Integrated population modeling reveals the impact of climate on the survival of juvenile

emperor penguins

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ABSTRACT

Early-life demographic traits are poorly known, impeding our understanding of population processes and sensitivity to climate change. Survival of immature individuals is a critical component of population dynamics and recruitment in particular. However, obtaining reliable estimates of juvenile survival (i.e., from independence to first year) remains challenging, as immatures are often difficult to observe and to monitor individually in the field. This is particularly acute for seabirds, in which juveniles stay at sea and remain undetectable for several years. In this work, we developed a Bayesian integrated population model to estimate the juvenile survival of emperor penguins (*Aptenodytes forsteri*), and other demographic parameters including adult survival and fecundity of the species. Using this statistical method, we simultaneously analyzed capture-recapture data of adults, the annual number of breeding females, and the number of fledglings of emperor penguins collected at Dumont d'Urville, Antarctica, for the period 1971-1998. We also assessed how climate covariates known to affect the species foraging habitats and prey (southern annular mode (SAM), sea-ice concentration (SIC)) affect juvenile survival. Our analyses revealed that there was a strong evidence for the positive effect of SAM during the rearing period (SAMR) on juvenile survival. Our findings suggest that this large-scale climate index affects juvenile emperor penguins body condition and survival through its influence on wind patterns, fast ice extent, and distance to open water. Estimating the influence of environmental covariates on juvenile survival is of major importance to understand the impacts of climate variability and change on the population dynamics of emperor penguins and seabirds in general, and to make robust predictions on the impact of climate change on marine predators.

INTRODUCTION

Climate is changing at an unprecedented rate with important ecological consequences on the structure and functioning of ecosystems (Walther *et al.*, 2002), marine ecosystems making no exception (Hoegh-guldberg & Bruno, 2010). Given the lack of progress in reducing global atmospheric greenhouse-gas emissions (IPCC 2014), understanding the threats (e.g. land use change, habitat loss, pollution, and invasive species) that interact with climate change, and that are potentially more tractable, is all the more important in the short term for animal populations and species conservation (de Chazal & Rounsevell, 2009; Mantyka-pringle *et al.*, 2012). In this context, assessing the impact of climate change on the dynamics of animal populations is fundamental to understanding ecosystems (Sillett, 2000; Crick, 2004; Bost *et al.*, 2015).

To date, most demographic studies used long term demographic information to assess the influence of climate change on life history traits (e.g. adult survival, breeding performance) of seabird species across several marine ecosystems worldwide (Sydeman *et al.*, 2012). Survival of immature individuals is critical for the recruitment into the population. In long lived species such as seabirds, younger age classes represent up to half of the total population and account for a large contribution to the total reproductive value and demographic stochasticity (Sæther *et al.*, 2013). Other studies (e.g. Gaillard *et al.*, 2000; Altwegg *et al.*, 2005) also showed that the immature stage is much more sensitive to environmental variation and it is one of the critical components of population growth in populations of mammals and reptiles. In addition, conditions experienced in early life may have long-term individual fitness consequences such as delayed reproduction, reduced survival probability of future reproductive success (Cam & Aubry, 2011). It is also a prerequisite to assess the impact of climate variables on immature survival to project the consequences of future climate change on animal population (Dybala *et al.*, 2013).

However, estimating the survival probability of immature seabirds remains challenging because most of them spend their early life at sea and are undetectable on land in breeding colonies monitored using capture-recapture (CR) methods. Because this subadult period lasts several years, it is also difficult to follow the fate of immature individuals using tracking devices such as Argos or GPS loggers. As a consequence, little is known about the links between immature survival and environmental factors (Fay *et al.*, 2015).

In this study, we simultaneously analyzed long-term CR data for adults, population counts, and productivity data of the emperor penguins *Aptenodytes forsteri* using a Bayesian integrated population model (IPM; Besbeas *et al.*, 2002; Abadi *et al.*, 2010). IPM is a powerful tool in conservation and management of seabird species (e.g. Véran & Lebreton, 2008) and other taxa (e.g. Schaub *et al.*, 2007). A detailed review of IPM and its applications can be found in Schaub & Abadi (2011). The main strength of our approach is that it efficiently combines multiple sources of data within a unified framework and allows the estimation of juvenile survival for which no explicit information is available. Hence, our main objectives were to estimate the juvenile survival of emperor penguins and to demonstrate how this demographic parameter was influenced by climate covariates.

MATERIALS AND METHODS

Study site and species

Emperor penguins were studied at Pointe Géologie Archipelago (66°40'S, 140°01'E), Terre Adélie, Antarctica from 1952 onward. The emperor penguin is the only Antarctic winter breeder and breeding adults forage within the pack ice at an average distance of 100 km from the breeding colony (Zimmer *et al.*, 2008). During breeding the diet of adults and chicks is mainly composed of fish (mainly *Pleuragramma antarcticum*), cephalopods (mainly *Psychroteuthis glacialis*) and Antarctic krill (mainly *Euphausia superba*) (Offredo & Ridoux,

1986; Cherel, 2008). Just after their departure at sea (end of December) and during their first 5 months at sea, juvenile emperor penguins disperse away from Antarctica up to 1250 km north of the pack-ice edge in the Polar Frontal Zone (i.e. the region of low salinity water between the Antarctic polar front and the subantarctic front), before moving southwards close to the extending pack-ice during autumn and winter (Thiebot *et al.*, 2013). Juvenile emperor penguins tracked at other colonies show the same northward movement towards the Polar Front following their departure from the colonies (Ross Sea: Kooyman & Ponganis, 2008; Mawson Coast: Wienecke *et al.*, 2010). This pattern seems consistent from year to year (Ross Sea: Kooyman *et al.*, 1996; Kooyman *et al.*, 2008; Pointe Géologie: Thiebot *et al.*, 2013; Orgeret *et al.*, unpublished data).

Counts and demographic data

The annual number of breeding pairs was estimated by adding the number of dead eggs and dead chicks counted daily at the colony during the breeding period and the number of live chicks just before their departure at sea (Barbraud *et al.*, 2011). The number of fledged chicks was estimated by direct counts and/or photograph counts. Here, we used counts made from 1971 to 1998 to match with the CR data.

From 1968 to 1988 penguins were individually marked using flipper bands (Barbraud & Weimerskrich, 2001). We only used individuals marked as adults. Marking stopped in 1988 as a precautionary approach since it was found that wing tagging affected reproductive success and mortality in Adélie penguins in the early 1980s, but banded birds have been recorded since then. Following goodness-of-fit validation in earlier studies (Barbraud & Weimerskrich, 2001; Jenouvrier *et al.*, 2005), the CR data was restricted to 873 histories of female adult individuals from 1971 to 1998 and excluded data prior the period 1971 during which most band loss occurred in the emperor penguins.

Climate covariates

We included a large-scale climate index, the Southern Annular Mode (SAM) defined as the difference in the normalized monthly zonal mean sea level pressure between 40°S and 65°S (Gong & Wang, 1999). SAM is the leading mode of atmospheric circulation variability in the Southern Hemisphere affecting wind condition in the Southern Ocean (Marshall, 2003). SAM may affect juvenile emperor penguins indirectly through stronger westerly winds and increased Ekman transport (i.e. the 90° net transport of the surface layer of a fluid by wind forcing) accentuating upwelling intensity and consequently the biological productivity and prey availability in the Antarctic Zone south of the Polar Front (Thompson *et al.*, 2011), where they forage during their first months at sea (Thiebot *et al.*, 2013). We obtained data from the online database of the British Antarctic Survey (http://www.nerc-bas.ac.uk/icd/gjma/sam.html). Since juvenile emperor penguins leave the pack ice and reach open water around the end of December, we used average yearly SAM (SAMY) calculated from January to December, following the departure of chicks at sea.

To build from previous results of Massom *et al.* (2009), we used an average of SAM during the rearing period (SAMR: July - December) in addition to SAMY as a covariate of juvenile survival. Massom *et al.* (2009) showed that SAM had a positive effect on breeding success of emperor penguins by influencing wind patterns and lower fast ice extent, and thereby decreasing the distance between the breeding colony and the nearest open water (i.e. foraging area) during the rearing period. SAMR could also have a positive effect on juvenile survival through its influence on chick body condition because adults had to travel a shorter distance to obtain food and hence could feed chicks more frequently.

We also considered sea ice concentration (SIC), which is the fraction of area covered by sea ice. High SIC may affect emperor penguins directly by increasing the length of the foraging trips and energetic costs of breeding adults, thereby decreasing the provisioning of chicks

(Massom *et al.*, 2009) or indirectly through its effects on abundance of penguin prey. Indeed, individual based studies suggest that juvenile emperor penguins south of the Polar Front feed on small mesopelagic fish such as myctophids but also on squid (e.g. Mawson coast: Wienecke *et al.*, 2010; Ross Sea: Kooyman *et al.*, 2008; Pointe Géologie: Thiebot *et al.*, 2013). We used averaged SIC during the rearing period (SICR: July-December) for the sector used for foraging by breeding adults during the chick rearing period (70°S-55°S; 130°E-150°E; (Zimmer *et al.*, 2008)) as a covariate of juvenile survival the following year. SIC values were obtained from the online database (http://iridl.ldeo.columbia.edu) where SIC data were calculated from a combination of *in situ* observations from ships and remote measurements from satellites (AVHRR and thermal infrared satellite images). Therefore, we used SAM following independence (i.e. SAMY) as an indicator of food availability in the oceanic areas frequented by juvenile penguins after they fledged, while SAMR and SICR were used as indicators of juvenile body condition before they fledge, which would then potentially influence their survival after fledging as shown in other penguin species (Saraux *et al.*, 2011; Horswill *et al.*, 2014). We also tested the effect of the 5-month average SAM (SAMM: January - May) to further understand what temporal scale of SAM was related to juvenile survival of emperor penguins.

Integrated population model (IPM) for emperor penguins

We built an age-structured integrated population model with 6 age classes (Jenouvrier *et al.*, 2005) to model juvenile survival as a function of environmental covariates, and to estimate adult survival and fecundity while accounting for detectability < 1. The model allows combining the counts and demographic data into a joint likelihood to estimate parameters. Our model ignored the dispersal processes because the Pointe Géologie colony of emperor penguin is the colony where some marking was done for demographic studies and no

observation of marked animals was made in neighboring colonies situated at 200 km for the

nearest one. Recent genetic studies also suggested dispersal occurs but at low annual rates ($\approx$

0.15-0.17% per year; Cristofari *et al.*, 2016; Younger *et al.*, 2016). Here we first describe the

likelihoods for the three datasets shown in Fig. 1, and we then describe the Bayesian

implementation of our model.

Likelihood for the population count data

For population count data, we used the state-space model formulation, which comprises the

state and observation equations. The state equations described the dynamics of true, but

unknown population sizes for different age classes over time. We defined the state equations

based on the female only age-structured matrix population model described in Jenouvrier *et*

al.(2005). Here, we used the Poisson (*Po*) and binomial (*bin*) distributions to account for

demographic stochasticity.

$N_{1,t+1} \sim Po(0.5 * \phi_{j,t} * f_t * N_{a,t})$

$N_{2,t+1} \sim bin(\phi_{a,t}, N_{1,t})$

$N_{3,t+1} \sim bin(\phi_{a,t}, N_{2,t})$

$N_{4,t+1} \sim bin(\phi_{a,t}, N_{3,t})$

$N_{5,t+1} \sim bin(\phi_{a,t}, ((1 - b_5) * N_{4,t} + (1 - b_6) * N_{5,t}))$

$N_{a,t+1} \sim bin(\phi_{a,t}, (b_5 * N_{4,t} + b_6 * N_{5,t} + N_{a,t}))$

where $\phi_{j,t}$ is the juvenile (from fledging to first year) apparent survival probability between

year t and $t + 1$, $\phi_{a,t}$ is the apparent survival probability for individuals over 1 year of age

between year t and $t + 1$, f_t is the fecundity (proportion of eggs that produced a fledgling) in

year t, which is multiplied by 0.5 to reflect the assumption of an even sex ratio, $N_{1,t}$ is the

population size of j year old individuals at time t (for $1 \leq j \leq 5$),and $N_{a,t}$ is the population

size of individuals older than 6 years at time t . b_5 and b_6 denote the proportion of

individuals that breed for the first time at age 5 and 6 years old, respectively. The values of b_5 and b_6 were set to 0.22 and 0.32 , respectively (Jenouvrier *et al.*, 2005). We also assumed that once recruited, individuals breed every year (Jenouvrier *et al.*, 2012).

The observation equation links the observed population count (i.e., number of breeding females, denoted by (y)) with the true population size (N), assuming an observation error. That is,

$$y_t = (0 \quad 0 \quad 0 \quad 0 \quad 0 \quad 1) \begin{pmatrix} N_1 \\ N_2 \\ N_3 \\ N_4 \\ N_5 \\ N_a \end{pmatrix}_t + \varepsilon_t , \qquad \varepsilon_t \sim N(0, \sigma_y^2)$$

where ε_t is the error term and σ_y^2 is the variance of the error term. The likelihood for the population count data is denoted as $L_{CO}(y|\phi_a, \phi_j, N, f)$.

Likelihood for the capture-recapture data

For adult capture-recapture data, we used the standard Cormack-Jolly-Seber (CJS) model (Lebreton *et al.*, 1992) that permits estimating the apparent adult survival (ϕ_a) and recapture (p) probabilities. The likelihood for the capture-recapture data is denoted as $L_{CR}(m|\phi_a, p)$.

Likelihood for the productivity data

We modeled the productivity data (i.e., the number of fledglings produced each year) using a binomial distribution with parameter (f), and number of breeders (y). The likelihood for the productivity data is denoted as $L_{PR}(J|f)$.

Joint likelihood for the IPM

Assuming independence, we constructed the joint likelihood as a product of the likelihoods for the three data sets. It is given by

$$L_{IPM}(m, y, J|\phi_a, \phi_j, f, p, N) = L_{CR}(m|\phi_a, p) \times L_{PR}(J|f) \times L_{CO}(y|\phi_a, \phi_j, N, f).$$

Therefore, the advantage of combining and analyzing the three datasets simultaneously using

an IPM was that it allowed us the estimation juvenile survival despite lack of explicit

information about this parameter. Details of the construction of the likelihoods are presented

in several papers (Besbeas *et al.*, 2002; Abadi *et al.*, 2010; Schaub & Abadi, 2011).

Assessing the effect of environmental covariates on juvenile survival

We used the following univariate logit-linear regressions to assess the effects of SIC and

three SAM covariates on juvenile survival.

$$logit(\phi_{j,t}) = \beta_0 + w * \beta_1 * SICR_t + \varepsilon_{j,t}$$

$$logit(\phi_{j,t}) = \beta_0 + w * \beta_1 * SAMY_t + \varepsilon_{j,t}$$

$$logit(\phi_{j,t}) = \beta_0 + w * \beta_1 * SAMR_t + \varepsilon_{j,t}$$

$$logit(\phi_{j,t}) = \beta_0 + w * \beta_1 * SAMM_t + \varepsilon_{j,t}$$

$$\varepsilon_{j,t} \sim N(0, \sigma_j^2)$$

where β_0 and β_1 are the intercept and slope, respectively, SICR, SAMY,SAMR and SAMM

are defined as above,, ε is the error term, σ_j^2 is the temporal variance (on logit scale) of

juvenile survival, and w is the inclusion probability that measures the importance of the

covariate (Royle, 2008; O'Hara & Sillanpää, 2009).

Note that each covariate was standardized to have a mean 0 and variance 1 in the modeling

process. The relationship between SICR and juvenile survival was investigated based on the

short time-series data (1979-1997) compared to SAM covariates (1971-1979). In the case of

the model with SICR covariate, we also constrained juvenile survival to be year-dependent

prior the period 1979 as no SICR information was available during this period. We set vague

priors for the parameters:$\beta_0 \sim N(0, 0.001)$, $\beta_1 \sim N(0, 0.001)$, $\sigma_j \sim U(0, 5)$, and

$w \sim Bin(1,0.5)$. We also computed the 95% credible intervals for the regression coefficients.

For the other parameters in the model, we assumed temporal random effects for fecundity and

recapture probability. We also constrained adult survival to be constant over time as an

earlier study (Jenouvrier *et al.*, 2005) showed that there was little temporal variability in this

parameter. Thus,

$$logit(\phi_{a,t}) = \alpha$$

$$logit(f_t) = \eta + \varepsilon_{f,t} , \quad \varepsilon_{f,t} \sim N(0, \sigma_f^2)$$

$$logit(p_t) = \gamma + \varepsilon_{p,t} , \quad \varepsilon_{p,t} \sim N(0, \sigma_p^2)$$

where α, η, and γ are the overall mean adult survival, fecundity, and recapture probabilities

on the logit scale, respectively, and σ_f^2 and σ_p^2 are the temporal variance (on logit scale) of

fecundity, and recapture probabilities, respectively. We specified vague priors for the

parameters: $\alpha \sim N(0, 0.001), \eta \sim N(0, 0.001), \gamma \sim N(0, 0.001), \sigma_f \sim U(0, 5)$, and

$\sigma_p \sim U(0, 5)$.

Model implementation

We used the Markov Chain Monte Carlo (MCMC) algorithms to approximate the posterior

distributions of model parameters. We generated 3 chains of 2,000,000 iterations with a burn-

in of 1,000,000 and thinned by 100. The Gelman-Rubin diagnostic convergence statistic ($\widehat{R}$-

hat, Brooks & Gelman, 1998) for each parameter was below 1.02 and the chains were also

well mixed. We performed the analyses using the program JAGS (Plummer, 2003) executed

from R with the package R2jags (Su & Yajima, 2012).

RESULTS

The results showed that the posterior inclusion probabilities for both SAM covariates (i.e.

SAMY and SAMR) were above 0.90, suggesting there was a strong support for the effects of

SAMY and SAMR on juvenile survival of emperor penguins. Our analysis also revealed that

both SAMY ($\widehat{\beta_1} = 2.316$; 95% CRI = (0.782, 3.551)) and SAMR ($\widehat{\beta_1} = 1.639$; 95% CRI =

(0.489, 2.664); Fig. 2) had significant positive effects on juvenile survival. However, the

effect of SAMM on juvenile survival was insignificant ($\widehat{\beta_1} = 0.140$; 95% CRI = (-1.033,

1.218)). Based on the model with SAMR covariate, the juvenile survival was estimated with mean 0.401 (SD =0.126) and temporal standard deviation (on logit scale) of 4.226 (SD = 0.578). Mean adult survival probability was estimated at 0.907 (SD = 0.002). The mean and temporal standard deviation (on logit scale) for fecundity was estimated at 0.458 (SD = 0.064), and 1.420 (SD = 0.224), respectively. The mean adult recapture probability was estimated with mean 0.651 (SD = 0.072) and temporal standard deviation (on logit scale) of 1.692 (SD = 0.372). The model with SICR covariate had low posterior inclusion probability (0.267). Further, the 95% credible interval for the effect of SICR did include zero ($\widehat{\beta_1}$ = 0.813; 95% CRI = (-0.288, 1.966)), indicating there was insufficient evidence for the effect of SICR on juvenile survival probability during the following year.

DISCUSSION

We provide evidence for a strong positive effect of SAM on the juvenile survival (i.e. survival from independence to first year) of emperor penguins. Our results clearly showed that juvenile survival was positively influenced by yearly average SAM (SAMY) as well as SAM during the previous rearing period (SAMR). However, the effect of the 5-month average SAM (SAMM) was insignificant. These results suggest that the yearly effect was due to SAM during the rearing period when juvenile emperor penguins are in the Antarctic Zone into the vicinity of the pack ice.

The SAM is the dominant mode of extratropical variability in the Southern Hemisphere (Simmonds & King, 2004). A positive phase of the SAM induces a poleward shift of the surface westerly winds, which creates anomalies in poleward and equatorward Ekman transport, driving increased upwelling of cold, iron-enriched water in the Antarctic Zone south of the Polar Front (Lovenduski & Gruber, 2005). This latter process increases the phytoplankton abundance in the Antarctic Zone (Lovenduski & Gruber, 2005).

Our results are coherent with previous findings showing a positive effect of SAM on breeding success (Massom *et al.*, 2009). Because SAM is related to both breeding success and the shortest distance separating the breeding colony from the nearest open water (i.e. foraging area) during the rearing period, this environmental covariate may influence fledging body condition which is known to affect juvenile survival in several penguin species (Saraux *et al.*, 2011; Horswill *et al.*, 2014).

The effect of SAM on sea ice, phytoplankton and penguins differs between the Antarctic Peninsula and all the other regions of Antarctica (Ainley *et al.*, 2005; Lovenduski & Gruber, 2005; Emmerson & Southwell, 2011; Saba *et al.*, 2014). This is because the Antarctic Peninsula is situated at more northern latitudes compared to the rest of the Antarctic continent. In the Antarctic Peninsula, a positive SAM seems to have negative effects on sea ice concentration, phytoplankton production, krill recruitment and penguins (Ainley *et al.*, 2005; Saba *et al.*, 2014), whereas in other regions of Antarctica (Ross Sea, Indian Ocean sector) a positive SAM is associated to increased sea ice concentration and enhances penguins demographic traits (Ainley *et al.*, 2005; Emmerson & Southwell, 2011; Hindell *et al.*, 2012). These contrasted patterns are probably due to the localized situation of the Antarctic Peninsula which extends further north than any other parts of Antarctica and is more directly exposed to warming associated with positive SAM (Yuan & Li, 2008). So far, all studies that investigated post-natal dispersal in juvenile emperor penguins revealed a pronounced northward dispersion up to the Polar Front followed by a stay at least 6 months in the Antarctic Zone (Kooyman *et al.*, 1996; Kooyman & Ponganis, 2008; Wienecke *et al.*, 2010; Thiebot *et al.*, 2013). Therefore, for the above reasons, we speculate that our findings of the relationship between SAM and juvenile survival may not hold for emperor penguins colonies situated in the Antarctic Peninsula, which however represent a small fraction (about 3%) of the global population (Fretwell & Trathan, 2009).

Present climate change projections suggest that the amplitude of the SAM will increase and become more positive in future decades (Cai *et al.*, 2003), which according to our results may favor juvenile survival except perhaps in the Antarctic Peninsula. Until now, emperor penguin population projections under climate change (decrease in sea ice) suggest a decrease of all populations by 2100 (Jenouvrier *et al.*, 2014). However, these projections only included the effects of sea ice on adult survival and breeding success. The effect of SAM on adult survival was never investigated in the emperor penguins, and SAM was found to be positively related to breeding success (Massom *et al.*, 2009). A previous study by Jenouvrier *et al.* (2005) showed that juvenile survival contributed 4 times less than adult survival and breeding success to variations in population growth rate. From a prospective point of view, the study also showed that juvenile survival will affect population growth rate 5 times less than adult survival and 1.2 times more than breeding success. Given that, in emperor penguins, juvenile survival is the demographic parameter to which population growth rate is the most sensitive following adult survival, our results highlight the need to take into account the effects of large-scale climate indices (particularly SAM) on juvenile survival and other demographic parameters in future population projection studies. In addition, it may also be important to account for the synergistic effects of large-scale climate indices and climate warming in population projection.

On a methodological side, our estimate of juvenile survival is comparable to survival rates inferred from a survey of remotely tracked juvenile emperor penguins obtained in different years and localities (Wienecke *et al.*, 2010; Thiebot *et al.*, 2013). Our model also provided estimates of the other demographic parameters (e.g. adult survival) of emperor penguins, which were consistent with previous studies (Jenouvrier *et al.*, 2005, 2012).The integrated population modeling approach allows the combination of multiple data sources to unravel the effects of climate on an important component of emperor penguins' demography. Although

no explicit information was available to directly estimate immature survival, we showed that this parameter could be studied by sharing information among demographic datasets, which holds great promise for understanding the impact of climate forcing on the dynamics of seabirds as well as other animal populations.

REFERENCE

Abadi F, Gimenez O, Arlettaz R, Schaub M (2010) An assessment of integrated population models: bias, accuracy, and violation of the assumption of independence. *Ecology*, **91**, 7–14.

Ainley DG, Clarke ED, Arrigo K, Fraser WR, Kato A, Barton KJ, Wilson PR (2005) Decadal-scale changes in the climate and biota of the Pacific sector of the Southern Ocean, 1950s to the 1990s. *Antarctic Science*, **17**, 171–182.

Altwegg R, Dummermuth S, Anholt BR, Flatt T (2005) Winter weather affects asp viper *Vipera aspis* population dynamics through susceptible juveniles. *Oikos*, **110**, 55–66.

Aubry LM, Rockwell RF, Cooch EG, Brook RW, Mulder CPH, Koons DN (2013) Climate change, phenology, and habitat degradation: drivers of gosling body condition and juvenile survival in lesser snow geese. *Global Change Biology*, **19**, 149–160.

Barbraud C, Weimerskrich H (2001) Emperor penguins and climate change. *Nature*, **411**, 183

– 186.

Barbraud C, Gavrilo M, Mizin Y, Weimerskirch H (2011) Comparison of emperor penguin declines between Pointe Géologie and Haswell Island over the past 50 years. *Antarctic Science*, **23**, 461–468.

Besbeas P, Freeman SN, Morgan BJT, Catchpole EA (2002) Integrating mark-recapture-recovery and census data to estimate animal abundance and demographic parameters. *Biometrics*, **58**, 540–547.

Bost CA, Cotté C, Terray P et al. (2015) Large-scale climatic anomalies affect marine predator foraging behaviour and demography. *Nature Communications*, doi:10.1038/ncomms9220.

Brooks SP, Gelman A (1998) General methods for monitoring convergence of iterative simulation. *Journal of Computational and Graphical Statistics*, **7**, 434–455.

Cai W, Whetton PH, Karoly DJ (2003) The response of the Antarctic Oscillation to increasing and stabilized atmospheric CO2. *Journal of Climate*, **16**, 1525–1538.

Cam E, Aubry L (2011) Early development, recruitment and life history trajectory in long-lived birds. *Journal of Ornithology*, **152**, 187–201.

Cherel Y (2008) Isotopic niches of emperor and Adélie penguins in Adélie Land, Antarctica. *Marine Biology*, **154**, 813–821.

Crick HQP (2004) The impact of climate change on birds. *Ibis*, **146**, 48–56.

Cristofari R, Bertorelle G, Ancel A et al. (2016) Full circumpolar migration ensures evolutionary unity in the Emperor penguin. *Nature Communications*, **7**, 11842.

de Chazal J, Rounsevell MDA (2009) Land-use and climate change within assessments of biodiversity change: A review. *Global Environmental Change*, **19**, 306–315.

Dybala KE, Eadie JM, Gardali T, Seavy NE, Herzog MP (2013) Projecting demographic responses to climate change: Adult and juvenile survival respond differently to direct

and indirect effects of weather in a passerine population. *Global Change Biology*, **19**, 2688–2697.

Fay R, Weimerskirch H, Delord K, Barbraud C (2015) Population density and climate shape early-life survival and recruitment in a long-lived pelagic seabird. *Journal of Animal Ecology*, **84**, 1423–1433.

Gaillard J-M, Festa-Bianchet M, Yoccoz NG, Loison A, Toigo C (2000) Temporal variation in fitness components and population dynamics of large herbivores. *Annual Review of Ecology and Systematics*, **31**, 367–393.

Gong D, Wang S (1999) Definition of Antarctic Oscillation index. *Geophysical Research Letters*, **26**, 459–462.

Hoegh-guldberg O, Bruno JF (2010) The Impact of climate change on the world's marine ecosystem. *Science*, **328**, 1523–1528.

Jenouvrier S, Barbraud C, Weimerskirch H (2005) Long-term contrasted responses to climate of two antarctic seabird species. *Ecology*, **86**, 2889–2903.

Jenouvrier S, Holland M, Stroeve J, Barbraud C, Weimerskirch H, Serreze M, Caswell H (2012) Effects of climate change on an emperor penguin population: Analysis of coupled demographic and climate models. *Global Change Biology*, **18**, 2756–2770.

Lebreton J-D, Burnham KP, Clobert J, Anderson DR (1992) Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs*, **62**, 67–118.

Lovenduski NS, Gruber N (2005) Impact of the Southern Annular Mode on Southern Ocean circulation and biology. *Geophysical Research Letters*, **32**, 1–4.

Mantyka-pringle CS, Martin TG, Rhodes JR (2012) Interactions between climate and habitat loss effects on biodiversity: A systematic review and meta-analysis. *Global Change Biology*, **18**, 1239–1252.

Marshall GJ (2003) Trends in the Southern Annular Mode from observations and reanalyses. *Journal of Climate*, **16**, 4134–4143.

Massom RA, Hill K, Barbraud C, Adams N, Ancel A, Emmerson L, Pook MJ (2009) Fast ice distribution in Adélie Land, East Antarctica: Interannual variability and implications for emperor penguins Aptenodytes forsteri. *Marine Ecology Progress Series*, **374**, 243–257.

O'Hara RB, Sillanpää MJ (2009) A review of Bayesian variable selection methods: what, how and which. *Bayesian Analysis*, **4**, 85–117.

Offredo C, Ridoux V (1986) The diet of Emperor Penguins Aptenodytes forsteri in Adelie Land, Antarctica. *Ibis*, **128**, 409–413.

Plummer M (2003) JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. In: *Proceedings of the 3rd International Workshop on Distributed Statistical Computing (DSC 2003), March 20–22, Vienna, Austria*, p. ISSN 1609–395X.

Royle JA (2008) Modeling individual effects in the Cormack-Jolly-Seber model: A state-space formulation. *Biometrics*, **64**, 364–370.

Sæther B-E, Coulson T, Grøtan V et al. (2013) How life history influences population dynamics in fluctuating environments. *The American Naturalist*, **182**, 743–759.

Saraux C, Le Bohec C, Durant JM et al. (2011) Reliability of flipper-banded penguins as indicators of climate change. *Nature*, **469**, 203–206.

Schaub M, Abadi F (2011) Integrated population models: a novel analysis framework for deeper insights into population dynamics. *Journal of Ornithology*, **152**, S227–S237.

Schaub M, Gimenez O, Sierro A, Arlettaz R (2007) Use of Integrated Modeling to Enhance Estimates of Population Dynamics Obtained from Limited Data. *Conservation Biology*, **21**, 945–955.

Sillett TS (2000) Impacts of a Global Climate Cycle on Population Dynamics of a Migratory Songbird. *Science*, **288**, 2040–2042.

Su Y-S, Yajima M (2012) R2jags: A Package for Running jags from R.

Sydeman WJ, Thompson SA, Kitaysky A (2012) Seabirds and climate change: roadmap for the future. *Marine Ecology Progress Series*, **454**, 107–117.

Thiebot J-B, Lescroël A, Barbraud C, Bost C-A (2013) Three-dimensional use of marine habitats by juvenile emperor penguins Aptenodytes forsteri during post-natal dispersal. *Antarctic Science*, **25**, 536–544.

Thompson DWJ, Solomon S, Kushner PJ, England MH, Grise KM, Karoly DJ (2011) Signatures of the Antarctic ozone hole in Southern Hemisphere surface climate change. *Nature Geoscience*, **4**, 741–749.

Véran S, Lebreton JD (2008) The potential of integrated modelling in conservation biology: a case study of the black-footed albatross (Phoebastria nigripes). *Canadian Journal of Statistics-Revue Canadienne De Statistique*, **36**, 85–98.

Walther G-R, Post E, Convey P et al. (2002) Ecological responses to recent climate change. *Nature*, **416**, 389–395.

Wienecke B, Raymond B, Robertson G (2010) Maiden journey of fledgling emperor penguins from the Mawson Coast, East Antarctica. *Marine Ecology Progress Series*, **410**, 269–282.

Younger JL, Hoff J Van Den, Wienecke B, Hindell M, Miller KJ (2016) Contrasting responses to a climate regime change by sympatric , ice-dependent predators. *BMC Evolutionary Biology*, **16**, 1–11.

Zimmer I, Wilson RP, Gilbert C, Beaulieu M, Ancel A, Plötz J (2008) Foraging movements of emperor penguins at Pointe Géologie, Antarctica. *Polar Biology*, **31**, 229–243.

FIGURE CAPTIONS

Fig. 1. Graphical representation of an integrated population model for emperor penguins. Elliptical nodes represent data and unknown quantities (parameters to be estimated), and Rectangle node represents the covariate (e.g. southern annular mode). Solid and dashed arrows represent stochastic and functional dependencies, respectively.

Fig. 2. Survival of juvenile emperor penguins (with 95% credible intervals) estimated from the model in relation to the standardized average SAM during the rearing period (SAMR).