



# Demographic responses to environmental change of the black-browed albatross, sentinel of the Patagonian Shelf Large Marine Ecosystem

Francesco Ventura<sup>1,\*</sup>, Paul M. Lukacs<sup>2</sup>, José Pedro Granadeiro<sup>1</sup>, Ricardo Matano<sup>3</sup>, Paulo Catry<sup>4</sup>

<sup>1</sup>CESAM, Departamento de Biologia Animal, Faculdade de Ciências, Universidade de Lisboa, Campo Grande, 1749-016 Lisboa, Portugal

<sup>2</sup>Wildlife Biology Program, Department of Ecosystem and Conservation Sciences, WA Franke College of Forestry and Conservation, University of Montana, Missoula, Montana 59812, USA

<sup>3</sup>College of Earth, Ocean and Atmospheric Sciences, Oregon State University, Corvallis, OR 97331, USA

<sup>4</sup>MARE — Marine and Environmental Sciences Centre, ISPA—Instituto Universitário, Rua Jardim do Tabaco 34, 1149-041 Lisboa, Portugal

**ABSTRACT:** In long-lived marine top-predators with delayed sexual maturity such as seabirds, adult survival is predicted to drive population dynamics. Major knowledge gaps exist for the cryptic sub-adult stages of the population. Yet as the oceans undergo dramatic change, investigating the trends of top-predator populations and their responses to environmental variability is key for a process-based understanding of climate change. Using integrated population models based on a longitudinal data set spanning nearly 2 decades, we investigated the demographic rates and environmental drivers shaping the dynamics of a longevous marine top-predator population, the black-browed albatross *Thalassarche melanophrys* in the Falklands. We quantified the dynamics of the whole population, including its cryptic sub-adult stages, and examined the effects of candidate environmental covariates on adult survival and productivity parameters. We found that high survival rates of both adults and juveniles are the main contributors to the growth of this albatross population, the only one that is increasing in the South Atlantic. The breeding parameters were affected by environmental fluctuations through bottom-up processes, with a negative effect of higher sea surface temperatures and a positive effect of wind intensity. The relatively constant adult survival was influenced by deeper ecosystem changes, captured by large-scale indices (Southern Annular Mode). Approximately half of the total population is composed of sub-adults, and the population dynamics are highly sensitive to changes in juvenile survival; addressing current knowledge gaps in these cryptic life-history stages is therefore a conservation goal of primary importance.

**KEY WORDS:** Juvenile survival · Demography · Integrated population model · Top-predator · Conservation · Seabird · Albatross

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## 1. INTRODUCTION

Due to their apex position in the trophic web and high sensitivity to perturbation, top-predators are often regarded as reliable indicators of environmental processes occurring in their supporting ecosystems and are particularly useful in attracting the attention of a broader audience, given their inherent

charisma and lever for public support for the conservation of biodiversity (Boyd & Murray 2001, Sergio et al. 2008). Marine ecosystems are being dramatically impacted by climate change (Poloczanska et al. 2013, Jones et al. 2018, IPCC 2019), but our understanding of these impacts remains limited. In this context, monitoring the population trends and demographic responses to environmental variability of marine top-

\*Corresponding author: fraventura.92@gmail.com

predators allows for a unique analytical viewpoint for understanding the effects of climate change on wild populations and for promoting the conservation of biodiversity (Sergio et al. 2008, Hazen et al. 2019).

As top-predators, seabirds play a key role in the equilibrium of marine ecosystems (Parsons et al. 2008), consuming yearly prey biomass comparable to that of global fisheries (Cury et al. 2011). In seabirds and other longevous species with delayed maturity, adult survival is predicted to be the main demographic contributor to population growth and to be buffered against adverse environmental conditions (Sæther & Bakke 2000, Forcada et al. 2008, Nevoux et al. 2010a). Sub-adults — which we hereby define as individuals in the juvenile, immature and pre-breeding stages — are often unobservable as they spend their first years of life at sea before recruiting into their breeding colonies (Phillips et al. 2017). Hence, due to the challenging nature of data collection for sub-adults and the key role of adult survival in shaping the dynamics of the population, substantial knowledge gaps exist for the cryptic sub-adult life-history stages (Hazen et al. 2012). Yet sub-adults often make up a substantial portion of the total population size, as estimated by Clay et al. (2019) and Carneiro et al. (2020) using age- and stage-structured matrix population models. Moreover, sub-adult birds are more vulnerable due to their inexperience (Gianuca et al. 2017). Thus, due to scarcity of information, the demographic contribution of the survival of sub-adult individuals to overall population dynamics is largely unknown.

Estimation of demographic parameters is a fundamental necessity for the development of mechanistic models and for process-oriented evaluation of population dynamics (Zipkin & Saunders 2018). A recent integrative modelling approach — using integrated population models (IPMs) — was developed to jointly analyse and capitalise on the strength of multiple demographic data sets (Abadi et al. 2010, Schaub & Abadi 2011), thus addressing the shortcomings of traditional separate analyses on survival, immigration and productivity. Compared to more conventional models that are applied to individual data sets, IPMs present a series of key advantages: proper error propagation by accounting for multiple sources of uncertainty and standardising the error structure across the different data sets incorporated in the model; increased precision of demographic estimates; and crucially, the capability of estimating hidden demographic parameters for cryptic life-history stages such as sub-adult stages in seabirds (Abadi et al. 2010, 2017, Schaub & Abadi 2011). IPMs have been utilised on mammals and other avian taxa (re-

viewed in Zipkin & Saunders 2018), but rarely in seabird population ecology studies (but see Véran & Lebreton 2008). Nevertheless, thanks to the accessibility of their breeding sites, several seabird species have been intensively monitored for decades, providing some of the best long-term ecological data sets available for the use of IPMs.

Here, we investigated the demographic responses of the black-browed albatross *Thalassarche melanophris* to environmental variability in the Falkland/Malvinas Islands region. Albatrosses (Family Diomedidae) are among the most threatened seabird groups, and many populations worldwide are in steep decline (Birdlife International 2018a, Dias et al. 2019). In the South Atlantic, the only documented exception is, in fact, the increasing population of the Falklands black-browed albatross (Birdlife International 2018b). The objectives of our study were to (1) investigate the Falklands black-browed albatross demographic rates underpinning the dynamics of the whole population, including the cryptic sub-adult life-history stages. We aimed to estimate the survival rate of juvenile birds (i.e. 1–3 yr old, see below) and quantitatively describe the full population structure by age-stage; (2) identify the main demographic contributors to population dynamics. In particular, we aimed to quantify the sensitivity of the population dynamics to the survival of juveniles; and (3) examine the temporal variability of the adult survival and productivity processes and elucidate the effects of candidate environmental covariates on albatross adult survival and productivity parameters.

To achieve these objectives, we implemented Bayesian IPMs and a prospective sensitivity analysis framework, making use of the most extensive demographic and tracking data sets available for the Falklands albatross. These data sets comprised a longitudinal data set on population counts; high resolution (at a daily to weekly temporal resolution during the breeding season, see below) capture–mark–recapture (CMR) data; productivity data spanning 2005–2006 to 2019–2020 (hereafter, 2005–2006 will be referred to as the 2005 season, etc.) and GPS tracking data (2008–2019).

## 2. MATERIALS AND METHODS

### 2.1. Study system and available data

The Falkland Islands are home to the largest black-browed albatross population (over 70 % of the global breeding population size), estimated at 475 500 to

535 000 pairs, distributed in 12 colonies across the archipelago (Wolfaardt 2012). The Falklands albatross population is mainly resident, foraging over the Patagonian Shelf Large Marine Ecosystem year-round (Ponchon et al. 2019). Food availability in the Patagonian Shelf is modulated by the Falklands/Malvinas current, which originates from the Antarctic Circumpolar Current bringing cold and nutrient-rich waters to lower latitudes. The Patagonian Shelf is one of the most productive marine ecosystems in the world (Croxall & Wood 2002); it is a biodiversity hotspot of fundamental importance for regional economies and home to large populations of marine mammals and seabirds (Augé et al. 2018, Baylis et al. 2019), with a large portion of its avian biomass represented by black-browed albatross.

Our demographic study was based on New Island, to the west of the Falklands/Malvinas archipelago, where Catry et al. (2011) have been collecting high-resolution CMR data, population counts and productivity data. New Island is home to approximately 15 500 black-browed albatross breeding pairs. Incubation begins in October, hatching in the second week of December and fledging in April. The intensive CMR effort is based on daily (during incubation and brooding) and weekly (during post-brooding) visits to the study plots and their neighbouring areas. Thanks to the data collection protocol adopted (see Text S1 in the Supplement at [www.int-res.com/articles/suppl/m668p107\\_supp.pdf](http://www.int-res.com/articles/suppl/m668p107_supp.pdf)), our data set also contains encounter histories of sub-adults that were ringed as chicks in our monitored plots and returned to the colony in the years prior to recruiting (Campioni et al. 2017), non-breeding adults and birds that emigrated from our study plots and recruited in the surrounding areas, collected on a daily to weekly basis. Every year, fieldwork started in the first days of October, prior to or at the onset of egg-laying, ensuring that the number of early failed breeders erroneously classified as non-breeders was minimal. This sampling strategy increased detectability rates, provided the IPM with recaptures of young and non-breeding birds and with explicit information on local immigration and emigration, thus improving the estimates of survival and breeding parameters. Our database comprised GPS tracking data from 2008–2019 (Text S1), which allowed for quantifying the areas of the southern Patagonian Shelf most intensively used by albatrosses using kernel utilization distributions (Worton 1989). The 90 % contour of the kernel utilization distribution was used to define the relevant spatial domain for the extraction of the Patagonian Shelf environmental variables (Text S2).

Recent DNA metabarcoding studies (McInnes et al. 2017a,b) revealed that the main dietary items of albatrosses breeding on New Island are fish (e.g. Fuegian sprat *Sprattus fuegensis* and rockcod *Patagonotothen* sp.) and crustaceans from the Family Munidae (lobster krill). To a lesser extent, their diet also includes scyphozoan jellyfish and cephalopods from the order Teuthida (squids). Due to the scarcity of information on prey distribution, we used environmental proxies for food availability and accessibility that may have affected albatross breeding and survival rates. Quantifying demographic responses to environmental variability is particularly challenging, as complex biological and oceanographic processes operate and interact at different spatio-temporal scales (Trathan et al. 2006). Here, we considered both fine-scale, short-lived proxies of the Patagonian Shelf physical and biological variability and large-scale climate indices. Specifically: sea surface temperature anomalies (SSTAs), which we predicted to have a negative effect on albatross demographic rates; net primary production (NPP), which we predicted to have a positive effect; and mean wind intensity (WIND), predicted to have a positive effect. SSTAs, which are driven by atmospheric heat fluxes and vertical mixing, modulate (directly or indirectly) the recruitment and abundance of prey (Waluda et al. 1999, Arkhipkin et al. 2010). It has been shown that warm SSTAs negatively affect the breeding processes of other seabirds in the region, such as thin-billed prions *Pachyptila belcherii* from New Island (Quillfeldt et al. 2007). NPP—which is higher in colder, nutrient-rich waters—shapes the distribution of prey supporting pelagic seabirds, such as mid-trophic-level fish, squid and crustacean species (Chassot et al. 2010). WIND not only enhances water mixing and nutrient supply, thus having a positive effect on primary productivity, but can also reduce the commuting costs and hence the accessibility of foraging areas, particularly for dynamic soaring birds such as albatrosses and petrels (Ventura et al. 2020). The region is characterised by strong westerly winds, which are largely consistent in direction from one season to the next. This limited temporal variability in average wind direction is the reason why, in the analysis, we only considered mean wind intensity, which shows much more pronounced temporal variability. As we predicted that adult survival would exhibit limited responses to local environmental variability in the Patagonian Shelf, we also modelled adult survival as a function of the 2 dominant modes of climate variability in the Southern Ocean, captured by the large-scale climatic indices the Southern Annular Mode (SAM) and Southern Os-

cillation Index (SOI) (Forcada & Trathan 2009, Turner et al. 2009). To model the effects of large-scale climatic indices on albatross survival rates, we considered these indices under different temporal lags (Text S2) to capture the impacts at both short and long lags (Forcada & Trathan 2009). We hypothesised that the effects of environmental and climatic variables propagated (at different temporal scales, which we accounted for using different temporal windows for the variables extraction; see Text S2, Fig. S3) to the upper trophic levels, altering ecosystem structure, regulating food availability and, ultimately, affecting albatross productivity and survival processes.

## 2.2. Definition of the IPM

We constructed an age-stage structured Bayesian IPM with 12 age-stage classes (Fig. 1, Text S3) using a multi-event framework with a state-space model-

ling formulation for the CMR component, a state-space modelling formulation for the population count component and a binomial univariate regression for the productivity component. The IPM was structured as follows: fledglings (J0) surviving to the first year (with juvenile survival probability,  $\phi_j$ ) move to the first juvenile age class (J1); if they survive, they move to J2, then to J3 and subsequently to the immature age class ('Imm', 4 yr old), all with  $\phi_j$ . Once in this stage, immature birds acquire the same survival probability as adults (i.e.  $\phi_a$ ) (Nevoux et al. 2010b, Pardo et al. 2017a). If they survive to the following year, they enter the first pre-breeder stage ('PreB1', 5 yr old). Those that survive to the 6<sup>th</sup> year—which is the first year at which recruitment occurred in our study colonies—and recruit (i.e. breed for the first time, with probability of recruitment when 6 or 7 yr old 'recr<sub>6-7y</sub>') become either successful (S) or failed (F) breeders, with a first-time-breeder probability of success (i.e. of successfully fledging a chick) equal to

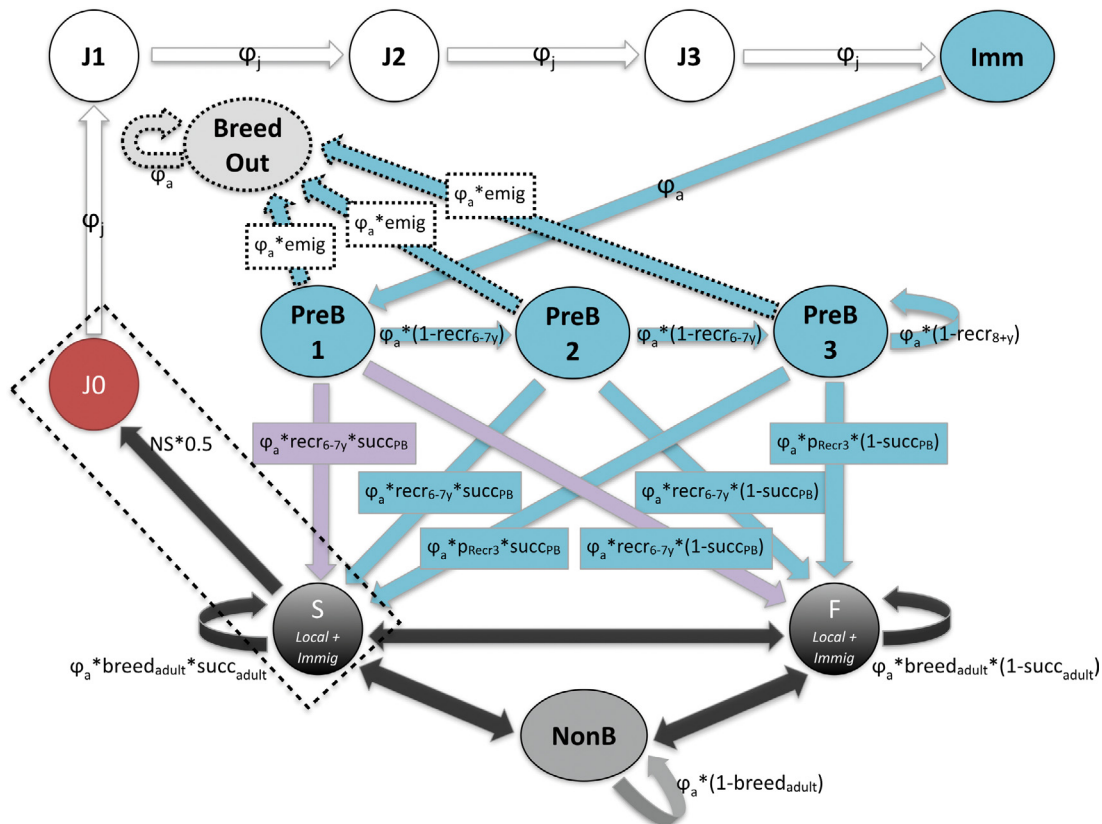


Fig. 1. Age-stage structured integrated population model describing the black-browed albatross population in New Island, Falklands. Different colours are used to visualise different detection probabilities: red:  $p_C$  (i.e. fledglings); white:  $p_J$  (juveniles); light blue:  $p_{ImmPB}$  (immatures and pre-breeders); light grey:  $p_{BreedOut}$  (birds that emigrated and recruited outside); black:  $p_{AdultB}$  (adult breeders); dark grey:  $p_{AdultNonB}$  (adult non-breeders). The states used to describe the albatross population are: fledglings (J0); juveniles of 1, 2 and 3 years of age (J1, J2, J3); immatures (Imm, 4 yr old); pre-breeders of 5, 6 and 7 years of age (PreB1, PreB2, PreB3); successful (S) or failed (F) breeders, including both the 'Local' birds that were born in the study cohort) and immigrant (Immig) adults that entered into our monitored plots as breeders; and non breeding birds (NonB), i.e. adult birds that skipped a reproductive attempt. At each pre-breeder stage, if birds emigrated and recruited outside of the study colonies, they entered the 'BreedOut' stage. See Table 1 for further parameter abbreviations

'succ<sub>PB</sub>'. Those that do not recruit move to the 2<sup>nd</sup> and 3<sup>rd</sup> pre-breeder stages ('PreB2' and 'PreB3'), with probabilities of recruitment equal to 'recr<sub>6-7y</sub>' and 'recr<sub>8+y</sub>', respectively. Birds in PreB3 remain at this stage until recruitment. After recruitment, birds may breed annually with an adult probability of breeding ('breed<sub>adult</sub>'; if not, they become non-breeders, 'NonB') and fledge a chick with an adult probability of success 'succ<sub>adult</sub>' (which we refer to as breeding success), becoming successful breeders, S (or failed breeders, F, if they attempt breeding but fail to produce a fledgling). At each pre-breeder stage, surviving birds can emigrate and recruit outside of the study colonies with probability 'emig', thus entering the 'BreedOut' stage. Once birds are in the latter stage they are permanently out of the study cohort, an assumption that is consistent with 99% of the encounter histories of emigrating birds in our data set. In accordance with the states defined in our IPM, we hereafter define adults as birds that have attempted breeding at least once; sub-adults collectively refers to the juveniles, immature and pre-breeding stages and juveniles refers to birds 1–3 yr old, all characterised by the same survival probability,  $\phi_i$ .

### 2.3. Sensitivity analysis

As succ<sub>adult</sub> showed the highest inter-annual fluctuations (see Section 3.1 below), the 'reference' IPM adopted for the sensitivity analysis and for the description of the demographic rates and population dynamics (below) was the one accounting for temporal variability in succ<sub>adult</sub>. Our framework was based on a prospective sensitivity analysis (Caswell 2000). The contribution of each parameter to future population growth ( $\lambda$ ) was quantified by the changes induced by that parameter on  $\lambda$  (rather than focussing on the contribution of the observed variation in different demographic traits on the past changes in  $\lambda$ , which is the objective of a retrospective analysis). Starting from the last age-stage population counts (2019 season), we simulated future population dynamics (structured by age-stage) for the next 50 yr. Each year, the population trajectory was estimated by drawing each demographic parameter from a normal distribution with the same mean and standard deviation as the respective posterior distribution in the reference IPM, thus yielding a population matrix with 50 rows (the years) and 11 columns (the population age-stages). Simulations were repeated for 1000 iterations, generating 1000 population matrices. In each matrix, yearly  $\lambda$  was estimated by dividing the total population size at

time-step  $t + 1$  by the total population size at  $t$ ;  $\lambda$  was then estimated for each simulated matrix as the geometric mean of the yearly  $\lambda$ . Finally, the average  $\lambda$  and the 25–75% confidence interval were estimated, representing the reference  $\lambda$  calculated based on the same demographic parameter distributions estimated by the reference IPM. The sensitivity of  $\lambda$  to changes in each focal demographic parameter (e.g.  $\phi_j$ ) was estimated using the same analysis described above, but drawing the focal parameter (for example,  $\phi_j$ ) from a distribution with a mean decreased by  $x\%$  (1, 2.5, 5 or 10%) compared to the mean of the parameter posterior distribution in the reference IPM, while the other parameters were kept as in the reference IPM. The sensitivity of  $\lambda$  (i.e. the % change of  $\lambda$ ) to changes in the following demographic parameters was quantified:  $\phi_a$ ,  $\phi_j$ , breed<sub>adult</sub>, succ<sub>adult</sub> and recruitment probabilities (i.e. simultaneous changes to both recr<sub>6-7y</sub> and recr<sub>8+y</sub>).

### 2.4. Analysis of temporal variability and effects of environmental variables

The demographic rates considered in this analysis were breed<sub>adult</sub>, succ<sub>adult</sub> and  $\phi_a$ . After fledging, birds spend their first years of life at sea, leading to very few (if any) recaptures of birds aged 1–3 yr. As a consequence, the temporal variability in  $\phi_j$  could not be estimated. The temporal variability of productivity (breed<sub>adult</sub> and succ<sub>adult</sub>) and  $\phi_a$  was modelled by including each breeding season as a temporal random effect. Because of the complex IPM formulation, the temporal random effects on breed<sub>adult</sub>, succ<sub>adult</sub> and  $\phi_a$  were separately included in 3 different IPMs (Text S3).

We then used univariate logistic regression to separately investigate the effect of the candidate covariates on  $\phi_a$ , breed<sub>adult</sub> and succ<sub>adult</sub>. Due to the model complexity, it was not possible to reach model convergence if we tested for the effect of every variable on each parameter. Thus, we created a set of IPMs including either the Patagonian Shelf environmental covariates or the large-scale climatic indices. Prior to model fitting, we standardised the explanatory variables to facilitate model convergence. We used variance inflation factors (VIFs) from the 'AED' package in R (Zuur et al. 2009) to check that the variables included in each model were not collinear; in all models, the VIFs calculated for the explanatory variables were smaller than 2, indicating no collinearity. The effect of climatic indices on survival was tested using different time lags (Text S2). The importance of each covariate was assessed using inclusion probability parameters (O'Hara & Sillanpää 2009) (Text S3).



## 2.5. Model implementation

Analyses were performed using the JAGS software executed through R v.3.6.2 (R Core Team 2019) via the 'R2jags' package (Su & Yajima 2012), which uses a Markov chain Monte Carlo (MCMC) algorithm to sample from the posterior distribution of each parameter in the model. For all models, we carried out the analysis generating 3 chains of at least 30 000 iterations. The chains were well mixed, and the Gelman-Rubin diagnostic convergence statistic (Brooks & Gelman 1998) was below 1.02 for all parameters, indicating that the chains converged adequately.

## 3. RESULTS

### 3.1. Demographic rates and population dynamics

The parameters  $\text{breed}_{\text{adult}}$  and  $\phi_a$  were considerably less variable than  $\text{succ}_{\text{adult}}$  (Fig. 2). The demographic rates calculated by the reference IPM (Table 1), i.e. the one accounting for temporal variability in  $\text{succ}_{\text{adult}}$ , revealed high  $\phi_a$  (estimated at 0.94; 95 % credible interval [CRI] = 0.936, 0.946) and  $\phi_j$  (estimated at 0.75; CRI = 0.727, 0.789), as well as high  $\text{breed}_{\text{adult}}$  (0.88; CRI = 0.872, 0.888) and  $\text{succ}_{\text{adult}}$  (0.68; CRI = 0.545, 0.789). The temporal variance of breeding success (on logit scale) was estimated at  $\sigma^2_{\text{succ}} = 1.04$  (CRI = 0.71, 1.97).

The estimated total number of black-browed albatrosses in our study (including individuals from all age classes at a given year, excluding chicks) increased from 724 (CRI = 585, 851) in 2005 to 1083 (CRI = 905, 1259) in 2019 (Fig. 3). Maximum population size of 1143 (CRI = 970, 1322) was recorded in 2015. During the entire period of the study,  $\lambda$  was 1.03 (CRI = 1.029, 1.035), with an average population increase of 3.3 %  $\text{yr}^{-1}$  (CRI = 2.49, 4.11). During the breeding season, adult birds (S, F and NonB) comprised the largest portion of the population (mean = 53.6 %, range = 49.7–60.4 %; these percentages and the ones below do not include chicks). On average, during the breeding season, adult birds (S, F and NonB) comprised 47.6 % (range = 43.6–54.4 %) and 6.1 %, (range = 4.2–7.6 %) of the total population size, respectively. Juvenile and immature birds made up, on average, 31.2 % of the total numbers (range = 23.5–40.5 %). Pre-breeders represented, on average, 15.1 % of the population (range = 6.2–19.4 %).

### 3.2. Sensitivity analysis

Adult survival had the highest impact on the population dynamics (Fig. 4): a decrease of 1 % in  $\phi_a$  caused a 0.83 % decrease in mean  $\lambda$  over the following 50 yr, leading to a yearly population decrease of 0.4 %. Juvenile survival was the second most important contributor to population dynamics (Fig. 4). In particular,  $\lambda$  decreased by 0.19 % as  $\phi_j$  decreased by 1 %. As  $\phi_j$  decreased by 5 and 10 %,  $\lambda$  decreased by 0.81 and 1.56 % and the population size decreased by 0.38 and 1.14 %  $\text{yr}^{-1}$ , respectively. A 1 % decrease in  $\text{breed}_{\text{adult}}$  and  $\text{succ}_{\text{adult}}$  caused a reduction of 0.05 and 0.04 % in  $\lambda$ , respectively. The sensitivity of  $\lambda$  to recruitment was marginal; in particular, a 1 % decrease in the means of the distributions of both recruit-

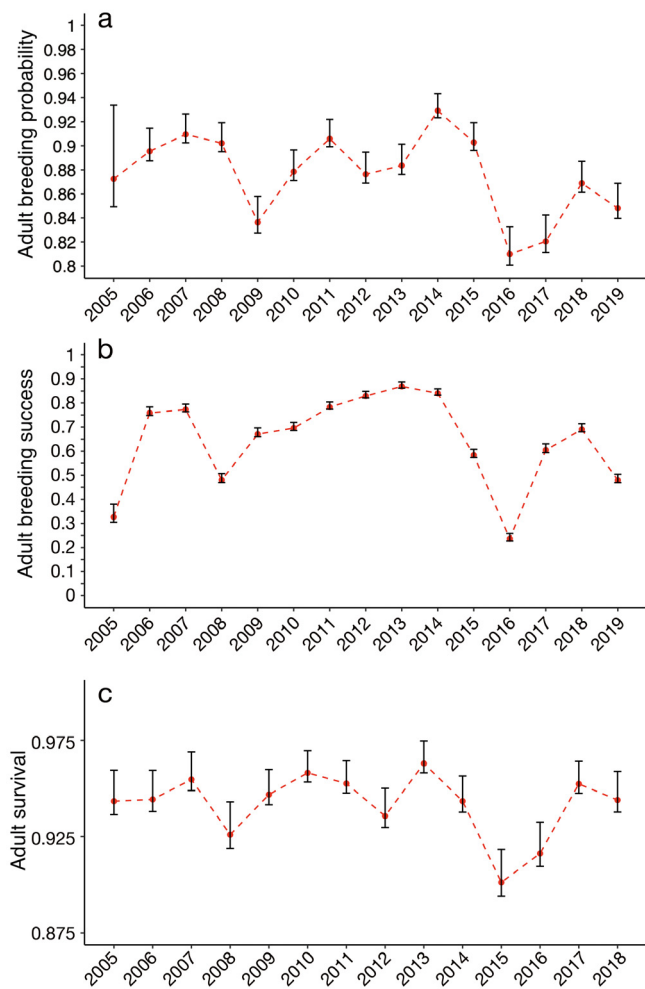


Fig. 2. Temporal variability of (a) breeding probability, (b) breeding success and (c) survival of adult black-browed albatrosses, estimated by the integrated population model. Dots: means; error bars: 95 % credible interval (ranging from the 2.5<sup>th</sup> to the 97.5<sup>th</sup> quantile) of the parameter posterior distributions

Table 1. Demographic parameters for black-browed albatross estimated by the ‘reference’ integrated population model, with temporal random effect on adult breeding success. As in this model adult breeding success varies temporally, we report the average success and its temporal variance on the logit scale. For each parameter, the 95 % credible interval (CRI) ranges from the 2.5<sup>th</sup> to the 97.5<sup>th</sup> quantile of its posterior distribution

Parameter	Mean (SD)	95 % CRI
Juvenile survival ( $\phi_j$ )	0.75 (0.03)	0.727, 0.789
Adult survival ( $\phi_a$ )	0.94 (0.003)	0.936, 0.946
Probability of recruitment at year 6 or 7 ( $\text{recr}_{6-7y}$ )	0.09 (0.01)	0.064, 0.112
Probability of recruitment at year 8 or above ( $\text{recr}_{8+y}$ )	0.31 (0.03)	0.263, 0.352
Adult probability of breeding ( $\text{breed}_{\text{adult}}$ )	0.88 (0.005)	0.872, 0.888
First-time breeder probability of success ( $\text{succ}_{\text{PB}}$ )	0.40 (0.03)	0.339, 0.457
Adult average breeding success ( $\text{succ}_{\text{adult}}$ )	0.68 (0.07)	0.545, 0.789
Adult success temporal variance, logit ( $\sigma^2_{\text{succ}}$ )	1.04 (0.48)	0.71, 1.97
Emigration and recruitment outside (emig)	0.31 (0.06)	0.241, 0.442
Chick detection probability ( $p_c$ )	0.99 (0.01)	0.96, 0.999
Juvenile year 1–3 recapture probability ( $p_j$ )	0.005 (0.001)	0.003, 0.006
Immature or pre-breeder recapture probability ( $p_{\text{ImmPreB}}$ )	0.25 (0.02)	0.165, 0.275
Adult breeder recapture probability ( $p_{\text{AdultB}}$ )	0.996 (0.004)	0.987, 1
Adult non breeder recapture probability ( $p_{\text{AdultNonB}}$ )	0.82 (0.03)	0.775, 0.864
Emigrated breeders recapture probability ( $p_{\text{AdultOut}}$ )	0.35 (0.07)	0.118, 0.437

ment probabilities  $\text{recr}_{6-7y}$  and  $\text{recr}_{8+y}$  led to a 0.01 % decrease in  $\lambda$ . In a simulated scenario in which the means of the recruitment probabilities distributions decreased by 99 %,  $\lambda$  decreased by 2.55 %, leading to a yearly population decrease of 2.4 %, further suggesting the low sensitivity of growth rate to recruitment.

### 3.3. Effect of candidate covariates

Our results highlight a strong influence of local environmental conditions on the albatross productivity pro-

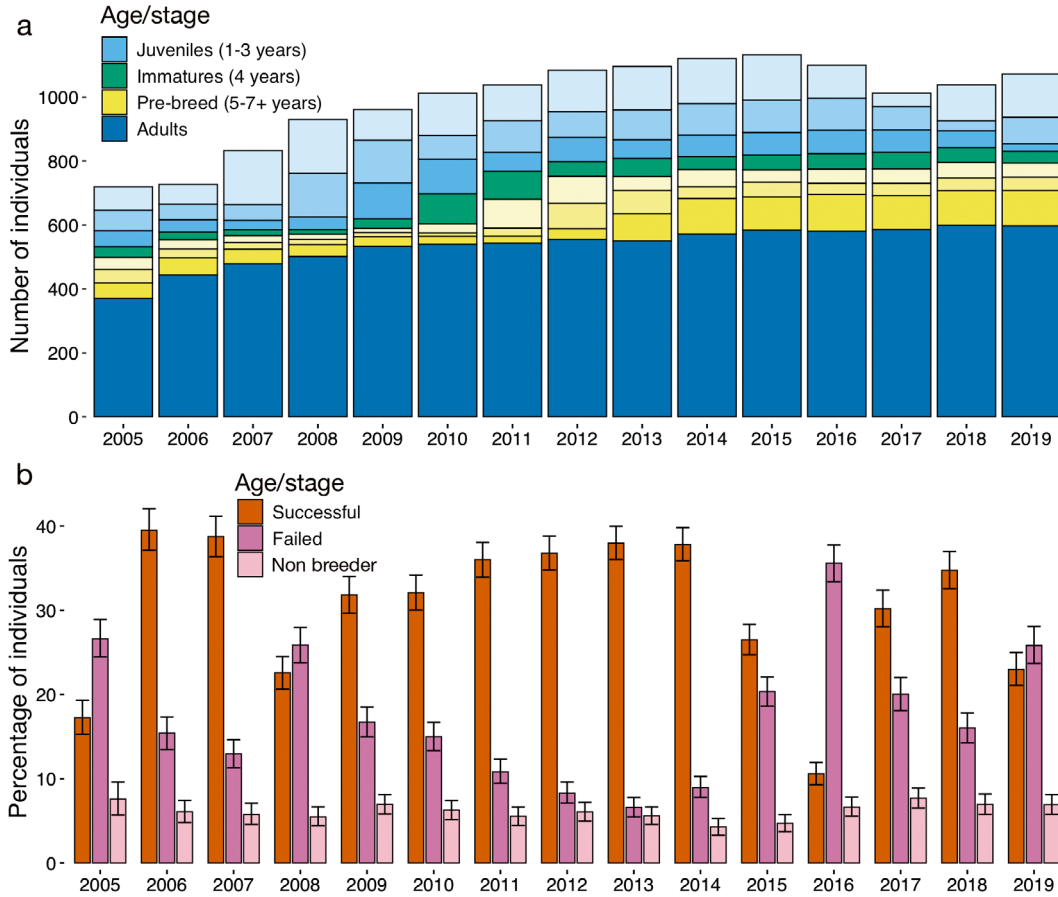


Fig. 3. (a) Number of black-browed albatrosses in each age-stage, each year, excluding chicks. Different shades of the same colour are used to represent different years of age within the same stage (for juveniles and pre-breeders, with the colours darkening as the birds get older). (b) The adult component of the population, with different colours depicting the percentage of successful, failed and non-breeding birds. Error bars: 95 % credible intervals

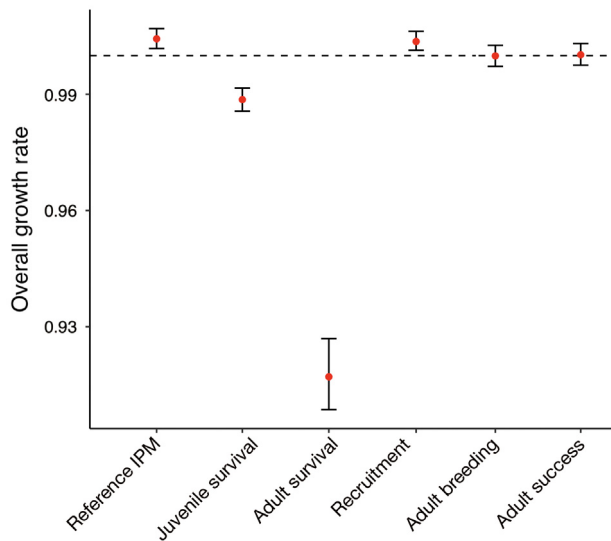


Fig. 4. Sensitivity of the overall black-browed albatross population growth rate to changes in the focal parameters juvenile survival, adult survival, recruitment rate, adult breeding probability and adult breeding success. The figure shows the overall population growth rate over the next 50 yr (y-axis) based on the unaltered 'reference' integrated population model (IPM; i.e. the one accounting for temporal variability in adult breeding success) and the overall growth rate as the mean value of each focal demographic parameter decreases by 10%. Dashed horizontal line: growth rate of 1 (i.e. a stable population). A growth rate below 1 indicates a population decrease. Dots: means; vertical error bars: 0.25, 0.75 quantiles

cesses (Fig. 5). Hereafter, we use the Greek letter  $\beta$  to denote the regression slopes quantifying the effect size and 'w' for the inclusion probability parameters. The  $\text{breed}_{\text{adult}}$  was significantly negatively affected by SSTA ( $w > 0.99$ ,  $\beta_{\text{SSTA}} = -0.20$ , CRI =  $-0.26, -0.15$ ; Fig. 5a) and, to a limited extent, by NPP ( $w > 0.99$ ,  $\beta_{\text{NPP}} = -0.17$ , CRI =  $-0.23, -0.11$ ; Fig. 5b). WIND ( $w > 0.99$ ,  $\beta_{\text{WIND}} = 0.11$ , CRI =  $0.06, 0.16$ ; Fig. 5d) and NPP ( $w > 0.99$ ,  $\beta_{\text{NPP}} = 0.24$ , CRI =  $0.20, 0.28$ ; Fig. 5e) had a significant positive effect on adult breeding success, whereas SSTA had a negative effect ( $w > 0.99$ ,  $\beta_{\text{SSTA}} = -0.48$ ; CRI =  $-0.54, -0.42$ ; Fig. 5c). Conversely,  $\phi_a$  was only marginally affected by local environmental covariates, and our IPMs only provided weak evidence for an inconclusive positive effect of WIND ( $w \sim 0.80$ ,  $\beta_{\text{WIND}} = 0.30$ , CRI =  $-6.04, 6.37$ ). When we considered large-scale climate indices, there was a strong significant negative effect of SAM with a 1 yr time lag on  $\phi_a$  ( $w > 0.99$ ,  $\beta_{\text{SAM}} = -0.32$ , CRI =  $-0.41, -0.24$ ; Fig. 5f), but not of SOI.

## 4. DISCUSSION

In this study, we provide among the first quantitative evaluations of the proportion of the total population size composed of sub-adults (juveniles, immatures and pre-breeders) in a long-lived marine top-predator. Additionally, we robustly quantified the sensitivity of the population growth to changes in juvenile survival, a traditionally overlooked demographic rate. Direct quantitative links were established between the demographic rates of albatrosses and the environmental variability in their supporting ecosystem, which is information of particular value for assessing the impact of climate-related changes on long-lived top-predators. Our results were obtained through a widely applicable IPM framework, which is among the most refined demographic modelling methodologies and, at present, is under-represented in the seabird literature despite its great potential for the analysis of longitudinal demographic data sets.

### 4.1. Objective 1: Demographic rates and population dynamics

Given the global conservation importance of the Falklands black-browed albatross population, we provide a qualitative comparison of the demographic rates estimated in this study and those computed (through non-integrated approaches) for other populations. As predicted for a species with high life expectancy (Gaillard & Yoccoz 2003, Forcada et al. 2008), we found high and relatively constant adult survival. In particular, the estimated  $\phi_a$  (0.94) is higher than the estimates of other monitored black-browed albatross populations in South Georgia (0.88; Pardo et al. 2017a) and Kerguelen (0.91; Nevoux et al. 2010b). Together with high adult survival, the estimated  $\phi_j$  (0.75) is also comparably high and in line with that of the Kerguelen population (0.78; Nevoux et al. 2010b) and higher than that of South Georgia over recent years (0.65; Pardo et al. 2017a). Moreover, the Falklands albatross population also had a high, relatively time-invariant  $\text{breed}_{\text{adult}}$  (0.88), lower than the estimated rate for Kerguelen (0.96; Pardo et al. 2013) but higher than that of South Georgia (0.77; Pardo et al. 2017a). The estimated  $\text{succ}_{\text{adult}}$  (0.68) was higher than the South Georgia estimate (0.3; Pardo et al. 2017a) and lower than the Kerguelen average rate for middle-aged ('optimal') birds (0.76, but this estimate was found to decrease significantly for younger and older ani-



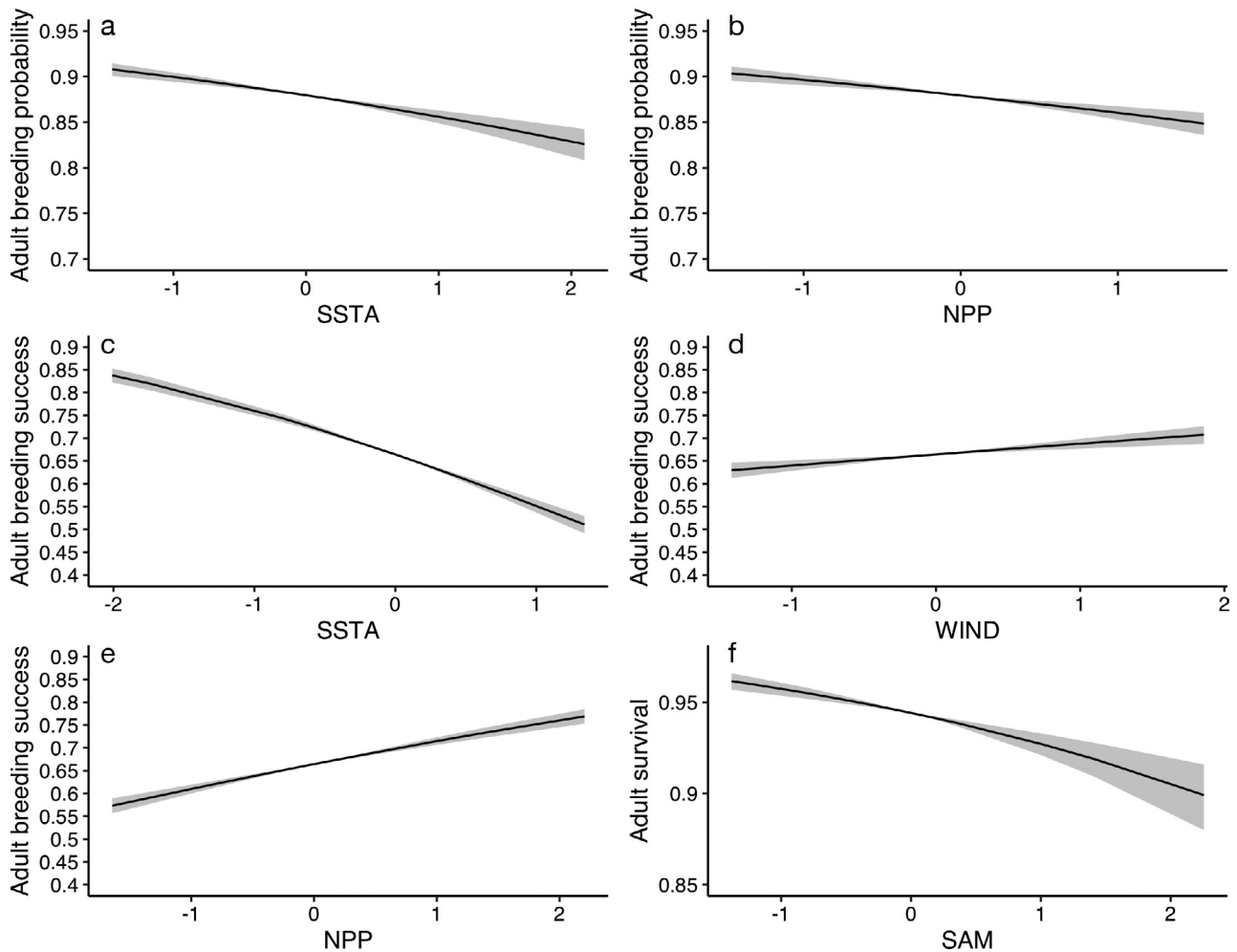


Fig. 5. The effect of (standardised) Patagonian Shelf environmental variables (sea surface temperature anomaly, SSTA; net primary production, NPP; wind intensity, WIND) and large-scale climate indices (Southern Annular Mode, SAM) on black-browed albatross productivity (breeding probability and breeding success) and survival parameters (adult survival). Shaded areas: 95 % credible intervals

mals; Pardo et al. 2013). In our population,  $\text{succ}_{\text{adult}}$  was the most variable demographic parameter, ranging from 0.24–0.87;  $\text{succ}_{\text{adult}}$  of experienced breeders was also the parameter with the highest temporal variability in Kerguelen and South Georgia, where it ranged from ~0.4–0.99 and from ~0–0.67, respectively (Nevoux et al. 2010a).

In albatrosses, as in other longevous iteroparous species, the survival of adult individuals is the trait with the highest sensitivity (see below) and it is therefore canalised against variability (Gaillard & Yoccoz 2003, Nevoux et al. 2010a, Hilde et al. 2020). Environmental disturbances on demography are therefore predicted to mainly affect productivity processes (Pons & Migot 1995, Oro et al. 1999, Thorne et al. 2015), with individuals investing less

in reproduction and more in their own survival when conditions become harsher (Nevoux et al. 2010a). The high  $\text{breed}_{\text{adult}}$ —and, despite its marked inter-annual variability, the relatively high  $\text{succ}_{\text{adult}}$ —is therefore likely supported by the high food availability in the rich waters of the Patagonian Shelf, particularly compared to the collapsing population in South Georgia (Pardo et al. 2017a, Poncet et al. 2017), which is surrounded by less productive and more variable oceanic conditions (Nevoux et al. 2010a). Indeed, thanks to the more favourable conditions in the Patagonian Shelf, the sedentary Falklands albatross population was found to allocate proportionately more energy to feather synthesis while breeding compared to the albatrosses from South Georgia (Catry et al. 2013b), which are long-

distance migrants in winter and experience harder conditions throughout their annual cycle (Rohwer et al. 2011, Catry et al. 2013b).

To the best of our knowledge, this is the first seabird study providing a strong estimate of the numbers of sub-adults and non-breeders based on a robust integrated approach. In this longevous population with delayed sexual maturity (a 'survivor' species at the slow end of the slow-fast continuum described in Sæther & Bakke 2000), the sub-adults (including juveniles, immatures and pre-breeders) represent a substantial part (just under half) of the whole population size. Hence, current knowledge gaps on the spatial and population ecology of these cryptic stages limit our understanding of the threats faced by such a large component of the whole population. In turn, this might critically hamper the design of effective conservation actions and mitigation measures in place for seabirds and other long-lived species with similar life histories (Clay et al. 2019, Carneiro et al. 2020).

#### 4.2. Objective 2: Demographic contributors to population dynamics

In accordance with the predictions of life-history theory, the main demographic contributor to the observed population dynamics was adult survival. Our analysis also showed that the population dynamics were highly sensitive to changes in a critical demographic rate: the survival probability of juveniles,  $\phi_j$ . All other parameters being equal, our results showed that if  $\phi_j$  decreased by 5%, the population would decrease at a rate of 0.38% yr<sup>-1</sup>. This finding emphasises once again the urgent need to address the ecological knowledge gaps for these cryptic stages that likely face higher survival risk due to naïve foraging behaviours (Gianuca et al. 2017). To a minor degree, population growth was also sensitive to  $\text{breed}_{\text{adult}}$  and  $\text{succ}_{\text{adult}}$ , whereas changes in recruitment probabilities only had a marginal effect on population dynamics. In the context of the observed decline of other albatross populations in the South Atlantic, our results shed light on the demographic drivers of the Falklands black-browed albatross population increase. Particularly compared to the population from South Georgia, the population growth seems to be underpinned firstly by the high survival probabilities of adults and juveniles and to a more limited extent by the high adult breeding probability and breeding success.

#### 4.3. Objective 3: Temporal variability of productivity and survival

Overall, adult survival and, to a lesser extent, adult breeding probability were generally constant. Nevertheless, these parameters did show small inter-annual fluctuations. For a given year  $t$ ,  $\phi_a$  from  $t$  to  $t + 1$  is significantly positively correlated with  $\text{breed}_{\text{adult}}$  at year  $t + 1$  (Pearson's correlation,  $r_{12} = 0.85$ ,  $p < 0.001$ ). This could be the consequence of 2 non-mutually exclusive processes. First, bottom-up environmental effects: when resources are plentiful (i.e. in 'good' years), survival throughout the previous ( $t$ ) breeding and non-breeding season will be higher; in turn, more birds might attempt breeding in the following ( $t + 1$ ) season, potentially facing reduced costs of reproduction owing to the more favourable conditions. Second, the mainly monogamous breeding strategy: if survival from the previous ( $t$ ) to the following ( $t + 1$ ) season is higher than average, adult breeders are more likely to reunite with their previous partners, which might in turn result in increased breeding probability in season  $t + 1$ .

The analysis of complementary data on the mean mass of chicks (Text S1) offered further insight into the survival and productivity temporal dynamics. Chick mass in season  $t$  was strongly positively correlated with  $\text{breed}_{\text{adult}}$  and  $\text{succ}_{\text{adult}}$  in the same season (Pearson's correlation,  $r_{12} = 0.72$ ,  $p = 0.004$ ;  $r_{12} = 0.87$ ,  $p < 0.001$ , respectively) and with  $\phi_a$  from season  $t$  to  $t + 1$  (Pearson's correlation,  $r_{11} = 0.69$ ,  $p = 0.01$ ). The correlations between productivity and survival processes highlight the role of environmental conditions. During resource-poor seasons, adult birds respond by investing less in breeding; additionally, fewer of them breed successfully because of limited parental investment and less food availability (Pons & Migot 1995, Oro et al. 1999, Nevoux et al. 2010a). These detrimental conditions, which are potentially exacerbated by the higher costs of reproduction faced by those birds that did not defer breeding, ultimately leads to a reduction of adult survival.

Breeding success showed the most pronounced fluctuations across the study period. Together with the role of environmental drivers (further discussed below), a portion of the variability in  $\text{succ}_{\text{adult}}$  might be caused by an unidentified infectious disease affecting albatross chicks, widespread in the albatross colonies across the Falklands, which can decrease breeding success by a minimum of 3.5% up to a maximum of 40% (Ventura et al. 2021).

Although  $\phi_a$  was mostly constant, it suffered its sharpest drop in 2015, when it decreased from 0.94

(survival from the 2014 to the 2015 breeding season) to 0.90 (survival from the 2015 to the 2016 season). During this period, widespread marine megafauna mortality affected not only the black-browed albatross population, but also southern rockhopper penguins *Eudyptes chrysocome* and gentoo penguins *Pygoscelis papua* (Crofts & Stanworth 2017). Penguins, in particular, died in large numbers due to starvation (Crofts & Stanworth 2017). Anomalously low catches of *Illex* squid *Illex argentinus*, which is one of the major contributors to the Falklands fishery revenue (Falkland Islands Government 2017), also evinced low productivity and food shortages. The results of our survival IPM suggest that the food shortages leading to this drop in survival might have been related to changes in the ecosystem structure and food chain associated with positive SAM phases (see below).

#### 4.4. Objective 3: Environmental drivers of productivity and survival

Warm SSTA had a strong negative effect on  $\text{breed}_{\text{adult}}$  and  $\text{succ}_{\text{adult}}$ . These matters are of concern in light of the current and predicted trends in sea temperatures (IPCC 2019) and the frequency of marine (Oliver et al. 2018) as a consequence of climate change. High SSTs, particularly in upwelling and frontal ecosystems, negatively affect primary and secondary production (Wilson & Adamec 2002, Behrenfeld et al. 2006, Barbraud et al. 2012), limiting food availability for seabirds through bottom-up mechanisms (Nevoux et al. 2010b, Barbraud et al. 2012, Sydeman et al. 2015, Pardo et al. 2017b). Our IPMs show that in cold and nutrient-rich waters, the higher NPP at the bottom of the food chain increases the availability of resources for higher level predators. Thus, during the breeding season, NPP positively affected  $\text{breed}_{\text{adult}}$  and  $\text{succ}_{\text{adult}}$ . However, the result showing a negative effect of winter NPP on the  $\text{breed}_{\text{adult}}$  is counter-intuitive (even if the effect size was weaker compared to that of SSTA). The non-breeding season (local winter) is characterised by low NPP, which might therefore be of limited significance in relation to food availability in this phase of the life cycle of the birds; rather, the negative effect of NPP might reflect potential interactions with biological or oceanographic processes unaccounted in our models. WIND positively affected  $\text{succ}_{\text{adult}}$  (and also had an inconclusive positive effect on  $\phi_a$ ), suggesting its role in favouring food availability by enhancing convective water mixing, and also its direct

effect on the accessibility of foraging patches by shaping the commuting costs. During breeding, seabirds act as central place foragers and undertake long foraging trips, reaching maximum flight effort (Ponchon et al. 2019) and often covering thousands of km (Ventura et al. 2020). During these trips they extract energy from the wind through a flight behaviour known as ‘dynamic soaring’ (Pennycuik 2002, Richardson 2011). Thus, wind conditions—especially wind intensity in areas where wind direction is relatively constant—shape the energy expenditure faced by commuting seabirds. In turn, this determines the spatial extent of the areas accessible for albatrosses to use and, ultimately, affects overall breeding success and, to a limited extent, adult survival. The non-significant effect of winter WIND on  $\text{breed}_{\text{adult}}$  could be caused by the decreased flight effort (Ponchon et al. 2019) and increased opportunity to remain in proximity to good foraging patches during the non-breeding season.

SAM is the dominant mode of inter-annual climate variability in the Southern Ocean, affecting the ocean and atmospheric circulation and, most germane to this study, SSTs and primary productivity (Stenseth et al. 2003, Lovenduski & Gruber 2005). Positive SAM phases, which are predicted to become more frequent in the near future as a consequence of climate change (Turner et al. 2009, 2014), are associated with a contraction of the westerly winds towards the Antarctic, warmer SSTA and increments of downwelling events in the foraging domain of the albatross population (Lovenduski & Gruber 2005, Catry et al. 2013a, Ponchon et al. 2019). Adult albatrosses survival was strongly negatively correlated with SAM at a lag of 1 yr (Pearson’s correlation,  $r_{12} = -0.82$ ,  $p = 0.0003$ ; Text S2, Fig. S4). This result is in agreement with the results of a recent study on Antarctic petrels *Thalassoica antarctica*, in which SAM (also considered at a 1 yr time lag) was found to negatively impact survival (Descamps et al. 2016). These studies suggest that SAM variability is associated with deep environmental changes affecting the ecosystem structure and the whole trophic web (Stenseth et al. 2003, Lovenduski & Gruber 2005), ultimately having repercussions on the highly sensitive  $\phi_a$ .

## 5. CONCLUSIONS

In this work, we provide a proof of concept on the fundamental importance of a process-based understanding in the demography of top-predator populations, only achievable through long-term monitoring.

Thanks to the analytical depth attained by IPMs based on a comprehensive longitudinal data set, our study unravelled the mechanistic links between albatross demographic processes and environmental variability. We showed that black-browed albatrosses exhibit clear demographic responses to changes in their ecosystem, highlighting their role as sentinels of the Patagonian Shelf (Sergio et al. 2008). Our robust quantitative description of the structure of the albatross population shows that juveniles, immatures and pre-breeders comprise approximately half of the total number of individuals. Thus, addressing current knowledge gaps on these stages is of primary importance to design effective conservation measures. This is particularly true given our findings highlighting the sensitivity of the population to the (traditionally overlooked) survival rate of juveniles. Even with high adult survival rates, failing to encompass the young and inexperienced stages into well-designed conservation actions will likely prove to have serious repercussions on the overall population dynamics.

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