Variable vital rates and the risk of population declines in Adélie penguins from the Antarctic Peninsula region

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Abstract. Predicting population responses in changing environments is an important task for ecologists. In polar regions, climate warming, loss of sea ice, and more frequent anomalous events suggest that further reductions in ice-dependent animal populations are likely. We assess the risk of near-term (30-year) depletion of an Adélie penguin (*Pygoscelis adeliae*) population with a stochastic matrix model parameterized with 30 yr (1982–2011) of data from the Copacabana colony on King George Island, Antarctica. The model was fitted to nest census data by estimating correction factors for survival rates estimated from a multi-state mark–recapture model. We modeled future survival and fecundity scenarios during the projection period (2012–2041) based on a two-state Markov chain that randomly assigned survival rates and reproductive success from their respective historical distributions to represent "good" and "poor" years. Monte Carlo simulation was used to estimate population trajectories across a range of progressively worse survival conditions. The results suggest that, given historical distributions of survival and reproductive success, a limited scope for recovery of the population is present, commensurate with recent stabilization in population size at the study site. However, our projections mainly suggest that the Adélie penguin population will decline if the frequency of years with poor survival remains at, or increases above, its 30-year mean. The risk of local depletion within 30 yr, defined according to International Union for Conservation of Nature categories for endangered and critically endangered species, was 33% for >90% declines, but near 100% for 50% declines given status-quo conditions. As survival conditions worsen, the risk of substantive depletions rose rapidly. Given expectations of further environmental and ecosystem changes in the northern Antarctic Peninsula region, continued declines in Adélie penguin population size at the northern extent of their range should be expected.

Key words: climate change; Commission for Conservation of Antarctic Living Marine Resources; demography; long-term monitoring; penguin; pygoscelis; South Shetland Islands.

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INTRODUCTION

As environmental conditions change, predicting population responses is an important task for ecologists. Soberingly, estimating the risk of extinction due to climate change has become a common task in conservation biology (Thomas et al. 2004, Maclean and Wilson 2011) and an important component of managing endangered resources (Beissinger and Westphal 1998). In polar marine ecosystems, extinction risks may be particularly acute given the rapid pace of

warming and consequent loss of physical habitat in the form of sea ice. Sea ice is an essential habitat for numerous marine mammals and seabirds; it is used as a substrate for reproduction, foraging, molting, and resting. Animals that have evolved a direct dependence on sea ice are of particular concern (Croxall et al. 2002, Laidre et al. 2008), and recent studies on Pacific walrus (*Odobenus rosmarus divergens*; Jay et al. 2011), polar bears (*Ursus maritimus*; Amstrup et al. 2007), and emperor penguins (*Aptenodytes forsteri*; Jenouvrier et al. 2009*b*) suggest a substantial probability of extinction due to climate change-induced reductions in sea ice within 100 yr.

In the Antarctic Peninsula region, the pace of climate change is particularly rapid (Vaughan et al. 2003). Positive trends in air and sea surface temperatures (Meredith and King 2005, Turner et al. 2005) and reductions in the extent and duration of winter sea ice (Stammerjohn et al. 2008) have been accompanied by potential declines in primary production (Ducklow et al. 2007) and the density of Antarctic krill (*Euphausia superba*; Atkinson et al. 2004). Krill are one of the main food resources for higher trophic-level predators in the Antarctic (Laws 1985). Among such predators is the Adélie penguin (*Pygoscelis adeliae*), an ice-obligate seabird whose populations in the northern Antarctic Peninsula region have declined by more than 50% since the mid-1970s (Trivelpiece et al. 2011, Lynch et al. 2012). Those declines have been attributed to loss of sea ice and reduced krill availability (Ducklow et al. 2007, Trivelpiece et al. 2011). Intergovernmental Panel on Climate Change (IPCC) projections suggest that future warming, loss of sea ice, and an increased frequency of anomalous environmental events are likely (IPCC 2013). For Adélie penguins at the northern limit of their circumpolar range, such environmental changes may increase emigration rates and/or decrease vital rates, hastening local population declines.

We integrated 30 yr of survival and reproductive data to develop a stochastic matrix population model to predict population responses to changes in the frequency of years with poor survival. The method is motivated by an analysis of mark–recapture data on Adélie penguins in the Copacabana colony on King George Island (Hinke et al. 2014) that revealed episodic occurrences of low adult survival rates that were not well explained by a suite of local, regional, and circumpolar environmental covariates. Such episodic events can have disproportionately large effects on population dynamics of long-lived species (Sæther and Bakke 2000), causing rapid declines in abundance (Frederiksen et al. 2008). Given climate projections with continued warming, loss of sea ice in the Antarctic Peninsula region, and expectation of more frequent anomalous events (IPCC 2013), changes in the frequency of years with poor survival of Adélie penguins may be likely. Our approach provides a framework to evaluate how historical changes in survival and reproductive indices influenced observed population sizes, and enables forecasting population trends across a range of future scenarios. Here, we fit the model to census data at the Copacabana colony and then estimate the risk of local depletion in the Copacabana colony across a range of future environmental scenarios. We define depletion risk as the probability of the population declining beyond a specific threshold over a 30-year period. We have chosen thresholds of 50%, 80%, and 90%. The first two levels correspond to the magnitude of population declines over three generations that meet International Union for Conservation of Nature (IUCN) Red List categories of endangered and critically endangered, respectively, based on A2 criteria (IUCN 2012). We note that Adélie penguin generation times for stable to increasing population have been estimated as 9.55 yr (Clarke et al. 2003). The 90% threshold has been used as a quasi-extinction threshold (e.g., Jenouvrier et al. 2009*b*) and corresponds to observed maximum reductions in breeding populations in the Antarctic Peninsula region over the last three decades (Schofield et al. 2010).

Methods

Study site

The Copacabana Adélie penguin colony (62°10′ S, 58°30′ W) is located within Admiralty Bay on the southern shore of King George Island. Breeding population size, survival rates, and indices of reproductive success were monitored annually from 1981/1982 through the 2012/2013 austral summer breeding seasons. During that time, the Adélie colony declined from a peak of roughly 9600 breeding pairs in 1988/1989 to a minimum of 2038 in 2012/2013, representing a nearly 79% decline in abundance. The magnitude

of decline is commensurate with population trends at other Adélie penguin colonies on King George Island (Sander et al. 2007, Carlini et al. 2009, Korczak-Abshire et al. 2013) and throughout the northern Antarctic Peninsula region across a wide range of colony sizes (Lynch et al. 2012).

Matrix model structure

We developed a post-breeding matrix model (Caswell 2001) that incorporates six age-classes (ages 0 through 5), a breeding adult stage, and a non-breeding adult stage. Ages 0 through 5 represent birds that have not yet bred, but birds aged 2 through 5 can recruit into the adult breeding stage in subsequent years. Once recruited to the adult breeding stage, birds can skip breeding periodically by entering a non-breeding adult stage. This model structure is motivated by the analysis of Hinke et al. (2007), who reported that 96% of recruitment to the Copacabana colony occurred by age 5. The model is based on female abundance, equivalent to the nest census, and female chick production, assuming a 50:50 sex ratio. The model was coded and run in the R environment (R Core Team 2015).

Transitions between age-classes are described by stage-specific (*a*) and time-specific (*t*) survival rates ($S_{a,t}$). Recruitment into the adult breeding state is modeled as $S_{a,t} \times Pb_i$, where Pb_i is the probability of breeding for the first time at age *i*. Birds that are older than the minimum age of first breeding can remain non-breeding birds with probability $S_{a,t} \times (1 - Pb_i)$. After recruiting to the adult breeding stage, the probability of reproducing in subsequent years is $S_{a,t} \times Pb_\alpha$, where Pb_α is the probability of breeding once adult status has been achieved. Adults in the breeding stage can skip breeding with probability $(1 - Pb_\alpha)$. First-time breeders contribute offspring to the population with a fecundity defined as $S_{a,t} \times Pb_i \times BS_i$, where BS_i is the average reproductive success of first-time breeders of age *i*. Adult birds with prior breeding experience have a fecundity defined as $S_{a,t} \times Pb_\alpha \times BS_{a,t}$, where $BS_{a,t}$ is the average reproductive success of all adult birds at time *t*.

The resulting model forms a generalized matrix population model

$$n_t + 1 = A_t \times n_t \qquad (1)$$

where A_t is a time-dependent population projection matrix and n is a vector of abundance for each age-class or stage in the model at time *t*. The time-varying A_t is based on the annual estimates of survival rates for adult and juveniles and reproductive success of adult birds with prior breeding experience, whose values are updated in the transition matrix each time step. All other parameters are held constant (see *Parameterization of the model*).

Parameterization of the model

We used a multi-state mark–recapture (MSMR) model to jointly estimate juvenile and adult survival rates ($S_{a,t}$) and transition probabilities from non-breeder to breeder status (Pb_i) for input into the population model. The MSMR model structure was modified from the best-fitting Cormack–Jolly–Seber mark–recapture model described by Hinke et al. (2014) to include estimation of age-dependent transition probabilities from non-breeder to breeder status. Briefly, apparent survival rates were estimated for two age-classes which represent juveniles (ages 0–2) and adults (ages 3+). Recapture probabilities were estimated for three age-classes representing age-1 returns, age-2 returns, and age-3+ returns. We modeled the transitions from non-breeder to breeder status as age dependent. Additional details on the MSMR model are provided in Appendix S1. The probability of annual breeding as an adult (Pb_a) was independently estimated from the life-long breeding histories of known-age individuals. The breeding history for all birds that bred multiple times ($N = 296$) was converted to an encounter history with a value of one indicating alive and breeding and a value of zero indicating either alive and not breeding or possibly not alive. In this format, each observed breeding attempt is equivalent to a live recapture in standard Cormack–Jolly–Seber mark–recapture models and we estimated a constant breeding probability from these data. The models were fit using Program Mark (White and Burnham 1999) interfaced with R (version 2.15, R Core Team 2015) via the RMark package (Laake 2013).

Data on reproductive success were estimated from two monitoring studies. Age-specific breeding success for first-time breeders was estimated from a "known-age" study. Individuals in the known-age study were marked with flipper bands at age 0 and monitored for reproductive success in all future years. Breeding parameters

for birds that had recruited into the breeding adult stage were derived from the "reproductive study." In the reproductive study, 20 to 40 sets of five adjacent nests with individuals of unknown age were monitored each year. During both studies, breeding attempts were monitored from egg laying until successful crèche or nest failure, whichever occurred first. A successful crèche was defined at the first observation of an unattended chick in the nest. An average, age-specific reproductive success of first-time breeders (BS_i) was estimated from the known-age study as the total number of chicks crèched per total number of individuals of age i that attempted to breed for the first time. Annual estimates of reproductive success of adults (BS_a) in the reproductive study were estimated similarly.

The initial vector of population abundance for all stages ($n_{t\,=\,1}$) was estimated using the mean nest census from 1977 to 1982 (7836, Trivelpiece et al. 2011), and the stable age distribution of the first transition matrix, $A_{t\,=\,1}$, was estimated as the right eigenvector.

Model fitting

We fit the population model to nest census data collected from 1982 to 2011. During the fitting procedure, the model was forced with the time series of adult reproductive success and the time-varying survival rates of adults and juveniles. Comparisons of the raw survival rate estimates with another published estimate of Adélie penguin survival rates (Emmerson and Southwell 2011) suggested that the estimated survival rates may have been biased low. Band loss or band-induced mortality can produce such bias (Conn et al. 2004). We note that survival rates in the model merge data from two different band types, aluminum and stainless steel, each with potentially different retention rates (Hinke et al. 2014). Aluminum bands were used from 1982 to 2000, and stainless steel bands were used from 1998 to 2011. Therefore, to correct the negative bias, we estimated four correction factors, one each for juvenile and adult survival rates for each band type, by embedding the model in an optimization routine and fitting to the nest census data via maximum likelihood. Following Arnason and Mills (1981), a correction factor (δ) for each band type (f) and life stage (j) was used to derive a corrected survival rate, $\hat{S}_{f,j,t}$, as:

$$\hat{S}_{f,j,t} = \text{logit}^{-1}\left(\frac{S_{f,j,t}}{\delta_{f,j}}\right) \qquad (2)$$

The corrected survival estimates were constrained to remain in the interval [0,1] with an inverse logit transformation. We also examined the effect of retention rates that were estimated from a double-banding study on Adélie penguins (see appendix 1 in Hinke et al. 2014) to compare performance with the model-estimated retention rates.

Projecting future population sizes

Inter-annual variation in future survival rates and reproductive success was modeled stochastically with a two-state Markov chain. The chain switches between nominal states of "good" and "poor" based on an expected frequency (ω) of poor survival or reproductive success and an estimate of the autocorrelation (ρ) in survival or reproductive success that determines the rate of switching between states. The reproductive success data were not correlated with the estimates of juvenile survival ($r = -0.12$, $P = 0.53$) or adult survival rates ($r = 0.24$, $P = 0.20$) and juvenile and adult survival rates also were not correlated ($r = -0.06$, $P = 0.77$). Therefore, we modeled future variability in each index independently. For each future time step, survival rates and adult reproductive success rates were randomly assigned based on the state of their Markov chain, respectively. If the state at time t was "good," a random quantile, q, was drawn from a $U(0.5, 1)$ distribution. If the environmental state was "poor," q was drawn from a $U(0, 0.5)$ distribution. A survival or reproductive rate was then extracted from the qth quantile of their respective historical distributions. The age- and stage-specific breeding propensity parameters (PB_x) in the projection matrix were held constant.

We used a projection period of 30 yr and conducted 1000 Monte Carlo trials for three future survival scenarios that each spanned conditions from $\omega = 0$ (all "good" years) to $\omega = 1$ (all "poor" years) to examine how the expected frequency of years with poor survival affects final population status. First, we modeled scenarios where future juvenile and adult survival rates both varied. Because the estimates of adult and juvenile survival were not correlated, we then simulated two additional scenarios to examine how future

variation in ω for only adult or juvenile survival impacted the risk of depletion. Therefore, we fixed juvenile survival rates to vary at historical levels, while only future adult survival rates varied across all levels of ω. Finally, we fixed adult survival rates to vary at historical levels, while only future juvenile survival rates varied across all levels of ω. In the latter two cases, historical means for juveniles and adults were estimated by the frequency of years with below-average survival in the fitted survival rate data. In these projection scenarios, annual adult reproductive success varied stochastically based on the frequency of years with below-average reproductive success (ω = 0.466).

We also assessed the effect of two additional factors that may contribute to population declines. First, the sensitivity of the projection results to variation in ρ was tested by setting $\hat{\rho} = \rho \pm 0.1$ and $\hat{\rho} = \rho \pm 0.25$ and re-running the projection scenarios. Second, we examined the effect of variation in average fecundity on the risk of depletion. Here, all simulations were based on status-quo survival conditions, but future reproductive success was modeled as either all good (ω = 0) or all poor (ω = 1). We compared these scenarios to the status-quo condition for reproductive success (ω = 0.466).

We calculated two quantities from the simulations to summarize population status. First, the risk of depletion in breeder abundance over 30 yr was estimated as the proportion of simulation ending with an abundance less than the respective threshold abundance for depletion thresholds of 50%, 80%, and 90%. The reference abundance for these calculations was the observed population size in 2011. Second, we calculated the mean annual rate of population change as

$$\lambda = \left(\frac{N_T}{N_0}\right)^{1/T} \quad (3)$$

where N_0 is the size of the adult breeding population at the start of the projection period and N_T is the adult breeding population size at the end of the projection period T. Whereas the risk of local depletion on a 30-year horizon may be small, consistently negative population growth rates would indicate that further population decline is likely.

Table 1. Mean and standard errors for breeding success (BS) and breeding propensity (PB) for first-time and adult breeders.

Age or stage	(BS)	(PB)
0	0	0
1	0	0
2	0.13 ± 0.04	0.06 ± 0.01
3	0.20 ± 0.03	0.3 ± 0.02
4	0.24 ± 0.06	0.45 ± 0.03
5	0.31 ± 0.12	0.47 ± 0.06
Adult	0.46 ± 0.16	0.94 ± 0.02

Note: Note that in the post-census matrix model, reproductive success applies to birds at the end of their respective age; that is, age 2 birds may breed just prior to turning age 3.

RESULTS

Reproductive success and breeding probability

Estimates of first-time reproductive success and the probability of breeding increased with age (Table 1). The average reproductive success of novice birds was between 28% and 67% of the average reproductive success of breeding adults. Similarly, the probability of transitioning from non-breeder to breeder status increased with age (Table 1). Adults with prior breeding experience returned to breed in their natal colony in consecutive years with high probability (Pb_a = 0.94). Reproductive success of adult females was variable over time (Table 2) and averaged 0.46 ± 0.15 female chicks per nest. For status-quo conditions, the reproductive success was characterized with ω = 0.466 and ρ = −0.03.

Model fitting

Without estimated correction factors for survival rates, the population became extinct within 10 yr (Fig. 1a). Applying the fixed retention rates that were estimated for adult birds from the double-banding study for aluminum and stainless steel bands (δ = 0.6, 0.97, respectively; Hinke et al. 2014) also failed to fit to the data (Fig. 1a). Moreover, the estimated retention rate for aluminum bands caused survival rates to exceed 1.0 in some years, which is not biologically possible. We improved the fit to the census data when correction factors were estimated by the model. The estimated correction factors for stainless steel bands were generally smaller than for aluminum

Table 2. Annual mean female chick production (±1 SD) of established adult breeders, final estimates of survival rates for juvenile and adult stages from model fitting, and the derived correction factors for juveniles ($\delta_{juvenile}$) and adults (δ_{adult}).

Year	Adult reproductive success	Juvenile survival	$\delta_{juvenile}$	Adult survival	δ_{adult}
1982	0.46 ± 0.31	0.59	0.61	0.91	0.49
1983	NA	0.66	0.99	0.91	0.49
1984	0.58 ± 0.3	0.61	0.68	0.88	0.43
1985	NA	0.79	1.00	0.94	0.55
1986	0.59 ± 0.09	0.59	0.60	0.95	0.59
1987	0.3 ± 0.15	0.59	0.61	0.98	0.81
1988	0.46 ± 0.2	0.62	0.78	0.96	0.65
1989	0.28 ± 0.1	0.63	0.82	0.86	0.40
1990	0.16 ± 0.1	0.61	0.70	0.81	0.34
1991	0.37 ± 0.09	0.57	0.48	0.97	0.68
1992	0.38 ± 0.14	0.88	1.00	0.98	0.74
1993	0.59 ± 0.09	0.53	0.24	0.94	0.55
1994	0.48 ± 0.03	0.59	0.61	0.92	0.52
1995	0.63 ± 0.14	0.56	0.42	0.98	0.76
1996	0.31 ± 0.1	0.64	0.87	0.79	0.32
1997	0.75 ± 0.13	0.58	0.55	0.97	0.67
1998	0.70 ± 0.08	0.63	0.82	0.98	0.72
1999	0.48 ± 0.06	0.56	0.39	0.77	0.30
2000	0.64 ± 0.1	0.62	0.78	0.87	0.57
2001	0.25 ± 0.07	0.65	0.91	0.84	0.54
2002	0.46 ± 0.08	0.58	0.56	0.91	0.81
2003	0.44 ± 0.06	0.60	0.68	0.72	0.44
2004	0.51 ± 0.17	0.89	1.00	0.83	0.63
2005	0.52 ± 0.15	0.57	0.50	0.77	0.52
2006	0.46 ± 0.18	0.69	1.00	0.90	0.81
2007	0.21 ± 0.1	0.65	0.90	0.88	0.75
2008	0.53 ± 0.19	0.66	0.98	0.86	0.70
2009	0.19 ± 0.17	0.57	0.48	0.84	0.66
2010	0.60 ± 0.19	0.66	0.98	0.78	0.55
2011	0.60 ± 0.24	0.53	0.20	0.84	0.67

bands (Table 2), but larger than those estimated from the double-banding study. We therefore used the model-corrected estimates of adult and juvenile survival for all future projections (Table 2).

The fitted model predicted the observed long-term decline in breeding population, including the steep decline in breeder abundance from 1989 to 1991 and more gradual decline of the population in the late 2000s. The model also reproduced the high degree of variation in chick production and the general decline in total chick production observed at the Copacabana colony (Fig. 1b). The corrected, mean adult

survival probabilities over the last 30 yr were 0.88 ± 0.07, compared to mean juvenile survival rates of 0.63 ± 0.09. The corrected adult survival rates retained the pattern of relatively high rates punctuated by years with relatively low survival; adult survival rates were below average in 15 of 30 yr (ω = 0.5). Juvenile survival rates were more skewed with 60% (ω = 0.6) of years having survival rates less than the mean. Based on lag-1 autocorrelations estimated, we estimated ρ for adult survival at ρ = 0.206 and for juvenile survival at ρ = −0.34. The frequency of low survival years, estimated for a 10-year moving average to approximate penguin generation times in the wild (e.g., Clarke et al. 2003), increased over time for adults, but decreased for juveniles (Fig. 2).
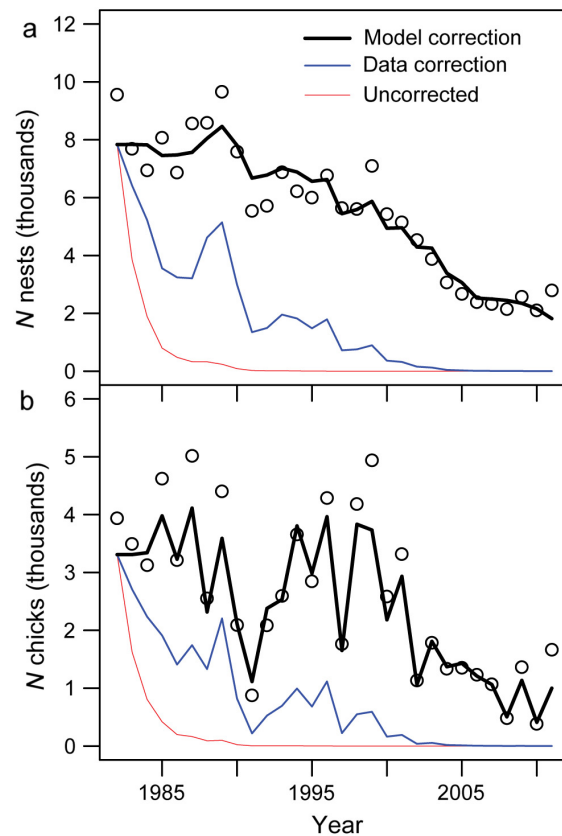

Fig. 1. Model estimates for the number of nests (a) and chick production (b) for uncorrected adult survival (red line), data-corrected survival (blue line), model-estimated survival based on correction factors (black line). Data are plotted as open circles.
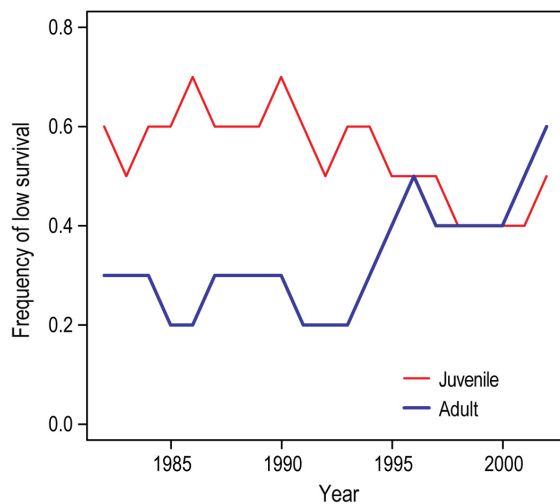
Fig. 2. Frequency of below-average survival during 10-year moving windows during the study period for the model-corrected juvenile (blue line) and adult survival rates.

Probability of depletion

Monte Carlo simulations identified a high risk of local depletion across a wide range of ω and depletion thresholds (Fig. 3). Risk was higher with lower depletion thresholds and greater ω in all cases. Notably, the risk of 80% and 90% depletions increased rapidly as ω increased beyond 0.3. If future survival rates vary in a manner similar to historical variation in adult survival rates, there is a nearly 33% risk that the population will fall >90% within 30 yr. The risk of 90% depletions nearly doubles with only a 10% increase in ω and approaches 100% once ω exceeds 0.8 (Fig. 3a). The model suggests that 50% declines in the Copacabana colony over the next 30 yr are near certain (Fig 3a) without reductions in the frequency of poor survival condition. Across all depletion thresholds, total increases in depletion risk were greater when adult survival rates were affected than when only juvenile survival rates were affected (this effect is illustrated only for simulations using the 90% depletion threshold in Fig. 3a).

The model suggests there is limited scope for recovery of the population. The risk of large depletions fell toward zero as ω decreased from historical means (Fig. 3a) and positive population growth rates were predicted for ω < 0.2 (Fig. 3b). This is generally consistent with the observed stabilization in the Copacabana population since about 2000 (Fig. 1). Nonetheless, simulations with low depletion risk are characterized by negative population growth rates (Fig. 3b) at levels of ω ≥ 0.2, a level less than the historical expectation.

The risk of depletion was less sensitive to small changes in the autocorrelation (ρ) in the proxy environmental index than to the expected proportion of years (ω) with poor survival. Neither the sign nor the magnitude of the autocorrelation in the projected environmental state caused our predictions to differ from the base case. Examples of this insensitivity are plotted for simulations that affected adult survival rates only (Fig. 3a).

Future variation in fecundity had a larger effect on the risk of depletion (Fig. 4). Assuming status-quo survival conditions, the risk of 90% depletion ranged from 13% to 57%, while the risk of 80% depletion ranged from 65% to 96% depending on the expected frequency of low reproductive success. The relatively high sensitivity of population status to variation in fecundity suggests that factors impacting breeding success alone can have important short-term consequences for local population growth rates.

Discussion

Increasingly negative population growth rates under more variable survival conditions suggest that the population of Adélie penguins at Copacabana will continue to decline if the frequency of years with poor adult survival remains at, or increases above, its current state. Under status-quo conditions, the risk of >90% declines within 30 yr was estimated to be roughly 33%, but increased rapidly with minor increases in the frequency of years with poor survival. Based on IUCN Red List criteria, this breeding population of Adélie penguins would be considered endangered (50% decline within 30 yr) with high probability given no further change in survival rates. Given expectations that warming trends and loss of sea ice in the Antarctic Peninsula region (IPCC 2013) will be chronic stressors, negative population growth rates of Adélie penguins throughout the Antarctic Peninsula region (Lynch et al. 2012) will likely remain negative over the long term.

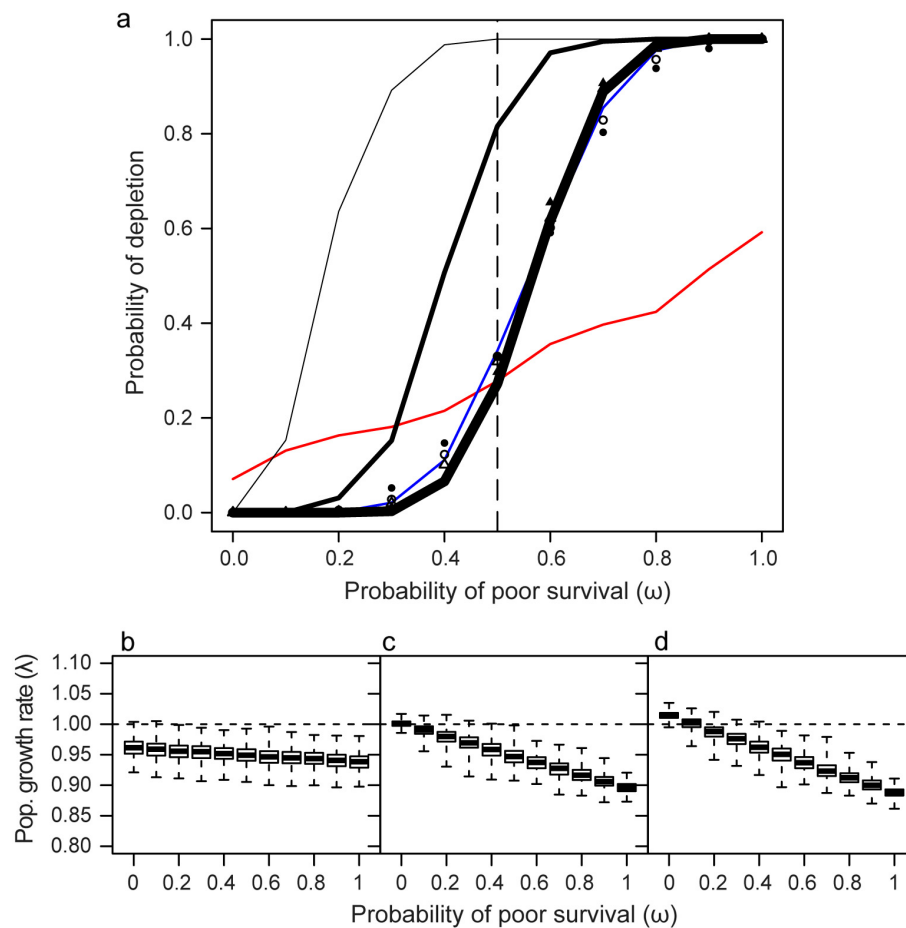A key uncertainty concerning the rate of population decline in this study arises from relatively

Fig. 3. Probability of local depletion and mean population growth rates of Adélie penguins under alternative scenarios about the expected frequency (ω) of future survival scenarios. (a) Probability of local depletion for depletion thresholds of 50% (thin black line), 80% (medium black line), and 90% (thick black line) during 30-year projections assuming historical levels of autocorrelation (ρ) in survival indices. Risk of depletion when only juvenile survival varies (red line) and when only adult survival varies (blue line) is included for the 90% threshold. The historical mean probability of years with poor survival is marked with the vertical dashed line. The effect of different degrees of autocorrelation in the proxy environmental index is displayed for positive (circles) and negative (triangles) shifts in autocorrelation values by 0.1 (open points) and 0.25 (closed points) on the adult-only projection scenario with a 90% depletion threshold. (b–d) Boxplots of population growth rates (λ) from 30-year projections under different expectations of the probability of poor survival events for juvenile-only (b), adult-only (c), and juvenile plus adult projection scenarios (d).

weak correlations between indices of environmental conditions and the estimates of penguin survival rates (Hinke et al. 2014). As noted by Hinke et al. (2014), regional sea ice extent anomalies were positively correlated with estimates of adult and juvenile survival rates at the Copacabana colony and those correlations persist in the MSMR model estimates here (see Appendix S1). Nonetheless, the relationship at the Copacabana colony

is weaker than findings of demographic studies of Adélie penguins from elsewhere in the Antarctic, where relatively stronger effects of sea ice extent have been reported (e.g., Jenouvrier et al. 2006, Ballerini et al. 2009, Emmerson and Southwell 2011). For example, Ballerini et al. (2009) reported that sea ice extent anomalies could explain up to 95% of the temporal variability in survival rates in the Ross Sea. Such strong relationships reflect the
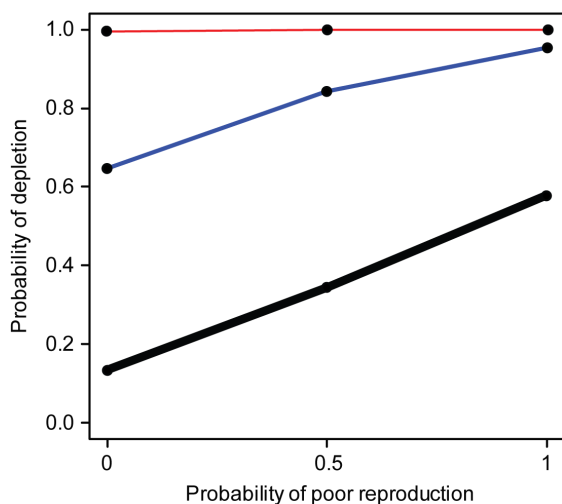
Fig. 4. Risk of depletion for 50% (red line), 80% (blue line), and 90% (black line) thresholds due to future variation in reproductive success assuming constant, status-quo survival conditions.

relatively dominant role of sea ice in dictating access to breeding and foraging areas in southern colonies (Wilson et al. 2001, Ballerini et al. 2009). This contrasts with the northern colonies of Adélie penguins, particularly those in the western Antarctic Peninsula, where losses of sea ice (Stammerjohn et al. 2008) appear to have cascaded through the ecosystem and resulted in reductions in primary production (Schofield et al. 2010) and episodic secondary production (e.g., krill recruitment; Fraser and Hofmann 2003, Trivelpiece et al. 2011). While sea ice conditions are correlated with survival rates at the Copacabana colony, it is not surprising that the magnitude of direct effects of physical drivers on demographic rates is lower in the western Antarctic Peninsula region. Such relatively weak relationships hinder development of robust population projections based on single environmental indices.

Statistical relationships between demographic rates and environmental drivers are not always clear or strong, potentially because of poor-quality demographic data (Beissinger and Westphal 1998) or synergistic effects of multiple climate and biological drivers that are difficult to identify a priori (Brook et al. 2008). Without good statistical underpinning, estimates of future survival rates and predictions of population trends based on IPCC-type model outputs (e.g., Jenouvrier et al.

2009*b*, Ballerini et al. 2015) are difficult. Despite the statistics, however, there is widespread recognition that environmental factors have important effects on Adélie penguin survival and reproduction (Ainley 2002, Forcada and Trathan 2009). To circumvent the lack of strong statistical relationships between vital rates and environmental indices at the Copacabana colony, we chose a simple stochastic Monte Carlo method to examine whether the variability observed in historical data was sufficient to drive further population decline. Implicit in this approach is an assumption that the historical distribution of survival rates adequately applies to future conditions; this cannot be known with certainty. Nonetheless, an advantage of constraining projections with historical distributions is that the assessment of future population trends is based on an observed range of survival, rather than on correlations between demographic rates and environmental indices that may change under changing environmental conditions (Scheffer et al. 2009).

Our results demonstrate that small increases beyond the historical average of the frequency of years with poor adult survival or reproductive success can substantially increase the risk of large population declines in the near term. The magnitude and rate of declines modeled here are commensurate with recent forecasts of Adélie penguin populations based on models that consider demographic data and environmental drivers in the Ross Sea (Ballerini et al. 2015) and from a circumpolar analysis of habitat suitability for Adélie penguins based on indices of novel climate conditions experienced by Adélie penguins (Cimino et al. 2016). The similarity of results from these different analytical approaches is worth highlighting; the weight of evidence clearly suggests that expectations for climate warming and loss in sea ice in the Antarctic, and in the Antarctic Peninsula region in particular, will perpetuate population declines among Adélie penguins throughout their breeding range.

In estimating the risk of depletion at the Copacabana colony, we mainly considered the effect of varying the frequency of poor survival rates to predict future population sizes. A focus on adult survival rates is useful for long-lived species like penguins because population growth rates are typically most sensitive to changes in adult survival rates in the long term (Sæther and

Bakke 2000). Nonetheless, the risk of local depletion may be substantially higher in the short term because of additional effects of stochastic variation in breeding success at small population sizes (e.g., Boersma 2008, Jenouvrier et al. 2009*a*). Indeed, while depletion risk in the Copacabana colony appeared to be most sensitive to adult survival rates, there were non-trivial effects of variation in future reproductive success. Finally, we note that depensatory dynamics arising from predation or other Allee effects (e.g., Watters et al. 2013), catastrophic events that can rapidly decrease population sizes (Gerber and Hilborn 2001, Ovaskainen and Meerson 2010), and potential dispersal to more suitable areas (e.g., Dugger et al. 2010) may further accelerate the rate of population decline. In particular, the apparent survival rates used in this analysis implicitly conflate, but cannot resolve, the processes of survival and permanent emigration. Opportunistic sightings of banded individuals are rare, although at least one banded animal from the Copacabana colony site has been resighted in a large breeding colony on Paulet Island, some 200 km southeast of the study colony (H. Lynch, *personal communication*). While anecdotal, this relative absence of inter-colony movement is a motivating factor for our focus on changes in survival. Thus, we feel the estimated risks of depletion presented here are conservative.

From local decline to regional concern

The Copacabana colony contains a small percentage of the global population of Adélie penguins, estimated recently to be near 3.65 million breeding pairs (Lynch and LaRue 2014). However, declines in abundance at the Copacabana colony are consistent with declines in abundance throughout the Antarctic Peninsula and South Atlantic region, home to roughly 29% of the global population of Adélie penguins (Lynch et al. 2012, Lynch and LaRue 2014). If our model results from the Copacabana colony reflect regional dynamics generally, then substantive declines in the abundance of Adélie penguins in the Antarctic Peninsula region might be expected to continue. Such regional declines, while contrasting the stable to increasing populations of Adélie penguins elsewhere in Antarctica (Southwell and Emmerson 2013, Lynch and LaRue 2014), will affect the Antarctic Peninsula ecosystem via vacated niche space, reduced predation pressure on krill and fish, reductions in marine–terrestrial nutrient exchange, and altered predator–prey interactions within the remaining marine food web. Such regional-scale losses of key ecological components have been related to reduced ecosystem resilience throughout the world's oceans (Worm et al. 2006). Given the backdrop of rapid climate and ecosystem change already underway in the Antarctic Peninsula region (Schofield et al. 2010), predicted depletions of Adélie penguins add uncertainty and urgency to management and conservation efforts in the Antarctic.

Implications for the fisheries management in the Southern Ocean

Fisheries management in the Southern Ocean is conducted by the Commission for Conservation of Antarctic Living Marine Resources (CCAMLR). A major objective of the Commission is to minimize the risk of changes in marine ecosystems due to harvesting that are not potentially reversible within two or three decades (CCAMLR 1980). Detection of a high risk of local depletion over a relatively short time frame is therefore applicable to the management protocols for Antarctic marine living resources. With respect to Adélie penguins, the Antarctic krill fishery is a potential competitor for krill. Assessments of the marginal impacts of the krill fishery on krill-dependent predators, such as Adélie penguins, have suggested that penguin populations are at risk of being depleted as catches increase (Plaganyi and Butterworth 2012, Watters et al. 2013). Therefore, observations of a sustained decline in Adélie penguin abundance might trigger a fisheries management action (e.g., re-distributing catches to areas not potentially used by Adélie penguins) aimed to mitigate ongoing negative population trends. However, an important question to resolve is whether (and to what extent) management of the krill fishery would affect the population growth rate of Adélie penguins. Functional relationships between krill abundance and indices of reproductive success and offspring growth have been described for krill-dependent predators and suggest improved growth and offspring production with higher krill density (Reid et al. 2005). However, the relationships between krill abundance and survival rates that largely influence population growth rates remain elusive. If variation in

Adélie penguin survival is attributable to changes in the availability of krill, then a management action to minimize the risks of krill harvesting on Adélie penguins might be effective (Watters et al. 2013). Nonetheless, climate change-induced increases in temperatures and consequent loss of sea ice will also impact the productivity and distribution of Antarctic krill (Loeb et al. 1997), which depend on winter sea ice to complete their life cycle (Nicol 2006). Given the underlying physical changes in the environment and expectation for further long-term degradation of the cryosphere (IPCC 2013), the marginal effects of management action on Adélie penguin population growth rates may be difficult to assess. This is a key challenge to resolve for effective ecosystem-based fisheries management and conservation of Antarctic fauna.

Acknowledgments

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