



Flying under the radar: the demographic importance of immatures in long-lived seabird populations

Francesco Ventura^{a,*}, Christian Che-Castaldo^b, Paulo Catry^c, Karine Delord^d, Amanda Kuepfer^e, Bertille Mohring^f, Steffen Oppel^g, Richard A. Phillips^h, Etienne Rouby^{i,j}, Caroline C. Ummenhofer^a, Henri Weimerskirch^d, Andrew G. Wood^h, Christophe Barbraud^d, Stéphanie Jenouvrier^j

^a Department of Physical Oceanography, Woods Hole Oceanographic Institution, Woods Hole, MA, USA

^b U.S. Geological Survey, Wisconsin Cooperative Wildlife Research Unit, Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, Madison, WI, USA

^c MARE – Marine and Environmental Sciences Centre/ARNET - Aquatic Research Network, Ispa Instituto Universitario, Lisbon, Portugal

^d Centre d'Études Biologiques de Chizé, UMR7372 CNRS-La Rochelle Université, Villiers-en-Bois, 79360, France

^e Falklands Conservation, Stanley, Falkland Islands

^f School of Environmental Sciences, University of Liverpool, Liverpool, UK

^g Swiss Ornithological Institute, Sempach, Switzerland

^h British Antarctic Survey, Cambridge, United Kingdom

ⁱ Institute of Arctic and Alpine Research, University of Colorado Boulder, Boulder, CO, USA

^j Department of Biology, Woods Hole Oceanographic Institution, Woods Hole, MA, USA

ARTICLE INFO

Keywords:

Conservation
Demography
Integrated population model
Immature survival
Seabird
Top-predator

ABSTRACT

Demographic assessments are essential for effective biological conservation management, allowing early detection of population declines and timely allocation of resources to avoid possible crises. For species with slow life-history strategies like seabirds, only the breeding adults are monitored routinely. The dynamics of immatures, often unobservable from fledging to recruitment, are less well understood and typically not accounted for in conservation status assessments.

Here, we quantify the importance of changes in the survival and abundance of immatures in shaping the past and forecasted dynamics of a long-lived marine top-predator. We use integrated population models (IPM) incorporating the dynamics of immatures, based on multi-decadal demographic monitoring of the black-browed albatross (*Thalassarche melanophris*) at three globally important breeding sites.

The populations showed differences in breeding and survival rates, highlighting a degree of life history flexibility in response to the environment. Using a retrospective sensitivity analysis, we consistently identified immature survival as the key contributor to population growth rate. At all sites, even those with increasing or stable breeding populations, the total population has been declining, largely due to decreases in immature survival. Although not directly apparent from counts, this decline is already underway and is projected to emerge at the level of the breeding population over the coming three generations. This contrasts with a model focusing solely on counts of breeding adults, which mostly indicate an overall population increase.

Collectively, our findings highlight that conservation assessments must account for the dynamics of subadult stages, or risk providing an inaccurate picture of population status.

1. Introduction

Global biodiversity is declining at an unprecedented rate (Pimm et al., 2014; Ceballos et al., 2015, 2020; IPBES, 2019; Wiens and Zelnika, 2024). The global ocean, once thought to be too vast and

productive to deplete (Lubchenco and Gaines, 2019), is suffering ever increasing impacts driven by anthropogenic climate change and other human activities, such as overfishing and habitat degradation (Halpern et al., 2015; IPCC, 2019). Yet, averting further dramatic collapses of biodiversity is possible through the successful implementation of

* Corresponding author.

E-mail address: fraventura.92@gmail.com (F. Ventura).

<https://doi.org/10.1016/j.biocon.2026.112102>

Received 12 December 2025; Received in revised form 27 August 2026; Accepted 4 September 2026

0006-3207/© 2026 Published by Elsevier Ltd.

conservation strategies (Hoffmann et al., 2010). Given the urgency of the task and the limited economic resources, filling gaps in knowledge of status and trends of biota is crucial to conservation prioritization and decision-making.

Seabirds play pivotal roles in marine conservation by serving as sentinels of ecosystem health (Boyd and Murray, 2001; Sergio et al., 2008). They also comprise some of the most threatened species among all vertebrates (Phillips et al., 2016; Dias et al., 2019). Being long-lived with delayed maturity and low reproductive output (Schreiber and Burger, 2001; Bird et al., 2020), seabird populations are particularly sensitive to even small decreases in the survival of adult individuals, which can lead to steep population declines (Rolland et al., 2008; Tuck et al., 2011). Unlike most other marine predators, adult seabirds are relatively accessible during breeding. As a result, breeding adults have been the focus of extensive longitudinal ecological monitoring and research, and the target of most conservation actions, often leading to immediate, tangible benefits (Croxall, 2008; Robertson et al., 2014; Da Rocha et al., 2021; Dasnon et al., 2022).

Beyond the breeding component of the population, a large proportion of the total population is composed of immature individuals. Unlike breeding adults, however, substantial gaps in knowledge exist for the years of immaturity (Witham, 1980), i.e. the period from fledging to recruitment. Immature individuals are largely unobservable during their first years of life at sea (Hazen et al., 2012; Phillips et al., 2017). Yet, they often make up a substantial portion of the total population size and may be more vulnerable to threats due to their inexperience (Nevoux et al., 2007; Gianuca et al., 2017; Clay et al., 2019; Carneiro et al., 2020). Decreases in these younger age classes can give rise to gradual shifts in the population age structure, triggering disequilibrium and transient dynamics (Stafoggia et al., 2006; Pardo et al., 2017a). These processes have more subtle repercussions than the more rapid decreases in the breeding population driven by decreases in adult survival or skipped breeding. Indeed, underlying hidden declines in the young age classes may be occurring even if the adult breeding population numbers are stable or increasing (Oppel et al., 2022). Clearly, failing to account for immatures leads to incomplete demographic assessments, potentially leading to a false sense of security in terms of the outlook for conservation. This is particularly relevant, as global climate change is shaping divergent and context-dependent responses in vital rates, producing different impacts on different life history stages within populations (Pardo et al., 2013; Cordes et al., 2020).

The overarching objective of this study is to quantify the importance of cryptic (i.e., not directly observable) changes in the survival and abundance of immatures for the population dynamics of a long-lived marine top-predator, the black-browed albatross (*Thalassarche melanophris*). Applying a consistent modelling framework, we analyse some of the longest individual-based multi-decadal demographic records available for any vertebrate, focusing on three study colonies that show different breeding population trajectories. Given the high adult survival rates, slow maturation and long generation time of our study species, we investigate when hidden changes in dynamics of subadults will become manifest as a changing trend in the breeding population. We assess the conservation relevance of immatures by comparing the population projections generated by demographic models incorporating dynamics of immatures (i.e., integrated population models, IPMs) vs. projections generated by simpler models of breeding abundance not accounting for immatures. Our comparative analysis reveals the demographic importance of immatures under different environmental contexts and a range of population trends (i.e., in increasing as well as decreasing breeding populations). Results are discussed in the context of drivers of these differences in life histories and implications for conservation.

2. Materials and methods

2.1. Study system

The black-browed albatross is a colonial species in the order Procellariiformes with a circumpolar distribution, ranging from subtropical to polar waters, and usually breeds annually. The total global breeding population is estimated at ~700,000 pairs, the majority (>70%) nesting on the Falkland Islands (Phillips et al., 2016). Largely due to reported increases at the Falklands colonies, the global population size is considered to be increasing and classified as Least Concern by the IUCN Red List (Birdlife International, 2018). However, concerns about potentially unsustainable levels of incidental mortality (bycatch) in fisheries led to listing of the species by the multilateral Agreement on the Conservation of Albatrosses and Petrels (ACAP), and the continuing steep decline of the globally important population at South Georgia later led to its inclusion as one of just nine ACAP High Priority Populations for conservation (Phillips et al., 2016).

Our comprehensive demographic database is the product of multi-decadal monitoring efforts at three colonies across their distributional range: New Island, Falklands (South Atlantic Ocean); Bird Island, South Georgia (South Atlantic Ocean); Canyon des Sourcils Noirs, southern Kerguelen Islands (Southern Indian Ocean) (Fig. 1). The long-term demographic data collected in the Falklands, South Georgia and Kerguelen comprise long-term breeding histories of ~3900, 9000 and 6500 individuals, respectively. A total of 3044, 5586 and 5097 birds were ringed as chicks in the Falklands, South Georgia and Kerguelen, respectively. We included data spanning 1979–2024 (South Georgia), 1987–2023 (Kerguelen) and 2003–2024 (Falklands). For all study populations we had the following demographic information: individual-based capture–mark–recapture datasets (“CMR”, i.e. encounter histories of ringed adults and chicks); population counts (number of breeding pairs); and productivity data (total number of fledglings produced per nesting adult). At South Georgia, standardised population counts and productivity data were only available from 1993 onwards, which was therefore used as the starting year of the abundance component of the South Georgia demographic model (see below). Data collection protocols varied across study sites, leading to site-specific data limitations and assumptions and, in turn, to slight differences in the formulation of the demographic models (outlined in the appendix).

2.2. Demographic modelling

In this study, we define: “immatures” as individuals from fledging to 4 years old; and “immature survival” as the annual survival over the first four years post-fledging. No birds (South Georgia) and only 0.6% (Falklands) and 0.3% (Kerguelen) of all birds have been recaptured prior to 4 years of age, making it impossible to estimate survival rates separately for these earlier years. Once individuals reach 4 years of age, we assume that they have the same survival probability as adults, as in Pardo et al., 2017b (see the description of the model formulation below). Demographic data from all colonies were analysed using integrated population models (IPMs, Schaub and Abadi, 2011; Schaub and Kéry, 2021). IPMs simultaneously capitalize on the strengths of each demographic data stream (i.e., CMR, counts and productivity) to better estimate demographic rates and population trajectories. Advantages over non-integrated analysis include: robust error propagation; improved demographic estimates; and the estimation of hidden parameters driving the dynamics of cryptic components of the population (Schaub and Abadi, 2011; Abadi et al., 2017; Zipkin and Saunders, 2018). This feature is particularly useful for the study of immatures, which are largely unobservable until they return to the colony.

We designed IPMs to quantify the demographic rates driving the dynamics of the total populations, including immatures, and capture the temporal variability in survival (of both adults and immatures), breeding probability and breeding success. The abundance process

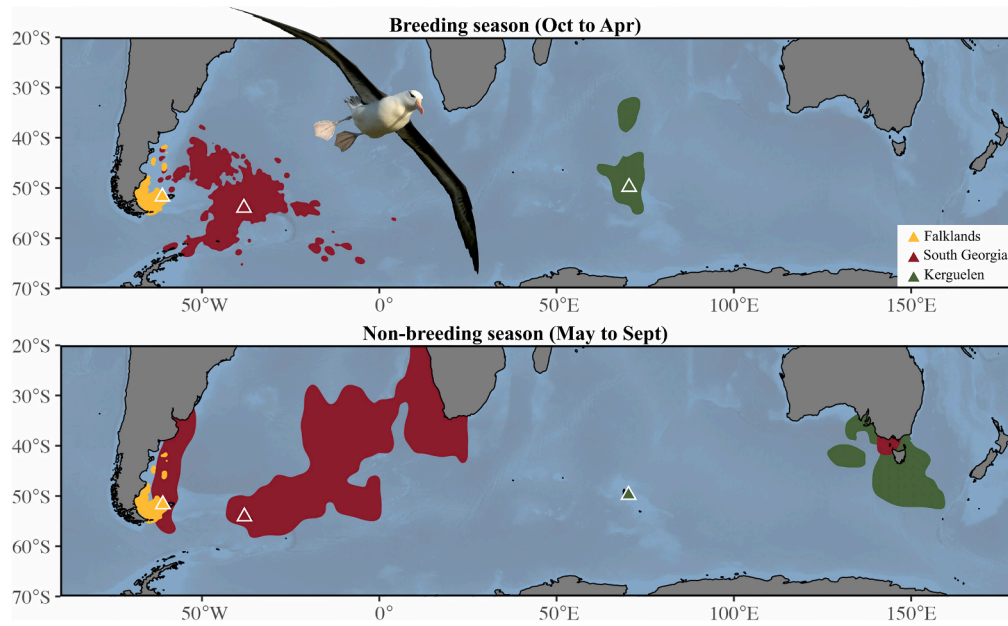


Fig. 1. The map depicts the at-sea distribution of the monitored black-browed albatross populations (*Thalassarche melanophris*) during the breeding and non-breeding seasons. The triangles represent the study colonies of New Island (Falklands) and Bird Island (South Georgia) in the South Atlantic, and Canyon des Sources Noirs (southern Kerguelen Islands) in the southern Indian Ocean. For each colony, the distribution contours encompass 90% of the kernel utilization distribution, adapted from Ventura et al., 2021 (Falklands), Phillips et al., 2005 (South Georgia) and Desprez et al., 2018 (Kerguelen).

models in the IPMs were female-based, estimating the dynamics of the female component of the population. We fitted one age-stage structured IPM per colony. At all sites, the IPM assumed equal sex ratio at birth and no dispersal, an assumption supported by the strong philopatry exhibited by fledglings, which virtually always return to breed at their natal colony (Prince et al., 1994; Nevoux et al., 2007). Following Ventura et al., 2021, for the Falklands colony we accounted for local patterns of emigration (see Section 1 in the Appendix), i.e., those individuals hatched in the study area that recruited outside of the monitored plots, as failing to do so would have artificially increased immature mortality estimates. Local emigration processes at the other study sites are negligible and were not incorporated in the models.

In the IPMs, we used a state-space modelling formulation for the population counts, a multi-state framework with a state-space modelling formulation for the CMR component and a binomial regression for the productivity component. The full likelihoods for these three components are specified in Section 1 in the Appendix. The multi-state modelling formulation assumes that individual states can be determined unambiguously upon recapture, an assumption that is well supported in our study system (see Appendix, Section 1). The structure of the model, adapted from Ventura et al. (2021), was specified as follows (see Section 2 in the Appendix for a diagram). Fledglings (J_0) surviving to the first year (with immature survival probability, ϕ_j) move to the first immature age class (J_1). Individuals then transition successively to the J_2 , then J_3 and subsequently J_4 age class (i.e., 2, 3 and 4-year-old immatures, respectively), with the same annual immature survival probability ϕ_j applied to all age classes. At this stage (J_4), following Pardo et al., 2017b, we assumed that birds acquired the same survival probability as adults (ϕ_a) to eventually enter the first pre-breeding stage at 5 years of age (PB_1). Upon reaching the sixth year of age, birds in PB_1 can either recruit (entering the breeding stage) with probability of recruitment at age 6 or 7 ($r_{6,7}$), or transition to the next pre-breeding stage (PB_2). Similarly, at stage PB_2 , birds can recruit (with same probability $r_{6,7}$) or transition to the third and last pre-breeding stage (PB_3). Once in PB_3 , birds remain at this stage until recruitment, which occurs with probability of recruitment at 8 or more years of age, equal to r_{8+} . Newly recruiting birds breeding for the first time have a probability of successfully fledging a chick equal to f_{PB} , in which case they would enter the successful breeder

stage (S). If they fail (with probability $1-f_{PB}$), they enter the failed breeder stage (F). Only in the Falklands, at each pre-breeder stage, birds can recruit outside the study colonies (with probability of local emigration), permanently moving out of the study cohort. The choice of modelling local emigration as a permanent process is consistent with 99% of the encounter histories of emigrating birds in our data set, which show that individuals recruiting outside the study area almost invariably retain their nests outside the colony in subsequent seasons. Local emigration was negligible at the other study sites and thus not accounted for in the model (see Appendix Sections 1 and 2). Once birds are adult breeders, they either remain in the breeding stage (with breeding probability b) or skip a breeding attempt (with probability $1-b$) thus entering the non-breeding stage (NB). Every year, breeding adults can either fledge a chick (becoming successful breeders S), with probability f (i.e., the breeding success), or fail reproduction (becoming failed breeders F , with probability $1-f$). In this formulation, as in previous demographic studies (e.g., Pardo et al., 2017b; Oppel et al., 2022), breeding success parameters (f_{PB} and f) are defined as the probability of successfully fledging a chick, and thus incorporate both reproductive output and the early nestling survival (from the egg stage until fledging). The yearly breeding population growth rates and yearly total population growth rates (i.e., including immatures, pre-breeders and non-breeders) were calculated as:

$$\lambda_t = N_{t+1}/N_t, \quad (1)$$

where N_t represents the breeding (or total) population size in year t , and N_{t+1} is the breeding (or total) population size the following year. The average growth rate across all study years (from year 1 to n) was calculated as the geometric mean of the yearly growth rates λ_t :

$$\lambda \equiv (\lambda_1 * \lambda_2 * \dots * \lambda_n)^{1/n}. \quad (2)$$

The IPMs modelled the temporal variability in adult survival ϕ_a , immature survival ϕ_j , breeding probability b and breeding success f using yearly random effects (Appendix Section 3). To reduce model complexity, ensure parameter identifiability and facilitate convergence, the other demographic rates (recruitment, first-time breeding success and, for the Falklands, local emigration) were assumed to be constant

over time. Different recapture probability rates were used for 1 to 3-year-old immatures (J_1 to J_3); older (4-year-old) immatures and pre-breeders (J_4 , PB_1 , PB_2 and PB_3), which are detected more frequently than younger individuals as they return as prospectors to the colony before recruitment; adult breeders; and adult non-breeders (Appendix Section 5).

For each population, we calculated the trends in ϕ_j , considering the years in which the capture recapture histories overlapped (i.e., starting from the 2003/04 season) and excluding the 10 final years (to control for incomplete return/recruitment of the last cohorts). To do so, we: extracted the annual ϕ_j estimates, for each IPM iteration; fitted a linear model; and calculated the slope of annual ϕ_j regressed against year (thus obtaining a full posterior distribution of regression slopes).

All IPMs were run using JAGS, executed via R v4.1.3 (R Core Team, 2022) through the “R2jags” package (Su and Yajima, 2012). The analysis was performed using 6 chains of 100,000 iterations, discarding 25,000 iterations as burn-in. The output was inspected using the R package “MCMCvis” (Youngflesh, 2018). The resulting chains were well mixed and the Gelman–Rubin diagnostic convergence statistic (Brooks and Gelman, 1998) was below 1.1 for all parameters, indicating convergence. To evaluate the performance of the model, we adopted a simulation-based parameter-recovery framework to determine: whether simulated datasets (with specified demographic rates), comparable in size and structure to our empirical data, contain sufficient information for the IPM to successfully recover the underlying data generating demographic parameters, with a particular focus on immature survival; and whether estimates of immature survival are robust to misspecification of priors for initial population stage sizes and priors for the temporal variance of immature survival (Appendix Section 6). Furthermore, we evaluated the goodness of fit of the IPMs using posterior predictive checks (Appendix Section 9).

2.3. Retrospective sensitivity analysis

Based on the IPMs results, we carried out a retrospective sensitivity analysis to identify the most important demographic contributors to the albatross population dynamics. To do so, we used transient Life Table Response Experiments (tLTRE, Koons et al., 2016; Knape et al., 2023; Christian et al., 2024). Unlike the more conventional life table response experiments (Caswell, 2001), tLTREs quantify the contributions of both demographic rates and age-stage abundances to the realized population dynamics, not relying on the assumption that the population reached a stable age distribution. To perform the tLTRE, we partitioned the temporal variance of the realized growth rate λ_t due to realized variability and covariation of demographic rates and of population structure, and then quantified the sensitivities of λ_t to the demographic parameters and population age-stage structure. Then, we measured the contribution of the temporal variability in the demographic rates and population structure to the differences in realized population growth rates ($\Delta\lambda_t$) between successive years, following the protocol in Schaub and Kéry (2021). Using a demographic simulation framework (Appendix Section 7), we assessed the robustness of the estimated demographic contribution of immature survival to changes in the temporal variance of immature survival.

2.4. Population projections

We projected population dynamics over three generations into the future, following the IUCN Red List criterion A3b to evaluate projected changes in abundance. We assumed a generation time of 24 years for the black-browed albatross (Bird et al., 2020) and extended the temporal horizon of the IPM (i.e., we extended the time loops for the models of the demographic rates and the population dynamics) by an additional 72 years. Based on the posterior distributions estimated from the observed period, the IPMs generated stochastic projections of future rates and abundances in a unified analysis that ensured full propagation of

uncertainty from both process stochasticity and parameter estimates.

To test whether the detailed demographic understanding facilitated by the IPM affected the projected population dynamics, we compared the IPM results with the output generated by a simpler, phenomenological state-space model. We used this simpler time-series model of abundance to project population size into the future based on a stochastic growth rate, without reference to vital rates. The (female) breeding population size over time N was modelled as a Markovian process in which population size at year $t + 1$ only depended on population size at year t and the population growth rate λ , described by the state-process equations:

$$N_{t+1} = N_t \lambda_t \quad (3)$$

$$\lambda_t \sim \text{Normal}(\lambda, \sigma_\lambda^2) \quad (4)$$

The yearly growth rates (λ_t) were assumed to be realizations of a normal random process with mean λ (representing the long-term population growth rate) and variance σ_λ^2 (capturing the environmental stochasticity). The observation equation, linking the observed population size (y_t) with the true population size (N_t), was simply:

$$y_t \sim \text{Poisson}(N_t), \quad (5)$$

reflecting the assumption that the magnitude of the observation error in the counts is proportional to the true population size. As above, we fit this model to the study years and then projected the female breeding population size for a 72-year period into the future.

3. Results

3.1. Integrated population modelling

The IPMs revealed differences in the demographic rates of the different populations (Fig. 2 and Table 1). Results of the simulation-based parameter-recovery analysis (Appendix Section 6) show that the IPM successfully captured the true (simulated) fluctuations of all parameters, both observable (e.g., breeding success) and unobservable (e.g. adult and immature survival). Importantly, immature survival estimates were robust to misspecification of priors for initial population size and for the temporal variance of immature survival. Posterior predictive checks further indicated an overall good model fit, with estimated breeding success and breeder abundance closely matching observations, despite small systematic discrepancies between estimated and observed productivity (~ 1 –5%; see Appendix Section 9). On average, compared to the other populations, albatrosses in the Falklands had the highest recruitment probability (both r_{8+} and $r_{6,7}$, although the latter was comparable to $r_{6,7}$ estimated at Kerguelen), as well as high breeding probability b and breeding success f , comparable to the estimates at Kerguelen. By inspecting the raw recapture histories of individual birds born between 2003/2004 (when the Falklands study started) and 2009/2010 that recruited in the study colonies, albatrosses in the Falklands had, on average, the lowest age at first reproduction: 8.6 years (sd = 1.6), compared to the 10.5 years (sd = 1.9) at South Georgia and 10.9 years (sd = 1.9) at Kerguelen. At South Georgia, albatrosses had, on average, the highest adult (ϕ_a) and immature (ϕ_j) survival rate, but lowest breeding rate b and breeding success f . At Kerguelen, breeding success f and breeding rate b were higher than those at South Georgia and comparable to the Falklands. For all populations, adult survival was less variable than the other rates. Instances of sharp declines in ϕ_a mostly occurred at South Georgia and Kerguelen until the first decade of the 2000s, after which ϕ_a exhibited little temporal fluctuations.

Since the early 2000s, immature survival ϕ_j underwent a decreasing trend in the Falklands and at Kerguelen; at South Georgia, ϕ_j did not exhibit a clear trend but it became more variable until the 2010s (Fig. 2). During the last decade of the study, estimates of ϕ_j became more variable at all colonies; however, this pattern may reflect the incomplete return/

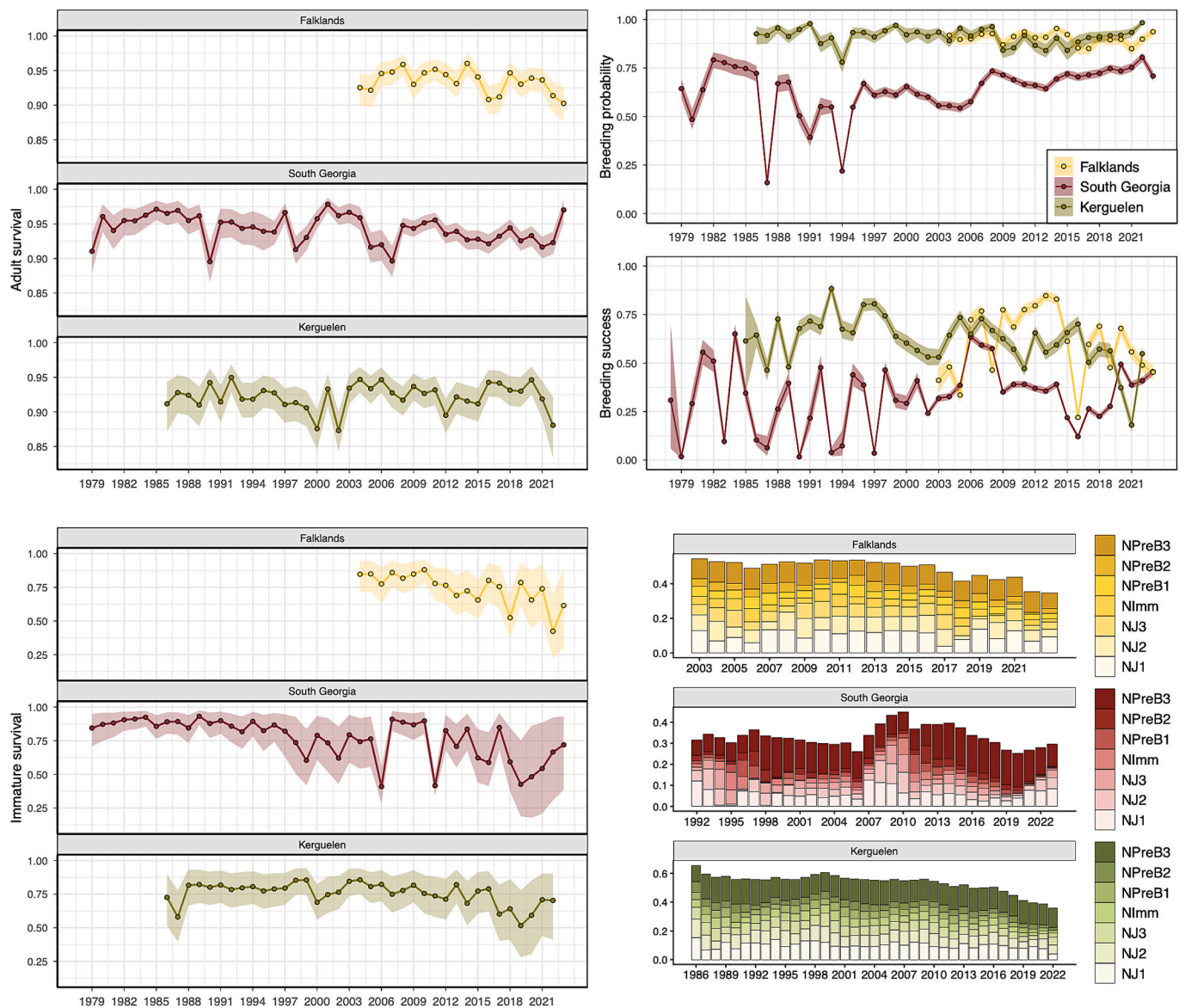


Fig. 2. Output of the integrated population models (IPMs) for the black-browed albatross populations at the Falklands (yellow), South Georgia (red), and Kerguelen (green). The figure shows temporal variability in adult survival (top left), breeding probability and breeding success (top right), and immature survival (bottom left). The solid lines represent the mean estimates, whereas the shaded areas represent the Bayesian 95% credible intervals. In the bottom right panel, we also show the temporal trends in the proportion of the total population made up of immatures and pre-breeders (i.e., from immatures J_1 to the last pre-breeding stage PB_3), estimated by our IPMs. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

recruitment of the most recent cohorts. In the second half of the study, in the years in which the capture-recapture histories overlapped (i.e., from the 2003/04 season onward), and excluding the final 10 years to account for the incomplete return/recruitment of the most recent cohorts, ϕ_j decreased at a rate of -1.26% [CRI = $(-2.06\%, -0.42\%)$] in the Falklands. At Kerguelen, when considering the entire study period (excluding the last 10 years), ϕ_j did not exhibit any significant trend; however, since 2003, it decreased at a rate of -1.39% [CRI = $(-2.29\%, -0.49\%)$]. In South Georgia, although the rate of change of ϕ_j since 2003 showed no clear increase or decrease (-0.19% [CRI = $-1.35\%, 0.99\%$]), it became more variable and showed the two lowest extremes of the entire study.

In turn, the proportion of the total population made up of immatures and pre-breeders (from J_1 to PB_3) declined in the Falklands (going from: 0.54 [CRI = $(0.44, 0.63)$] to 0.34 [CRI = $(0.26, 0.42)$]) and at Kerguelen (from 0.65 [CRI = $(0.53, 0.74)$] to 0.36 [CRI = $(0.29, 0.42)$]), and fluctuated substantially at South Georgia (Fig. 2). The estimates of ϕ_j

towards the final years of the study are not explicitly informed by data (as immatures are seldom recaptured before recruitment). Given the lack of data, the estimates for these last years are more uncertain (i.e., higher credible intervals) and centered around the average ϕ_j across the entire study period (Fig. 2).

The IPMs accurately described the observed breeding population dynamics, with the estimated yearly number of breeding pairs closely matching the observed number of pairs (Fig. 3). During the study period, the (female) breeding population size estimated by the IPMs underwent a moderate increase in the Falklands (average growth rate $\lambda^- = 1.010$ [CRI = $(1.004, 1.016)$]), i.e. an average yearly percentage change of 1.01% [CRI = $(0.44\%, 1.59\%)$]. Breeding population size was stable at Kerguelen ($\lambda^- = 0.998$ [CRI = $(0.995, 1.001)$]), i.e. an average yearly percentage change of -0.18% [CRI = $(-0.50\%, 0.14\%)$], and declining substantially at South Georgia ($\lambda^- = 0.974$ [CRI = $(0.972, 0.975)$]), i.e. an average yearly percentage change of -2.63% [CRI = $(-2.76\%, -2.50\%)$]. Over the study period for which standardised population

Table 1

The demographic parameters for the black-browed albatross populations in the Falklands, South Georgia and Kerguelen, estimated using integrated population models. As adult breeding success, breeding probability, adult survival and immature survival are time-varying in these models, for these parameters we report the posterior means of the average rates and the posterior mean of the coefficient of variation across years. The other rates (recruitment at age 6 or 7; recruitment at age 8 or more; first-time breeding success; local emigration probability, for the Falklands colony) were assumed to be constant over time. For each parameter, we report the symbol used in the text and the 95% credible interval (CRI), which ranges from the 2.5th to the 97.5th quantile of its posterior distribution.

Parameter	Symbol	Falklands	South Georgia	Kerguelen
		Mean (95%CRI)	Mean (95%CRI)	Mean (95% CRI)
Adult survival	ϕ_a	0.94 (0.93, 0.95)	0.95 (0.94, 0.95)	0.93 (0.92, 0.93)
Mean coefficient of variation of ϕ_a	$CV(\phi_a)$	0.02 (0.02, 0.03)	0.02 (0.02, 0.03)	0.02 (0.02, 0.03)
Immature survival	ϕ_j	0.76 (0.70, 0.80)	0.81 (0.77, 0.84)	0.77 (0.73, 0.80)
Mean coefficient of variation of ϕ_j	$CV(\phi_j)$	0.19 (0.14, 0.25)	0.22 (0.20, 0.25)	0.15 (0.11, 0.20)
breeding probability	b	0.91 (0.89, 0.92)	0.64 (0.60, 0.68)	0.92 (0.91, 0.94)
Mean coefficient of variation of b	$CV(b)$	0.04 (0.03, 0.04)	0.21 (0.20, 0.22)	0.05 (0.04, 0.06)
breeding success	f	0.61 (0.55, 0.68)	0.28 (0.23, 0.33)	0.62 (0.58, 0.67)
Mean coefficient of variation of f	$CV(f)$	0.29 (0.28, 0.31)	0.53 (0.51, 0.56)	0.21 (0.20, 0.23)
Recruitment at age 6 or 7	$r_{6,7}$	0.06 (0.05, 0.08)	0.01 (0.01, 0.01)	0.05 (0.05, 0.07)
Recruitment at age 8 or more	(r_{8+})	0.29 (0.26, 0.33)	0.15 (0.14, 0.15)	0.20 (0.19, 0.22)
First-time breeding success	f_{PB}	0.43 (0.36, 0.49)	0.17 (0.15, 0.19)	0.48 (0.43, 0.52)
Local emigration probability	p_{emig}	0.38 (0.33, 0.44)	NA	NA

counts were available at South Georgia (1993–2024), the breeding population decreased by 56.21% [CRI = (−57.98%, −54.36%)]. The IPMs also estimated the dynamics of the total (female) population (Fig. 3), including younger age classes (immatures, pre-breeders) and adult non-breeders. The total size of each of the three populations declined at different rates, even though the breeding population was increasing (Falklands) or stable (Kerguelen). Specifically, the average growth rate λ^- was estimated at 0.987 [CRI = (0.977, 0.997)] in the Falklands, i.e. an average yearly percentage change of −1.29% [CRI = (−2.28%, −0.34%)]; 0.967 [CRI = (0.963, 0.971)] in South Georgia, i.e. an average yearly percentage change of −3.29% [CRI = (−3.71%, −2.89%)]; and 0.979 [CRI = (0.972, 0.985)] at Kerguelen, i.e. an average yearly percentage change of −2.12% [CRI = (−2.83%, −1.49%)].

3.2. Retrospective sensitivity analysis

The results of the retrospective tLTRE showed that, consistently across colonies, immature survival ϕ_j , breeding success f and adult survival ϕ_a were the most important demographic contributors to the realized total population growth rate (Fig. 4). Importantly, the simulation work confirms that the inferred key demographic contribution of ϕ_j is robust to potential overestimation of the temporal variance in ϕ_j . The key demographic contribution of immature survival ϕ_j was also robust to the removal of the final years of the study (see Appendix Sections 7 and 8). Furthermore, the contribution of breeding success f was proportionally higher at South Georgia than at the other colonies. The retrospective analysis of the observed fluctuations in the total population growth rate between successive years highlighted the importance of

changes of these three demographic rates, which contributed positively in some seasons and negatively in others (Fig. 4).

3.3. Population projections

The projections produced by the IPMs and by the phenomenological state-space models were markedly different (Fig. 3). Over the next three generations, IPMs project a 90% probability of a decrease in the breeding population in the Falklands (i.e., 90% of the posterior distribution of the average breeding population growth rate λ^- over the next three generations is below 1). Specifically, λ^- was estimated at 0.989 [CRI = (0.972, 1.005)], representing a projected decrease of −44.66% in the breeding population, albeit with substantial uncertainty [CRI = (−87.55%, 41.01%)]. At South Georgia, the breeding population is projected to approach local extinction, with λ^- estimated at 0.970 [CRI = (0.957, 0.982)], i.e. an average future decline of −85.25% [CRI = (−94.25%, −69.91%)]. At Kerguelen, λ^- was estimated at 0.979 [CRI = (0.965, 0.991)], representing an average projected decrease of the breeding population over three generations of −75.50% [CRI = (−92.15%, −46.92%)].

In contrast, the simpler phenomenological state-space model projected a breeding population decline only at South Georgia, estimated at −62% [CRI = (−94%, 36%)]. With large uncertainties surrounding the mean estimates, the breeding populations in the Falklands had an 80% probability of increase (i.e., 80% of the posterior distribution of the population growth rate over three generations was above 1). Over three generations, the breeding population in the Falklands was projected to experience an average increase of 138% [CRI = (−59%, 695%)]. At Kerguelen, the projected breeding population increase over three generations was estimated at a mean of 113% [CRI = (−63%, 591%)].

4. Discussion

Our modelling work revealed the key role of immature survival in population dynamics, and profound differences in the perceived population trajectory if the hidden declines of these cryptic age classes were not considered. The difference in observed population trend solely based on adult breeders, and the actual trend once all population components are taken into account, is further amplified in projections. As we discuss below, focusing on only a fraction of the population (i.e., the adult breeders) can be misleading and may mask ongoing declines.

4.1. Cryptic shifts in albatross population structure and dynamics

Whether due to anthropogenic mortality or climate stressors, the decrease in immature survival and in the number of subadults, as well as the fluctuations in breeding success, have major consequences for population dynamics of black-browed albatrosses. Our model highlights that, despite a stable or even increasing breeding population trend, the overall population size has been decreasing at all colonies, though at different rates. Our retrospective sensitivity analysis revealed that immature survival (followed by breeding success and adult survival) was the main rate driving overall population dynamics and realized growth rate at all colonies. Through the use of IPMs, which jointly estimate the demographic rates and the outcome of these rates (i.e. the resulting abundance of all age groups), we were able to detect a shift in the population age structure, with a substantial decrease in the numbers and proportion of subadults at all colonies.

By projecting the estimated vital rates and population dynamics into the future, we forecasted that within three generations, the impact of cryptic changes in the immature component of the population would emerge at the level of the breeding population, contributing to their declines (severe at South Georgia, more moderate in the Falklands and at Kerguelen). In this context, further insights are offered by the comparison with the simpler phenomenological state-space models, which focus exclusively on the breeding population size. While these models

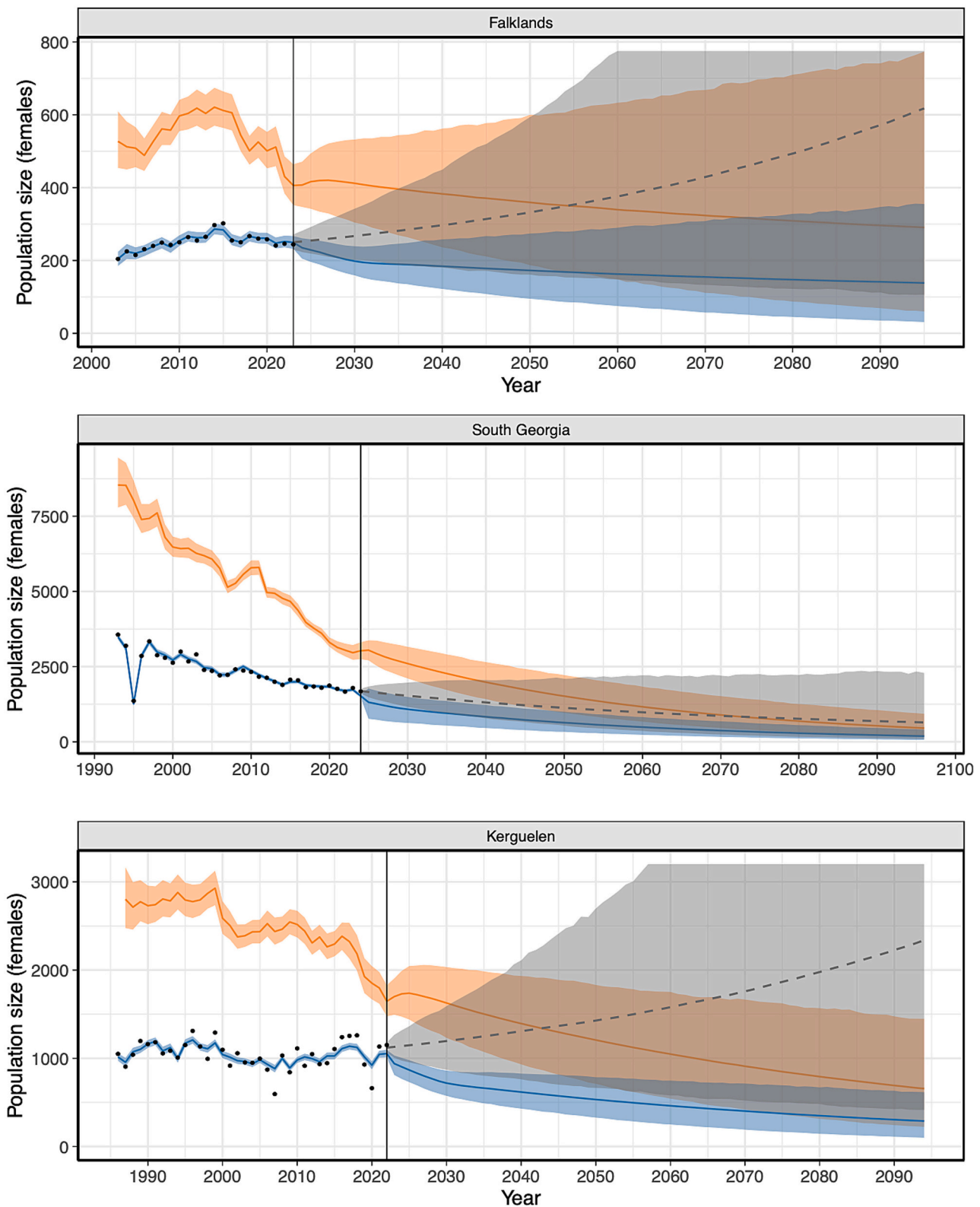


Fig. 3. The dynamics of the population of breeding females (in blue) and total (i.e., including immatures, pre-breeders and non-breeders) female population (in orange) of black-browed albatrosses at the three study colonies in the Falklands, South Georgia and Kerguelen, estimated by the integrated population model (IPM). The shaded areas represent the 95% credible interval. For each colony, the subplot depicts the observed breeding population size (black points) recorded until the breeding season of 2023/24 (Falklands and South Georgia) and 2022/23 (Kerguelen), the last monitoring season included in the study (marked by the solid vertical line). The IPM projected the breeding and total population size (colored lines and shaded area). The dashed grey line (with associated grey shaded area, representing the 95% credible interval) shows the mean breeding population projections yielded by a simpler, purely phenomenological state-space model, in which the population size was a function of the population size in the previous year and of the population growth rate λ . (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



Fig. 4. Results of the retrospective sensitivity analysis based on the transient life table response experiment (tLTRE) applied to demographic data from black-browed albatrosses at the three study colonies in the Falklands, South Georgia and Kerguelen. The main contributors to the observed changes in the realized overall (left column) and year-to-year (right column) population growth rate were immature survival ϕ_j , breeding success f , and adult survival ϕ_a . In the left column panel, the y-axis represents the total relative contribution of each parameter; in the right column, the positive/negative values on the y-axis depict contributions of each parameter to both negative and positive year-to-year growth rates.

could accurately describe observed (past) dynamics in the breeding population, they did not account for any change in the population structure. As a result, their future projections suggested a markedly different scenario, with increases at the Falklands and at Kerguelen (albeit with very large uncertainty) and a more moderate decrease at South Georgia. In other words, if breeding population counts were the only available data stream for our assessment, projections would be highly uncertain and would indicate a population increase. These results would be consistent with the empirical evidence on the improvements in mitigation of seabird bycatch in fisheries in several key exclusive economic zones (EEZs) used by our study populations (Collins et al., 2021; Delord et al., 2010; Wolfaardt, 2013; Mackley et al., 2025), and the conventional understanding of the importance of adult survival. However, our IPMs suggest that, despite the high and conserved adult survival, the current rates of immature survival and breeding success, and the reduced numbers of subadults are insufficient to sustain a growing population.

The important role of subadults in driving population trends has been documented in other seabird populations. For instance, declines in species such as the Tristan albatross (*Diomedea dabbenena*), sooty albatross (*Phoebastria fusca*) and Indian yellow-nosed albatross (*Thalassarche carteri*) have been linked to reduced breeding success and limited recruitment of subadults into the breeding population, as well as disease outbreaks (Rolland et al., 2009; Jaeger et al., 2018; Weimerskirch et al., 2018; Oppel et al., 2022). Conversely, management actions that reduce subadult mortality enhance population growth (Finkelstein et al., 2010), and pre-breeders returning to the colony at atypically young ages can accelerate population recovery following sharp declines, e.g. after disease outbreaks (Sceviour et al., 2025).

4.2. Decrease in immature survival

Our study provides relevant evidence for decreasing trends in immature survival (albeit at different rates between colonies) and associated shifts in population structures. Since the early 2000s (specifically, since the beginning of the demographic monitoring work in the Falklands in 2003), immature survival has decreased in the Falklands. Over the same time span, immature survival has also decreased at Kerguelen (although no clear linear trend is evident when considering the full time series beginning in 1986). In South Georgia, despite the lack of a clear linear trend, immature survival fluctuated substantially and showed the two most extreme decreases in the study. We assumed that younger immatures (0 to 4-year-old) share the same survival rate and that this differs from adult birds (after Pardo et al., 2017b). This assumption does not account for the likely lower survival immediately after fledging and gradual increase thereafter (Oppel et al., 2022). However, no birds in South Georgia and very few in the Falklands and Kerguelen (less than 1%) have been recaptured before age four, limiting the ability of our model to detect potential differences in survival during these early years. The uncertainty as to when or where – given the limited data on distribution – immatures die contributes to the challenges of understanding the environmental drivers (but see Clay et al., 2019). While this task would require the development of climate-dependent demographic models, which is beyond the scope of this current study, we can nevertheless speculate on the potential drivers at play. Apart from potential carry-over effects of natal conditions (Fay et al., 2017), immature survival is affected by processes occurring after birds fledge and before they recruit, a period in which they spend virtually the entirety of their time at sea. Any mechanisms leading to decreased survival should therefore primarily reflect sources of mortality at sea, possibly linked to bycatch in fisheries and the impacts of

climate change on marine ecosystems (Barbraud et al., 2012).

Major efforts have been made to reduce bycatch of seabirds in parts of the Southern Ocean, with considerable success in several fisheries, primarily within EEZs (Robertson et al., 2014; Phillips et al., 2016; Da Rocha et al., 2021; Danson et al., 2022; Kuepfer et al., 2022). This includes greatly reduced bycatch rates within the EEZ around the three study colonies during the breeding season (Collins et al., 2021; Delord et al., 2010; Wolfaardt, 2013; Mackley et al., 2025). However, at non-breeding grounds, which may be used year-round by immatures, there is a higher overlap with fisheries, involving demersal and pelagic longliners, and demersal trawlers operating in the waters off the northern Patagonian Shelf, the Benguela upwelling region and South Australian Bight and Tasman Sea (Rolland et al., 2008, 2010; Clay et al., 2019). The limited data from most pelagic longline fleets operating in international waters indicate that seabird bycatch rates remain high, and there is weak monitoring or enforcement of compliance (Phillips et al., 2016; Michael et al., 2017; Jiménez et al., 2020). In addition, the scale of the mortality associated with illegal, unreported, and unregulated fishing vessels, which typically do not implement any mitigation measures, is unknown but likely to be high (Michael et al., 2017). As a major portion of the year-round distribution of subadults includes the high seas, the effect of incidental mortality in fisheries may be disproportionately high for immatures (Clay et al., 2017, 2019; Carneiro et al., 2020). Ultimately, this evidence indicates the need to identify the at-sea areas primarily used by immatures, which are still poorly understood for most seabirds. Furthermore, beyond immature survival, breeding success f (which incorporates both reproductive output and early nestling survival) is the second most important contributor to population growth. This further emphasises the importance of early life-history stages and suggests that on land interventions targeting chick survival (e.g. invasive species eradication and disease control) may be critical for reversing population declines.

Recent research has greatly advanced our understanding of the impacts of climate change on marine ecosystems (IPCC, 2019), and improved our understanding of the effects of long-term shifts in oceanographic variables and climate indices on the demography and distribution of marine top predators (Barbraud et al., 2012; Phillips et al., 2016; Hazen et al., 2019). Being at the apex of the marine food web, top predators play a key role as ecosystem sentinels, often showing responses to changes in their ecosystems (Sergio et al., 2008). For instance, rising ocean temperatures likely impacting the food web negatively affect reproductive success of black-browed albatrosses (Pardo et al., 2017b; Ventura et al., 2021), and potentially alter the migratory schedules (Desprez et al., 2018; Jenouvrier et al., 2018). While major gaps remain in our knowledge of the environmental mechanisms that determine the survival of immature age classes (Desprez et al., 2018), some of the regions used year-round by subadults have experienced long-term oceanographic changes. Over the past decades, the Patagonian Shelf waters and shelf break front have experienced significant changes in physical conditions, with repercussions for productivity, species distribution and abundance, and ecosystem structure (Franco et al., 2022; Saraceno et al., 2022). An increase in the severity and frequency of marine heatwaves may pose further risks to ecosystem structure and stability (Smith et al., 2023), including in the South Atlantic (Pujol et al., 2022), and in the Tasman Sea, a global warming hotspot with frequent, intense, and long-lasting marine heatwave occurrence (e.g., Gregory et al., 2023; Capotondi et al., 2024, and references therein). Importantly, the Southern Ocean has experienced substantial changes in atmospheric circulation over the past decades, recording the largest increases in marine surface wind speeds (Young and Ribál, 2019; Gulev et al., 2021; Sharman et al., 2021). The movement ecology of albatrosses and other long-ranging pelagic seabirds is largely shaped by the wind, which determines the energetic costs of flight and modulates movement and foraging efficiency (Nourani et al., 2023; Thorne et al., 2023). An intensification and poleward shift of the westerly winds in the southern Indian Ocean resulted in an increase in

the travel speed of foraging wandering albatrosses (*Diomedea exulans*), which in turn reduced foraging trip duration and improved breeding success (Weimerskirch et al., 2012). The extent to which the smaller and lighter black-browed albatross or other seabirds might benefit from increased wind speeds is unknown, including immatures, which may have lower flight capabilities than adults (Shaffer et al., 2001; Delord et al., 2024; Thorne et al., 2023). Lastly, stronger winds and the increased frequency and severity of storms may be another important, direct driver of mortality (Thorne et al., 2023; Ventura et al., 2023).

4.3. Differences in life histories among populations

Our models identify immature survival as key driver of population dynamics at all breeding colonies, despite the contrasting breeding population trajectories. Importantly, immature survival was consistently the key contributor despite the ecological differences in the life-histories of the three populations identified by our models. Black-browed albatrosses in the Falklands have high breeding probability (in line with estimates from Kerguelen) and earlier recruitment compared to other populations. This can be attributed to the more benign environmental conditions and year-round high productivity of the Patagonian Shelf (Romero et al., 2006; Marrari et al., 2017). Albatrosses in the Falklands are resident, able to use highly productive feeding grounds on the Patagonian Shelf to replenish their body reserves after reproduction (Ponchon et al., 2019). This contrasts with the migratory populations at Kerguelen and South Georgia (Phillips et al., 2005; Mackley et al., 2010; Desprez et al., 2018). Birds at the Falklands also moult more feathers during the breeding season (and, overall, more feathers per year), than conspecifics at South Georgia (Catry et al., 2013), further suggesting that the former benefit from a highly productive environment capable of supporting the energetically demanding overlap of moulting and breeding. At Kerguelen, marine productivity shows typical seasonal patterns, characterized by large phytoplankton and zooplankton blooms during the austral spring and summer and drastic declines in productivity during the winter (Park et al., 2014; Halfter et al., 2020). These predictable seasonal patterns in marine food resources trigger long-range migration during the austral winter (Desprez et al., 2018). During spring and summer, the high productivity in the Kerguelen plateau sustains high breeding probability and breeding success, comparable to the Falklands and higher than at South Georgia. Conversely, the oceanographic conditions at South Georgia are three times more variable than at Kerguelen (Nevoux et al., 2010). Albatrosses at South Georgia rely heavily on Antarctic krill *Euphausia superba* (Mills et al., 2020), the availability of which can be highly variable between years (Fielding et al., 2014). Years with poor krill abundance and prey shortages, interacting with a fluctuating predation pressure on chicks (Catry et al., 2010), were associated with recurring instances of steep declines in breeding success, particularly during the first half of the study at South Georgia.

Previous research by Nevoux et al. (2010) documented higher yearly survival rates in South Georgia than at Kerguelen until the early 2000s, and suggested that individuals allocate a fixed energy budget, prioritizing survival over reproduction in more variable environments (“bet-hedging”). Here, however, we show that after the early 2000s (following the implementation of bycatch mitigation measures, see below), the survival of adult birds at Kerguelen increased, reaching levels consistent with South Georgia. Over the last two decades, adult survival was high, stable and comparable in the three populations, regardless of whether reproductive costs were higher (Falklands, Kerguelen) or lower (South Georgia). Once they reach adult age, albatrosses have high survival, which is preserved against environmental fluctuations (Sæther and Bakke, 2000; Gaillard and Yoccoz, 2003) and remains high both in variable (South Georgia) and more benign (Kerguelen, Falklands) environments. Combined, our findings highlight that the life history of allopatric populations of the same species exhibits a degree of flexibility in response to context-dependent selective pressures linked to prevailing

environmental conditions (Schatz et al., 2025). We suggest that the environment primarily modulates the life history of long-lived species by shaping the acquisition of resources and, ultimately, the energy that can be invested in reproduction. Harsher conditions and a resultant higher cost of reproduction are paid in terms of a lower investment in reproduction (Hamel et al., 2010), which seems to be the case in South Georgia.

Several studies attributed the lower survival of black-browed albatrosses in the 1980s or 1990s, including of the Chilean populations (which are not considered here), to unsustainable levels of bycatch in fisheries (Michael et al., 2017; Pardo et al., 2017a, 2017b; Robertson et al., 2014, 2017). In addition to the potential environmental drivers, the improvement in survival after the early 2000s at Kerguelen largely coincides with the implementation of bird-scaring (streamer) lines, heavier line weighting and night-setting in longline fisheries, and more strict management practices in commercial longline fisheries (Delord et al., 2005, 2010; Collins et al., 2021; Dasnon et al., 2022). These mitigation measures have reduced bycatch of seabirds to minimal levels within longline fisheries in the EEZs around Kerguelen, South Georgia and the Falklands (Collins et al., 2021; Delord et al., 2010). Black-browed albatrosses were also one of the most common species killed or injured in collisions with warps and net monitoring cables in several trawl fisheries in the Southern Ocean, but bycatch rates have reduced considerably in the last 1–2 decades with the requirement to use bird-scaring lines and offal management to reduce the attractiveness of vessels during high-risk operations (Phillips et al., 2024). Efforts to mitigate bycatch in trawl fisheries in the South Georgia, South African and Namibian EEZs may also underpin the more stable adult survival and slowing of the population declines after the mid-2000s (Mackley et al., 2025).

4.4. The need for integrated assessments in conservation

As climate change and other ubiquitous anthropogenic pressures continue to exacerbate threats to biodiversity (IPBES, 2019), biological conservation heavily relies on comprehensive extinction risk assessments. This requires the detection of processes that are often not immediately reflected by changes in observed population abundance, particularly so in species with slow life histories. The conservation status of populations could be assessed in a more timely fashion by monitoring a temporal sequence of warning signals that precede population declines, such as changes in individual behaviour, shifts in body condition and growth rates, and changes in population structure or dynamics (Cerini et al., 2023; Rouby et al., 2025). Key additional information can be gained through the integrated analysis of body condition (Pirotta et al., 2024) and tracking data, e.g. to quantify expansions or contractions of distributions potentially indicative of changes in food availability and competition for resources (Fayet et al., 2021). Recent studies in molecular ageing biomarkers led to the discovery of an “epigenetic clock”, a DNA methylation-based predictor of age (De Paoli-Iseppi et al., 2019; Roman et al., 2024). If this technique is transferable across species, it could provide an instantaneous snapshot of the age structure of seabird breeding populations, representing a clear example of the type of multi-dimensional dataset that could be integrated into conservation assessments. With the rapid advances in demographic modelling (Zipkin and Saunders, 2018), it is now possible to incorporate these processes as additional data streams into integrated evaluations of population dynamics. These types of integrated assessments will be critical for moving beyond the conventional demographic modelling typically focused on a (visible) fraction of populations, ultimately enabling the timely design and implementation of proactive conservation measures.

CRediT authorship contribution statement

Francesco Ventura: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Funding

acquisition, Formal analysis, Data curation, Conceptualization. **Christian Che-Castaldo:** Writing – review & editing, Writing – original draft, Validation, Resources, Methodology, Formal analysis. **Paulo Catry:** Writing – review & editing, Writing – original draft, Resources, Methodology, Investigation, Funding acquisition, Data curation. **Karine Delord:** Writing – review & editing, Writing – original draft, Resources, Methodology, Investigation, Funding acquisition, Data curation. **Amanda Kuepfer:** Writing – review & editing, Writing – original draft, Resources, Investigation, Data curation. **Bertille Mohring:** Writing – review & editing, Writing – original draft, Resources, Methodology, Data curation. **Steffen Oppel:** Writing – review & editing, Writing – original draft, Resources, Methodology, Formal analysis. **Richard A. Phillips:** Writing – review & editing, Writing – original draft, Resources, Methodology, Investigation, Funding acquisition, Data curation. **Etienne Rouby:** Writing – review & editing, Writing – original draft, Resources, Methodology, Data curation. **Caroline C. Ummenhofer:** Writing – review & editing, Writing – original draft, Visualization, Resources, Methodology. **Henri Weimerskirch:** Writing – review & editing, Writing – original draft, Resources, Methodology, Investigation, Funding acquisition. **Andrew G. Wood:** Writing – review & editing, Writing – original draft, Resources, Data curation. **Christophe Barbraud:** Writing – review & editing, Writing – original draft, Resources, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Stéphanie Jenouvrier:** Writing – review & editing, Writing – original draft, Supervision, Resources, Methodology, Investigation, Formal analysis, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

No artificial intelligence tools were used.

Declaration of competing interest

We declare no competing interests.

Acknowledgments

We thank all the field workers who provided invaluable contributions to the long-term studies in the Falklands, South Georgia and Kerguelen. The New Island Conservation Trust, Falklands Conservation and the South Atlantic Environmental Research Institute supported field studies on New Island, Falklands, by providing logistic help and research facilities. Financial support for the Falklands study was through the Environmental Studies Budget of the Falkland Islands Government and through UID/04292 - Centro de Ciencias do Mar e do Ambiente (MARE) and through the project LA/P/0069/2020 granted to the Associate Laboratory ARNET by FCT – Portugal. Logistical and financial support at South Georgia was provided by the Government of South Georgia and the South Sandwich Islands, Friends of South Georgia Island, South Georgia Heritage Trust, Antarctic Research Trust, Peter Smith Charitable Trust for Nature, UK Blue Belt Programme and Natural Environment Research Council (NERC). We acknowledge the Institut Paul Emile Victor (project IPEV 109-ORNITHO2E), Terres Australes et Antarctiques Françaises and Zone Atelier Antarctique et Terres Australes (LTSER France, CNRS) for logistical and financial support in Kerguelen. This study is part of the long-term Studies in Ecology and Evolution (SEE-Life) program of the CNRS. The Ethics Committee of IPEV and Comité de l'Environnement Polaire approved all field procedures. F.V. acknowledges support by the National Science Foundation (NSF) Office of Polar Programs grant 2037561 and by the National Aeronautics and Space Administration (NASA) under grant 80NSSC25K7836 (to F.V. and C.C.U.), and the *Independent Research & Development Program at WHOI* (to C.C.U.).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2026.112102>.

Data availability

The data and R scripts to reproduce the analysis are available from the Figshare digital repository (<https://figshare.com/s/c3815569130beab73e3a>).

This draft manuscript is distributed solely for purposes of scientific peer review. Its content is deliberative and predecisional, so it must not be disclosed or released by reviewers. Because the manuscript has not yet been approved for publication by the U.S. Geological Survey (USGS), it does not represent any official USGS finding or policy.

References

- Abadi, F., Barbraud, C., Gimenez, O., 2017. Integrated population modeling reveals the impact of climate on the survival of juvenile emperor penguins. *Glob. Change Biol.* 23, 1353–1359.
- Barbraud, C., Rolland, V., Jenouvrier, S., Nevoux, M., Delord, K., Weimerskirch, H., 2012. Effects of climate change and fisheries bycatch on Southern Ocean seabirds: a review. *Mar. Ecol. Prog. Ser.* 454, 285–307.
- Bird, J.P., Martin, R., Akçakaya, H.R., Gilroy, J., Burfield, I.J., Garnett, S.T., Symes, A., Taylor, J., Şekercioglu, Ç.H., Butchart, S.H.M., 2020. Generation lengths of the world's birds and their implications for extinction risk. *Conserv. Biol.* 34, 1252–1261.
- Birdlife International, 2018. *Thalassarche melanophris*. The IUCN Red List of Threatened Species 2018. Available from: <https://doi.org/10.2305/IUCN.UK.2018-2.RLTS.T22698375A132643647.en%0ACopyright>.
- Boyd, I.L., Murray, A.W.A., 2001. Monitoring a marine ecosystem using responses of upper trophic level predators. *J. Anim. Ecol.* 70, 747–760.
- Brooks, S.P., Gelman, A., 1998. General methods for monitoring convergence of iterative simulations. In: *Journal of Computational and Graphical Statistics*, 7. Taylor & Francis, pp. 434–455. <https://doi.org/10.1080/10618600.1998.10474787>.
- Capotondi, A., Rodrigues, R.R., Sen Gupta, A., Benthuyssen, J.A., Deser, C., Frölicher, T. L., Lovenduski, N.S., Amaya, D.J., Le Grix, N., Xu, T., Hermes, J., 2024. A global overview of marine heatwaves in a changing climate. *Commun. Earth Environ.* 5. <https://doi.org/10.1038/s43247-024-01806-9>.
- Carneiro, A.P.B., et al., 2020. A framework for mapping the distribution of seabirds by integrating tracking, demography and phenology. *J. Appl. Ecol.* 57, 514–525.
- Caswell, H., 2001. Matrix population models.
- Catry, P., Phillips, R.A., Forster, I.P., Matias, R., Lecoq, M., Granadeiro, J.P., Strange, I.J., 2010. Brood-guarding duration in black-browed albatrosses *Thalassarche melanophris*: temporal, geographical and individual variation. *J. Avian Biol.* 41, 460–469.
- Catry, P., Poisbleau, M., Lecoq, M., Phillips, R.A., 2013. Differences in the timing and extent of annual moult of black-browed albatrosses *Thalassarche melanophris* living in contrasting environments. *Polar Biol.* 36, 837–842.
- Ceballos, G., Ehrlich, P.R., Barnosky, A.D., García, A., Pringle, R.M., Palmer, T.M., 2015. Accelerated modern human-induced species losses: entering the sixth mass extinction. *Sci. Adv.* 1, 9–13.
- Ceballos, G., Ehrlich, P.R., Raven, P.H., 2020. Vertebrates on the brink as indicators of biological annihilation and the sixth mass extinction. *Proc. Natl. Acad. Sci. U. S. A.* 117, 13596–13602.
- Cerini, F., Childs, D.Z., Clements, C.F., 2023. A predictive timeline of wildlife population collapse. In: *Nature Ecology and Evolution*, 7. Springer US, pp. 320–331.
- Christian, M., Oosthuizen, W.C., Bester, M.N., de Bruyn, P.J.N., 2024. Robustly estimating the demographic contribution of immigration: simulation, sensitivity analysis and seals. *J. Anim. Ecol.* 93, 632–645.
- Clay, T.A., Small, C., Carneiro, A.P.B., Mulligan, B., Pardo, D., Wood, A.G., Phillips, R.A., 2017. Identifying areas, seasons and fleets of potential highest bycatch risk to South Georgia albatrosses and petrels. In: *Iotc-Wp613*.
- Clay, T.A., Phillips, R.A., Clay, T.A., Small, C., Tuck, G.N., Pardo, D., Carneiro, A.P.B., Wood, A.G., Croxall, J.P., Crossin, G.T., 2019. A comprehensive large - scale assessment of fisheries bycatch risk to threatened seabird populations. *J. Appl. Ecol.* 1882–1893.
- Collins, M.A., Hollyman, P.R., Clark, J., Söffker, M., Yates, Oliver, Phillips, R.A., 2021. Mitigating the impact of longline fisheries on seabirds: lessons learned from the South Georgia Patagonian toothfish fishery (CCAMLR Subarea 48.3). *Mar. Policy* 131, 104618.
- Cordes, L.S., Blumstein, D.T., Armitage, K.B., CaraDonna, P.J., Childs, D.Z., Gerber, B.D., Martin, J.G.A., Oli, M.K., Ozgul, A., 2020. Contrasting effects of climate change on seasonal survival of a hibernating mammal. *Proc. Natl. Acad. Sci. U. S. A.* 117 (30), 18119–18126.
- Croxall, J.P., 2008. The role of science and advocacy in the conservation of Southern Ocean albatrosses at sea. *Bird Conserv. Int.* 18, S13–S29.
- Da Rocha, N., et al., 2021. Reduction in seabird mortality in Namibian fisheries following the introduction of bycatch regulation. *Biol. Conserv.* 253, 108915.
- Dasnon, A., Delord, K., Chaigne, A., Barbraud, C., 2022. Fisheries bycatch mitigation measures as an efficient tool for the conservation of seabird populations. *J. Appl. Ecol.* 00, 1–12.
- De Paoli-Iseppi, R., Deagle, B.E., Polanowski, A.M., McMahon, C.R., Dickinson, J.L., Hindell, M.A., Jarman, S.N., 2019. Age estimation in a long-lived seabird (*Ardenna tenuirostris*) using DNA methylation-based biomarkers. *Mol. Ecol. Resour.* 19, 411–425.
- Delord, K., Gasco, N., Weimerskirch, H., Barbraud, C., Micol, T., 2005. Seabird mortality in the Patagonian toothfish longline fishery around Crozet and Kerguelen Islands, 2001–2003. *CCAMLR Sci.* 12, 53–80.
- Delord, K., Gasco, N., Barbraud, C., Weimerskirch, H., 2010. Multivariate effects on seabird bycatch in the legal Patagonian toothfish longline fishery around Crozet and Kerguelen Islands. *Polar Biol.* 33, 367–378.
- Delord, K., Weimerskirch, H., Barbraud, C., 2024. The challenges of independence: ontogeny of at-sea behaviour in a long-lived seabird. *Peer Community J.* 4.
- Desprez, M., Jenouvrier, S., Barbraud, C., Delord, K., Weimerskirch, H., 2018. Linking oceanographic conditions, migratory schedules and foraging behaviour during the non-breeding season to reproductive performance in a long-lived seabird. *Funct. Ecol.* 32, 2040–2053.
- Dias, M.P., Martin, R., Pearmain, E.J., Burfield, I.J., Small, C., Phillips, R.A., Yates, O., Lascelles, B., Borboroglu, P.G., Croxall, J.P., 2019. Threats to seabirds: a global assessment. *Biol. Conserv.* 237, 525–537.
- Fay, R., Barbraud, C., Delord, K., Weimerskirch, H., 2017. Contrasting effect of climate and population density over time and life-stages in a long-lived seabird. *Funct. Ecol.* 31, 1275–1284.
- Fayet, A.L., Lucas, G. V., Anker-Nilssen, T., Syposz, M., Hansen, E.S., 2021. Local prey shortages drive foraging costs and breeding success in a declining seabird, the Atlantic puffin. *J. Anim. Ecol.* 90, 1152–1164.
- Fielding, S., Watkins, J.L., Trathan, P.N., Enderlein, P., Waluda, C.M., Stowasser, G., Tarling, G.A., Murphy, E.J., 2014. Interannual variability in Antarctic krill (*Euphausia superba*) density at South Georgia, Southern Ocean: 1997–2013. *ICES J. Mar. Sci.* 71, 2578–2588.
- Finkelstein, M.E., Doak, D.F., Nakagawa, M., Sievert, P.R., Klavitter, J., 2010. Assessment of demographic risk factors and management priorities: impacts on juveniles substantially affect population viability of a long-lived seabird. In: *Animal Conservation*, 13. Wiley Online Library, pp. 148–156.
- Franco, B.C., Ruiz-Etcheverry, L.A., Marrari, M., Piola, A.R., Matano, R.P., 2022. Climate change impacts on the Patagonian shelf break front. *Geophys. Res. Lett.* 49, 1–9.
- Gaillard, J.M., Yoccoz, N.G., 2003. Temporal variation in survival of mammals: a case of environmental canalization? *Ecology* 84, 3294–3306.
- Gianuca, D., Phillips, R.A., Townley, S., Votier, S.C., 2017. Global patterns of sex- and age-specific variation in seabird bycatch. In: *Biological Conservation*, 205. Elsevier B.V., pp. 60–76. <https://doi.org/10.1016/j.biocon.2016.11.028>. Available from.
- Gregory, C.H., Holbrook, N.J., Marshall, A.G., Spillman, C.M., 2023. Atmospheric drivers of Tasman Sea marine heatwaves. *J. Clim.* 36, 5197–5214.
- Gulev, S.K., et al., 2021. *Changing State of the Climate System*. Cambridge University Press.
- Halfter, S., Cavan, E.L., Swadling, K.M., Eriksen, R.S., Boyd, P.W., 2020. The role of zooplankton in establishing carbon export regimes in the Southern Ocean – a comparison of two representative case studies in the Subantarctic region. *Front. Mar. Sci.* 7, 1–8.
- Halpern, B.S., et al., 2015. Spatial and temporal changes in cumulative human impacts on the world's ocean. In: *Nature Communications*, 6. Nature Publishing Group, pp. 1–7.
- Hamel, S., Gaillard, J.-M., Yoccoz, N.G., Loison, A., Bonenfant, C., Descamps, S., 2010. Fitness costs of reproduction depend on life speed: empirical evidence from mammalian populations. In: *Ecology letters*, 13. Wiley Online Library, pp. 915–935.
- Hazen, E.L., Maxwell, S.M., Bailey, H., Bograd, S.J., Hamann, M., Gaspar, P., Godley, B. J., Shillinger, G.L., 2012. Ontogeny in marine tagging and tracking science: technologies and data gaps. *Mar. Ecol. Prog. Ser.* 457, 221–240.
- Hazen, E.L., Abrahms, B., Brodie, S., Carroll, G., Jacox, M.G., Savoca, M.S., Scales, K.L., Sydeman, W.J., Bograd, S.J., 2019. Marine top predators as climate and ecosystem sentinels. *Front. Ecol. Environ.* 17, 565–574.
- Hoffmann, M., et al., 2010. The impact of conservation on the status of the world's vertebrates. *Science* 330, 1503–1509. <https://doi.org/10.1126/science.1194442>.
- IPBES, 2019. *Global Assessment Report on Biodiversity and Ecosystem Services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. Zenodo. <https://doi.org/10.5281/zenodo.6417333> (Available from, May).
- IPCC, 2019. In: Pörtner, H.O., et al. (Eds.), *IPCC Special Report on the Ocean and Cryosphere in a Changing Climate* (Page).
- Jaeger, A., et al., 2018. Avian cholera outbreaks threaten seabird species on Amsterdam Island. In: *PLOS ONE*, 13. Public Library of Science, pp. 1–17. <https://doi.org/10.1371/journal.pone.0197291>. Available from.
- Jenouvrier, S., Desprez, M., Fay, R., Barbraud, C., Weimerskirch, H., Delord, K., Caswell, H., 2018. Climate change and functional traits affect population dynamics of a long-lived seabird. *J. Anim. Ecol.* 87, 906–920.
- Jiménez, S., Domingo, A., Winker, H., Parker, D., Gianuca, D., Neves, T., Coelho, R., Kerwath, S., 2020. Towards mitigation of seabird bycatch: large-scale effectiveness of night setting and Tori lines across multiple pelagic longline fleets. *Biol. Conserv.* 247, 108642.
- Knappe, J., Paquet, M., Arlt, D., Kačergytė, I., Pärt, T., 2023. Partitioning variance in population growth for models with environmental and demographic stochasticity. *J. Anim. Ecol.* 92, 1979–1991.
- Koons, D.N., Iles, D.T., Schaub, M., Caswell, H., 2016. A life-history perspective on the demographic drivers of structured population dynamics in changing environments. *Ecol. Lett.* 19, 1023–1031.

- Kuepfer, A., Sherley R., B., Brickle, P., Arkhipkin, A., Votier S., C., 2022. Strategic discarding reduces seabird numbers and contact rates with trawl fishery gears in the Southwest Atlantic. *Biol. Conserv.* 266, 109462.
- Lubchenko, J., Gaines, S.D., 2019. A new narrative for the ocean. *Science* 364, 911.
- Mackley, E.K., Phillips, R.A., Silk, J.R.D., Wakefield, E.D., Afanasyev, V., Fox, J.W., Furness, R.W., 2010. Free as a bird? Activity patterns of albatrosses during the nonbreeding period. *Mar. Ecol. Prog. Ser.* 406, 291–303.
- Mackley, E.K., et al., 2025. Endurance or extinction: long-term declines in albatrosses at South Georgia highlight threats from South Atlantic fisheries and climate change. In: *Endangered Species Research*, 57. Inter-Research Science Center, pp. 437–451. <https://doi.org/10.3354/esr01427>. Available from.
- Marrari, M., Piola, A.R., Valla, D., 2017. Variability and 20-year trends in satellite-derived surface chlorophyll concentrations in large marine ecosystems around South and Western Central America. *Front. Mar. Sci.* 4, 1–17.
- Michael, P.E., Thomson, R., Barbraud, C., Delord, K., De Grissac, S., Hobday, A.J., Strutton, P.G., Tuck, G.N., Weimerskirch, H., Wilcox, C., 2017. Illegal fishing bycatch overshadows climate as a driver of albatross population decline. *Mar. Ecol. Prog. Ser.* 579, 185–199.
- Mills, W.F., Xavier, J.C., Bearhop, S., Cherel, Y., Votier, S.C., Waluda, C.M., Phillips, R.A., 2020. Long-term trends in albatross diets in relation to prey availability and breeding success. In: *Marine Biology*, 167. Springer Berlin Heidelberg, pp. 1–12. <https://doi.org/10.1007/s00227-019-3630-1>.
- Nevoux, M., Weimerskirch, H., Barbraud, C., 2007. Environmental variation and experience-related differences in the demography of the long-lived black-browed albatross. *J. Anim. Ecol.* 76, 159–167.
- Nevoux, M., Forcada, J., Barbraud, C., Croxall, J., Weimerskirch, H., 2010. Bet-hedging response to environmental variability, an intraspecific comparison. *Ecology* 91, 2416–2427.
- Nourani, E., et al., 2023. Seabird morphology determines operational wind speeds, tolerable maxima, and responses to extremes. *Curr. Biol.* 1–6.
- Oppel, S., et al., 2022. Cryptic population decrease due to invasive species predation in a long-lived seabird supports need for eradication. *J. Appl. Ecol.* 59, 2059–2070.
- Pardo, D., Barbraud, C., Authier, M., Weimerskirch, H., 2013. Evidence for an age-dependent influence of environmental variations on a long-lived seabird's life-history traits. *Ecology* 94, 208–220.
- Pardo, D., Jenouvrier, S., Weimerskirch, H., Barbraud, C., 2017a. Effect of extreme sea surface temperature events on the demography of an age-structured albatross population. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* 372 (1723), 20160143.
- Pardo, D., Forcada, J., Wood, A.G., Tuck, G.N., Ireland, L., Pradel, R., Croxall, J.P., Phillips, R.A., 2017b. Additive effects of climate and fisheries drive ongoing declines in multiple albatross species. *Proc. Natl. Acad. Sci. U.S.A.* 114 (50), E10829–E10837. <https://doi.org/10.1073/pnas.1618819114>.
- Park, Y.-H., Durand, I., Kestenare, E., Rougier, G., Zhou, M., D'Ovidio, F., Cotté, C., Lee, J.-H., 2014. Polar front around the Kerguelen Islands: an up-to-date determination and associated circulation of surface/subsurface waters. *J. Geophys. Res. Oceans* 3868–3882. Available from. <https://doi.org/10.1002/jgrc.20353/abstract>.
- Phillips, R.A., Silk, J.R.D., Croxall, J.P., Afanasyev, V., Bennett, V.J., 2005. Summer distribution and migration of nonbreeding albatrosses: individual consistencies and implications for conservation. *Ecology* 86, 2386–2396.
- Phillips, R.A., Gales, R., Baker, G.B., Double, M.C., Favero, M., Quintana, F., Tasker, M.L., Weimerskirch, H., Uhart, M., Wolfaardt, A., 2016. The conservation status and priorities for albatrosses and large petrels. In: *Biological Conservation*, 201. Elsevier Ltd., pp. 169–183. <https://doi.org/10.1016/j.biocon.2016.06.017>. Available from.
- Phillips, R.A., Lewis, S., González-solis, J., Daunt, F., 2017. Causes and consequences of individual variability and specialization in foraging and migration strategies of seabirds. *Mar. Ecol. Prog. Ser.* 578, 117–150.
- Phillips, R.A., Fox, E., Crawford, R., Prince, S., Yates, O., 2024. Incidental mortality of seabirds in trawl fisheries: a global review. *Biol. Conserv.* 296, 110720.
- Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P. H., Roberts, C.M., Sexton, J.O., 2014. The biodiversity of species and their rates of extinction, distribution, and protection. *Science* 344, 1246752. Available from. <https://doi.org/10.1126/science.1246752>.
- Pirotta, E., Bierlich, K.C., New, L., Hildebrand, L., Bird, C.N., Fernandez Ajó, A., Torres, L.G., 2024. Modeling individual growth reveals decreasing gray whale body length and correlations with ocean climate indices at multiple scales. *Glob. Change Biol.* 30, 1–13.
- Ponchon, A., Cornulier, T., Hedde, A., Granadeiro, J.P., Catry, P., 2019. Effect of breeding performance on the distribution and activity budgets of a predominantly resident population of black-browed albatrosses. *Ecol. Evol.* 9, 8702–8713.
- Prince, P.A., Rothery, P., Croxall, J.P., Wood, A.G., 1994. Population dynamics of Black-browed and Grey-headed Albatrosses *Diomedea melanophrys* and *D. chrysostoma* at Bird Island, South Georgia. *Ibis* 136, 50–71. Available from. <https://doi.org/10.1111/j.1474-919X.1994.tb08131.x>.
- Pujol, C., Pérez-Santos, I., Barth, A., Alvera-Azcárate, A., 2022. Marine heatwaves offshore Central and South Chile: understanding forcing mechanisms during the years 2016–2017. *Front. Mar. Sci.* 9, 1–20.
- R Core Team, 2022. R: A Language and Environment for Statistical Computing (R Foundation for Statistical Computing, Vienna, Austria). R Foundation for Statistical Computing, Vienna, Austria. Available from. <http://www.r-project.org/>.
- Robertson, G., Moreno, C., Arata, J.A., Candy, S.G., Lawton, K., Valencia, J., Wienecke, B., Kirkwood, R., Taylor, P., Suazo, C.G., 2014. Black-browed albatross numbers in Chile increase in response to reduced mortality in fisheries. *Biol. Conserv.* 169, 319–333. Elsevier Ltd. Available from. <https://doi.org/10.1016/j.biocon.2013.12.002>.
- Robertson, G., Wienecke, B., Suazo, C.G., Lawton, K., Arata, J.A., Moreno, C., 2017. Continued increase in the number of black-browed albatrosses (*Thalassarche melanophrys*) at Diego Ramírez, Chile. *Polar Biol.* 40, 1035–1042.
- Rolland, V., Barbraud, C., Weimerskirch, H., 2008. Combined effects of fisheries and climate on a migratory long-lived marine predator. *J. Appl. Ecol.* 45, 4–13.
- Rolland, V., Barbraud, C., Weimerskirch, H., 2009. Assessing the impact of fisheries, climate and disease on the dynamics of the Indian yellow-nosed Albatross. In: *Biological Conservation*, 142. Elsevier Ltd., pp. 1084–1095. <https://doi.org/10.1016/j.biocon.2008.12.030>. Available from.
- Rolland, V., Weimerskirch, H., Barbraud, C., 2010. Relative influence of fisheries and climate on the demography of four albatross species. *Glob. Change Biol.* 16, 1910–1922.
- Roman, L., Mayne, B., Anderson, C., Kim, Y., O'Dwyer, T., Carlile, N., 2024. A novel technique for estimating age and demography of long-lived seabirds (genus *Pterodroma*) using an epigenetic clock for Gould's petrel (*Pterodroma leucoptera*). *Mol. Ecol. Resour.* 1–11.
- Romero, S.L., Piola, A.R., Charo, M., Garcia, C.A.E., 2006. Seasonal to interannual variability along the Patagonia shelf and shelf-break based on satellite ocean color data. *J. Geophys. Res.* 111, C05021.
- Rouby, E., Plard, F., Ridoux, V., Mauchamp, A., Dabin, W., Spitz, J., Authier, M., 2025. Longevity collapse in dolphins: a growing conservation concern in the Bay of Biscay. *Conserv. Lett.* 18 (5), e13142.
- Sæther, B.E., Bakke, Ø., 2000. Avian life history variation and contribution of demographic traits to the population growth rate. *Ecology* 81, 642–653.
- Saraceno, M., Martín, J., Moreira, D., Pisoni, J.P., Tonini, M.H., 2022. Physical changes in the Patagonian Shelf. In: Helbling, E.W., Narvarte, M.A., González, R.A., Villafañe, V.E. (Eds.), *Global Change in Atlantic Coastal Patagonian Ecosystems. Natural and Social Sciences of Patagonia*. Springer, Cham.
- Sceviour, M.P., Ward, C.R.E., Wilhelm, S.I., 2025. Immature Northern Gannets (*Morus bassanus*) increase colony attendance following highly pathogenic avian influenza. *Ibis* 167, 711–719.
- Schatz, C., Delord, K., Joubert, D., Peroteau, S., Sun, R., Barbraud, C., 2025. Inter-population variation in demographic responses to environmental changes: insights from four seabird populations. *Oikos*, e11364.
- Schaub, M., Abadi, F., 2011. Integrated population models: a novel analysis framework for deeper insights into population dynamics. *J. Ornithol.* 152, S227–S237.
- Schaub, M., Kéry, M., 2021. *Integrated Population Models: Theory and Ecological Applications With R and JAGS*. Academic Press.
- Schreiber, E.A., Burger, J., 2001. *Biology of Marine Birds*. CRC Press.
- Sergio, F., Caro, T., Brown, D., Clucas, B., Hunter, J., Ketchum, J., McHugh, K., Hiraldo, F., 2008. Top predators as conservation tools: ecological rationale, assumptions, and efficacy. *Annu. Rev. Ecol. Syst.* 39, 1–19.
- Shaffer, S.A., Weimerskirch, H., Costa, D.P., 2001. Functional significance of sexual dimorphism in wandering albatrosses, *Diomedea exulans*. *Funct. Ecol.* 15 (2), 203–210.
- Sharma, V.D., Markina, M.Y., Gulev, S.K., 2021. Global ocean wind-wave model hindcasts forced by different reanalyses: a comparative assessment. In: *Journal of Geophysical Research: Oceans*, 126. Wiley Online Library, e2020JC016710.
- Smith, K.E., Burrows, M.T., Hobday, A.J., King, N.G., Moore, P.J., Sen Gupta, A., Thomsen, M.S., Wernberg, T., Smale, D.A., 2023. Biological impacts of marine heatwaves. *Annu. Rev. Mar. Sci.* 15, 119–145.
- Stafoggia, M., et al., 2006. Vulnerability to heat-related mortality: a multicity, population-based, case-crossover analysis. *Epidemiology* 17, 315–323.
- Su, Y.-S., Yajima, M., 2012. R2jags: A Package for Running Jags From R.
- Thorne, L.H., Clay, T., Phillips, R., Silvers, L., Wakefield, E., 2023. Effects of wind on the movement, behavior, energetics, and life history of seabirds. In: *Marine Ecology Progress Series*, 723. Inter-Research Science Center, pp. 73–117. <https://doi.org/10.3354/meps14417>. Available from.
- Tuck, G.N., Phillips, R.A., Small, C., Thomson, R.B., Klaer, N.L., Taylor, F., Wanless, R.M., Arrizabalaga, H., 2011. An assessment of seabird – fishery interactions in the Atlantic Ocean. *ICES J. Mar. Sci.* 68, 1628–1637.
- Ventura, F., Lukacs, P., Granadeiro, J., Matano, R., Catry, P., 2021. Demographic responses to environmental change of the black-browed albatross, sentinel of the Patagonian Shelf Large Marine Ecosystem. *Mar. Ecol. Prog. Ser.* 668, 107–120.
- Ventura, F., Stanworth, A., Crofts, S., Kuepfer, A., Catry, P., 2023. Local-scale impacts of extreme events drive demographic asynchrony in neighbouring top predator populations. *Biol. Lett.* 19 (2), 20220408.
- Weimerskirch, H., Louzao, M., de Grissac, S., Delord, K., 2012. Changes in wind pattern alter albatross distribution and life-history traits. *Science* 335, 211–214.
- Weimerskirch, H., Delord, K., Barbraud, C., Le Bouard, F., Ryan, P.G., Fretwell, P., Marteau, C., 2018. Status and trends of albatrosses in the French Southern Territories, Western Indian Ocean. In: *Polar Biology*, 41. Springer Berlin Heidelberg, pp. 1963–1972. <https://doi.org/10.1007/s00300-018-2335-0>. Available from.
- Wiens, J.J., Zelnika, J., 2024. How many species will Earth lose to climate change? *Glob. Change Biol.* 30, e17125. Available from. <https://doi.org/10.1111/gcb.17125>.
- Witham, R., 1980. The “lost year” question in young sea turtles. In: *American Zoologist*, 20. Oxford University Press, UK, pp. 525–530.
- Wolfaardt, A., 2013. An assessment of the population trends and conservation status of black-browed albatrosses in the Falkland Islands. In: *First Meeting of the Population and Conservation Status Working Group of the Agreement on the Conservation of Albatrosses and Petrels*, pp. 29–30 (La Rochelle, France).

- Young, I.R., Ribal, A., 2019. Multiplatform evaluation of global trends in wind speed and wave height. In: *Science*, 364. American Association for the Advancement of Science, pp. 548–552.
- Youngflesh, C., 2018. MCMCvis: tools to visualize, manipulate, and summarize MCMC output. *J. Open Source Softw.* 3, 640.
- Zipkin, E.F., Saunders, S.P., 2018. Synthesizing multiple data types for biological conservation using integrated population models. In: *Biological Conservation*, 217. Elsevier, pp. 240–250. <https://doi.org/10.1016/j.biocon.2017.10.017>. Available from.