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## Unravelling the relative roles of top-down and bottom-up forces driving population change in an oceanic predator

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### Abstract

In the open ocean ecosystem, climate and anthropogenic changes have driven biological change at both ends of the food chain. Understanding how the population dynamics of pelagic predators are simultaneously influenced by nutrient-driven processes acting from the “bottom-up” and predator-driven processes acting from the “top-down” is therefore considered an urgent task. Using a state-space demographic model, we evaluated the population trajectory of an oceanic predator, the macaroni penguin (*Eudyptes chrysolophus*). This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1002/ecy.1452

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and numerically assessed the relative importance of bottom-up and top-down drivers acting through different demographic rates. The population trajectory was considerably more sensitive to changes in top-down control of survival compared to bottom-up control of survival or productivity. This study integrates a unique set of demographic and covariate data and highlights the benefits of using a single estimation framework to examine the links between covariates, demographic rates and population dynamics.

Keywords: Density-dependence; El Niño Southern Oscillation; Macaroni penguin; Monte Carlo Markov Chain; Population model; Predation; Seabird; Sea Surface Temperature; Stochastic variable selection.

### **Introduction**

The predator-driven or “top-down” view of population control appears to be widely accepted by researchers considering terrestrial (Hairston et al. 1960), fresh water (Carpenter et al. 1985) and intertidal ecosystems (Paine 1980). In contrast, the majority of population change in the pelagic zone, apart from those resulting from human exploitation and fisheries by-catch, is thought to be nutrient-driven, or controlled from the “bottom-up” (Aebischer et al. 1990, Stenseth et al. 2002). The overall structure and functioning of the pelagic system is dominated by physical processes and nutrient fluxes (Pace et al. 1999, Behrenfeld et al. 2006), however the consequences of removing pelagic predators remains unclear, and a number of studies have linked the overexploitation of these species to marked changes in community structure at lower trophic levels, indicative of top-down control (e.g. Estes & Duggins, 1995; Bascompte *et al.*, 2005; Frank *et al.*, 2005; Springer & van Vliet, 2014).

Polar ecosystems are receiving growing attention because anthropogenic drivers have precipitated biological change at both ends of the food chain. In the Antarctic system, rapid regional warming has had a major impact on lower trophic levels (Vaughan et al. 2003, Atkinson et al. 2004), furthermore the composition of predators occupying the upper trophic level has been repeatedly changed by “boom and bust” sealing, whaling and fishing industries (Agnew 2004). Regulating exploitation pressures at sustainable levels and reliably predicting the population response to future climate change requires certainty in the ecological processes that influence population dynamics. Consequently, unravelling the effects of bottom-up and top-down forcing in this region, particularly on species that utilise the open ocean, is considered an urgent task (Smetacek and Nicol 2005). To reliably separate these effects requires diverse demographic and covariate data that are difficult to collect for ocean-scale populations. Consequently, studies comparing the relative importance of these population drivers are largely lacking for this system.

The early view was that Antarctic and Sub-Antarctic oceanic systems were relatively simple, characterised by a large prey resource, principally Antarctic krill (*Euphausia superba*), supporting an assemblage of apex predators (Laws 1977). However, an increasing number of studies have demonstrated that the demographic processes of particular Antarctic predators are controlled by trophic levels both above and below them (Schwarz et al. 2013, Horswill et al. 2014). By considering specific species of seals and seabirds as occupants of intermediate trophic levels, we improve our ability to evaluate the drivers of their population dynamics. This is best assessed using integrated population models (Francis and Sagar 2011, Maunder and Punt 2013, Thomson et al. 2015, Tuck et al. 2015). In particular, Bayesian state-space approaches permit relationships between covariates and demographic processes to reflect the available knowledge of the system (Buckland et al. 2004). Furthermore, missing data can be

imputed and the measurement errors inherent in ecological data can be accounted for in the estimation and prediction uncertainty (Buckland et al. 2004).

Many populations of Antarctic and Sub-Antarctic marine predators declined between the 1980s and early 2000s (Reid and Croxall 2001, Woehler et al. 2001, Lyver et al. 2014). For example, macaroni penguin (*Eudyptes chrysolophus*) colonies on South Georgia, had a net decline of approximately 70% during this time (Trathan et al. 2012; Fig. 1A). Several studies have attributed this to a single driver, including climate (Forcada and Trathan 2009), as well as elevated levels of competition associated with recovering populations of Antarctic fur seals (*Arctocephalus gazella*; Trathan et al. 2012). However, the relative importance of these effects is not understood. Furthermore, a recent examination of macaroni penguin survival rates highlighted that top-down control mechanisms should also be considered when examining the demography of this species (Horswill et al. 2014).

In this study, we used an age-structured state-space model to integrate a unique set of demographic and covariate data to examine the links between individual covariates, demographic rates, and the overall population trajectory of macaroni penguins. This included 28 years of abundance and productivity data, 8 years of survival data and a diverse set of covariates. By subjecting this model to a sensitivity analysis, we also estimated the relative contributions of top-down and bottom-up forces in generating year-to-year variation in demography and population dynamics.

## Methods

### Study system

This study uses data collected from the Fairy Point macaroni penguin colony on Bird Island, South Georgia (54° 00' S, 38° 03' W). Abundance and productivity were monitored annually between 1985 and 2012 (Table 1); the total number of breeding pairs was counted at the start of the incubation phase (29 November-10 December), and the number of chicks was counted shortly before fledging (16 February). Productivity is defined as the proportion of breeding pairs that reared a chick to the fledging count date. Each annual count was repeated at least three times in the field, or to within 10% of the other estimates (methods are further detailed in CCAMLR, 2004). Survival data were obtained from a mark-recapture study conducted between 2003 and 2012 based on passive integrated transponders (PIT; Horswill *et al.*, 2014). To remove any temporal correlation introduced by the covariates that were retained in this earlier study, the estimates of survival utilised in the current study were re-estimated from a model without covariates, that incorporated age and time-specific variation and included year as a nominal factor variable (recapture and transition rates were specified in agreement with the best candidate model reported by Horswill *et al.*, 2014). This maximally flexible model produced year-specific estimates of survival with associated yearly measures of uncertainty.

### State-space population model

Simultaneous estimation of parameters and hidden states was carried out alongside model selection in a state-space population model that included: (1) coefficients describing the relationship between different covariates and demographic processes between 1985 and 2012 (Appendix S1); (2) Bernoulli selection coefficients that determined the inclusion of each covariate; (3) missing (and thus imputed) segments of demographic and covariate time series; and (4) the magnitude and direction of different observation biases and imprecision (code

listed in the accompanying Data File S1). Inference was undertaken in OpenBUGS (<http://www.mrc-bsu.cam.ac.uk/bugs/>). Models were fitted by running three Monte Carlo Markov Chains (MCMC) for  $1 \times 10^6$  iterations and retaining every 100<sup>th</sup> step in order to increase the effective MCMC sample size for the same amount of computer memory. The first 5000 MCMC draws were removed as burn-in. Each chain was initialised at different points in parameter space, and mixing and convergence of the MCMC was examined for each parameter and state. The amount of mixing between the three chains indicated the ability of the model to reach a steady state distribution. Convergence of the chains was confirmed using the Brooks-Gelman-Rubin diagnostic tool in the OpenBUGS software (all values  $< 1.02$ ). The final model structure was validated by removing the demographic data and simulating the population time series using the influential covariates and the marginal posterior distributions for the respective parameters. This procedure demonstrated whether the observed population time series could be recreated from the functional structure, the parameter estimates and the covariate data, and by not including the implicit covariance embedded in the MCMC samples was considered a stringent method for testing the descriptive power of the variables (Appendix S2).

### *Covariates*

The demographic function of survival included covariates that were demonstrated to be influential at the population-level in our earlier analysis of deviance study; i.e., predation pressure and local sea surface temperature anomalies (SSTa) (equations 2-3; Table 1; Horswill et al. 2014). Wider testing of candidate covariates in the survival function reduced model convergence and was therefore avoided. For the demographic function of productivity, we selected candidate covariates from information across Spheniscidae (Table 1). Top-down control was assessed using a proxy of predation pressure. Bottom-up control was assessed

using female body mass at the start of the breeding season, two measures of competition, as well as one local and two quasi-remote climatic variables: (i) SSTa; (ii) the El Niño/Southern Oscillation (ENSO) phenomenon; and (iii) the Southern Annular Mode (SAM).

The influence of predation pressure was examined using the number of northern (*Macronectes halli*) and southern (*M. giganteus*) giant petrel chicks successfully reared to fledging. Northern and southern giant petrels are large birds that are predators and scavengers. On Bird Island these species breed sympatrically at densities that at the time of publication were among the highest in the world. Nesting pairs of giant petrels in three study areas close to the penguin study colony were visited weekly during incubation and chick-rearing to determine the local productivity. This measure represents the number of adult giant petrels that will be foraging within a restricted range for the whole of the penguin breeding season, including when the macaroni penguin chicks fledge. Penguins form a major component of giant petrel diet during the breeding season (Bonner and Hunter 1982, Hunter and Brooke 1992), and at Bird Island, this is thought to consist predominantly of adult macaroni penguins (Hunter 1983) scavenged from predation events by sub-adult Antarctic fur seals (Bonner and Hunter 1982). More recently, anecdotal accounts from Bird Island report macaroni penguin chicks also being heavily predated by giant petrels as they fledge (J. A. Green; P. N. Trathan; R. A. Phillips pers. obs.), as well as an adult macaroni penguin being killed by a giant petrel in waters close to the study colony (J. Gillham pers. comm.). Therefore, the predation pressure index is taken to reflect predation by both giant petrels and sub-adult Antarctic fur seals.

To examine the annual variation of macaroni penguin body condition on productivity we included the body mass of adult females at the start of the breeding season (n=49-59). The

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macaroni penguin breeding season is highly synchronous, and birds were weighed annually between the 8<sup>th</sup> and 9<sup>th</sup> November using a spring balance ( $\pm 0.05$ kg; Pesola, Baar). A study of macaroni penguins breeding in the Indian Ocean did not identify a significant relationship between arrival mass and productivity, however a positive correlation has been reported in other crested penguins (rockhopper penguins *E. chrysocome filholi*, Crawford et al. 2006). The influence of competition during the breeding season was examined using proxies of inter- and intra-specific effects. The foraging grounds and diets of breeding macaroni penguins and Antarctic fur seals overlap extensively during the breeding season (Reid et al. 1996, Trathan et al. 2006, Staniland et al. 2012), and we used the number of Antarctic fur seal pups born on the fur seal study beach at Bird Island (minus those found dead) to provide a measure of female seals foraging within a restricted foraging range during the macaroni penguin breeding season. To examine intra-specific competition we used the number of macaroni penguin breeding pairs at the study colony. The trajectory of the study colony mirrored other, much larger colonies in the same region (Trathan et al. 2012), and therefore, this measure was taken to reflect the wider population density of penguins.

SSTa are considered to have a major influence on prey biomass within the South Georgia continental shelf zone (Trathan et al. 2003). To reflect local conditions we used SSTa in the foraging area used by macaroni penguins during the breeding season (35.5°W to 44.5°W; 52.5°S to 54.5°S). These data were obtained from the National Oceanographic and Atmospheric Administration (NOAA) International Research Institute ([http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCEP/.EMC/.CMB/.GLOBAL/.Reyn\\_SmithOlv2/.monthly/.SSTa/](http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCEP/.EMC/.CMB/.GLOBAL/.Reyn_SmithOlv2/.monthly/.SSTa/)). Ocean-scale climate effects, such as the El Niño Southern Oscillation (ENSO) phenomenon and the Southern Annular Mode (SAM), are associated with major changes in upwelling, SSTa, circumpolar winds (Meredith et al. 2008) and local



prey availability (Murphy et al. 2007). These data were obtained from the NOAA Climate Diagnostics Center (<http://www.cdc.noaa.gov/people/cathy.smith/best/>), and the NOAA Climate Prediction Center (<http://www.cpc.ncep.noaa.gov/>). Candidate temporal lags for these climatic variables were calculated by summing plausible physical and biological process lags (following Horswill et al. 2014, Appendix S2). El Niño events are associated with warmer temperatures in the Scotia Sea region after approximately a 2 year lag, whereas the effects of SAM are typically more immediate, i.e. no lag (Meredith et al. 2008). Biological lags associated with the recruitment of krill to South Georgia were added to the physical lags in two potential spawning and dispersal scenarios. Either spawning occurs across the Scotia Sea with recruitment maintained within that year in all shelf regions (Brierley et al. 1999), or spawning and successful survival through the first year occurs mainly in central and southern areas of the Scotia Sea, with dispersal occurring through interactions with the ocean and sea ice over the next 1–2 years (Hofmann et al. 1998). All covariates were standardised to have a zero mean and unit variance to promote convergence across parameters with different scales (Congdon 2003). Annual values were calculated following Horswill *et al.* (2014; Appendix S2).

#### *Demographic model*

Incomplete attendance histories at the individual level caused by variable recapture rates within seasons precluded the identification of recruitment and missed breeding events. Studies of crested penguins marked with flipper bands report that recruitment can occur within the same year as first return following deferred reproduction (+1 yr; Guinard et al., 1998). The mean age of recruitment was therefore taken to correspond with the maximum age of first return for this population (4 years; Horswill et al., 2014). In the absence of evidence for a significant sex difference in survival rates (Horswill 2015) we assumed a 1:1

sex ratio in the population. To account for the production of one chick per two adults, the model was based on female numbers only, i.e., the number of breeding females (equal to the number of breeding pairs), and the number of female chicks fledged (equal to half the total productivity). The model assumed that all birds aged 4 and above will breed annually. Although macaroni penguins may skip an individual breeding attempt following particularly adverse winter conditions (Williams and Rodwell 1992, Crawford et al. 2006), the study population did not fluctuate widely between years, and the PIT reader used in this study achieved very high recapture rates when it was fully operational (99%; Horswill et al., 2014). Consequently, it appears that intermittent breeding was not a common source of variation for this population.

The deterministic transition matrix was based on breeding success ( $b_t$ ) and 5 state variables; one fledgling (from fledging to 1 year of age;  $\phi_{f,t}$ ), three sub-adult (age classes 2-4 have the same survival probability as an adult) and one adult stage ( $\phi_{a,t}$ ):

$$R_t = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & \phi_{a,t} \frac{b_t}{2} \\ \phi_{f,t} & 0 & 0 & 0 & 0 & 0 \\ 0 & \phi_{a,t} & 0 & 0 & 0 & 0 \\ 0 & 0 & \phi_{a,t} & 0 & 0 & 0 \\ 0 & 0 & 0 & \phi_{a,t} & 0 & 0 \\ 0 & 0 & 0 & 0 & \phi_{a,t} & \phi_{a,t} \end{pmatrix} \quad (1)$$

Macaroni penguins lay two eggs, but near-complete failure of the first-laid egg means that they effectively produce a single-egg clutch (Williams 1995). This permitted individual productivity and survival events to be modelled using binomial demographic stochasticity, estimating the probability of success for each time step using a logit function that incorporated candidate covariates (following Matthiopoulos *et al.*, 2013), as well as variable selection priors to numerically evaluate the probability of inclusion for each covariate (Lunn

et al. 2012; eqns. 2-4). For purposes of model selection, a switch variable with an independent Bernoulli 0/1 indicator was used to determine whether a specific covariate was allowed to operate within the model for any given parameterisation (George and McCulloch 1993). By using a uniform prior bounded between 0 and 1 to estimate the parameter of this indicator, we were also able to estimate the probability of inclusion for each covariate. All prior distributions are detailed further in Appendices S1-S2.

The logit functions for adult and fledgling survival rates are shown in eqn. 2 and 3. The age-specific drivers included changing combinations of top-down control from predation pressure ( $P$ ) and bottom-up control from SSTa (with a year lag,  $S_{t-1}$ ):

$$\text{logit}(\phi_{f,t}) = \alpha_{f,0} + (I_1\alpha_1 + I_2\alpha_2)P_t + I_3\alpha_3S_{t-1} \quad (2)$$

$$\text{logit}(\phi_{a,t}) = \alpha_{a,0} + (I_1\alpha_1)P_t + I_3\alpha_3S_{t-1} \quad (3)$$

Here,  $f$  and  $a$  denote birds in the fledging year and birds that are older than 1 year, respectively. Age dependence was determined by using different parameters for the baseline survival of each age class ( $\alpha_{f,0}, \alpha_{a,0}$ ). Following Horswill *et al.* (2014) the parameters for the predation ( $\alpha_1$ ) and SSTa terms ( $\alpha_3$ ) replicated the effect of these covariates across both age classes, and an extra coefficient ( $\alpha_2$ ) was included in the function for fledgling survival to allow for an additional component of predation on fledglings (Horswill et al. 2014).

The productivity function (eqn. 4) included female arrival mass ( $A$ ), environmental forces (SSTa  $S$ , SAM  $M$ , and ENSO  $E$ ), inter- ( $D$ ) and intra-specific competition ( $C$ ) and predation pressure ( $P$ ):

$$\text{logit}(b_t) = \beta_0 + I_1\beta_1A_t + I_2\beta_2P + I_3\beta_3S_t + I_4\beta_4S_{t-1} + I_5\beta_5M_t + I_6\beta_6M_{t-1} + I_7\beta_7E_{-2} + I_8\beta_8E_{-3} + I_9\beta_9D_t + I_{10}\beta_{10}C_t \quad (4)$$

The number of breeding females estimated by the process model was fed back into the

productivity function as the auto-covariate  $C$ .

### *Observation model*

Observation error was stochastically assigned in each time step to account for annual variation associated with detection and unspecified covariates. For survival, the maximum range of uncertainty was set using the 95% confidence intervals (CIs) from the mark-recapture analysis to encompass both process variability and observation error. The true range of residuals for survival within the state-space model will be narrower because some variability will be accounted for by the inclusion of covariates. Survival estimates were assumed to have a normal error distribution where the mean was equal to the mark-recapture estimate, and the variance was set from a uniform distribution. Here, the maximum value was stochastically assigned from a gamma distribution that represented the available range of 95% CIs. For productivity, observation error was also applied through a normal error structure on the number of breeding females and the number of female chicks. The mean was equal to the colony count estimate and the variance was derived from the range of the repeated counts. These data were available for 5 years between 2007 and 2012, and therefore the same variance was applied to all years. The variance ( $s^2$ ) was calculated using the mean variance of the annual counts ( $\bar{\sigma}^2=1727.3$ ) and the mean number of counts ( $\bar{n} = 4.7$  repeated counts):

$$s^2 = \frac{\bar{\sigma}^2}{\bar{n}} = 0.0028 \quad (5)$$

As with simpler regression analyses, the covariate data will also contain some observation error. Ignoring these uncertainties in a typical regression framework that uses model selection (e.g. via information criteria) can lead to spurious correlations. It was not computationally feasible to propagate these sources of uncertainty through the state-space model, however the

embedded model selection approach essentially operates as a Bayesian equivalent to model averaging (Lunn et al. 2012), and therefore should reduce the probability of spurious correlations (Burnham and Anderson 2002).

#### *Missing data*

Missing data on female mass at the start of the breeding season were estimated as a normal variate with an expectation equal to the observed data (Table 1; Appendices S2-S3). The missing segment of the predation pressure time series was modelled as a random walk through time to enable serial autocorrelation to be included in the process (Table 1; Appendices S2-S3).

#### Variables influencing the population trajectory

To identify a suitable splitting point for presenting summary statistics on the early and later parts of the time series we fitted a broken-stick GLM to the raw data using the statistical package *segmented* in Program R (Muggeo 2008). To quantify the relative importance of each covariate in determining the observed population trajectory, we compared the estimated population size between model iterations where specific covariates were indicated as being included or excluded based on the variable selection terms. For covariates that were included in all model iterations, we refitted the model with the covariate term indicator set to 0. Years where the imputed values of missing covariate data may have been overestimated were removed from this analysis to minimise bias. This was assessed by examining the population trajectory for anomalous changes that may result in residual variation being artificially attributed to a covariate value (Appendix S2). Repeated bootstrap sampling (5000 samples) was used to undertake multiple pairwise comparisons of the population trajectories estimated with and without the covariate included, calculating the squared residuals between randomly

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selected MCMC iterations from each scenario. The covariates were then ranked by these statistics to determine their relative influence. Higher values and greater variability indicated that when a covariate was excluded the model's ability to re-create the population size was reduced.

## Results

### Model fit

The observed population trajectory was recreated convincingly by the full model (Fig. 1A) and the validation model that did not include the demographic time series (Appendix S4). Therefore, we infer that the population trajectory was adequately described by the parameters and covariates considered.

### Missing covariate data

The imputed segment of the predation pressure time series was slightly higher and more variable (de-standardised  $\bar{x}_{<2000} = 302, SD_{<2000} = 75$ ; Fig. 2A) than the segment of observed data (de-standardised  $\bar{x}_{\geq 2000} = 269, SD_{\geq 2000} = 68$ ; Fig. 2A). This was largely attributed to elevated estimates during 1986, 1987, 1990 and 1994. These values may have been inflated in order to describe the concurrent population declines (Fig. 1A & Fig. 2B), and therefore were removed from the sensitivity analysis. The imputed values for body mass of females at the start of the breeding season were highly similar to the observed values (de-standardised imputed values  $\bar{x}_{<1989} = 4.99, SD_{<1989} = 0.19$ , de-standardised observed values  $\bar{x}_{\geq 1989} = 5.04, SD_{\geq 1989} = 0.16$ ).

### Variables influencing survival rates

In the fledgling age class, mean survival rates were slightly lower during the period of

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population decline compared to the period of population stability ( $\bar{x}_{<2000} = 0.37, \bar{x}_{\geq 2000} = 0.43$ ) and the variability was consistently high ( $SD_{<2000} = 0.20, SD_{\geq 2000} = 0.22$ ; Fig. 1B; Appendix S5). Mean survival rates also increased slightly in the older age class ( $\bar{x}_{<2000} = 0.87, \bar{x}_{\geq 2000} = 0.89$ ) and variability was consistently low ( $SD_{<2000} = 0.07, SD_{\geq 2000} = 0.05$ ; Fig. 1C; Appendix S5). Based on variable selection, both of the age specific predation effects were influential (Fig. 3A), and the directional influence followed Horswill *et al.* (2014; Appendix S1). The probability of inclusion for the main predation term was consistently above 0.5; therefore this term was included in all model iterations. The effect of SSTa on survival rates was not resolvable from variable selection or posterior credible intervals (Appendix S1; Fig. 3A). Despite this, the estimates of survival from the state-space model predominantly occurred within the confidence interval of the covariate model that was reported in our earlier study (Horswill *et al.* 2014), with lower values of survival estimated for the older age class during 2003 and 2004 (Fig. 1B&C).

#### Variables influencing productivity rates

Productivity increased during the study period (lm:  $F=5.11, df=25, p=0.03$ ), and values were lower during the period of population decline ( $\bar{x}_{<2000} = 0.51, \bar{x}_{\geq 2000} = 0.55$ ; Fig. 1D; Appendix S5). Based on variable selection and posterior credible intervals, annual productivity was positively influenced by body mass of females at the start of the breeding season, and negatively influenced by intra-specific competition and ENSO with a 3 year lag (Fig. 3A). The remaining covariates were not resolvable based on variable selection or posterior credible intervals (Fig. 3A).

#### Variables influencing the population trajectory

The breeding population declined at 6.5% (SE=0.6) per year from 1985 until *c.* 2000, the  
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trend thereafter could not be reliably resolved; declining at 1.2% (SE=1.1) (Fig. 1A). Prior to 2000, the proportion of a cohort that recruited to the breeding population at Bird Island was 0.06 ( $SD = 0.04$ ) and the mean rate of adult mortality was 0.13 ( $SD = 0.07$ ) (Appendix S5). After 2000, the rate of recruitment was 0.09 ( $SD = 0.04$ ) and the rate of adult mortality was 0.11 ( $SD = 0.05$ ) (Appendix S5). The sensitivity analysis was carried out using a 24 year time series (Appendix S2), and this population trajectory was most sensitive to the removal of the predation pressure terms from the survival functions, especially the main predation term (Fig. 3B). The other covariates were relatively similar in their effect on population size (Fig. 3B).

## Discussion

Unravelling the relative importance of bottom-up and top-down forcing in the pelagic zone is central to regulating fishery pressures at sustainable levels and predicting how these communities will be influenced by future climatic changes. We sought to examine the links between individual covariates, demographic rates and the overall population trajectory of macaroni penguins, and quantify the relative importance of bottom-up and top-down drivers acting through different demographic rates.

### Variables influencing survival rates

Between 1987 and 1990 the survival rate of Bird Island macaroni penguins marked with flipper-bands was estimated to be  $\bar{x} \sim 0.75$  ( $\sigma \sim 0.06$ ) (Williams and Rodwell 1992). We estimated adult survival for the same period to be higher, and infer that flipper-banding may have impaired survival rates (Saraux et al. 2011) during the Williams & Rodwell (1992) study, or alternatively, survival rates estimated from visual recapture assuming 100% recapture may have resulted in underestimation. When operational, the automated gateway



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system used in our study achieved very high recapture probabilities (0.88-0.99; Horswill *et al.*, 2014). In agreement with Horswill *et al.* (2014), survival rates were generally lower during the fledgling year, and increased from age one. However, under certain conditions (low predation pressure), the survival rates of the two age classes were comparable (Fig. 1B-C).

The estimates of survival during the period of population stability were highly similar to those reported by Horswill *et al.* (2014) for the same time period. The difference in survival estimates for the older age class during 2008 and 2009 is likely to represent the lack of inference attributed to SSTa by the model. This also demonstrates the relative significance of the predation pressure covariate in resolving this demographic process. A negative relationship between survival and predation pressure agrees with dietary analysis that shows macaroni penguins form a major component of giant petrel diet during the breeding season (Hunter 1983). However, years with particularly low survival rates for macaroni penguins also coincided with years when other species of marine predators that breed on Bird Island experienced a decrease in vital rates. For example, during 1987, the survival rates of macaroni and gentoo penguins (*Pygoscelis papua*) decreased (Williams and Rodwell 1992), and following the 1987 winter, the breeding season of gentoo penguins and Antarctic fur seals was delayed (Duck 1990, Williams 1990). A delay in the onset of breeding may indicate adverse climatic conditions during the preceding winter (e.g. Barbraud & Weimerskirch, 2006). Rates of productivity at Bird Island were also reduced for several marine predator species during 1994 (Reid and Croxall 2001), and gentoo penguins experienced high adult mortality and very low productivity during 2009 (British Antarctic Survey, unpublished data). The predation pressure index may therefore also represent mechanisms acting at the community-level, and further work is needed to examine the interaction between bottom-up

and top-down forces during adverse climatic conditions (e.g. Votier *et al.*, 2004).

#### Variables influencing productivity

The mean productivity rate during the period of population decline was similar to other decreasing populations of macaroni penguins breeding in colonies of comparable size ( $\bar{x} = 0.46 - 0.57$  chicks pair<sup>-1</sup>; Crawford *et al.*, 2006). However, by the end of the study period, annual rates were comparable to an increasing population of rockhopper penguins ( $\bar{x} = 0.64$  chicks pair<sup>-1</sup>; Baylis *et al.*, 2013). Observational studies indicate that giant petrels can depredate penguin chicks at the colony (Le Bohec *et al.* 2003), however this foraging strategy has rarely been observed at Bird Island, where predation of macaroni penguin chicks appears to be focused on the fledging period. In agreement with this, top-down control was not identified as being influential to productivity. Instead, low rates of productivity were consistently associated with a decrease in female body mass at the start of the breeding season and a higher value of ENSO; i.e., an El Niño event. A positive relationship between arrival mass and productivity has not been previously shown for this species, however it has been reported for other crested penguins (Crawford *et al.* 2006). Likewise, a negative relationship between penguin productivity and ENSO has been observed in other populations (e.g. Chambers, 2004). Both of these processes are likely to represent local prey availability immediately before and during the breeding season (Murphy *et al.* 2007), when macaroni penguins from Bird Island are foraging locally (Horswill *et al.* *in press*).

The arrival body mass of female macaroni penguins decreased between 1988 and 1992 (Reid and Croxall 2001). Furthermore, the ENSO had a marked preponderance of El Niño compared with La Niña events between 1983 and 2008 (Meredith *et al.* 2008). Consequently, the overall increase in productivity between 1985 and 2012 cannot be attributed to these

variables; i.e. the predicted trend based on the observed change in these covariates would have been in the opposite direction to that observed. Productivity rates also demonstrated a negative relationship with intra-specific competition, such that productivity increased at lower population densities. Here, the proposed mechanism is principally a product of resource competition, whereby per capita availability of prey and high quality nesting sites increased as the population declined. A negative relationship between population density and productivity has been documented in several species of seabird (e.g. Weimerskirch & Jouventin, 1987; Frederiksen & Bregnballe, 2001), including penguins (rockhopper penguins; Baylis *et al.*, 2013). At higher population densities, a saturation of good quality foraging habitat may force some individuals to forage in poorer habitat that requires greater energetic demands to exploit (Lewis *et al.* 2001, Ballance *et al.* 2009).

#### Variables influencing the population trajectory

The colony of macaroni penguins examined in this study declined rapidly between 1985 and the early 2000s because recruitment did not sufficiently balance adult mortality rates (Appendix S5). The rate of decline was similar to other, much larger colonies in the same region (Trathan *et al.*, 2012), and therefore it seems likely that the mechanisms discussed here were influential to the population more broadly. The model's ability to replicate the change in population trajectory without the observed time-series of demographic data indicates that the principal contributing mechanisms were captured, namely predation, arrival mass, ENSO and intra-specific competition. In agreement with life history theory on long-lived species, population size was considerably more sensitive to influential covariates acting on adult survival rates, compared to those acting on juvenile survival and productivity (Sæther and Bakke 2000). The main predation term in the survival functions was considerably more influential in resolving the observed population trajectory than the bottom-

up climatic variable. However, the additional component of predation pressure acting on fledgling survival rates also appeared to be slightly more influential than bottom-up control of adult survival rates. This is likely to reflect the lack of influence attributed to SSTa in the survival function. Therefore, as time-series data are extended, it would be worthwhile evaluating alternative bottom-up covariates as drivers of survival. The variables acting through productivity generated a similar effect on the population size to SSTa acting through survival. Based on these results, it appears that the population dynamics of macaroni penguins are relatively canalized (i.e., preserved) against climate variations.

### **Conclusions**

This study integrates a unique set of demographic and covariate data in order to assess how an ocean-scale population is influenced by bottom-up and top-down drivers. We conclude that the population of macaroni penguins at Bird Island rapidly declined between 1985 and the early 2000s following an imbalance between recruitment to the breeding population and adult mortality. The population later stabilised following an increase in survival and productivity. It was not possible to reliably attribute the increase in survival to a single factor; however the increase in productivity appeared to be driven by a bottom-up negative feedback with population size. Despite this, population size was considerably more sensitive to changes in top-down control of survival rates than all of the bottom-up covariates included. Under the observed conditions, we can predict that a continued increase in the population size of giant petrels or a shift in their predatory behaviour (to include chicks at the colony) could rapidly destabilise the penguin population. More broadly, this study highlights the importance of considering how pelagic predators are influenced by multiple drivers when examining their population dynamics and assessing options for conservation management.

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The following appendices are available for this article.

- S1. Prior and posterior information on the integrated population model's parameters;
- S2. Detailed methods;
- S3. Time series of available covariate data;

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S4. The result of the model validation exercise;

S5. Mean and standard deviation of demographic rates before and after the change in macaroni penguin population trajectory.

The following data file is available for this article:

S1. OpenBUGS code.

## Tables

Table 1. The candidate covariates and the relative importance of each covariate (sensitivity) in resolving the population trajectory of macaroni penguins at Bird Island, South Georgia. The length of available time series are also illustrated in Appendix S3.

Process	Covariate	Data availability	Reference of effect
Survival (Fledging)	Predation pressure	2001-2012	Horswill <i>et al.</i> 2014
	SSTa	1985-2012	Horswill <i>et al.</i> 2014
Survival (>1 year)	Predation pressure	2001-2012	Horswill <i>et al.</i> 2014
	SSTa	1985-2012	Horswill <i>et al.</i> 2014
Productivity	Female arrival mass	1989-2012	Crawford <i>et al.</i> 2006
	Predation	2001-2012	Le Bohec <i>et al.</i> 2003
	SSTa	1985-2012	Chambers 2004
	SAM	1985-2012	Forcada & Trathan 2009
	ENSO	1985-2012	Chambers 2004
	Intra-specific competition	1985-2012	Baylis <i>et al.</i> 2013
Inter-specific competition	1985-2012	Trathan <i>et al.</i> 2012	

## Figures

Figure 1. The population dynamics and demography of macaroni penguins at Bird Island, South Georgia between 1985 and 2011. A) The population trajectory. Observed trajectory with confidence interval estimated from the repeated colony counts in grey. The approximate point where the gradient of the population trajectory changed ( $\pm$ standard error) is shown with a vertical dashed line. In all figures the median modelled trajectory (black points) is shown with 95% credible interval (dashed line). B-C) Posterior estimates of survival rates B) birds >1-year; C) fledglings. The 95% confidence intervals of the independent survival estimates (from capture-mark-recapture data), are shown as the light grey shaded band (fully time dependent model), and dark grey band (covariate model). D) Time series of posterior estimates of productivity rates (scaled to reflect chicks pair<sup>-1</sup>). Observed productivity estimates are shaded in grey with confidence interval taken from the repeated colony counts.

Figure 2. A) Approximate predation rate of macaroni penguins per giant petrel (based on the total number of giant petrels in the study areas, methods detailed in Appendix S2; penguins older than 1-year - black circles, and fledglings - white squares); B) The predation pressure index, estimated from northern and southern giant petrels productivity at Bird Island, South Georgia. Observed values (i.e., number of chicks fledged from the study area) shown as black circles, and imputed values shown as black triangles with 95% credible interval.

Figure 3. A) The probability of inclusion in the model for each covariate, estimated using stochastic variable selection. Dashed line shows probability of 0.5; a covariate scoring predominantly above this will operate in more than 50% of model parameterisations. B) The relative importance of each covariate in resolving the population trajectory; higher values and greater variability indicates more influence. Covariates are ordered by the median, those

indicated as being included in the majority of model iterations based on variable selection are shown in grey; those excluded are shown in white (box metrics: central line, median; box, interquartile range; whisker, 1.5\*inter-quartile range).





