RESEARCH ARTICLE

Global Change Biology WILEY

Ninety years of change, from commercial extinction to recovery, range expansion and decline for Antarctic fur seals at South Georgia

Jaume Forcada[1] | Joseph I. Hoffman[1,2] | Olivier Gimenez[3] | Iain J. Staniland[4] | Pete Bucktrout[1] | Andrew G. Wood[1]

[1]British Antarctic Survey, Natural Environment Research Council, UKRI, Cambridge, UK

[2]Department of Animal Behavior, University of Bielefeld, Bielefeld, Germany

[3]CEFE, CNRS, Univ Montpellier, EPHE, IRD, Montpellier, France

[4]International Whaling Commission, Impington, UK

Correspondence
Jaume Forcada, British Antarctic Survey, Natural Environment Research Council, UKRI, Cambridge, UK.
Email: jfor@bas.ac.uk

Abstract

With environmental change, understanding how species recover from overharvesting and maintain viable populations is central to ecosystem restoration. Here, we reconstruct 90 years of recovery trajectory of the Antarctic fur seal at South Georgia (S.W. Atlantic), a key indicator species in the krill-based food webs of the Southern Ocean. After being harvested to commercial extinction by 1907, this population rebounded and now constitutes the most abundant otariid in the World. However, its status remains uncertain due to insufficient and conflicting data, and anthropogenic pressures affecting Antarctic krill, an essential staple for millions of fur seals and other predators. Using integrated population models, we estimated simultaneously the long-term abundance for Bird Island, northwest South Georgia, epicentre of recovery of the species after sealing, and population adjustments for survey counts with spatiotemporal applicability. Applied to the latest comprehensive survey data, we estimated the population at South Georgia in 2007–2009 as 3,510,283 fur seals [95% CI: 3,140,548–3,919,604] (ca. 98% of global population), after 40 years of maximum growth and range expansion owing to an abundant krill supply. At Bird Island, after 50 years of exponential growth followed by 25 years of slow stable growth, the population collapsed in 2009 and has thereafter declined by −7.2% [−5.2, −9.1] per annum, to levels of the 1970s. For the instrumental record, this trajectory correlates with a time-varying relationship between coupled climate and sea surface temperature cycles associated with low regional krill availability, although the effects of increasing krill extraction by commercial fishing and natural competitors remain uncertain. Since 2015, fur seal longevity and recruitment have dropped, sexual maturation has retarded, and population growth is expected to remain mostly negative and highly variable. Our analysis documents the rise and fall of a key Southern Ocean predator over a century of profound environmental and ecosystem change.

KEYWORDS
Antarctic fur seal, Antarctic krill, *Arctocephalus gazella*, decline, depletion, environmental change, integrated population model, pinniped, range expansion, recovery dynamics

1 | INTRODUCTION

The unregulated harvesting of marine predators causes defaunation and trophic downgrading with negative repercussions for ecosystem processes (Dulvy et al., 2021; Estes et al., 2011; Luypaert et al., 2020; McCauley et al., 2015). When harvesting ceases, the targeted species are often heavily depleted and their path to recovery is thereafter determined by novel ecosystem states, predator–prey interactions, harvesting regimes and environmental stressors (Hobbs et al., 2009; Jachowski et al., 2015; McNellie et al., 2020; Stier et al., 2016). Because these effects create transient population states (Hastings, 2004), only long-term analyses can identify which novel conditions enable recovery (Hastings et al., 2018), and inform best management practices (e.g. Larkin, 1996; Lindegren et al., 2009). However, as the supporting population data are often unavailable, the status of many affected species remains uncertain.

A major case is in the Southern Ocean, where historical unregulated extraction sequentially reduced fur seal, whale and finfish populations to commercial extinction levels (Gulland, 1983; Laws, 1977; Miller, 1991). This is hypothesised to have altered ecosystem trophodynamics (Hoffman et al., 2022; Laws, 1977; Sladen, 1964; Surma et al., 2014) and after harvesting ceased, the various targeted species recovered to varying degrees (Calderan et al., 2020; Hollyman, Hill, et al., 2021; Jackson et al., 2020; Zerbini et al., 2019). In the Southwest Atlantic sector, the Antarctic fur seal (*Arctocephalus gazella*) at South Georgia staged one of the fastest recoveries (Bonner, 1968; Laws, 1973; Payne, 1977) thanks to reduced mortality, high reproductive success and a locally abundant food supply (Bonner, 1968; Mackintosh, 1973; Marr, 1961; Siegel & Watkins, 2016). After near extirpation by 1907 and rediscovery in 1933–1936 (Mackintosh, 1967), the total population grew to an estimated 369,000 animals in 1976 (Payne, 1979), and from there to 1.55 million animals in 1991 (Boyd, 1993). This represents 95%–98% of the species' global abundance (Boyd, 1993; Forcada & Staniland, 2018), making the Antarctic fur seal at South Georgia the second most abundant pinniped in the Southern Hemisphere and the most abundant eared seal in the World (Costa et al., 2006). This abundant predator is considered a prime indicator species for resource management in the Southern Ocean ecosystem (Agnew, 1997; Croxall & Prince, 1979).

However, the status of this population remains uncertain because the latest abundance estimate did 'not reflect the pup production had 1990/91 been an average year' (Boyd, 1993, p. 22). Furthermore, the adjustment made to estimate the total population size was also derived from unrepresentative data, because 'nothing is [was] known of the structure of the male herd other than the mean age of a small sample of breeding bulls' (Payne, 1979, p. 9). Subsequently, and without any additional population surveys and supporting data, South Georgia was reported to carry between 4.5 and 6.2 million fur seals in 1999/2000. This is of concern because accurate population estimates are essential to evaluate the conservation status of a species and to grant adequate levels of protection.

Without a real and credible baseline, the notion of the Antarctic fur seal as super-abundant species contributed to (i) unwarrantedly depicting it as an ever-increasing environmental nuisance (Bonner, 1985; Convey & Hughes, 2022; Foley & Lynch, 2019), despite this being a naturally abundant species (Cook, 1777, v. 2, p. 213; Weddell, 1825, p. 54); and (ii) delisting it as a 'Specially Protected Species' in 2006 by the Antarctic Treaty Consultative Parties (SCAR, 2006), without a specific action plan for monitoring and reassessment (Jabour, 2008). Almost coincident with this decision, the population of Bird Island, the likely epicentre of historical recovery at South Georgia, collapsed in 2009 and has continued to decline ever since (Forcada & Hoffman, 2014). Antarctic fur seals have increasingly become more sensitive to external stressors (Forcada et al., 2008; Forcada & Hoffman, 2014; Krause et al., 2022), and their numbers are also declining elsewhere in the Southwest Atlantic sector of the Southern Ocean (Hofmeyr, 2016; Krause et al., 2022), where most of the global population currently resides.

To produce an improved population trajectory and to identify the drivers of population size changes, we develop new methods for long-term population assessment. Conventional methods to estimate pinniped abundance are based on counts of animals at breeding locations on land or ice taken at peak breeding dates (Buckland & York, 2018; Hammond et al., 2021). These counts are subsequently adjusted for detectability bias, which occurs when animals are within detection range but cannot be perceived by observers; and when they are unavailable while within or outside detection range. This availability bias is typically modelled from haul out studies (Southwell et al., 2008; Thompson et al., 1997; Womble et al., 2020), which may not account for the absences of individuals due to delayed accession to breeding, and sexual segregation in haul out behaviour due to variable rates of fecundity, breeding propensity, immigration and temporary emigration. This leads to additional adjustments typically based on life tables (e.g. Hammill et al., 2013; LaRue et al., 2021; Pitcher et al., 2007). However, these require demographic parameters that are often unavailable (e.g. Payne, 1979), which may not be specific to the focal population and may not account for spatiotemporal variation as required in serial abundance estimates.

Instead, we use integrated population models (IPMs), which jointly analyse individual and population-level data in a single statistical model, allowing the use of available information, and to achieve comprehensive error propagation throughout the model (Besbeas et al., 2002; Newman et al., 2014; Schaub & Abadi, 2011; Schaub & Kéry, 2021). IPMs allow for imperfect detection and observation error and carry this uncertainty over datasets, producing better and often more precise inference than other methods. They effectively combine in situ population counts and demographic data to directly infer demographic rates and availability bias. Here, we jointly analyse age-at-count and reproduction data, as well as capture–mark–recapture (CMR) data from the tagging and genetic sampling of individuals to obtain key demographic rates. Using flexible CMR model structures, we account for observed (counted) and unobserved states, estimate recruitment and breeding probabilities in both females and males, and temporary emigration in territorial males, allowing us to infer total population numbers while deriving adjustments for survey counts. Moreover, we produce the first robust life history and demographic assessment for the male of this species, which is the key to accurately evaluating the total Antarctic fur seal population size.

We apply these methods to photographic counts from the latest dedicated aerial surveys of South Georgia (2006/07 and 2008/09),

which we combine with genetic, demographic, reproductive and count data from an extensively studied representative population at Bird Island (Doidge et al., 1984; Forcada & Hoffman, 2014). We thus provide an assessment of total population and range expansion at South Georgia, and a population trajectory spanning the 90 years since commercial extinction, subsequent increase, range expansion and local decline at Bird Island, in relation with external drivers.

2 | MATERIALS AND METHODS

2.1 | South Georgia survey data

Two helicopter surveys of the entire South Georgia archipelago, conducted from 11 to 14 December 2006 and from 3 to 9 December 2008, provided aerial photographs from digital SLR cameras of the seal breeding range near the peak pupping days. Counts were extracted from images by at least two observers working independently using consistent training and methodology, and according to four categories: pups, females, territorial males and non-territorial males (Appendix S1). The pupping season (mid-November to mid-January) typically peaks between 6 and 10 December with high spatial synchrony and around the peak pupping day, numbers of newborn pups, breeding females and territorial males at each location reach their maximum values and the counts are less variable than at later dates (Duck, 1990; Forcada et al., 2005; Hofmeyr et al., 2007).

Antarctic fur seals at Bird Island (54°00′ S, 38°02′ W), South Georgia, were surveyed through complete island counts on seven more occasions. Visual counts were conducted from elevated vantage points by trained fur seal biologists in December 1988, 1989, 1990, 1994 and 1997. In December 2003 and 2016, additional counts were obtained

onwards (Duck, 1990; Forcada et al., 2008). At this site, the mean annual pup production was 709 (SE=22) from 1984 to 2010, and 409 (SE=34) from 2010 to date, after a major population decline (Forcada & Hoffman, 2014). Detailed data collection methods (Forcada et al., 2008; Forcada & Hoffman, 2014) are available in Appendix S1.

Genetic samples were collected during daily surveys of nearly all the territorial individuals observed at SSB since 1995, and between-year genetic recaptures are available for 13 seasons (1995–2007 inclusive). For each sample, total genomic DNA was extracted using a modified phenol-chloroform protocol and genotyped at nine highly polymorphic microsatellite loci as described by Hoffman et al. (2003). None of the loci showed significant deviations from Hardy–Weinberg or linkage equilibrium and the genotyping error rate was very low at <0.005 per reaction. The probability of identity was also very low (1.354×10^{-12}), indicating that identical genotypes most likely represent resampled individuals. To identify genetic recaptures, the microsatellite genotypes were checked for duplicate entries using the program *identity* (Allen et al., 1995) as described in detail by Hoffman et al. (2006).

2.3 | Integrated population models

2.3.1 | Females

We used a different IPM for each sex with an age–stage-structured population projection model (Caswell, 2001) as main building block, assuming a birth pulse and a pre-breeding census. The female model describes survival and accession to breeding (recruitment) for immature females (pre-breeders; P) of ages 3–7, and the transition of individuals through breeding states breeder (B) and mature non-breeder (N). The expected number of females in year $t+1$ is

$$E\left([N_{t+1}|N_t]\right) = E\left[\begin{bmatrix} N_{1,t+1}|N_{1,t} \\ N_{2,t+1}|N_{2,t} \\ N_{3,t+1}|N_{3,t} \\ \vdots \\ N_{7,t+1}|N_{7,t} \\ N_{N,t+1}|N_{N,t} \\ N_{B,t+1}|N_{B,t} \end{bmatrix}\right] = \begin{bmatrix} 0 & \varsigma_F\phi_0\phi_1\phi_3 a_3 & \cdots & \varsigma_F\phi_0\phi_1\phi_7 a_7 & \varsigma_F\phi_0\phi_1(\phi_N\psi_{NB}) & \varsigma_F\phi_0\phi_1(\phi_B\psi_{BB}) \\ \phi_2 & 0 & 0 & 0 & 0 & 0 \\ 0 & \phi_3(1-a_3) & 0 & 0 & 0 & 0 \\ 0 & 0 & \ddots & 0 & 0 & 0 \\ 0 & 0 & 0 & \phi_7(1-a_7) & 0 & 0 \\ 0 & 0 & 0 & 0 & \phi_N\psi_{NN} & \phi_B\psi_{BN} \\ 0 & \phi_3 a_3 & \cdots & \phi_7 a_7 & \phi_N\psi_{NB}+\iota & \phi_B\psi_{BB}+\iota \end{bmatrix}_t \begin{bmatrix} N_{1,t}|N_{1,t-1} \\ N_{2,t}|N_{2,t-1} \\ N_{3,t}|N_{3,t-1} \\ \vdots \\ N_{7,t}|N_{7,t-1} \\ N_{N,t}|N_{N,t-1} \\ N_{B,t}|N_{B,t-1} \end{bmatrix}$$

based on digital SLR camera images. Hereafter, an Antarctic fur seal breeding season is referred to by the second year of the split-year austral summer (e.g. 2007–2008 is referred to as 2008).

2.2 | Demographic, productivity, genetic and count data

Annual mark–recapture, pup production and individual count data of Antarctic fur seals at a designated Special Study Beach (SSB) from Bird Island (Doidge et al., 1984), have been consistently collected since 1984

where $N_{j,t}$ is the number of females for ages $j=1,\dots,7$, and $N_{N,t}$ and $N_{B,t}$ are number of mature non-breeders and breeders respectively at year t. Apparent survival parameters are: $\phi_{0,t}$ for pups from birth to tagging at 1.5 months of age, $\phi_{1,t}$ from tagging to the end of the first year (census year), $\phi_{j,t}$ for ages $j=2,\dots,7$, and $\phi_{N,t}$ and $\phi_{B,t}$ for mature non-breeders and breeders, between years t and $t+1$. Transition parameters between t and $t+1$ are $a_{j,t}$, defined as the probability that an immature female (pre-breeder) of age j starts to breed at that age (Pradel & Lebreton, 1999); parameters $\psi_{B-,t}$ and $\psi_{N-,t}$ are the probabilities of being in states B or N in year t and in year B or N at $t+1$, conditional on surviving between years. ς_F is the proportion of females

at birth, and ι is the immigration rate, defined as number of breeding immigrants in year $t+1$ per mature female in the population in year t (Abadi, Gimenez, Ullrich, et al., 2010).

Here, CMR data contribute to estimate survival, recruitment and breeding probability. A multistate Cormack–Jolly–Seber mark–recapture model (MSCJS) was formulated as a Bayesian state-space model (Gimenez et al., 2007), including 11 states: P_j, for $j=0$–7, where P_0 is pups, states P_1 to P_{7+} are pre-breeders of ages 1–7 and above, B is breeders, N is mature non-breeders or skippers and D is an absorbing state for dead or permanently emigrated females. Pre-breeders at ages $j=3$–7 access breeding (state B) with probability a_j, or stay as pre-breeders with probability $1-a_j$. Some pre-breeders, typically of ages seven 7 or more, are never observed breeding.

The state process equation for marked individual i and year t, is formulated as

$$z_{i,t+1} \sim \begin{pmatrix} 0 & \phi_{i,t}^1 & 0 & 0 & 0 & 0 & 0 & 0 & 1-\phi_{i,t}^1 \\ 0 & 0 & \phi_{i,t}^2 & 0 & 0 & 0 & 0 & 0 & 1-\phi_{i,t}^2 \\ 0 & 0 & 0 & \phi_{i,t}^3\left(1-a_{i,t}^3\right) & 0 & 0 & \phi_{i,t}^3 a_{i,t}^3 & 0 & 1-\phi_{i,t}^3 \\ 0 & 0 & 0 & 0 & \ddots & 0 & \vdots & 0 & \vdots \\ 0 & 0 & 0 & 0 & 0 & \phi_{i,t}^7\left(1-a_{i,t}^7\right) & \phi_{i,t}^7 a_{i,t}^7 & 0 & 1-\phi_{i,t}^7 \\ 0 & 0 & 0 & 0 & 0 & \phi_{i,t}^P & 0 & 0 & 1-\phi_{i,t}^P \\ 0 & 0 & 0 & 0 & 0 & 0 & \phi_{i,t}^B\psi_{i,t}^{BB} & \phi_{i,t}^B\psi_{i,t}^{BN} & 1-\phi_{i,t}^B \\ 0 & 0 & 0 & 0 & 0 & 0 & \phi_{i,t}^N\psi_{i,t}^{NB} & \phi_{i,t}^N\psi_{i,t}^{NN} & 1-\phi_{i,t}^N \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{pmatrix}$$

where rows and columns are departure and arrival states, both P_0 to P_{7+}, B, N and Dead, between years t and $t+1$.

The observation process $Y_{i,t}$, conditional on $z_{i,t}$, maps the true state at season t on the observed state, and is based on five types of observations of females: seen as tagged pup (1), seen as pre-breeder (2), with probabilities $p_{i=1-3,t}^{P1}$ and $p_{i=4+,t'}^{P2}$ seen as breeder (3), with probability p_t^B, seen as mature non-breeder (4) and with probability p_t^N, and not seen (5). This is formulated as

$$Y_{i,t+1}\,|\,z_{i,t+1} \sim \begin{pmatrix} 0 & 0 & 0 & 0 & 1 \\ 0 & p_t^{P1} & 0 & 0 & 1-p_t^{P1} \\ 0 & p_t^{P1} & 0 & 0 & 1-p_t^{P1} \\ 0 & p_t^{P1} & 0 & 0 & 1-p_t^{P1} \\ 0 & p_t^{P2} & 0 & 0 & 1-p_t^{P2} \\ 0 & p_t^{P2} & 0 & 0 & 1-p_t^{P2} \\ 0 & p_t^{P2} & 0 & 0 & 1-p_t^{P2} \\ 0 & p_t^{P2} & 0 & 0 & 1-p_t^{P2} \\ 0 & 0 & p_t^B & 0 & 1-p_t^B \\ 0 & 0 & 0 & p_t^N & 1-p_t^N \\ 0 & 0 & 0 & 0 & 1 \end{pmatrix}$$

where rows are states P_0 to P_{7+}, B, N and Dead, and columns are observation types (1–5) at year t. We denote the CMR likelihood as $\mathcal{L}_{MSCJS}(h\,|\,\phi, a, \psi, p)$, where h is the female recapture history as defined by observation types. Further details on Bayesian multistate model implementations can be found in Gimenez et al. (2007) and Kéry and Schaub (2012).

Data on pup production, equivalent to the breeding female population, contribute to estimate population sizes and demographic rates, including immigration. The state-space formulation is thus further composed of a state process defined by the matrix population model, with likelihood $\mathcal{L}_{sys}(N\,|\,\phi, a, \psi, \iota)$, and uses Poisson distributions to introduce demographic stochasticity as follows.

$$N_{P_1,t+1} \sim \text{Poisson}\left(\varsigma_F\,\phi_{0,t}\,\phi_{1,t}N_{BI,t}\right)$$

$$N_{P_2,t+1} \sim \text{Poisson}\left(\phi_{2,t}N_{2,t}\right)$$

$$N_{P_j,t+1} \sim \text{Poisson}\left(\phi_{j,t}\left(1-a_{j,t}\right)N_{P_{j-1},t}\right), \text{for } j=3, \dots, 7$$

$$N_{N,t+1} \sim \left[\text{Poisson}\left(N_{N,t}, \phi_{N,t}\,\psi_{NN,t}\right) + \text{Poisson}\left(N_{B,t}, \phi_{B,t}\,\psi_{BN,t}\right)\right]$$

and

$$N_{BI,t+1} \sim \left[\text{Poisson}\left(N_{N,t}, \phi_{N,t}\,\psi_{NB,t}\right) + \text{Poisson}\left(N_{B,t}, \phi_{B,t}\,\psi_{BB,t}\right) + \sum_j \text{Poisson}\left(\phi_{j,t}a_{j,t}N_{P_{j-1},t}\right) + \text{Poisson}\left(\left(N_{N,t}+N_{B,t}\right)\iota\right)\right],$$

where

$$N_{B,t+1} \sim \left[\text{Poisson}\left(N_{N,t}, \phi_{N,t}\,\psi_{NB,t}\right) + \text{Poisson}\left(N_{B,t}, \phi_{B,t}\,\psi_{BB,t}\right) + \sum_j \text{Poisson}\left(\phi_{j,t}a_{j,t}N_{P_{j-1},t}\right)\right],$$

N_B includes new recruits and returning mature females as breeders, and N_{BI} includes the same demographic groups plus immigrants. The distinction between N_B and N_{BI} allows for estimates of number of immigrants N_I, and the fecundity (or pregnancy) rate, F_t, which is the number of mature females ($N_B + N_N$) in year t which survive and breed in year $t+1$ (excluding recruits and immigrants in year $t+1$), divided by the number of mature females surviving to year $t+1$.

The observation process conditional on this state process is based only on the count of breeding animals (n_{BI}), equivalent to the sum of daily pups produced in each season, $y_{2,t}$, which is observed with little error (Forcada et al., 2005). We model these counts as $y_{2,t} \sim \text{Poisson}(N_{BI,t})$, where $N_{BI,t}$ is the number of breeders including immigrants, with likelihood $\mathcal{L}_{obs}(y_2\,|\,N_B)$. The product of state and

observed process likelihoods is the likelihood of the state-space model, $\mathcal{L}_{\text{sys}}(\boldsymbol{N} \,|\, \boldsymbol{\phi}, \boldsymbol{a}, \boldsymbol{\psi}, \iota) \times \mathcal{L}_{\text{obs}}(\boldsymbol{y}_2 \,|\, N_B)$.

To evaluate the proportion of the estimated study population, $E\left(\begin{bmatrix} N_{t+1} | N_t \end{bmatrix}\right)$, that represents a female count at the SSB (denoted with superscript S) obtained between 1 November and 31 December (e.g. n_j^s for day j), we model the observed daily total female counts with a generalised additive mixed model (GAMM). We select a Poisson–log-normal structure (Gelman & Hill, 2006), because the daily count series data tend to be overdispersed, with

$$n_j \sim \text{Poisson}(\mu_j),$$

$$\log(\mu_j) = \beta_0 + \sum_k b_k(d_j)\beta_k + \varepsilon_j,$$

where d_j is the jth day of the survey season, b_k is the basis of a penalized regression spline and ε_j are temporal random effects, with $\varepsilon_j \sim N(0, \sigma_\varepsilon^2)$. The hyperparameter σ_ε measures overdispersion, with $\sigma_\varepsilon = 0$ corresponding to a simple Poisson generalised additive model. Alternatively, we consider

$$E\left(\begin{bmatrix} N_{t+1} | N_t \end{bmatrix}\right) = E\left(\begin{bmatrix} N_{1,t+1}|N_{1,t} \\ N_{2,t+1}|N_{2,t} \\ \vdots \\ N_{8,t+1}|N_{8,t} \\ \vdots \\ N_{11,t+1}|N_{11,t} \\ N_{N,t+1}|N_{N,t} \\ N_{T,t+1}|N_{T,t} \end{bmatrix}\right) = \begin{bmatrix} \varsigma_M \phi_0 \phi_1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \phi_2 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & \ddots & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & \phi_8(1-a_8) & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & \ddots & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \phi_{11}(1-a_{11}) & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & \phi_N\psi_{NN} & \phi_T\psi_{TN} \\ 0 & 0 & 0 & \phi_8 a_8 & \cdots & \phi_{11}a_{11} & \phi_N\psi_{NT}+\iota & \phi_T\psi_{TT}+\iota \end{bmatrix}_t \begin{bmatrix} N_{1,t}|N_{1,t-1} \\ N_{2,t}|N_{2,t-1} \\ \vdots \\ N_{8,t}|N_{8,t-1} \\ \vdots \\ N_{11,t}|N_{11,t-1} \\ N_{N,t}|N_{N,t-1} \\ N_{T,t}|N_{T,t-1} \end{bmatrix}_t$$

$$\log(\mu_{j,t}) = \beta_0 + \sum_k b_k(d_{j,t})\beta_k + \varphi\epsilon_{j,t-1} + \zeta_{i,t},$$

$$\zeta_{i,t} \sim N(0, \sigma_\varepsilon^2),$$

where φ is an autocorrelation parameter with values between −1 and 1, and $\epsilon_{j,t-1}$ is the residual associated with observation at day t−1. The likelihood is $\mathcal{L}_c(\boldsymbol{n} \,|\, \boldsymbol{\beta}, \mathbf{b}, \lambda, \varphi, \zeta)$, where β are unknown parameters (penalties), $\mathbf{b}$ is the vector of k basis functions and λ are smoothing parameters.

With the daily female count model, the likelihood of the IPM is the joint likelihood of the different parts;

$$\mathcal{L}(\boldsymbol{h}, \boldsymbol{\phi}, \boldsymbol{a}, \boldsymbol{\psi}, \boldsymbol{p}, \boldsymbol{y}, \boldsymbol{n}_s | N_B, \iota) = \mathcal{L}_{\text{MSCJS}}(\boldsymbol{h} \,|\, \boldsymbol{\phi}, \boldsymbol{a}, \boldsymbol{\psi}, \boldsymbol{p}) \times \mathcal{L}_{\text{sys}}(\boldsymbol{N} \,|\, \boldsymbol{\phi}, \boldsymbol{a}, \boldsymbol{\psi}, \iota) \times \mathcal{L}_{\text{obs}}(\boldsymbol{y} \,|\, N_B) \times \mathcal{L}_c(\boldsymbol{n}_s \,|\, \boldsymbol{\beta}, \mathbf{b}, \lambda, \varphi, \zeta)$$

The combined likelihood produces two derived quantities, $N_{M,t}^S / E\left(n_j^s\right)$ and $N_{B,t}^S / E\left(n_j^s\right)$, where M is for mature females, B for breeders and $E\left(n_j^s\right)$ is the predicted count at SSB on the jth day. These are used as multipliers of observed counts at other locations to obtain estimates of total number of mature $\hat{N}_M = \sum_c n_j^c \hat{N}_M^S / E\left(n_j^s\right)$ and breeding females $\hat{N}_B = \sum_c n_j^c \hat{N}_B^S / E\left(n_j^s\right)$, where n_j^c is the female count at colony c on day j, and the second quantity is equivalent

to pup production. These equations assume that the dynamics of daily counts at SSB and other locations are highly correlated, which is accurate within Bird Island and across other locations (see Section 3).

To account for pre-breeders and obtain an estimate of total number of females at South Georgia, we use

$$\hat{N}_F = \left(1 + \frac{\sum_k \hat{N}_{P_k}^S}{\hat{N}_M^S}\right) \frac{\hat{N}_M^S}{E\left(n_j^s\right)} \sum_c n_j^c$$

where $\hat{N}_{P_k}^S$ is the estimated number of pre-breeders of age k, for k=1 to 7+, at SSB.

2.3.2 | Males

The male IPM has a combined age–stage matrix model with pre-territorial males (P) of ages 1–11+ (ages 11 or older), and mature states including territorial (T) and mature non-territorial (N). The expected number of males in year t+1 is

where $N_{j,t}$ is the number of males for ages j=1–11, and $N_{N,t}$ and $N_{T,t}$ are numbers of mature non-territorial and territorial in year t. Apparent survival parameters are $\phi_{0,t}$ for male pups from birth to tagging, and between year t and year t+1 are $\phi_{1,t}$ for weanlings, from tagging to the end of the first year; $\phi_{j,t}$ for males of ages j=2–11; and $\phi_{N,t}$ and $\phi_{T,t}$ for mature males. Transition parameters between years t and t+1 are $a_{j,t}$, defined as the probability that an immature male of age j starts to hold territory at that age; and $\psi_{T-,t}$ and $\psi_{N-,t}$ are the probabilities of being in states T or N in year t and in T or N at t+1, conditional on surviving between years. The proportion of males at birth is ς_M, and ι is the proportion of immigrants among territorial males.

CMR data contribute to estimate apparent survival, first-time accession to territory and probability of being territorial having held a territory before. Pup production data contribute to estimate population sizes and all demographic rates. For implementation, the CMR analysis was split into separate likelihoods given the different type, sample size and short temporal overlap between datasets. Thus, pups with implanted PIT-tags at birth (since 2001) represent the pre-territorial component, and are used to model $\phi_{j,t}$ and $a_{j,t}$; while genetic samples from territorial males (1995–2007) contribute to estimate their survival, territory tenure and temporary emigration

rates. Because the elapsed time between birth and accession to territory can be 10 years or more, observations of pre-breeders were limited and sparse (over 22 years, only 4.6% of 1773 PIT-tagged male pups were observed as territorial males), making IPM fitting and selection inefficient. As a valid alternative (Besbeas et al., 2002), we therefore use estimates from a simplified MSCJS recruitment model (Pradel & Lebreton, 1999) of the PIT-tag data as informative priors for $\phi_{j,t}$ and $a_{j,t}$ in the IPMs.

Nearly all the territorial males are genetically sampled every season, allowing for robust estimates of abundance using CMR models. We use a multistate Jolly–Seber model, selecting a hierarchical state-space formulation (Kéry & Schaub, 2012) with parameter-expanded data augmentation (Royle & Dorazio, 2009). Here, the number of individuals alive during the study is N^s, and b_t is the probability that a new territorial male enters the population in year t, so that the number of new territorial males in a year is $B_t = N^s b_t$. The augmented dataset contains M individuals, of which N^s is a subset, allowing for derivation of b_t in a restricted dynamic occupancy model framework (Royle & Dorazio, 2009). This relies on γ_t, defined as the probability that a male from M holds territory for the first time in year t, so that $E(B_t) = M \prod_{i=1}^{t-1} (1 - \gamma_i)\gamma_t$ and $N^s = \sum B$. The state process for sampled male i and year t, is then formulated as

$$z_{i,t+1} \sim \begin{pmatrix} 1-\gamma_t & \gamma_t & 0 & 0 \\ 0 & \phi_{i,t}^{\mathsf{T}}\left(1-\psi_{i,t}^{\mathsf{TN}}\right) & \phi_{i,t}^{\mathsf{T}}\psi_{i,t}^{\mathsf{TN}} & 1-\phi_{i,t}^{\mathsf{T}} \\ 0 & \phi_{i,t}^{\mathsf{N}}\psi_{i,t}^{\mathsf{NT}} & \phi_{i,t}^{\mathsf{N}}\left(1-\psi_{i,t}^{\mathsf{NT}}\right) & 1-\phi_{i,t}^{\mathsf{N}} \\ 0 & 0 & 0 & 1 \end{pmatrix}$$

where the states in rows and columns are P (not yet territorial in the population), T, N and Dead (or permanently emigrated), between years t and $t+1$. The corresponding observation process is

$$Y_{i,t+1} \mid z_{i,t+1} \sim \begin{pmatrix} 0 & 1 \\ p_t^{\mathsf{T}} & 1-p_t^{\mathsf{T}} \\ 0 & 1 \\ 0 & 1 \end{pmatrix}$$

where p_t^{T} is the recapture probability of territorial males. As non-territorials went unobserved, the multistate formulation part is analogous to a temporary emigration model (Schaub et al., 2004). We denote the likelihood as $\mathcal{L}_{\mathsf{MSJS}}(\gamma, \phi, \psi, p, N|h)$. Because the number of new territorial males each year (B_t) confounds locally born males starting to hold territory with immigrants that never held a territory at SSB before, these two components were separated with the demographic part of the IPM and the combined datasets (see below).

Data on pup production contribute to estimate population sizes of pre-territorial males and all demographic rates, including immigration. The state-space formulation is thus further composed of a state or system process, defined by the matrix population model with likelihood $\mathcal{L}_{\mathsf{sys}}(N|\phi, a, \psi, \iota)$ and uses Poisson distributions to introduce demographic stochasticity:

$$N_{\mathsf{P}_1,t+1} \sim \mathrm{Poisson}\left(\varsigma_{\mathsf{F}}\,\phi_{0,t}\,\phi_{1,t}N_{0,t}\right);$$

$$N_{\mathsf{P}_j,t+1} \sim \mathrm{Poisson}\left(\phi_{j,t}N_{2,t}\right), \text{for } j = 2, \ldots, 7;$$

$$N_{\mathsf{P}_k,t+1} \sim \mathrm{Poisson}\left(\phi_{k,t}(1-a_{k,t})N_{\mathsf{P}_{k-1},t}\right), \text{for } j = 8, \ldots, 11.$$

The observation process conditional on this state process is based on the count of male pups produced each year, $N_{0,t}$, and demographic rates from the PIT-tag recaptures for the pre-territorial component. Estimates of $N_{N,t+1}$, $N_{T,t+1}$ and B_t are directly obtained from the MSJS model component, which allows for immigration, and an estimate of immigrants is obtained as

$$N_{I,t+1} \sim B_t - \sum_j \mathrm{Poisson}\left(\phi_{j,t}a_{j,t}N_{\mathsf{P}_{j-1},t}\right).$$

The proportion of the estimated study population, $E\left(\left[\begin{array}{c}N_{t+1}|N_t\end{array}\right]\right)$, that represents a territorial male count at SSB, obtained between 1 November and 31 December, is obtained from daily total male counts $\left(n_j^s\right)$ and a Poisson GAMM (see female IPM). The combined IPM likelihood produces the derived quantities $N_{\mathsf{M},t}^{\mathsf{S}}/E\left(n_j^s\right)$ and $N_{\mathsf{T},t}^{\mathsf{S}}/E\left(n_j^s\right)$, where M and T are for mature and territorial males respectively, and $E\left(n_j^s\right)$ is the predicted count at SSB on the jth day. Used as multipliers of observed counts at other locations, we obtain estimates of total number of mature males $\hat{N}_{\mathsf{M}} = \sum_c n_j^c \hat{N}_{\mathsf{M}}^{\mathsf{S}}/E\left(n_j^s\right)$, and territorial males $\hat{N}_{\mathsf{T}} = \sum_c n_j^c \hat{N}_{\mathsf{T}}^{\mathsf{S}}/E\left(n_j^s\right)$, where n_j^c is the male count at colony c on day j. Adjusting for pre-territorial males, an estimate of total number of males at South Georgia is

$$\hat{N}_{\mathsf{M}} = \left(1 + \frac{\sum_k \hat{N}_{\mathsf{P}_k}^{\mathsf{S}}}{\hat{N}_{\mathsf{M}}^{\mathsf{S}}}\right)\frac{\hat{N}_{\mathsf{M}}^{\mathsf{S}}}{E\left(n_j^s\right)}\sum_c n_j^c$$

where $\hat{N}_{\mathsf{P}_k}^{\mathsf{S}}$ is the estimated number of pre-territorials of age k, for $k = 1$–11+, at SSB.

2.3.3 | Model implementation and selection

The total likelihood in IPMs is the product of likelihoods for the different datasets, which are assumed to be independent (Besbeas et al., 2002), although our counts include seals that were also marked. As shown elsewhere, violation of the independence assumption has little impact on model estimation and performance (Abadi, Gimenez, Arlettaz, et al., 2010; Weegman et al., 2021), and thus a significant bias in our results is highly unlikely.

We use Markov Chain Montel Carlo methods in BUGS language and the program JAGS (Plummer, 2003), run from R (v4.2.2; R Core Team, 2022) with the packages *jagsUI* (Kellner, 2021) and *rjags* (Plummer, 2022) to fit the IPMs. To specify priors, we use normal distributions with numbers of pre-breeders, breeders and mature non-breeders observed in the first year for the initial population sizes. For the capture–recapture part, model fit was initially assessed with frequentist multistate goodness-of-fit testing (Pradel et al., 2003) using *R2ucare* (Gimenez et al., 2018). Selection of best models was subsequently based on WAIC (Gelman et al., 2014; Watanabe, 2010),

and the IPMs were fitted with the best mark–recapture modelling options. We selected temporal variation in parameters to better reflect the population state at the time of the surveys. For the female model, we used independent temporal random effects for ϕ_j and a_j for ages 1–7 and 3–7 respectively, ψ_{NB}, $\log(\iota)$, p^{P1}, p^{P2}, p^B and p^N (e.g. $\mathrm{logit}\left(\psi_{i,t}^{NB}\right) = \mu_i^{NB} + \epsilon_{i,t}^{NB}$, where $\epsilon_{i,t}^{NB} \sim \mathrm{Normal}(0, \sigma_{NB}^2)$), with diffuse Uniform priors for σ_*^2. We used correlated temporal random effects for ϕ_B, ϕ_N and, ψ_{BN}, where $\epsilon_{i,t}^\theta \sim \mathrm{MVN}(0, \Sigma_{\theta,t})$ (multivariate normal distribution), where $\Sigma_{\theta,t}$ is the temporal variance–covariance matrix describing the temporal variance of each parameter (θ) and the temporal covariance among multiple parameters (Link & Barker, 2005). For this matrix, we chose priors from an inverse Wishart distribution (Gelman & Hill, 2006) with scale matrix Ω as the identity matrix and four degrees of freedom.

In the male IPM, we chose the best combinations of γ, ϕ and ψ with temporal random effects or constant values over time depending on WAIC-based model selection. As the available data for the Jolly–Seber likelihood did not support estimation with complex model structures, to test full time variation in ϕ_T, ϕ_N, ψ_{TN} and ψ_{NT}, we used correlated temporal random effects. For juveniles and pre-territorials, ϕ_j and a_j were selected as informative Beta priors with shape parameters obtained from an independent best fit of a multistate mark–recapture model of the PIT-tag data set. These priors incorporate temporal variation as observed in the data record, which reflects uncertainty due to environmental stochasticity at the time of the survey counts.

In both IPMs, the GAMMs of daily counts were implemented using the methods of Wood (2016), using multivariate normal priors on the smooth coefficients in the JAGS models; and the smoothing parameters and smoothing penalty matrices directly specified the prior multivariate normal precision matrix. We implemented preliminary model selection based on WAIC to evaluate the need to incorporate overdispersion and autocorrelation before incorporating the Poisson models in the IPMs.

For inference, we produced 200,000 iterations of three Markov chains using dispersed parameter values as starting values and discarded the first 50,000 samples of each chain as burn-in, thinning the remainder to every 10th sample. We assessed chain convergence visually using trace plots, through the mixing of the chains and sample autocorrelation plots, and using the $\hat{R}$ (potential scale reduction factor) statistic (Gelman & Shirley, 2011).

We used posterior simulations for inference on generation time and longevity, based on the core matrix model of the female IPM. Longevity was the age at which survivorship for a cohort fell below a critical value; and the generation time was the time required for a population to increase by a factor equivalent to the net reproductive rate (R0; average number of offspring produced by an individual in its lifetime taking mortality into account; Caswell, 2001).

2.4 | Range expansion, trends and trajectory

We produced a total abundance estimate for South Georgia from the latest surveys, and evaluated range expansion comparing the distribution of breeding females (and total pup production) for three surveys conducted in 1971–1975, 1991 and 2007–2009 respectively.

To obtain a population trajectory at Bird Island, we combined all of the pup production data available since the cessation of sealing. This includes data from 1933, 1936 and 1950 with estimated pup counts of 29, 56 and 1140 respectively (Bonner, 1968); field counts from 1957/58 to 1963/64 (Bonner, 1968); corrected field counts from 1971/72 to 1973/74 (Payne, 1977) and from 1975/76 to 1976/77 (Croxall & Prince, 1979); and eight estimates of pup productivity for 1989–1991, 1995, 1998, 2004, 2009 and 2017 based on comprehensive whole island counts. We produced estimates of mature female abundance from 1989 to 2017, and productivity from 1933 to 2017, extending the SSB capture–recapture analysis back to the 1985 season and using a simplified IPM for mature females (Appendix S2).

We identified phases of change in external pressures on the fur seal population including climate, the physical and biological environment, and commercial extraction of Antarctic krill (*Euphausia superba*). For climate effects, we used the Southern Annular Mode index (Marshall, 2003), available at http://www.nerc-bas.ac.uk/icd/gjma/sam.html, which is the leading mode of variability in the Southern Hemisphere atmospheric circulation, and contributes to sea surface temperature (SST) variability at South Georgia (Meredith et al., 2008). We used records of satellite SST Daily Optimum Interpolation (OI), AVHRR Only, Version 2.1 (Huang et al., 2020), averaged over a grid of 0.25° latitude (−54 to −53.5°) and longitude (−39 to −38°) resolution, from 1981 to the current day. We obtained commercial krill extraction for the CCAMLR management Area 48.3, which includes South Georgia, from 1977 to 2020 via https://www.ccamlr.org/en/fisheries/krill-fisheries. And we used seasonal mean krill size in the fur seal diet at Bird Island as indicator of krill availability (Reid & Arnould, 1996), from 1990 to date; a high mean size in a given year reflects a reduced recruitment of juvenile krill and correlates with low krill biomass, with repercussions in the current and following fur seal breeding seasons (Forcada et al., 2008; Reid et al., 1999). Even though krill density estimates obtained with fishery-independent acoustic surveys are available (Fielding et al., 2022), the temporal resolution, interannual sampling consistency and the extreme variation in the annual estimates were deemed inadequate for this analysis due to a lack of precision and statistical power in any analysis based on this covariate.

We used time-frequency maps of coherence (correlation) between Southern Annular Model (SAM), SST, krill size and estimated log-population growth rate [$\ln(\lambda)$] using wavelet transform multivariate analyses to investigate levels of synchrony in cycles among variables based on their wavelet modulus ratio (Keitt, 2008). This uncovered the non-stationary and temporal relationship between associated fluctuations in climate, physical and biological environments, and fur seal prey and fur seal population dynamics.

2.5 | Animal ethics

All animal handling procedures were evaluated and approved by the Animal Welfare and Ethics Review Body at the British Antarctic Survey, and this research was conducted under annual Regulated Activity Permits issued by the Government of South Georgia and the South Sandwich Islands (GSGSSI). Samples originating from South Georgia Islands were imported under permits from the Convention on International Trade in Endangered Species, and exported under permits issued by the GSGSSI and the UK Department for Environment, Food and Rural Affairs, under European Communities Act 1972.

3 | RESULTS

The assessment of IPMs, including mark–recapture and GAMM model choices is detailed in Appendix S3. The following results describe estimates of vital and life history rates, demographic parameters, population structure and population size changes at SSB, Bird Island and across South Georgia.

3.1 | Female vital rates

The mean recapture probability was 0.128 [95% credible interval: 0.112, 0.147] during the first 3 years of life (p^{P_1}) when most individuals were unobserved. During the next 4 years, the mean recapture probability increased to 0.242 [0.242, 0.341] in pre-breeders (p^{P_2}). For breeders (p^B) it was 0.878 [0.856, 0.898] and it was best modelled as constant over time, like p^{P_1} and p^{P_2}. Recaptures of mature non-breeders (p^N) were best modelled with temporal random effects and a population mean of 0.791 [0.671, 0.925].

Mean apparent survival rates were 0.35 [0.03, 0.82] for pre-weaned and weaned pups (first year females, ϕ^{P_1}); they were high for pre-breeders aged 1 and 2, and were highly variable but lower for pre-breeders of ages 3–8 and above (Figure 1a). First year female survival was lowest in 2006 and 2010 after strong climatic anomalies. For 2002–2015, the temporal mean was 0.441 [0.388, 0.493], and for 2016–2022, shortly after the most severe El Niño on record, it was reduced to 0.150 [0.114, 0.193] (Figure 2b).

The mean survival of breeders (ages 3–20 combined; ϕ^B) was 0.81 [0.52, 0.96] (Figure 1a), with high temporal variation (Figure 2a). Prior to the surveys, the survival of breeders was higher, at 0.93 [0.87, 0.97] in 2007 and 0.95 [0.89, 0.98] in 2009 (Figure 2b). For the period 2002–2015, the temporal mean was 0.826 [0.809, 0.842], and for 2016–2022, the mean dropped significantly, by 5.9% to 0.778 [0.748, 0.809]. In mature non-breeders, mean survival (ϕ^N) was 0.76 [0.43, 0.91]; for 2007 it was 0.77 [0.65, 0.87], and for 2009 it was 0.80 [0.66, 0.91] (Figure 1a).

For females, the probability of first pupping at age (α^{3-7}) increased from 0.06 [0.01, 0.13] at age 3 to 0.43 [0.38, 0.53] at age 5, and decreased subsequently (Figure 1c). Estimates during the
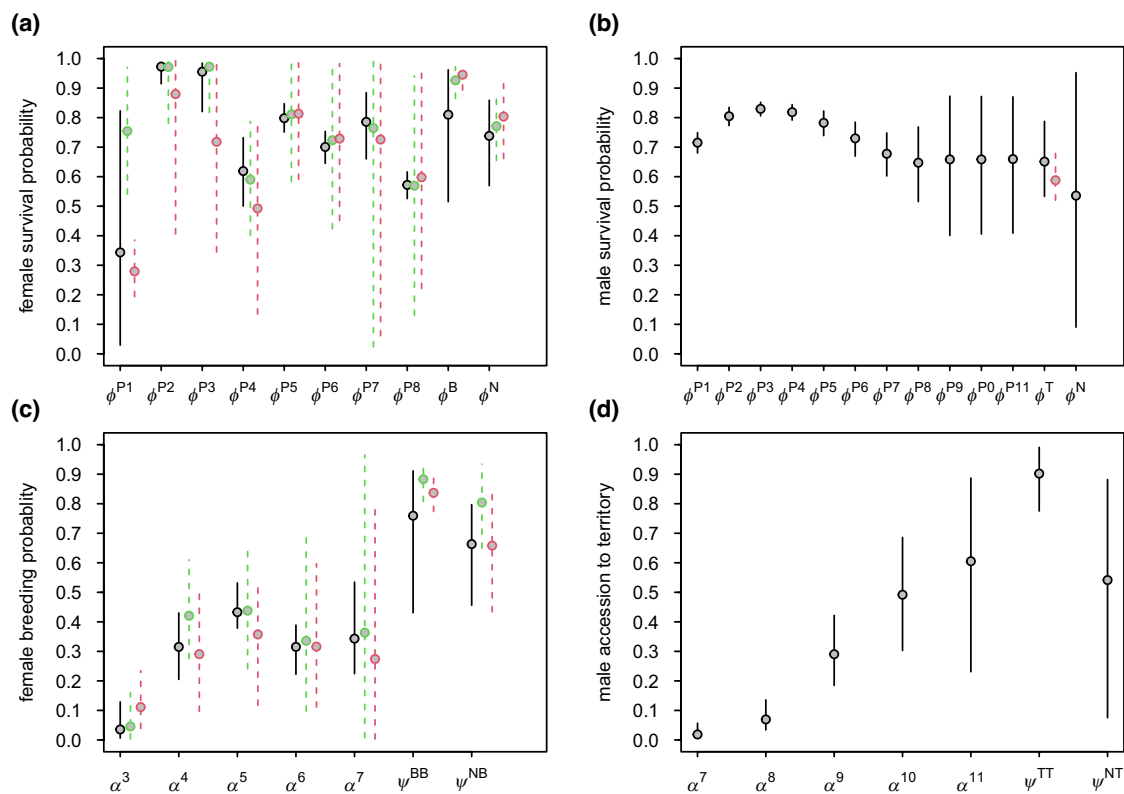

FIGURE 1 Medians and 95% credible intervals of (a) female apparent survival for each breeding stage, (b) male apparent survival, (c) recruitment and breeding probability in females and (d) male accession to territory tenure for pre-territorials and experienced territorials. Black points and solid black bars are temporal means, and green and red points with dashed bars are estimates for the South Georgia surveys in 2007 and 2009.
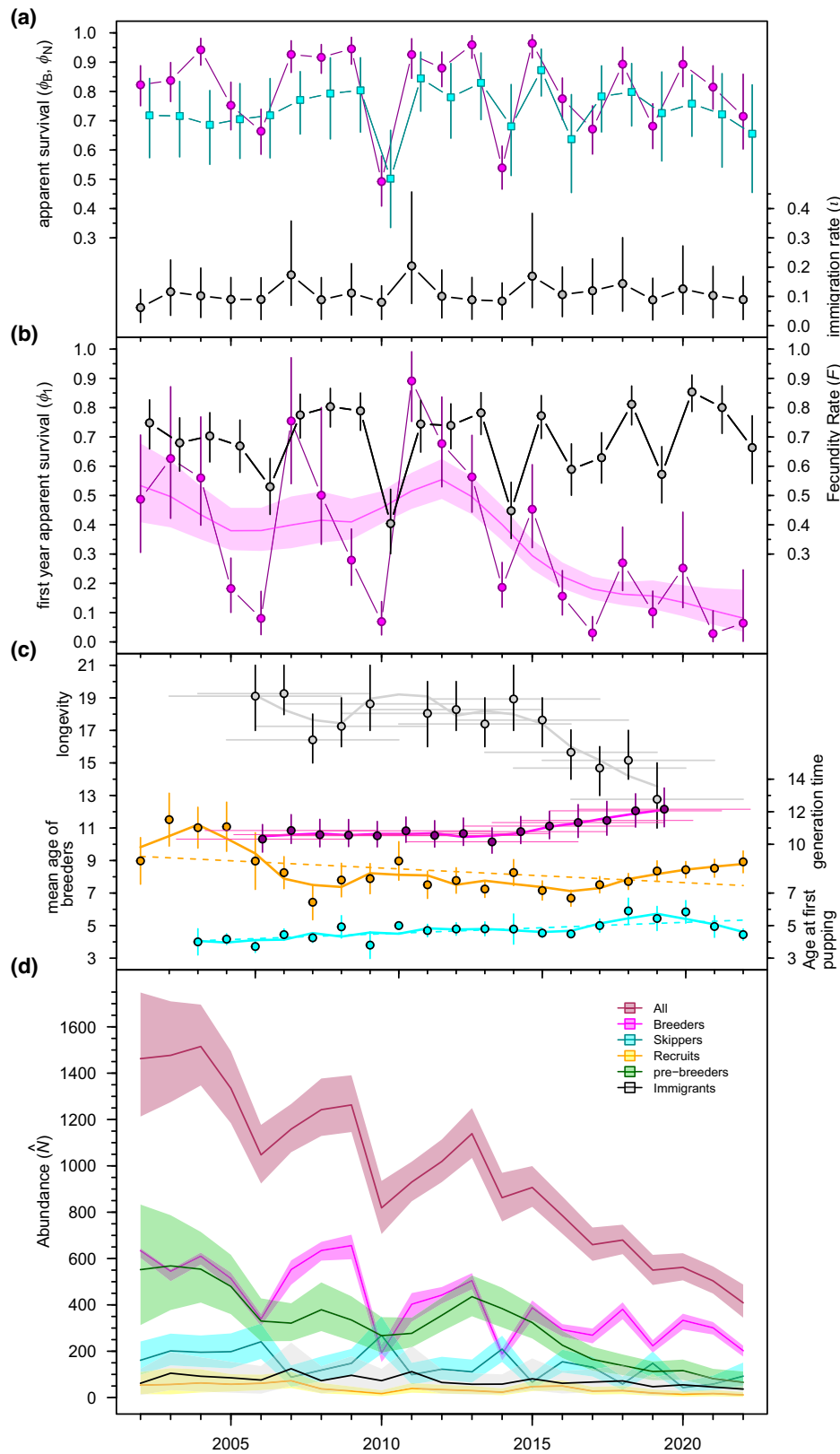
FIGURE 2 Annual medians and 95% credible intervals of vital and life history rates, and abundance at Special Study Beach (representative population) estimated from the integrated population models. (a) Apparent survival of experienced breeders (magenta) and skippers (cyan) and the immigration rate of breeders (black); (b) apparent survival of first year females, including a moving average filtering of order three (points, lines and polygon in magenta), and the fecundity rate (black); (c) seven-year rolling window estimates of longevity, the generation time and the observed mean age at breeding; and (d) abundance by demographic group at the representative female population.

survey years were comparable to the long-term mean but were more variable (Figure 1c). The mean probability of experienced breeders to return as breeders (ψ^{BB}) was 0.76 [0.43, 0.91], and the probability of skippers to return as breeders (ψ^{NB}) was 0.66 [0.46, 0.80]. During the survey years, breeding probabilities were very high and less variable for both stages (Figure 1c). Fecundity (i.e. the observed pregnancy rate) was high and was similar between the survey years (F_{07} = 0.775 [0.697, 0.846]; F_{09} = 0.789 [0.723, 0.850]) (Figure 2b) compared to the long-term mean rate of 0.691 [0.663, 0.719], and the equivalent rate for the period 2010–2022 (0.678 [0.646, 0.710]) (Figure 2b). In comparison, the pregnancy rate in 1991, during the previous large-scale survey of South Georgia, was 0.580 [0.492, 0.665].

The mean immigration rate (ι) of breeders from adjacent beaches to SSB was estimated as 0.099 [0.059, 0.132] for period 2002–2022. The highest immigration was observed in years following environmental declines in survival until 2014 but this pattern did not persist thereafter (Figure 2a,c).

Longevity was stable from 2001 to 2015, at around 18.4 [17–20] years, and declined significantly after 2015 to 14.2 [13–15.7] (Figure 2c). The observed mean age of breeding females declined significantly until 2015, and then increased during a subsequent period of persistently high juvenile mortality that started after 2015 as the surviving population aged. Similarly, the mean observed age at maturation increased from 4.4 (SE = 0.2) to 5.3 (SE = 0.1), contributing to a higher mean age of breeders, and therefore increasing the estimated mean generation time, from 10.6 [10.1–11.3] to 11.9 [11–13] (Figure 2c).

3.2 | Male vital rates

The recapture probability of pre-territorial males (p^P), which was best modelled as constant over time and across ages 1–11, was 0.120 [0.101, 0.141]. The recapture probability of territorial males (p^T), also best modelled as constant, was 0.925 [0.847, 0.999]. Apparent survival rates for pre-territorial males were higher at ages 2–4 and declined in older individuals. After age 8, when most pre-territorials started to be competitive, survival estimates were highly variable, with a similar mean to territorial males (Figure 1b). For these animals, the temporal mean was 0.651 [0.533, 0.787], and the mean estimate prior to the surveys was slightly lower (0.588 [0.520, 0.679]). For temporary emigrants, survival was lower but highly variable (0.534 [0.090, 0.952]).

The probability of defending a territory for the first time ($\alpha^{7–11}$) increased from 0.019 [0.006, 0.057] at age 7 to 0.605 [0.231, 0.887] at age 11 (Figure 2d), with the average age at first territory being 9.8 [9.5, 10.1] and the mean age of all territorial males being 10.6 [10.3, 10.9] (range: 7–14). Once territorial, the probability to emigrate temporarily was ψ^{TN} = 0.098 [0.009, 0.225], and after skipping a year, the probability to return was extremely variable (ψ^{NT} = 0.541 [0.076, 0.882]). Most surviving males only held territories in two or fewer years (mean = 1.85 years [1.55, 2.28]), and after emigration

they were unlikely to return. For a territorial male, the mean life expectancy (confounded with permanent emigration) was 2.59 years [1.82, 3.74], and when an animal was non-territorial, the estimated apparent average life expectancy (i.e. as a future territorial male) was 1.50 years [1.08, 2.38].

3.3 | Population structure, size and trends at SSB, Bird Island

Male population proportions were 0.797 [0.757, 0.829] for pre-territorials of ages 1–11, 0.022 [0.009, 0.041] for recruiting territorials (born at SSB), 0.111 [0.089, 0.138] for territorials returning as territorials, 0.054 [0.032, 0.074] for immigrant territorials, and 0.016 [0.000, 0.042] for skippers or returning emigrants. For the data record (1995–2007), the population of mature males (territorials and skippers) had an estimated geometric mean growth rate (λ) of 0.990 [0.969, 1.012].

The female population structure at SSB as defined by breeding stages is described in Table 1. For the period 2001–2022, the major population components were pre-breeders (32% [29, 35]) and breeders (54% [51, 57]), of which only 4% [3, 5] were recruits, and 8% [6, 9] were breeding immigrants from adjacent beaches. From 2010 to 2015 the percentage of breeders declined significantly by 12.6% with respect to 2001–2009, and the proportions of skippers and pre-breeders increased. After 2015, breeders increased by 11.4% and 22.6% in relation to 2010–2015 and 2001–2009 respectively, while pre-breeders declined by 39.3% and 34.7% for the same periods, and the proportions of skippers remained stable throughout.

The SSB female population declined from 2002 to 2022 (Figure 2d), with an estimated mean λ of 0.948 [0.938, 0.958]. The fastest decline (λ = 0.927 [0.904, 0.953]) occurred from 2016 to 2022 (Figure 2d), when the survival of breeders and first year females decreased significantly (Figure 2b). This resulted in very low numbers of older juveniles (ages 1–7) in subsequent years. Extending the data series back to 1984, the long-term mean λ for mature females was 0.972 [0.966, 0.977]. Most of the decline occurred during the last 13 years (2010–2022) of the 39-year series (Figures 2d and 4b), during which the mean λ was 0.930 [0.917, 0.944], corresponding to an annual decline of 7%. Previously, the time series was characterised by two phases of near stability, from 1984 to 1990 (mean λ = 0.983 [0.957, 1.012]), and from 1991 to 2009 (mean λ = 0.997 [0.991, 1.004]), with an abrupt decline in 1991.

Declines in ln(λ) were best explained by significant increases in SAM, summer SST and mean krill size (Figure 4c–e). The SAM has been mostly in its positive phase since the early 1990s, with a steady decline in variation while increasing its mean; and summer SST (December–February) increased by 0.88°C over 40 years (Figure 4a). The time-frequency map of coherence (correlation) between these indices showed a time-varying relationship between coupled fluctuations in climate and the physical environment, which propagated

TABLE 1 Female population structure at the Special Study Beach (SSB) of Bird Island, South Georgia.

Stage	2001–2022	2001–2009	2010–2015	2016–2022	2007	2009
Pre-breeders	0.318 [0.285, 0.350]	0.334 [0.284, 0.382]	0.359 [0.321, 0.397]	0.218 [0.178, 0.260]	0.277 [0.224, 0.330]	0.264 [0.207, 0.323]
Recruits	0.039 [0.032, 0.047]	0.041 [0.030, 0.054]	0.034 [0.026, 0.043]	0.041 [0.031, 0.052]	0.063 [0.036, 0.097]	0.022 [0.010, 0.038]
Breeders	0.424 [0.398, 0.449]	0.428 [0.390, 0.467]	0.374 [0.342, 0.406]	0.483 [0.443, 0.525]	0.478 [0.386, 0.559]	0.521 [0.446, 0.594]
Immigrants	0.076 [0.059, 0.093]	0.068 [0.045, 0.090]	0.079 [0.056, 0.105]	0.093 [0.064, 0.122]	0.107 [0.045, 0.202]	0.076 [0.025, 0.138]
Skippers	0.143 [0.123, 0.164]	0.129 [0.105, 0.155]	0.154 [0.126, 0.185]	0.165 [0.137, 0.196]	0.076 [0.040, 0.117]	0.117 [0.078, 0.161]

Note: In each season, the total number of breeders is the sum of new breeders born at SSB (Recruits), returning breeders (Breeders) and immigrants from other areas. Skippers or non-breeders are mature breeders which defer breeding in each season. In parentheses are 95% credible intervals.

to mean krill size and $\ln(\lambda)$ (Figure 4f–h), especially during the decade preceding the abrupt 2009 decline. Under similar climate-temperature coupling, with current values of mean summer SST (3.34°C [3.03, 3.65] since 2010) and highly positive SAM values, the mean $\ln(\lambda)$ is expected to be mostly negative and highly variable (Figure 4d,e).

In contrast, the interannual variation of commercial krill extraction was uncorrelated with $\ln(\lambda)$, and the annual mean extraction represented a small percentage of the extant krill stock (see Section 4).

3.4 | Daily counts and adjustment factors

In 2007, the peak of the pupping season was on 8 December and the survey of South Georgia was conducted from 11 to 14 December. In 2009, the peak day, 6 December, was the central day of the survey, from 3 to 9 December (Figure 3). The best GAMM fit for daily numbers of seals at SSB in 2007 and 2009 indicated a higher overdispersion in female counts ($\sigma_\varepsilon^{F,07} = 0.141$ [0.106, 0.184] and $\sigma_\varepsilon^{F,09} = 0.101$ [0.069, 0.140]), than in territorial male counts ($\sigma_\varepsilon^{M,07} = 0.022$ [0.001, 0.061] and $\sigma_\varepsilon^{M,09} = 0.026$ [0.001, 0.069]) (Figure 3).

The absolute mature female abundance in 2007 was 2.488 [2.259, 2.743] times the predicted survey count $\left(N_{M,t}^S / E\left(n_j^s \right) \right)$, and the productivity was 2.227 [2.039, 2.429] times the predicted survey count $\left(N_{B,t}^S / E\left(n_j^s \right) \right)$. For 2009, the estimates were 3.237 [2.963, 3.537] and 2.721 [2.518, 2.938] respectively; these values are the mean of the estimated daily values over the survey period. Among mature males, the absolute abundance was 3.266 [2.746, 3.970] times the predicted survey count, and the absolute abundance of territorials was 2.960 [2.500, 3.602] times the predicted survey count in 2007. For 2009, the estimates were 3.249 [3.195, 3.306] and 2.985 [2.935, 3.037] respectively.

The results of our analyses of 8 years with complete surveys of Bird Island are shown in Appendix S4 (Table S1), and the best models for the corresponding SSB female counts are shown in Appendix S4 (Figure S1). Four of eight surveys were in years affected by environmental anomalies and low pup production, which provided a good representation of long-term variation in peak female counts. Because most of the surveys were conducted when female numbers were close to the highest daily SSB counts (Figure S1), variation in mean counts over the survey dates was relatively low (%CV = 1.6%–12%), and was well reflected in the GAMM predictions $\left(E\left(n_{j,t}^s \right) \right)$.

The Pearson's product moment correlation coefficient for paired whole Bird Island counts and predicted SSB counts ($E\left(n_{j,t}^s \right)$; Table S1) was 0.992 [95% CI: 0.959, 0.999] and the correlation between the Bird Island counts and mean SSB counts was 0.982 [0.902, 0.997]. Additionally, the correlation between the Bird Island counts and total SSB productivity was 0.875 [0.444, 0.977]. The correlation for paired predicted SSB counts and counts at Maiviken (−54.2435°, −36.5033°), another long-term monitoring site situated
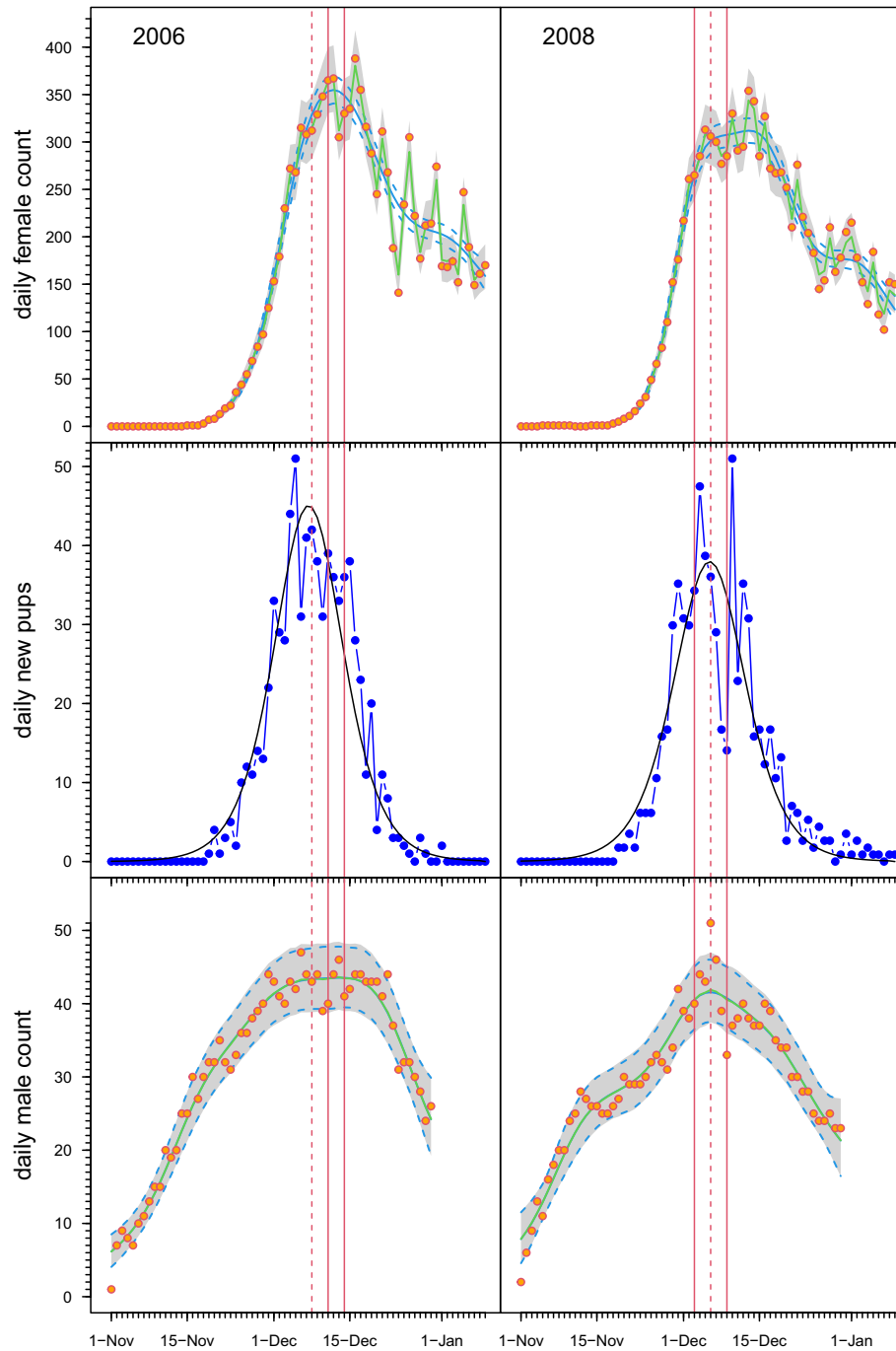
FIGURE 3 Seasonal daily counts of mature females, newborn pups and territorial males at the representative population (Special Study Beach) for the years of aerial surveys of South Georgia. Top and bottom panels show observed counts in red/orange, and the best fit of a Poisson generalised additive model (blue lines) and an overdispersed Poisson generalised additive mixed model (green lines and grey polygon). Central panels show daily newborn pups (blue) with a fitted logistic model (black) of the cumulative daily number. Vertical solid red lines delimit the survey windows and dashed red lines the estimated peak pupping day.

approximately 105 km to the east, on the South Georgia mainland (data from Hollyman, Trathan, & Collins, 2021), at peak pupping over 11 years was 0.899 [95% CI: 0.650, 0.974]. Thus, there is a high level of synchrony in the counts and productivity across South Georgia, supporting the applicability of SSB correction factors throughout the entire range.

3.5 | Mature female abundance and pup production at Bird Island

Bird Island estimates of the absolute abundance of mature females and pup production by year are shown in Figure 4b (also Appendix S4; Table S1). Abundance fluctuated between 1989 and 2009,
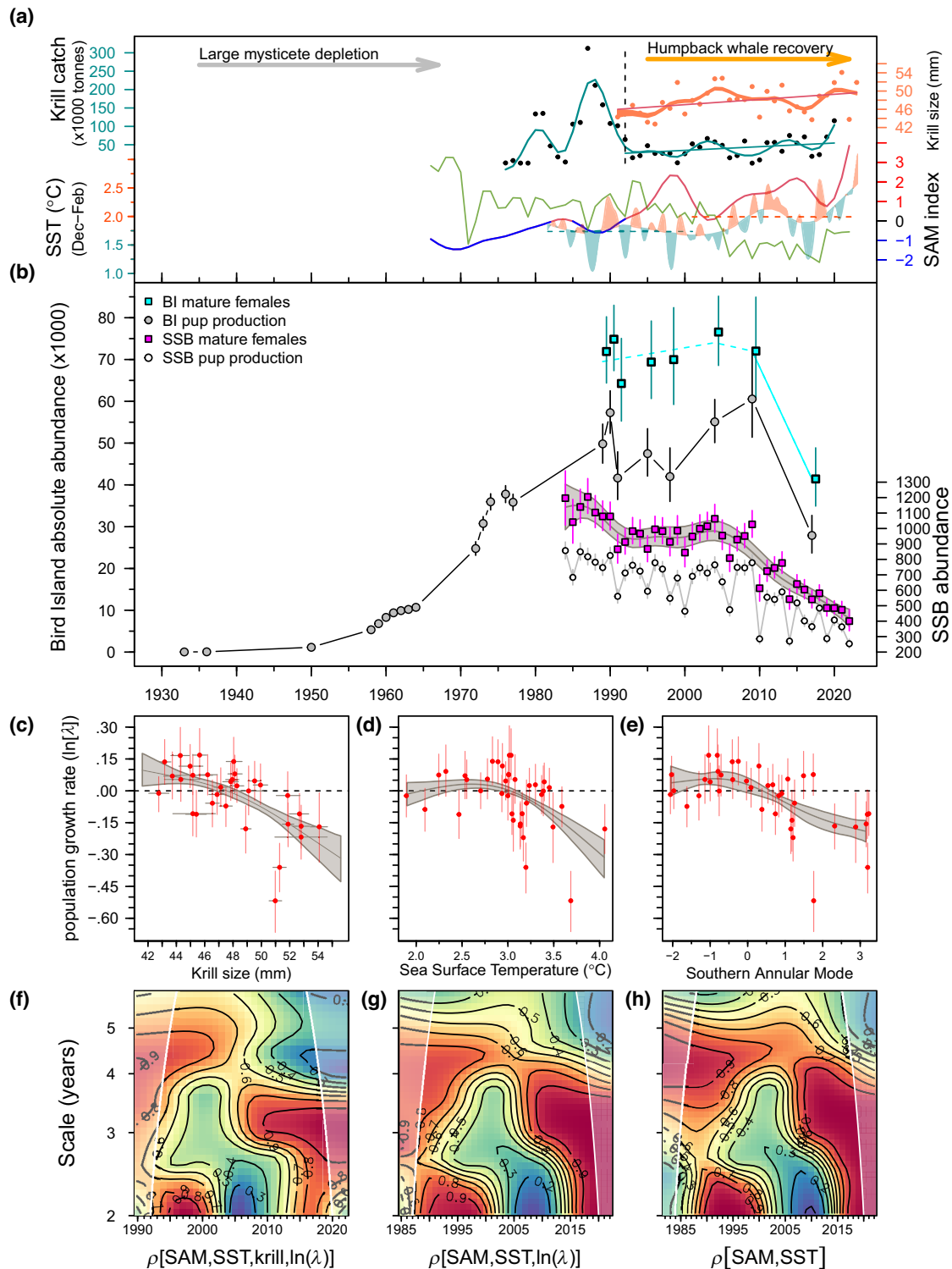
FIGURE 4 (a) Increases in the Southern Annular Mode (SAM) index, with the green line showing the coefficient of variation of a 6-year sliding window; South Georgia sea surface temperature (SST; dashed lines for baseline means); mean krill size in the seal's diet; and commercial krill extraction, with the collapse of the USSR fishery marked by the vertical dashed black line. Lines in the krill data indicate significant linear trends. (b) Median abundance of mature females and breeding females (i.e. pup production) at Bird Island (BI) in northwest South Georgia, and at its representative study population (Special Study Beach). The grey polygon is a moving average filter of order three; and the cyan line is a segmented regression model with significant (solid lines) and non-significant trends (dashed lines). Vertical bars are 95% credible intervals. (c–e) The relationships between fur seal population growth rate (ln(λ)) and krill size, SST and SAM; grey polygons show estimates from fitted generalised additive models. (f–h) Time-varying relationships between SAM, SST, krill size and ln(λ) obtained with a wavelet transform multivariate analysis; contours show levels of synchrony ($\rho \in [0, 1]$) in cycles for combinations of variables. Lighter shades are cones of influence containing less reliable values.

and declined by 42.1% [27.0, 54.5] from 2010 to 2017, which represents a mean annual rate of decline of 6.7% [3.9, 9.4] (Figure 4). High levels of variation between 1989 and 2009 precluded the effective detection of significant trends in pup production, but after 2010 it fell by 44.8% [34.8, 53.4] over 8 years. This represents a mean annual rate of decline of 7.2% [5.2, 9.1]. Given the high synchrony between SSB and Bird Island, we expect this trend to continue after 2017. Extending the time series of available productivity estimates back to the first half of the 20th century, Figure 4b shows a rapid exponential increase until 1975 (Payne, 1977). The mean productivity reached a maximum in the early 1980s, which was followed by a period of relative stability, and then the most recent drop after the abrupt decline of 2009 to values comparable to or below those of the early 1970s.

3.6 | South Georgia surveys, abundance and range expansion

Female breeder abundance (pup production) at South Georgia was estimated as 1,185,587 [1,090,178; 1,287,551], from a mature female population of 1,401,917 [1,276,716; 1,540,903] and a total female population of 1,907,905 [1,703,956; 2,129,438], of which 505,988 [366,281; 665,590] were pre-breeders. The abundance of territorial males was 309,073 [266,876; 369,738], from a mature population of 340,610 [292,520; 408,713] and a total male population of 1,602,378 [1,308,588; 1,950,838], of which 1,261,768 [991,155; 1,568,012] were pre-territorial males. This corresponds to a total abundance of 3,510,283 [3,140,548; 3,919,604] Antarctic fur seals as of 2009. The total abundance represents 2.96 [2.64, 3.33] times the total pup production, the pup production at South Georgia in 2007–2009 represents approximately 97.5% [97.3, 97.7] of the global pup production for the species (Appendix S4; Table S2), and the pup production at Bird Island is approximately 4.98% [4.59, 5.38] of the global pup production.

The geographical distribution of breeding females is shown in Figure 5c, along with the distribution range from the nearly complete surveys in 1971–1975 and in 1991 (Boyd, 1993; Payne, 1977) to illustrate range expansion. The fur seal population of Bird Island comprised approximately 37% of the South Georgia total in 1975, but thereafter declined to 17.1% in 1991 and 5.2% [4.7, 5.6] in 2009. The breeding distribution in 2007–2009 extends eastwards along most of the suitable breeding habitat on the north coast, excluding unsuitable glacier and fjord ends, mostly at the northeast end. In the south, the breeding range only expands along the southwest.

4 | DISCUSSION

This is the first assessment of the Antarctic fur seal population at South Georgia over a century of global change. We document its recovery from near extinction to become the most abundant otariid in the world, followed by a local decline. Such information provides the basis for an improved assessment of the conservation of the species worldwide, which is timely given the profound ecosystem changes occurring in the SW Atlantic region of the Southern Ocean, where the species is currently declining.

Using CMR and reproduction data from a representative study population, and visual and photographic count data on various geographical scales, we developed IPMs to address availability bias, one of the most common problems of evaluating marine predator populations. Methods to account for availability bias that rely on life tables have limitations when demographic data are inaccurate and unrepresentative (Hammond et al., 2021). To address this, Bayesian state-space population models can provide a flexible framework for data integration including detailed demographic parameters and other effects (e.g. Thomas et al., 2019). They can be extended to evaluate population viability and conservation management strategies (Saunders et al., 2018), assess population collapses (Maunder, 2004) and gain detailed insights into the drivers of population dynamics with limited data on marked individuals and study periods (Nater et al., 2021). We extended this framework to estimate availability bias, based on the proportion of the abundance of a representative population (SSB, Bird Island) that constituted a mature individual count, obtained in a given survey area, day and year. We incorporated uncertainty from different data sources, supported repeatability over past survey years and accounted for temporal specificity (Appendix S5), without making additional assumptions other than spatial synchrony in counts.

Spatial synchrony is often assumed, but untested, when applying abundance adjustments from data obtained at a single location to other locations (e.g. LaRue et al., 2021; Russell et al., 2019). In contrast, our results support the hypothesis of maximum temporal synchrony in numbers of breeders among locations, the high temporal correlation between peak female counts and total productivity, and the assumption that SSB count-based population adjustments have a wider spatial application, including at the opposite geographical end of the breeding distribution within South Georgia.

The IPMs considered separate demography and population dynamics by sex, given the large differences in life history between females and males. Sex structure in IPMs is preferable, although uncommon (but see Cleasby et al., 2017; Gamelon et al., 2021; Péron & Koons, 2012; Plard et al., 2019), and in our case it was justified by between- and within-sex differences in data types and data record periods, in a species with a high degree of sexual dimorphism. This allowed for the most comprehensive demographic analysis for the male of the species to date, including first estimates of survival, recruitment, breeding propensity and temporary emigration; which highlighted major differences in population components by sex.

The estimated percentage of females in the breeding population was 68, whereas in males it was only 18, and the majority of these held active territories. This difference is typically observed in highly polygynous pinnipeds (e.g. Condit et al., 2014; Oosthuizen et al., 2019), and reflects strong survival-reproduction trade-offs. Once becoming territorial at a mean age of 10 years, survival was limited to 3 years on average, reflecting the high survival cost of
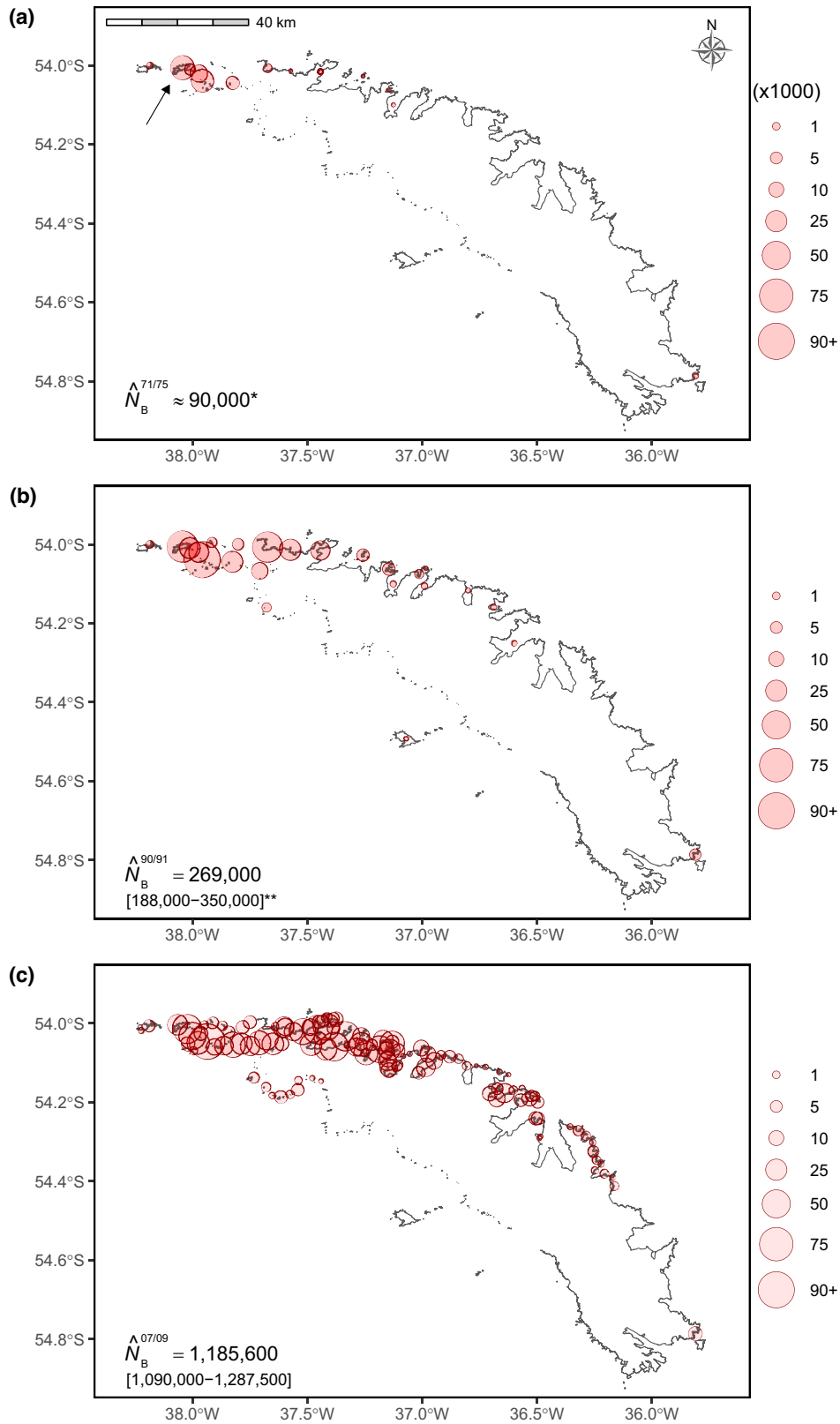
FIGURE 5 Distribution and range expansion of the female Antarctic fur seal breeding population of South Georgia based on available comprehensive surveys in 1975–1976 [(a) Payne (1977)], 1990–1991 [(b) Boyd (1993)] and 2007–2009 [(c) this analysis]. In (a), the location arrow points to Bird Island, identified in the early 1930s as the probable epicentre of the recovery of the species after sealing. Values for panels (a) (*) and (b) (**) are from the literature cited.

territoriality. If a territorial male emigrated, the probability to return as a territory holder was very low. As a result, up to 80% of males were pre-territorial, whereas the proportion of female pre-breeders was much lower, at around 32%. This indicates that most males were unobserved during counts of breeding beaches, and were hence unavailable to the observers during the survey period (see also Boyd et al., 1998; Staniland & Robinson, 2008). This is commonly found in pinniped surveys (e.g. LaRue et al., 2021; Pitcher et al., 2007), but requires representative and accurate adjustment estimates from non-count data.

The female IPM showed changes in vital rates and associated changes in female population structure, which since 2015 have been exacerbated by the continuing population decline at Bird Island (Forcada & Hoffman, 2014). The same pattern most likely occurs in nearby areas of South Georgia, where the species shares common foraging grounds and is affected by common climate–environment drivers (Meredith et al., 2008). This includes an unprecedented declining trend in first-year survival, which subsequently affects age at maturation, recruitment, mean breeding age and longevity. As a result, the population of Bird Island, which comprises approximately 5% of the global population, has declined by over 42% in less than one fur seal generation (9–11 years). This decline has been even more precipitous at the South Shetland Islands (Krause et al., 2022), and has also been observed to a lesser extent in Bouvet Island (Hofmeyr, 2016), although present data for Bouvet are lacking. Nonetheless, this increases conservation concerns for the Southern Ocean's South Western Atlantic region, which includes three of the four main island groups that have distinct population genetic structures (Humble et al., 2018; Paijmans et al., 2020), and where the species is globally most abundant, but declining.

South Georgia is in the Scotia Sea, which holds over half of the estimated global Antarctic krill biomass (Siegel & Watkins, 2016), is also the area with the highest regulated commercial krill extraction (Nicol & Foster, 2016), and where greenhouse warming is driving increases in ocean temperatures, changes in sea-ice seasonality and extent, increases in UV radiation and ocean acidification, affecting the marine biota (Constable et al., 2014). Here, the krill distribution is likely to be contracting Poleward, while increasing migration towards the seabed (Atkinson et al., 2019; McBride et al., 2021; Schmidt et al., 2011), both of which decrease its availability to millions of highly dependent predators such as Antarctic fur seals.

In the wider krill fishery management area encompassing South Georgia, CCAMLR Area 48.3, the commercial extraction of Antarctic krill peaked in the late 1980s, declined in the early 1990s (Figure 4a) with the collapse of the Soviet Union fishing fleet, and significantly increased since then (Nicol & Foster, 2016), although to much lower levels. Thus, the cumulative extraction between 1985 and 1991 was 1,108,473 tonnes, or between 6.4% and 7.1% of the available krill biomass estimates of 17,211,300 and 15,563,986 for that area for 2000 and 2019 (Hill et al., 2016; Krafft et al., 2021). Whereas subsequently, the extracted percentage has reduced to a mean of around 0.67%–0.74% per annum. This extraction is temporally uncorrelated with fur seal population growth, and is probably marginal compared to the fur seal peak demand on krill. This suggests that commercial krill extraction in the area encompassing a large part of the female Antarctic fur seal foraging summer and winter ranges (Arthur et al., 2017; Bamford et al., 2021; Boyd et al., 1998; Staniland & Robinson, 2008) could be sustainable. However, the effects of krill extraction on fur seal populations should be re-evaluated in the light of increasing environmental pressures on both the krill and the fur seals. Besides climate warming, these pressures include the effects of regional humpback whale recovery (Zerbini et al., 2019) and its direct competition for food with fur seals and other abundant krill-dependent predators such as macaroni penguins. The present humpback whale annual krill consumption could be between 7% and 10% of the total krill stock (data from Baines et al., 2021), but data on the effects on fur seals and the wider ecosystem are largely unavailable.

We have shown that accurate and representative abundance estimates are the key to evaluating the recovery of depleted species, not only retrospectively, but also from the contemporary perspective of greenhouse warming, habitat degradation and shifting harvesting practices, which increasingly affect marine food webs (Daskalov et al., 2007; du Pontavice et al., 2020; Hocevar & Kuparinen, 2021). We show that some of these effects have resulted in transient population states in Antarctic fur seals at South Georgia via changes in population structure and fertility, which carry over as negative population momentum (Forcada et al., 2008) and limit the ability of this population to recover from perturbations while facing new external pressures. As the fur seal recovery trajectory is expected to be fundamentally different from the long-term population at equilibrium (Hastings et al., 2018), previous projections of observed fur seal populations based on previous transient states, particularly without corroborating survey data, are very inaccurate, with an estimated upward bias of between 0.6 and 2.7 million seals (e.g. Bonner, 1985; Boyd, 2002; Foley & Lynch, 2019; SCAR, 2006). Therefore, these should not replace current abundance data in support of policy, and to achieve management objectives.

Research with Comparative Investigations in Arctic Ice Areas' (project number 424119118).

DATA AVAILABILITY STATEMENT
Helicopter survey data counts and demographic data, together with R script files for analysis of the female and male IPMs are available at the Dryad repository (https://datadryad.org/stash/share/9FJgp9eSQoOE7sjKVs-fWnwxk-UknJFRf09tMy2jNME), with unique digital object identifier (DOI): 10.5061/dryad.2rbnzs7tc. These are also available on request from the lead author.

ORCID
Jaume Forcada https://orcid.org/0000-0002-2115-0150
Joseph I. Hoffman https://orcid.org/0000-0001-5895-8949
Olivier Gimenez https://orcid.org/0000-0001-7001-5142
Iain J. Staniland https://orcid.org/0000-0003-2736-9134

REFERENCES
Abadi, F., Gimenez, O., Arlettaz, R., & Schaub, M. (2010). An assessment of integrated population models: Bias, accuracy, and violation of the assumption of independence. *Ecology*, 91(1), 7–14. https://doi.org/10.1890/08-2235.1

Abadi, F., Gimenez, O., Ullrich, B., Arlettaz, R., & Schaub, M. (2010). Estimation of immigration rate using integrated population models. *Journal of Applied Ecology*, 47(2), 393–400. https://doi.org/10.1111/j.1365-2664.2010.01789.x

Agnew, D. J. (1997). The CCAMLR ecosystem monitoring programme. *Antarctic Science*, 9(3), 235–242.

Allen, P. J., Amos, W., Pomeroy, P. P., & Twiss, S. D. (1995). Microsatellite variation in grey seals (*Halichoerus grypus*) shows evidence of genetic differentiation between two British breeding colonies. *Molecular Ecology*, 4(6), 653–662. https://doi.org/10.1111/j.1365-294X.1995.tb00266.x

Arthur, B., Hindell, M., Bester, M., De Bniyn, P. J. N., Trathan, P., Goebel, M., & Lea, M. A. (2017). Winter habitat predictions of a key Southern Ocean predator, the Antarctic fur seal (*Arctocephalus gazella*). *Deep-Sea Research Part II – Topical Studies in Oceanography*, 140, 171–181. https://doi.org/10.1016/j.dsr2.2016.10.009

Atkinson, A., Hill, S. L., Pakhomov, E. A., Siegel, V., Reiss, C. S., Loeb, V. J., Steinberg, D. K., Schmidt, K., Tarling, G. A., Gerrish, L., & Sailley, S. F. (2019). Krill (*Euphausia superba*) distribution contracts southward during rapid regional warming. *Nature Climate Change*, 9, 142–147. https://doi.org/10.1038/s41558-018-0370-z

Baines, M., Kelly, N., Reichelt, M., Lacey, C., Pinder, S., Fielding, S., Murphy, E., Trathan, P., Biuw, M., Lindstrøm, U., Krafft, B. A., & Jackson, J. A. (2021). Population abundance of recovering humpback whales *Megaptera novaeangliae* and other baleen whales in the Scotia Arc, South Atlantic. *Marine Ecology Progress Series*, 676, 77–94.

Bamford, C. C. G., Warwick-Evans, V., Staniland, I. J., Jackson, J. A., & Trathan, P. N. (2021). Wintertime overlaps between female Antarctic fur seals (*Arctocephalus gazella*) and the krill fishery at South Georgia, South Atlantic. *PLoS One*, 16(3), e0248071. https://doi.org/10.1371/journal.pone.0248071

Besbeas, P., Freeman, S. N., Morgan, B. J. T., & Catchpole, E. A. (2002). Integrating mark-recapture-recovery and census data to estimate animal abundance and demographic parameters. *Biometrics*, 58(3), 540–547. https://doi.org/10.1111/j.0006-341X.2002.00540.x

Bonner, W. N. (1968). *The fur seal of South Georgia (British Antarctic survey scientific reports issue)*.

Bonner, W. N. (1985). Impact of fur seals on the terrestrial environment at South Georgia. In W. R. Siegfried, P. R. Condy, & R. M. Laws (Eds.), *Antarctic nutrient cycles and food webs* (pp. 641–646). Springer.

Boyd, I. L. (1993). Pup production and distribution of breeding Antarctic fur seals (*Arctocephalus gazella*) at South Georgia. *Antarctic Science*, 5(1), 17–24.

Boyd, I. L. (2002). Estimating food consumption of marine predators: Antarctic fur seals and macaroni penguins. *Journal of Applied Ecology*, 39(1), 103–119. https://doi.org/10.1046/j.1365-2664.2002.00697.x

Boyd, I. L., McCafferty, D. J., Reid, K., Taylor, R., & Walker, T. R. (1998). Dispersal of male and female Antarctic fur seals (*Arctocephalus gazella*). *Canadian Journal of Fisheries and Aquatic Sciences*, 55(4), 845–852. https://doi.org/10.1139/cjfas-55-4-845

Buckland, S. T., & York, A. E. (2018). Abundance estimation. In B. Würsig, J. G. M. Thewissen, & K. M. Kovacs (Eds.), *Encyclopedia of marine mammals* (3rd ed., pp. 1–6). Academic Press. https://doi.org/10.1016/B978-0-12-804327-1.00001-7

Calderan, S. V., Black, A., Branch, T. A., Collins, M. A., Kelly, N., Leaper, R., Lurcock, S., Miller, B. S., Moore, M., Olson, P. A., Sirovic, A., Wood, A. G., & Jackson, J. A. (2020). South Georgia blue whales five decades after the end of whaling. *Endangered Species Research*, 43, 359–373. https://doi.org/10.3354/esr01077

Caswell, H. (2001). *Matrix population models: Construction, analysis, and interpretation* (2nd ed.). Sinauer Associates.

Cleasby, I. R., Bodey, T. W., Vigfusdottir, F., McDonald, J. L., McElwaine, G., Mackie, K., Colhoun, K., & Bearhop, S. (2017). Climatic conditions produce contrasting influences on demographic traits in a long-distance Arctic migrant. *Journal of Animal Ecology*, 86(2), 285–295. https://doi.org/10.1111/1365-2656.12623

Condit, R., Reiter, J., Morris, P. A., Berger, R., Allen, S. G., & Le Boeuf, B. J. (2014). Lifetime survival rates and senescence in northern elephant seals. *Marine Mammal Science*, 30(1), 122–138. https://doi.org/10.1111/mms.12025

Constable, A. J., Melbourne-Thomas, J., Corney, S. P., Arrigo, K. R., Barbraud, C., Barnes, D. K. A., Bindoff, N. L., Boyd, P. W., Brandt, A., Costa, D. P., Davidson, A. T., Ducklow, H. W., Emmerson, L., Fukuchi, M., Gutt, J., Hindell, M. A., Hofmann, E. E., Hosie, G. W., Iida, T., … Ziegler, P. (2014). Climate change and Southern Ocean ecosystems I: How changes in physical habitats directly affect marine biota. *Global Change Biology*, 20(10), 3004–3025. https://doi.org/10.1111/gcb.12623

Convey, P., & Hughes, K. A. (2022). Untangling unexpected terrestrial conservation challenges arising from the historical human exploitation of marine mammals in the Atlantic sector of the Southern Ocean. *Ambio*, 52, 357–375. https://doi.org/10.1007/s13280-022-01782-4

Cook, J. (1777). A voyage towards the south pole, and round the world. Performed in his Majesty's ships the Resolution and Adventure, in the years, 1772, 1773, and 1775 [volume 2]. https://open.library.ubc.ca/collections/chungpub/items/1.0129127

Costa, D., Weise, M., & Arnould, J. (2006). *Potential influences of whaling on the status and trends of pinniped populations*. University of California Press. https://doi.org/10.1525/california/9780520248847.003.0027

Croxall, J. P., & Prince, P. A. (1979). Antarctic seabird and seal monitoring studies. *Polar Record*, 19(123), 573–595. https://doi.org/10.1017/S0032247400002680

Daskalov, G. M., Grishin, A. N., Rodionov, S., & Mihneva, V. (2007). Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. *Proceedings of the National Academy of Sciences of the United States of America*, 104(25), 10518–10523. https://doi.org/10.1073/pnas.0701100104

Doidge, D. W., Croxall, J. P., & Baker, J. R. (1984). Density-dependent pup mortality in the Antarctic fur-seal *Arctocephalus gazella* at South Georgia. *Journal of Zoology*, *202*, 449–460. https://doi.org/10.1111/j.1469-7998.1984.tb05095.x

du Pontavice, H., Gascuel, D., Reygondeau, G., Maureaud, A., & Cheung, W. W. L. (2020). Climate change undermines the global functioning of marine food webs. *Global Change Biology*, *26*(3), 1306–1318. https://doi.org/10.1111/gcb.14944

Duck, C. D. (1990). Annual variation in the timing of reproduction in Antarctic fur seals, *Arctocephalus gazella*, at Bird Island, South-Georgia. *Journal of Zoology*, *222*, 103–116. https://doi.org/10.1111/j.1469-7998.1990.tb04032.x

Dulvy, N. K., Pacoureau, N., Rigby, C. L., Pollom, R. A., Jabado, R. W., Ebert, D. A., Finucci, B., Pollock, C. M., Cheok, J., Derrick, D. H., Herman, K. B., Sherman, C. S., VanderWright, W. J., Lawson, J. M., Walls, R. H. L., Carlson, J. K., Charvet, P., Bineesh, K. K., Fernando, D., … Simpfendorfer, C. A. (2021). Overfishing drives over one-third of all sharks and rays toward a global extinction crisis. *Current Biology*, *31*(21), 4773–4787. https://doi.org/10.1016/j.cub.2021.08.062

Estes, J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., Jackson, J. B. C., Marquis, R. J., Oksanen, L., Oksanen, T., Paine, R. T., Pikitch, E. K., Ripple, W. J., Sandin, S. A., Scheffer, M., Schoener, T. W., … Wardle, D. A. (2011). Trophic downgrading of planet earth. *Science*, *333*(6040), 301–306. https://doi.org/10.1126/science.1205106

Fielding, S., Enderlein, P., Stowasser, G., Tarling, G. A., & Manno, C. (2022). *Antarctic krill (Euphausia superba) biomass density estimates derived from acoustic backscatter data collected in the Western Core Box survey, South Georgia, South Atlantic: 1996–2019 (Version 1.0)*. NERC EDS UK Polar Data Centre. https://doi.org/10.5285/e85a9312-8531-4261-a2f6-1c58f40cfc71

Foley, C. M., & Lynch, H. J. (2019). A method to estimate pre-exploitation population size. *Conservation Biology*, *34*, 256–265. https://doi.org/10.1111/cobi.13416

Forcada, J., & Hoffman, J. I. (2014). Climate change selects for heterozygosity in a declining fur seal population. *Nature*, *511*(7510), 462. https://doi.org/10.1038/nature13542

Forcada, J., & Staniland, I. J. (2018). Antarctic fur seal: *Arctocephalus gazella*. In B. Würsig, J. G. M. Thewissen, & K. M. Kovacs (Eds.), *Encyclopedia of marine mammals* (3rd ed., pp. 25–27). Academic Press. https://doi.org/10.1016/B978-0-12-804327-1.00046-7

Forcada, J., Trathan, P. N., & Murphy, E. J. (2008). Life history buffering in Antarctic mammals and birds against changing patterns of climate and environmental variation. *Global Change Biology*, *14*(11), 2473–2488. https://doi.org/10.1111/j.1365-2486.2008.01678.x

Forcada, J., Trathan, P. N., Reid, K., & Murphy, E. J. (2005). The effects of global climate variability in pup production of Antarctic fur seals. *Ecology*, *86*(9), 2408–2417. https://doi.org/10.1890/04-1153

Gamelon, M., Nater, C. R., Baubet, E., Besnard, A., Touzot, L., Gaillard, J. M., Lebreton, J. D., & Gimenez, O. (2021). Efficient use of harvest data: A size-class-structured integrated population model for exploited populations. *Ecography*, *44*(9), 1296–1310. https://doi.org/10.1111/ecog.05738

Gelman, A., & Hill, J. (2006). *Data analysis using regression and multilevel/hierarchical models*. Cambridge University Press. https://doi.org/10.1017/CBO9780511790942

Gelman, A., Hwang, J., & Vehtari, A. (2014). Understanding predictive information criteria for Bayesian models. *Statistics and Computing*, *24*(6), 997–1016. https://doi.org/10.1007/s11222-013-9416-2

Gelman, A., & Shirley, K. (2011). Inference from simulations and monitoring convergence. In S. Brooks, A. Gelman, G. Jones, & X.-L. Meng (Eds.), *Handbook of Markov chain Monte Carlo* (1st ed., pp. 163–174). Chapman and Hall/CRC. https://doi.org/10.1201/b10905

Gimenez, O., Lebreton, J. D., Choquet, R., & Pradel, R. (2018). R2ucare: An r package to perform goodness-of-fit tests for capture-recapture models. *Methods in Ecology and Evolution*, *9*(7), 1749–1754. https://doi.org/10.1111/2041-210x.13014

Gimenez, O., Rossi, V., Choquet, R., Dehais, C., Doris, B., Varella, H., Vila, J. P., & Pradel, R. (2007). State-space modelling of data on marked individuals. *Ecological Modelling*, *206*(3–4), 431–438. https://doi.org/10.1016/j.ecolmodel.2007.03.040

Gulland, J. A. (1983). The development of fisheries and stock assessment of resources in the Southern Ocean. *Memoirs of National Institute of Polar Research*, *27*, 233–246.

Hammill, M., Gosselin, J.-F., & Stenson, G. (2013). *Abundance of Northwest Atlantic grey seals in Canadian waters*. NAMMCO Scientific Publications. https://doi.org/10.7557/3.2726

Hammond, P. S., Francis, T. B., Heinemann, D., Long, K. J., Moore, J. E., Punt, A. E., Reeves, R. R., Sepúlveda, M., Sigurðsson, G. M., Siple, M. C., Víkingsson, G., Wade, P. R., Williams, R., & Zerbini, A. N. (2021). Estimating the abundance of marine mammal populations. *Frontiers in Marine Science*, *8*, 735770. https://doi.org/10.3389/fmars.2021.735770

Hastings, A. (2004). Transients: The key to long-term ecological understanding? *Trends in Ecology & Evolution*, *19*(1), 39–45. https://doi.org/10.1016/j.tree.2003.09.007

Hastings, A., Abbott, K. C., Cuddington, K., Francis, T., Gellner, G., Lai, Y.-C., Morozov, A., Petrovskii, S., Scranton, K., & Zeeman, M. L. (2018). Transient phenomena in ecology. *Science*, *361*(6406), eaat6412. https://doi.org/10.1126/science.aat6412

Hill, S., Atkinson, A., Darby, C., Fielding, S., Krafft, B., Godø, O., Skaret, G., Trathan, P., & Watkins, J. (2016). Is current management of the Antarctic krill fishery in the Atlantic sector of the Southern Ocean precautionary? *CCAMLR Science*, *23*, 31–51.

Hobbs, R. J., Higgs, E., & Harris, J. A. (2009). Novel ecosystems: Implications for conservation and restoration. *Trends in Ecology & Evolution*, *24*(11), 599–605. https://doi.org/10.1016/j.tree.2009.05.012

Hocevar, S., & Kuparinen, A. (2021). Marine food web perspective to fisheries-induced evolution. *Evolutionary Applications*, *14*(10), 2378–2391. https://doi.org/10.1111/eva.13259

Hoffman, J. I., Boyd, I. L., & Amos, W. (2003). Male reproductive strategy and the importance of maternal status in the antarctic fur seal *Arctocephalus gazella*. *Evolution*, *57*(8), 1917–1930. https://doi.org/10.1111/j.0014-3820.2003.tb00598.x?sid=nlm%3Apubmed

Hoffman, J. I., Chen, R. S., Vendrami, D. L. J., Paijmans, A. J., Dasmahapatra, K. K., & Forcada, J. (2022). Demographic reconstruction of Antarctic fur seals supports the krill surplus hypothesis. *Genes*, *13*(3), 541.

Hoffman, J. I., Trathan, P. N., & Amos, W. (2006). Genetic tagging reveals extreme site fidelity in territorial male Antarctic fur seals *Arctocephalus gazella*. *Molecular Ecology*, *15*(12), 3841–3847. https://doi.org/10.1111/j.1365-294X.2006.03053.x

Hofmeyr, G. J. G. (2016). *Arctocephalus gazella. The IUCN red list of threatened species. 2016: e.T2058A66993062* (The IUCN red list of threatened species 2016 issue). IUCN.UK.2016-1.RLTS.T2058A66993062.en.

Hofmeyr, G. J. G., Bester, M. N., Pistorius, P. A., Mulaudzi, T. W., de Bruyn, P. J. N., Ramunasi, J. A., Tshithabane, H. N., McIntyre, T., & Radzilani, P. M. (2007). Median pupping date, pup mortality and sex ratio of fur seals at Marion Island. *South African Journal of Wildlife Research*, *37*(1), 1–8. https://doi.org/10.3957/0379-4369-37.1.1

Hollyman, P., Trathan, P., & Collins, M. (2021). *Counts of Antarctic fur seals at Maiviken, South Georgia, from 2008 to 2020 (version 1.0)* [Data set]. NERC EDS UK Polar Data Centre. https://doi.org/10.5285/41BFD98C-1A36-4689-A578-AD584426F9D2

Hollyman, P. R., Hill, S. L., Laptikhovsky, V. V., Belchier, M., Gregory, S., Clement, A., Collins, M. A., & Godo, O. R. (2021). A long road to recovery: Dynamics and ecology of the marbled rockcod (*Notothenia*

rossii, family: Nototheniidae) at South Georgia, 50 years after over-exploitation. *ICES Journal of Marine Science*, 78(8), 2745–2756. https://doi.org/10.1093/icesjms/fsab150

Huang, B., Liu, C., Banzon, V. F., Freeman, E., Graham, G., Hankins, B., Smith, T. M., & Zhang, H.-M. (2020). *NOAA 0.25-degree daily optimum interpolation sea surface temperature (OISST), version 2.1. [ncdcOisst21Agg_LonPM180]*. NOAA National Centers for Environmental Information. https://doi.org/10.25921/RE9P-PT57

Humble, E., Dasmahapatra, K. K., Martinez-Barrio, A., Gregorio, I., Forcada, J., Polikeit, A. C., Goldsworthy, S. D., Goebel, M. E., Kalinowski, J., Wolf, J. B. W., & Hoffman, J. I. (2018). RAD sequencing and a hybrid Antarctic fur seal genome assembly reveal rapidly decaying linkage disequilibrium, global population structure and evidence for inbreeding. *G3 – Genes Genomes Genetics*, 8(8), 2709–2722. https://doi.org/10.1534/g3.118.200171

Jabour, J. (2008). Successful conservation—Then what? The de-listing of *Arctocephalus* fur seal species in Antarctica. *Journal of International Wildlife Law & Policy*, 11(1), 1–29. https://doi.org/10.1080/13880290801960712

Jachowski, D. S., Kesler, D. C., Steen, D. A., & Walters, J. R. (2015). Redefining baselines in endangered species recovery. *The Journal of Wildlife Management*, 79(1), 3–9. https://doi.org/10.1002/jwmg.800

Jackson, J. A., Kennedy, A., Moore, M., Andriolo, A., Bamford, C. C. G., Calderan, S., Cheeseman, T., Gittins, G., Groch, K., Kelly, N., Leaper, R., Leslie, M. S., Lurcock, S., Miller, B. S., Richardson, J., Rowntree, V., Smith, P., Stepien, E., Stowasser, G., … Carroll, E. L. (2020). Have whales returned to a historical hotspot of industrial whaling? The pattern of southern right whale *Eubalaena australis* recovery at South Georgia. *Endangered Species Research*, 43, 323–339.

Keitt, T. H. (2008). Coherent ecological dynamics induced by large-scale disturbance. *Nature*, 454(7202), 331–334. https://doi.org/10.1038/nature06935

Kellner, K. (2021). *jagsUI: A wrapper around 'rjags' to streamline 'JAGS' analyses*. R package version 1.5.2. https://CRAN.R-project.org/package=jagsUI

Kéry, M., & Schaub, M. (2012). Chapter 9 – Estimation of survival and movement from capture–recapture data using multistate models. In M. Kéry & M. Schaub (Eds.), *Bayesian population analysis using WinBUGS* (pp. 263–313). Academic Press. https://doi.org/10.1016/B978-0-12-387020-9.00009-2

Krafft, B. A., Macaulay, G. J., Skaret, G., Knutsen, T., Bergstad, O. A., Lowther, A., Huse, G., Fielding, S., Trathan, P., Murphy, E., Choi, S.-G., Chung, S., Han, I., Lee, K., Zhao, X., Wang, X., Ying, Y., Yu, X., Demianenko, K., … Hoem, N. (2021). Standing stock of Antarctic krill (*Euphausia superba* Dana, 1850) (Euphausiacea) in the Southwest Atlantic sector of the Southern Ocean, 2018–19. *Journal of Crustacean Biology*, 41(3), 046. https://doi.org/10.1093/jcbiol/ruab046

Krause, D. J., Bonin, C. A., Goebel, M. E., Reiss, C. S., & Watters, G. M. (2022). The rapid population collapse of a key marine predator in the northern Antarctic peninsula endangers genetic diversity and resilience to climate change. *Frontiers in Marine Science*, 8, 796488. https://doi.org/10.3389/fmars.2021.796488

Larkin, P. A. (1996). Concepts and issues in marine ecosystem management. *Reviews in Fish Biology and Fisheries*, 6(2), 139–164. https://doi.org/10.1007/BF00182341

LaRue, M., Salas, L., Nur, N., Ainley, D., Stammerjohn, S., Pennycook, J., Dozier, M., Saints, J., Stamatiou, K., Barrington, L., & Rotella, J. (2021). Insights from the first global population estimate of Weddell seals in Antarctica. *Science Advances*, 7(39), eabh3674. https://doi.org/10.1126/sciadv.abh3674

Laws, R. M. (1973). Population increase of fur seals at South Georgia. *Polar Record*, 16(105), 856–858. https://doi.org/10.1017/S003224740006397X

Laws, R. M. (1977). Seals and whales of the Southern Ocean. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, 279(963), 81–96. https://doi.org/10.1098/rstb.1977.0073

Lindegren, M., Möllmann, C., Nielsen, A., & Stenseth, N. C. (2009). Preventing the collapse of the Baltic cod stock through an ecosystem-based management approach. *Proceedings of the National Academy of Sciences of the United States of America*, 106(34), 14722–14727. https://doi.org/10.1073/pnas.0906620106

Link, W. A., & Barker, R. J. (2005). Modeling association among demographic parameters in analysis of open population capture-recapture data. *Biometrics*, 61(1), 46–54. https://doi.org/10.1111/j.0006-341X.2005.030906.x

Luypaert, T., Hagan, J. G., McCarthy, M. L., & Poti, M. (2020). Status of marine biodiversity in the Anthropocene. In S. Jungblut, V. Liebich, & M. Bode-Dalby (Eds.), *YOUMARES 9 – The oceans: Our research, our future: Proceedings of the 2018 conference for YOUng MArine RESearcher*. Oldenburg, Germany (pp. 57–82). Springer International Publishing. https://doi.org/10.1007/978-3-030-20389-4_4

Mackintosh, N. A. (1967). Estimates of local seal populations in the Antarctic, 1930–37. *Norsk Hvalfangst-Tidende*, 3, 57–64.

Mackintosh, N. A. (1973). Distribution of post-larval krill in the Antarctic. *Discovery Reports*, 36, 95–156.

Marr, J. W. S. (1961). *The natural history and geography of the Antarctic krill (Euphausia superba Dana)*. Cambridge University Press.

Marshall, G. J. (2003). Trends in the southern annular mode from observations and reanalyses. *Journal of Climate*, 16(24), 4134–4143. https://doi.org/10.1175/1520-0442(2003)016<4134:TITSAM>2.0.CO;2

Maunder, M. N. (2004). Population viability analysis based on combining Bayesian, integrated, and hierarchical analyses. *Acta Oecologica*, 26(2), 85–94. https://doi.org/10.1016/j.actao.2003.11.008

McBride, M. M., Schram Stokke, O., Renner, A. H. H., Krafft, B. A., Bergstad, O. A., Biuw, M., Lowther, A. D., & Stiansen, J. E. (2021). Antarctic krill *Euphausia superba*: Spatial distribution, abundance, and management of fisheries in a changing climate. *Marine Ecology Progress Series*, 668, 185–214.

McCauley, D. J., Pinsky, M. L., Palumbi, S. R., Estes, J. A., Joyce, F. H., & Warner, R. R. (2015). Marine defaunation: Animal loss in the global ocean. *Science*, 347(6219), 1255641 10.1126/science.1255641.

McNellie, M. J., Oliver, I., Dorrough, J., Ferrier, S., Newell, G., & Gibbons, P. (2020). Reference state and benchmark concepts for better biodiversity conservation in contemporary ecosystems. *Global Change Biology*, 26(12), 6702–6714. https://doi.org/10.1111/gcb.15383

Meredith, M. P., Murphy, E. J., Hawker, E. J., King, J. C., & Wallace, M. I. (2008). On the interannual variability of ocean temperatures around South Georgia, Southern Ocean: Forcing by El Niño/southern oscillation and the southern annular mode. *Deep Sea Research Part II: Topical Studies in Oceanography*, 55(18), 2007–2022. https://doi.org/10.1016/j.dsr2.2008.05.020

Miller, D. G. M. (1991). Exploitation of Antarctic marine living resources – A brief-history and a possible approach to managing the krill fishery. *South African Journal of Marine Science-Suid-Afrikaanse Tydskrif Vir Seewetenskap*, 10, 321–339.

Nater, C. R., Eide, N. E., Pedersen, Å. Ø., Yoccoz, N. G., & Fuglei, E. (2021). Contributions from terrestrial and marine resources stabilize predator populations in a rapidly changing climate. *Ecosphere*, 12(6), e03546. https://doi.org/10.1002/ecs2.3546

Newman, K. B., Buckland, S. T., Morgan, B. J. T., King, R., Borchers, D. L., Cole, D. J., Besbeas, P., Gimenez, O., & Thomas, L. (2014). Integrated population modelling. In *Modelling population dynamics: Model formulation, fitting and assessment using state-space methods* (pp. 169–195). Springer. https://doi.org/10.1007/978-1-4939-0977-3_9

Nicol, S., & Foster, J. (2016). The fishery for Antarctic krill: Its current status and management regime. In V. Siegel (Ed.), *Biology and ecology of Antarctic krill* (pp. 387–421). Springer International Publishing. https://doi.org/10.1007/978-3-319-29279-3_11

Oosthuizen, W. C., Postma, M., Altwegg, R., Nevoux, M., Pradel, R., Bester, M. N., & de Bruyn, P. J. N. (2019). Individual heterogeneity in life-history trade-offs with age at first reproduction in capital breeding elephant seals. *Population Ecology*, 61(4), 421–435. https://doi.org/10.1002/1438-390X.12015

Paijmans, A. J., Stoffel, M. A., Bester, M. N., Cleary, A. C., De Bruyn, P. J. N., Forcada, J., Goebel, M. E., Goldsworthy, S. D., Guinet, C., Lydersen, C., Kovacs, K. M., Lowther, A., & Hoffman, J. I. (2020). The genetic legacy of extreme exploitation in a polar vertebrate. *Scientific Reports*, 10(1), 5089. https://doi.org/10.1038/s41598-020-61560-8

Payne, M. R. (1977). Growth of a fur seal population. *Philosophical Transactions of the Royal Society of London Series B-Biological Sciences*, 279(963), 67–79. https://doi.org/10.1098/rstb.1977.0072

Payne, M. R. (1979). Growth in the Antarctic fur seal *Arctocephalus gazella*. *Journal of Zoology*, 187(Jan), 1–20.

Péron, G., & Koons, D. N. (2012). Integrated modeling of communities: Parasitism, competition, and demographic synchrony in sympatric ducks. *Ecology*, 93(11), 2456–2464. https://doi.org/10.1890/11-1881.1

Pitcher, K. W., Olesiuk, P. F., Brown, R. F., Lowry, M. S., Jeffries, S. J., Sease, J. L., Perryman, W. L., Stinchcomb, C. E., & Lowry, L. F. (2007). Abundance and distribution of the eastern North Pacific Steller sea lion (*Eumetopias jubatus*) population. *Fishery Bulletin*, 105(1), 102–115.

Plard, F., Fay, R., Kéry, M., Cohas, A., & Schaub, M. (2019). Integrated population models: Powerful methods to embed individual processes in population dynamics models. *Ecology*, 100(6), e02715. https://doi.org/10.1002/ecy.2715

Plummer, M. (2003). JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. *International workshop on distributed statistical computing (DSC 2003)*. Vienna, Austria.

Plummer, M. (2022). *rjags: Bayesian graphical models using MCMC*. R package version 4-13. https://CRAN.R-project.org/package=rjags

Pradel, R., & Lebreton, J. D. (1999). Comparison of different approaches to the study of local recruitment of breeders. *Bird Study*, 46, 74–81.

Pradel, R., Wintrebert, C. M. A., & Gimenez, O. (2003). A proposal for a goodness-of-fit test to the Arnason-Schwarz multisite capture-recapture model. *Biometrics*, 59(1), 43–53. https://doi.org/10.1111/1541-0420.00006

R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Reid, K., & Arnould, J. P. Y. (1996). The diet of Antarctic fur seals *Arctocephalus gazella* during the breeding season at South Georgia. *Polar Biology*, 16(2), 105–114. https://doi.org/10.1007/Bf02390431

Reid, K., Watkins, J. L., Croxall, J. P., & Murphy, E. J. (1999). Krill population dynamics at South Georgia 1991–1997, based on data from predators and nets. *Marine Ecology Progress Series*, 177, 103–114. https://doi.org/10.3354/meps177103

Royle, J. A., & Dorazio, R. M. (2009). 10 – Modeling population dynamics. In J. A. Royle & R. M. Dorazio (Eds.), *Hierarchical modeling and inference in ecology* (pp. 325–345). Academic Press. https://doi.org/10.1016/B978-0-12-374097-7.00012-0

Russell, D. J. F., Morris, C. D., Duck, C. D., Thompson, D., & Hiby, L. (2019). Monitoring long-term changes in UK grey seal pup production. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 29(S1), 24–39. https://doi.org/10.1002/aqc.3100

Saunders, S. P., Cuthbert, F. J., & Zipkin, E. F. (2018). Evaluating population viability and efficacy of conservation management using integrated population models. *Journal of Applied Ecology*, 55(3), 1380–1392. https://doi.org/10.1111/1365-2664.13080

SCAR. (2006). *Proposal to de-list Antarctic fur seals as specially protected species*. Working Paper 39. Antarctic Treaty Consultative Meeting XXIX, Edinburgh, UK, 12–23 June, 2006.

Schaub, M., & Abadi, F. (2011). Integrated population models: A novel analysis framework for deeper insights into population dynamics. *Journal of Ornithology*, 152, 227–237. https://doi.org/10.1007/s10336-010-0632-7

Schaub, M., Gimenez, O., Schmidt, B. R., & Pradel, R. (2004). Estimating survival and temporary emigration in the multistate capture-recapture framework. *Ecology*, 85(8), 2107–2113. https://doi.org/10.1890/03-3110

Schaub, M., & Kéry, M. (2021). *Integrated population models: Theory and ecological applications with R and JAGS*. Academic Press.

Schmidt, K., Atkinson, A., Steigenberger, S., Fielding, S., Lindsay, M. C. M., Pond, D. W., Tarling, G. A., Klevjer, T. A., Allen, C. S., Nicol, S., & Achterberg, E. P. (2011). Seabed foraging by Antarctic krill: Implications for stock assessment, bentho-pelagic coupling, and the vertical transfer of iron. *Limnology and Oceanography*, 56(4), 1411–1428. https://doi.org/10.4319/lo.2011.56.4.1411

Siegel, V., & Watkins, J. L. (2016). Distribution, biomass and demography of Antarctic krill, *Euphausia superba*. In V. Siegel (Ed.), *Biology and ecology of Antarctic krill* (pp. 21–100). Springer International Publishing. https://doi.org/10.1007/978-3-319-29279-3_2

Sladen, W. J. L. (1964). The distribution of the Adelie and chinstrap penguins. In R. Carrick, M. W. Holdgate, & J. Prevost (Eds.), *Biologie Antarctique* (pp. 359–365). Hermann.

Southwell, C., Paxton, C. G. M., Borchers, D., Boveng, P., & De La Mare, W. (2008). Taking account of dependent species in management of the Southern Ocean krill fishery: Estimating crabeater seal abundance off east Antarctica. *Journal of Applied Ecology*, 45(2), 622–631. https://doi.org/10.1111/j.1365-2664.2007.01399.x

Staniland, I. J., & Robinson, S. L. (2008). Segregation between the sexes: Antarctic fur seals, *Arctocephalus gazella*, foraging at South Georgia. *Animal Behaviour*, 75, 1581–1590. https://doi.org/10.1016/j.anbehav.2007.10.012

Stier, A. C., Samhouri, J. F., Novak, M., Marshall, K. N., Ward, E. J., Holt, R. D., & Levin, P. S. (2016). Ecosystem context and historical contingency in apex predator recoveries. *Science Advances*, 2(5), e1501769. https://doi.org/10.1126/sciadv.1501769

Surma, S., Pakhomov, E. A., & Pitcher, T. J. (2014). Effects of whaling on the structure of the Southern Ocean food web: Insights on the "krill surplus" from ecosystem modelling. *PLoS One*, 9(12), e114978. https://doi.org/10.1371/journal.pone.0114978

Thomas, L., Russell, D. J. F., Duck, C. D., Morris, C. D., Lonergan, M., Empacher, F., Thompson, D., & Harwood, J. (2019). Modelling the population size and dynamics of the British grey seal. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 29(S1), 6–23. https://doi.org/10.1002/aqc.3134

Thompson, P. M., Tollit, D. J., Wood, D., Corpe, H. M., Hammond, P. S., & Mackay, A. (1997). Estimating harbour seal abundance and status in an estuarine habitat in north-east Scotland. *Journal of Applied Ecology*, 34(1), 43–52. https://doi.org/10.2307/2404846

Watanabe, S. (2010). Asymptotic equivalence of Bayes cross validation and widely applicable information criterion in singular learning theory. *Journal of Machine Learning Research*, 11, 3571–3594.

Weddell, J. (1825). *A voyage towards the south pole, performed in the years 1822–1824*. BHL.

Weegman, M. D., Arnold, T. W., Clark, R. G., & Schaub, M. (2021). Partial and complete dependency among data sets has minimal consequence on estimates from integrated population models. *Ecological Applications*, 31(3), 2258. https://doi.org/10.1002/eap.2258

Womble, J. N., Ver Hoef, J. M., Gende, S. M., & Mathews, E. A. (2020). Calibrating and adjusting counts of harbor seals in a tidewater glacier fjord to estimate abundance and trends 1992 to 2017. *Ecosphere*, 11(4), e03111. https://doi.org/10.1002/ecs2.3111

Wood, S. N. (2016). Just another Gibbs additive modeler: Interfacing JAGS and mgcv. *Journal of Statistical Software*, 75(7), 1–15. https://doi.org/10.18637/jss.v075.i07

Zerbini, A. N., Adams, G., Best, J., Clapham, P. J., Jackson, J. A., & Punt, A. E. (2019). Assessing the recovery of an Antarctic predator from historical exploitation. *Royal Society Open Science*, *6*(10), 190368. https://doi.org/10.1098/rsos.190368

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