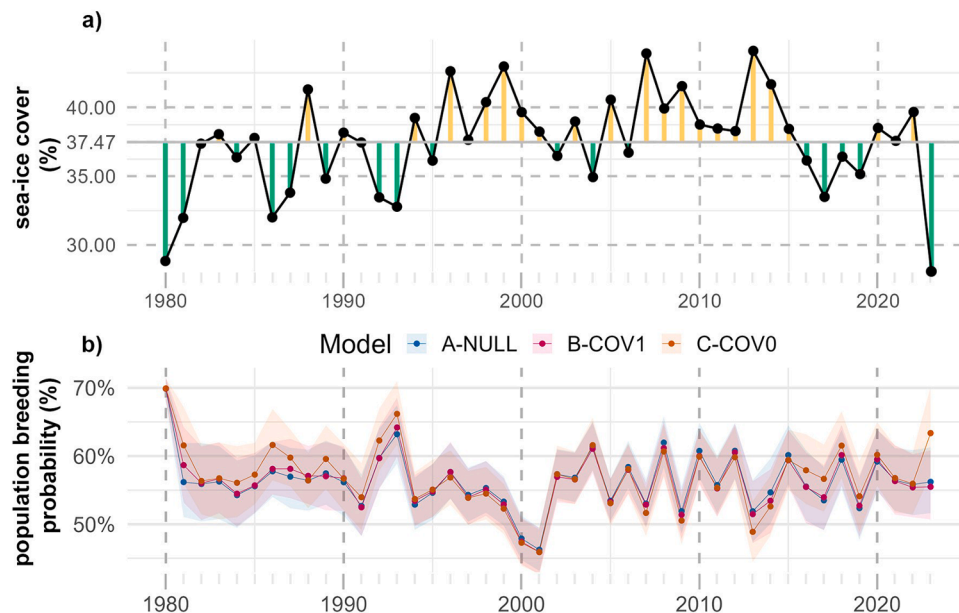


Figure 3. a) Average percentage sea-ice cover (area with greater than 15% sea-ice concentration) within the major foraging region identified for female southern elephant seals from Macquarie Island in the Southern Ocean (Hindell et al. 2025). Monthly satellite-derived (NSIDC 25 km) sea-ice concentrations were extracted from Niles Software at the Australian Antarctic Data Centre (Steketee, Chua, & Commonwealth of Australia 2023); aggregated and averaged from 1980 – 2023 over the months of March to October every year. Annual totals were then converted to annual anomalies by taking the difference from the mean of the timeseries, which is noted by the grey bar that divides the colouration of the anomalies on the y-axis. b) The estimated population breeding probability over time computed from an integrated population model of female southern elephant seals from Macquarie Island using capture-mark-recapture data and abundance counts. Estimates extracted from the NULL model (A-NULL), and models considering a lag-1 (B-COV1) and unlagged (C-COV0) sea-ice covariate effect on population-level breeding probability.

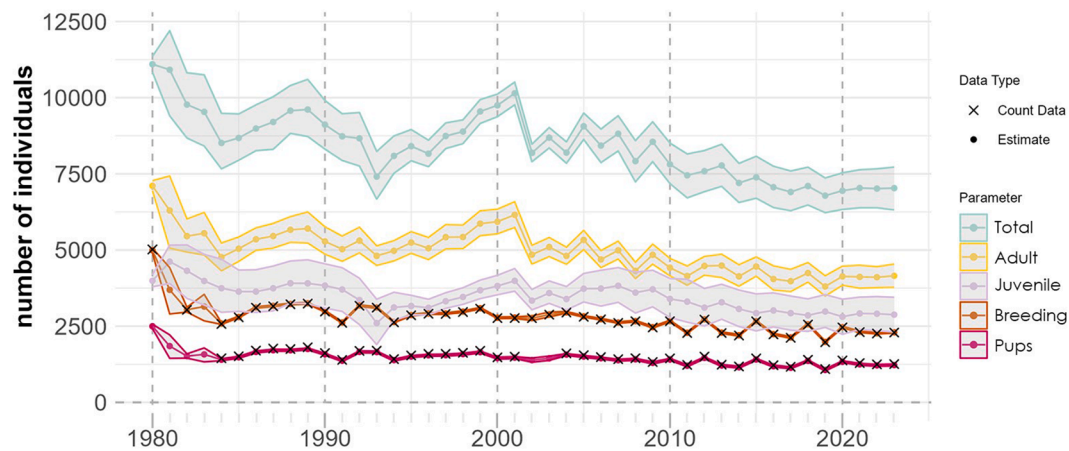


Figure 4. The estimated number of females (N) within a continuously monitored breeding site of southern elephant seals at the northern isthmus beach of Macquarie Island. Mean estimates of individuals (dots) and grey confidence intervals were derived from an Integrated Population Model (extracted from the best fit model B-COV1) with inputs from abundance counts (crosses) and capture-mark-recapture data. Different life-history groups are denoted by colour, including the total number of adults (yellow), which includes the sub-group of the number of breeding adults (orange), which is an observed component with data input. The total number of juveniles (purple) is estimated and includes the number of pups (pink), which is derived from data inputs as well as re-estimated by a state-space model. These estimates represent an important sub-sample of the Macquarie Island population from the main (isthmus) breeding site between 1980 and 2023.

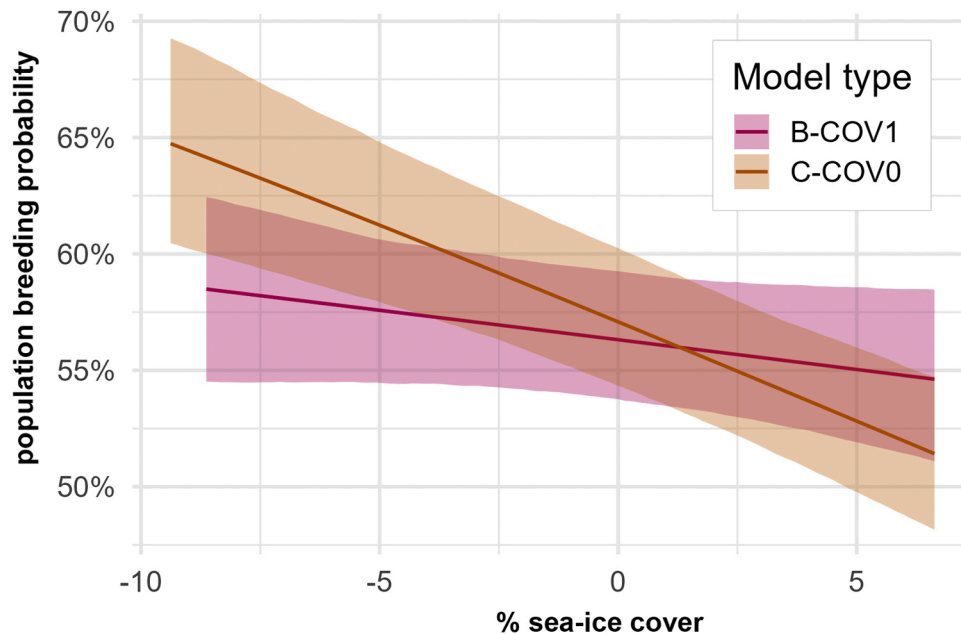


Figure 5. Estimated change in population breeding probability per percent increase of sea-ice cover within the key foraging habitat of adult female southern elephant seals from Macquarie Island. Output from a Generalised Linear Model estimates within a Bayesian Integrated Population Model.

with Bayesian model selection identifying the lagged model (B-COV1) as best fit by WAIC, though the LOO showed only a minor improvement (2 pt difference) (Table 1). Since none are definitive criteria, we present results for both covariate models. While the rate of change differs, the confidence intervals overlap, revealing either a weak negative relationship of ($\beta_{B-COV1} = -0.0103$; CI: [-0.025; 0.0037]) in the 1-year-lagged (B-COV1) model or a stronger, more definitive effect of sea-ice cover ($\beta_{C-COV0} = -0.0345$; CI: [-0.049; -0.021]) within the same year (C-COV0).

3.4. Historical scenarios

The projected population trends differed markedly among the four explored sea-ice scenarios (Figure 6; Table 2). The best-case (persistently low sea-ice cover anomaly) produced the slowest rate of decline, with an annual growth rate of -0.495% over the 43 year period. Under

neutral conditions (zero anomaly), the projected decline was stronger (-1.977% per year), and very closely resembled the observed annual decline of -2.144% . The worst-case scenario (persistently high sea-ice cover anomaly) resulted in the steepest population decline of -3.126% per year. Notably, the cumulative difference between scenarios varies, visually evident as the gap from neutral to worst (-1.15%) is smaller than the gap from neutral to best ($+1.48\%$). The final population size $N_{(2023)}$ for each scenario was extracted and listed in Table 2.

4. Discussion

4.1. Sea ice influencing breeding dynamics

Using an integrated population model, we investigated factors contributing to the long-term and continuing decrease in numbers of

Table 1

Model comparison between Integrated Population Models (IPMs) that compare the effects of a sea-ice covariate on population breeding probability. The IPM structure combines multiple data sources (pup counts, adult counts, and capture histories) into demographic estimates for a population of southern elephant seals from Macquarie Island. Three alternative covariate models were constructed, with log-likelihood functions calculated for each data input. Two information criteria (WAIC and LOO) were used to assess model fit and complexity (penalty terms: pWAIC and pLOO) as well as standard deviation (SE: LOO). Table sorted by WAIC with the best fit model (lowest WAIC) highlighted in bold.

Model	WAIC	p WAIC	LOO	p LOO	SE: LOO
Model B – COV1	5679.295	587.07	5664.521	579.69	471.80
Model C – COV0	5688.454	590.79	5666.748	579.93	470.51
Model A – NULL	5696.806	590.91	5687.181	586.10	474.25

southern elephant seals at Macquarie Island. By integrating census counts, demographic data and regionally relevant sea-ice conditions, we found new evidence of a long-hypothesized link between winter Antarctic sea-ice cover and the number of seals returning to Macquarie Island to breed (Hindell et al. 2017). Our IPM analysis revealed substantial temporal variation in population breeding probability (~45–65%), a latent parameter representing the proportion of the adult population breeding each year. This parameter describes a key unobserved demographic process, allowing us to test for external influences without requiring individual-level breeding information.

Three model scenarios were constructed to test the hypothesis that sea-ice cover within the foraging ground of adult females has an influence on breeding dynamics. Both covariate models consistently outperformed the null model according to WAIC and LOO metrics, supporting the inclusion of a sea-ice covariate in modelling population breeding probability. However, the estimated effect size was small in range and model predictions remained broadly similar among competing formulations. The covariate models documented a negative

relationship between high sea-ice cover and subtle changes in declining population breeding probability annually. Tracking studies found that around half of adult females forage along the Antarctic shelf in the austral winter (Pascoe et al. 2016, Hindell et al. 2017). This area can be covered by sea ice during the winter, which could mean spatial exclusion from this foraging region occurs in years when sea-ice extends farther north (Hindell et al. 2017). However, as not all adult females utilise this strategy, only a portion of the population is subjected to this covariate influence. Notably, the Southern Ocean off East Antarctica near the Ross Sea has seen an increase in sea-ice cover during La Niña years (Cai et al. 2023), with known negative consequences for adult female survival (Volzke et al. 2021). These regional differences in sea-ice dynamics illustrate a circumpolar trend of declining average sea-ice concentration (Rignot et al. 2019) may mask regionally relevant changes in habitat conditions for marine predators, who have physiological and behavioural limitations within their migratory ranges.

4.2. Lagged and unlagged effects on maternal investment

Female southern elephant seals who seasonally venture south shift their distribution with the ice edge as it expands and contracts over the winter months (Hindell et al. 2016). Unfortunately, our model selection did not clearly resolve which annual season of sea-ice conditions (lagged or unlagged) was most relevant to predicting how many females returned to the island to breed. Because both lagged and unlagged covariate models received similar support from model selection criteria, neither formulation was considered unequivocally superior. Consequently, differences between models are interpreted primarily as alternative hypotheses regarding the timing of environmental influence rather than competing explanations of population dynamics. Sea-ice conditions that extend beyond the continental shelf where females prefer to forage may spatially exclude them from their preferred foraging ground during a key period of energy acquisition, prior to returning to the sub-Antarctic to pup and mate (Hindell 1991). Having

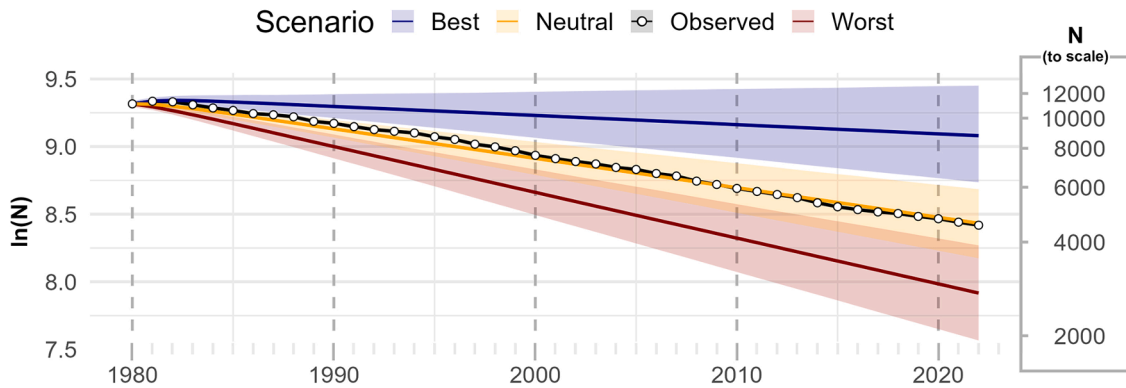


Figure 6. Posterior-predictive projections of total female population size (N , on natural log scale) for Macquarie Island southern elephant seals under four persistent sea ice anomaly scenarios. Observed population estimates (black points) are shown alongside posterior projections under persistent best (lowest anomaly– blue), neutral (zero anomaly– orange), and worst (highest anomaly– red) sea-ice conditions. Lines show median posterior estimates for each scenario. Shaded ribbons represent 95% credible intervals derived from forward-simulating IPM model C-COV0, illustrating increasing uncertainty in population trajectories through time.

Table 2

The intrinsic growth rates (r) of four projected scenarios of sea-ice cover anomaly conditions affecting population breeding probability, and thereby total population size in a modelled population of southern elephant seals from Macquarie Island. Linear regression models were applied to scenario-specific modelled total population size over time to derive the slope. The standard error (r_{SE}) and confidence intervals (r_{lo} ; r_{hi}) are given, as well as the same r values converted into the format of λ (annual population growth rate, calculated as: $1-r$) and percent growth rate (r_{pct}). The last column lists the final estimate of population size $N_{(2023)}$.

Scenario	r	r_{SE}	r_{lo}	r_{hi}	λ	r_{pct}	$N_{(2023)}$
Best	-0.00496	0.00095	-0.00688	-0.00304	0.995	-0.495	7106.275
Neutral	-0.01997	0.00092	-0.02182	-0.01812	0.980	-1.977	3740.652
Observed	-0.02167	0.00082	-0.02333	-0.02001	0.979	-2.143	3582.192
Worst	-0.03176	0.00090	-0.03358	-0.02993	0.969	-3.125	2261.260

to adapt and search for prey in a different region or extend their foraging duration can incur energetic costs that have been well documented for other seal species and there is no reason to expect that this does not hold for elephant seals (e.g., Hiruki-Raring et al. 2012; Jeanniard-Du-Dot et al. 2017; Kienle et al. 2022; Speakman, McHuron, & Arnould 2024). This increased cost can affect reproductive capacity in two ways; short-term because the current years' pup will gain less resources through lactation; and long-term if the mothers' own energetic resources are depleted to levels that increases their risk of mortality at sea. Both mechanisms are relevant to population processes as they ultimately result in fewer individuals in the breeding population. Considering short-term and long-term consequences is relevant to our results that the lagged and unlagged sea-ice models similarly contributed to a decline in population breeding probability, which may indicate both play a role.

Due to the phenology of their annual reproductive cycle, adult female seals return to their natal colony to give birth, even if they experienced poor winter foraging conditions that year (Oosthuizen et al. 2023). However, pup weaning mass is directly influenced by maternal investment (McMahon et al. 2017), as mothers acquire their energetic reserves from prey and store them as blubber, which is then converted to protein during lactation (Fedak, Arnborn, & Boyd 1996). Weaning mass has a strong influence on early juvenile survival (Postma, Bester, & De Bruyn 2013), which plays a significant role in population viability (McMahon et al. 2005b). Therefore, maternal energy is an important factor influencing pup survival (Burton et al. 1997) and even the pups' future reproductive success or age at breeding (Oosthuizen et al. 2015). Curiously, we documented that in some years, early maturing females (recruiting from juveniles) partially compensated for periods of reduced adult survival and breeding activity (Figure 4; Appendix B). But early maturation carries trade-offs for maternal fitness, pup survival and lifetime reproductive output (Arnborn, Fedak, & Rothery 1994), with further implications for long-term recruitment and population stability. The modelled parameter of population breeding probability captures a lot of the variation that is influenced by demographic processes. Indirect effects influencing reproductive effort may underpin the finding that model B-COV1, which included a one-year time lag, featured a more subtle negative influence of sea-ice cover on breeding probability; indicative of indirect effects being associated with overall high levels of natural variability in the data.

It is possible that some female seals do not return to breed in the same year they encounter high sea ice within their foraging range. If a pup does not survive their first three weeks prior to weaning, the mother may return to sea, in which case they may be missed from the recorded dataset. A direct response such as this may be captured by the stronger negative relationship in the unlagged model C-COV0. However, we once again argue that this direct effect only applies to a small proportion of the overall adult population. Therefore, it is likely that the answer lies within a combination of direct and indirect effects, with both covariate models identifying a clear and profound negative relationship with years of high sea-ice cover resulting in fewer adult females returning to breed on Macquarie Island.

4.3. Population rate of decline

Four projected population growth scenarios were run to visualise the sensitivity of long-term population dynamics to environmental conditions. We successfully reproduced the ongoing slow (2%) rate of decline observed in this population with our sea-ice covariate model, while both the best- and worst-case scenarios did not follow the same observed trend. This finding lends strong support to including sea-ice cover in conversations about this population's rate of recovery. Although all scenarios indicated continued mean population decline, the magnitude of variation between them was substantial. Notably, the gap between the best- and worst-case projected outcomes was large (>2.5 percentage points), illustrating that relatively small reductions in sea-ice conditions could yield disproportionately positive demographic outcomes over

decadal timescales. Confidence intervals of the best-case scenario hinted at a possible stabilising trend, including positive population growth rate estimates in the upper quantile. The modelled effect was cumulative, resulting in the projected N having doubled in size from ~3580 individuals (observed) to ~7100 individuals (under the 'best' case scenario), by 2023. In contrast, the 'worst' estimated $N_{(2023)}$ was indeed reduced (2260 individuals), but not half of the observed total. The apparent asymmetry reflects the nonlinear transformation of population breeding probability with a logistic link function. The sea-ice covariate was standardised, and all projections used the same demographic relationships estimated within the IPM. So, differences among scenarios arise solely from the imposed sea-ice conditions rather than from changes in model structure or parameterisation, while the nonlinear logistic transformation together with projected cumulative effects of demographic rates amplified these differences over time and produce asymmetric population trajectories.

Our results confirm that sea-ice conditions over recent decades have been largely unfavourable. In years when conditions were favourable (i.e. low sea-ice years), foraging access to the continental shelf waters increases for some females allowing them access to their preferred foraging ground during a critical time in their annual cycle when they are accumulating resources to fund their breeding effort. Notably, adult females display high site fidelity to marine foraging regions (Bradshaw et al. 2004; Robinson et al. 2012). If favourable conditions persisted, the observed effect could have almost stabilised the population as seen under the best-case projected scenario. Instead, females using the shelf encountered ongoing unfavourable conditions after 1995, which were initially compensated by early maturing juveniles. However, early maturing carries its own consequences for individual survival and lifetime reproductive capacity (Desprez et al. 2014), which may be what underpinned the observed high variability in population breeding probability post-2003. Overall, the historical projections emphasise how local-regional habitat conditions can have population-level consequences and that even small shifts in external environmental variables like sea-ice concentration can meaningfully alter population trajectories at scales relevant to the question of species recovery (growth versus decline, or in our case moderate versus weak decline).

Sea-ice changes south of Macquarie Island along the East Antarctic Coast between 130°E & 160°E differs from global trends. In this region sea-ice has been growing (Verfaillie et al. 2022) whereas it has been decreasing elsewhere (Pan, Li, & Watanabe 2022; Massom and Stammerjohn 2010). Sea-ice increase in the East Antarctic region coincides with atmospheric conditions such as the Southern Annular Mode (Verfaillie et al. 2022) and Southern Oscillation Index (Kwok & Comiso 2002) switching to consistently negative phases. The resulting changes in heat exchange between atmosphere and ocean influences circulation of the Antarctic Circumpolar Current and the location of winter sea-ice edge (Goosse et al. 2025). It is possible that female elephant seals feeding in this region over the Antarctic Shelf may benefit from reduced ice cover permitting access to their preferred foraging ground. However, this simplification does not account for other ecological factors and flow-on effects, such as sea-ice mediated primary production and bottom-up processes that influence prey availability and thus, needs to be treated with caution.

The IPM presents a flexible, quantitative framework for testing potential external drivers of change. It also provides new capability for simulation-based analyses, including population viability analyses and future projections. Quantifying annual variation in population breeding probability is an important finding itself. As a latent state, we acknowledge the limitations of estimating a population-level effect with assumed individual-level ecological processes that were simplified. Disentangling the difference between breeding adults versus non-breeding adult females (i.e., skipped breeding events) would be a useful future extension of this model. However, this will require retaining individual-level data for thousands of seals and producing estimates for each year in the time series, adding substantial processing time and cost

to the model. For this first iteration of the IPM, retaining flexibility was prioritised as the model was easily customised and tested, forming a baseline for future demographic analyses.

4.4. Demography in a Changing Climate

We show how external habitat conditions can shape the trajectory of a marine predator population in the Southern Ocean. This is especially relevant for protected marine mammal species that are undergoing a population recovery from commercial harvesting and would be expected to exhibit continued population increases. Many marine predators are subject to climate-mediated pressures on breeding success, including terrestrial-breeding pinnipeds, seabirds (Sojitra et al. 2024) and cetaceans (Vermeulen et al. 2025), many of which rely on the Southern Ocean ecosystem as their primary foraging ground. Similar population-level consequences have been documented for Northern Hemisphere marine mammals subject to anthropogenic disturbances (Pirrotta et al. 2019). Quantifying these demographic links continues to be a key hurdle for conservation and management, especially for data-poor marine mammal species (Keen et al. 2021). This challenge reflects a broader issue in ecological research: disentangling the interacting biological and environmental processes that drive population dynamics. Process-based approaches provide a powerful framework for linking observational data to underlying ecological mechanisms, and IPMs are especially well suited to this context. By combining multiple, incomplete data sources within a single hierarchical framework, IPMs allow demographic parameters to be estimated while accounting for observation error, variability in sampling effort, and gaps in the data. This is particularly valuable for long-lived marine predators in the Southern Ocean, where logistical constraints limit data availability. By jointly analysing multiple input data sources and environmental covariates, IPMs strengthen inference relative to analysing each dataset in isolation. Using an invaluable set of southern elephant seal field data, we demonstrated how this enables the estimation of otherwise unobservable processes such as breeding probability.

The modelling approach we presented here provides a practical framework for understanding population dynamics and supporting conservation management in data-poor systems. Individuals born today encounter rapidly changing ecological conditions across their range, driven by both localised pressures (e.g. coastal development at breeding sites) and broader-scale changes such as shifts in prey availability and marine food webs (McCormack et al. 2021). These pressures contribute to complex and interacting challenges, including climate change, habitat modification, and ongoing anthropogenic disturbance, as many species continue to recover from past exploitation. The IPM model structure is readily transferable to other taxa with similar life histories, including Southern Ocean pinnipeds (fur seals), long-lived seabirds (albatross and penguins), and other data-limited marine or terrestrial mammals, for which incorporating environmental variability into demographic models is critical for understanding population responses under changing conditions. In this context, the continued development and application of integrative modelling frameworks represent a key tool for improving population assessments and informing robust, evidence-based conservation and management strategies.

CRedit authorship contribution statement

Volzke Sophia: Writing – review & editing, Writing – original draft, Visualization, Validation, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Wotherspoon Simon J:** Writing – review & editing, Supervision, Software, Methodology, Formal analysis, Data curation, Conceptualization. **Corney Stuart P:** Writing – review & editing, Visualization, Supervision, Investigation, Funding acquisition. **Cleeland Jaimie B:** Writing – review & editing, Supervision, Investigation, Funding acquisition, Data curation. **Bestley Sophie:** Writing – review & editing, Validation,

Software, Methodology, Funding acquisition. **McMahon Clive R:** Writing – review & editing, Visualization, Validation, Supervision, Methodology, Investigation, Data curation, Conceptualization. **Hindell Mark A:** Writing – review & editing, Validation, Methodology, Investigation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.ecolmodel.2026.111854](https://doi.org/10.1016/j.ecolmodel.2026.111854).

Data availability

Research Link Provided
Southern elephant seal demography (Original data) (IMAS Metadata Catalogue)

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