

Warming effects in the western Antarctic Peninsula ecosystem: the role of population dynamic models for explaining and predicting penguin trends

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Abstract The western Antarctica Peninsula and Scotia Sea ecosystems appear to be driven by complex links between climatic variables, primary productivity, krill and Avian predators. There are several studies reporting statistical relationships between climate, krill and Penguin population size. The Adélie (*Pygoscelis adeliae*), Chinstrap (*P. antarctica*) and Gentoo (*P. papua*) penguins appear to be influenced by interannual variability in sea-ice extent and krill biomass. In this paper we developed simple conceptual models to decipher the role of climate and krill fluctuations on the population dynamics of these three *Pygoscelis* penguin species inhabiting the Antarctic Peninsula region. Our results suggest that the relevant processes underlying the population dynamics of these penguin species at King George Island (South Shetland Islands) are intra-specific competition and the combined effects of krill abundance and sea-ice cover. Our results using population theoretical models appear to support that climate change, specifically regional warming on the western Antarctic Peninsula, represents a major driver. At our study site, penguins showed species-specific responses to climate change. While Chinstrap penguins were only influenced by krill abundance, the contrasting population trends of Adélie and Gentoo penguins appear to be better

explained by the “sea-ice hypothesis”. We think that proper population dynamic modeling and theory are essential for deciphering and proposing the ecological mechanisms underlying dynamics of these penguin populations.

Keywords Climate change · Dynamics · Krill · Penguin populations · Predictions

Introduction

One of the pressing contemporary issues in ecology is predicting the response of natural populations to climate change (Stenseth et al. 2002; Walther et al. 2002). Population dynamics models are simple tools based on logical and ecological principles that can be applied to analyze ecological time series to understand and predict the effects of climate change (Royama 1992; Sæther et al. 2000; Stenseth et al. 2002; Berryman and Lima 2006; Lima and Beryman 2006; Lima et al. 2006, 2008a, b; Lima and Naya 2011; Estay and Lima 2010).

In the Southern Ocean, the region of the Western Antarctic Peninsula (WAP) is undergoing one of the most rapid environmental and ecological changes. In this region, important effects of global climate warming have been detected, such as an increase in air temperature and the associated drop in sea-ice cover (Smith et al. 1999; Vaughan et al. 2001; Gille 2002; Cook et al. 2005). These changes have profoundly affected several biological processes at different ecological levels (Croxall et al. 2002; Atkinson et al. 2004; Murphy et al. 2007; McClintock et al. 2008). For example, the continuous decline in the winter sea-ice extent and the increase in the sea surface temperature have impacted the recruitment and abundance of the

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Antarctic krill populations (*Euphausia superba*) (Atkinson et al. 2004; Murphy et al. 2007). Because krill is a key component in the Antarctic marine food webs (Atkinson et al. 2004), the magnitude of these changes may affect the population dynamics of top predators such as albatrosses, penguins, seals and whales (Croxall et al. 2002; Fraser and Hofmann 2003). Therefore, understanding how climatic variability may propagate its effects across the upper tropic levels is fundamental for predicting ecosystem responses.

In particular, some penguin populations have responded to the recent changes in sea-ice cover and krill population trends (Fraser et al. 1992; Croxall et al. 2002; Fraser and Hofmann 2003; Forcada et al. 2006; Carlini et al. 2009; Lynch et al. 2010). The Adélie (*Pygoscelis adeliae*), Chinstrap (*P. antarctica*) and Gentoo (*P. papua*) penguins appear to be influenced by the inter-annual variability in the sea-ice cover extent (Fraser et al. 1992; Trathan et al. 1996; Ainley et al. 1998; Wilson et al. 2001; Kato et al. 2002; Fraser and Hofmann 2003; Trivelpiece et al. 2011; Lynch et al. 2012). However, contrasting population trends have been recorded between species and localities (Croxall et al. 2002; Trivelpiece et al. 2011; Lynch et al. 2012). For example, Adélie penguin populations breeding at the Ross Sea and eastern Antarctica have been increasing during the last decades (Croxall et al. 2002; Kato et al. 2002), while the breeding populations from the Antarctic Peninsula and South Orkney Islands have exhibited a decreasing trend (Croxall et al. 2002; Forcada et al. 2006; Carlini et al. 2009; Lynch et al. 2010). Because Chinstrap penguins (*P. antarctica*) are essentially confined to the Antarctic Peninsula, almost all the populations showed negative trends during the last decade (Forcada et al. 2006). On the other hand, Gentoo penguins are mainly sub-Antarctic with a subspecies confined to the Antarctic Peninsula (Forcada et al. 2006). The latter species showed a positive population trend during the last years (Carlini et al. 2009; Lynch et al. 2010). The population trends observed in these penguin species seem to be caused by the reduction in the sea-ice cover and krill abundance (Croxall et al. 2002; Fraser and Hofmann 2003; Forcada et al. 2006). However, given the close relationship between sea-ice cover and krill recruitment (Atkinson et al. 2004; Murphy et al. 2007), the exact causal path between climate, food availability and penguin population dynamics may be difficult to decipher.

To date there are several studies reporting statistical relationships between climate, krill and penguins abundance and demography at Western Antarctic Peninsula ecosystem (Croxall et al. 2002; Atkinson et al. 2004; Forcada et al. 2006; Murphy et al. 2007; Trivelpiece et al. 2011; Lynch et al. 2012). Considering the large amount of previous studies, it is valid to question whether something new can be said about the role of climate warming on population trends of penguins. Although statistical analyses

are useful tools to detect relationships between variables and to show common signatures in the time or frequency domain, they do not provide causal explanations based on general ecological principles (Berryman 1999; Turchin 2003; Ginzburg and Colyvan 2004). Therefore, we propose the use of theoretical population dynamics models as a platform that may allow us to decipher the effects of climate change on the population trends of these species, providing a solid and simple background to analyze and interpret fluctuations in animal populations (Royama 1992; Berryman 1999; Ginzburg and Colyvan 2004; Ginzburg and Jensen 2004). Moreover, the models used in the present study are easy to fit to data, their parameters are ecologically interpretable, and their predictions can be tested against independent data (Berryman and Lima 2006; Lima et al. 2008a, b; Lima and Naya 2011), all of which make them essential tools in any efforts to anticipate unknown effects of climate change.

In consequence, based on the previous knowledge about the links between climate, krill and penguin dynamics, we will develop simple conceptual models to decipher the role of climate and krill fluctuations on the population dynamics of these three *Pygoscelis* penguin species inhabiting the Antarctic Peninsula region.

Methods

Climatic data

Sea surface temperature (SST) was obtained from the Hadley centre data sets (<http://www.metoffice.gov.uk/hadobs/hadsst2/>). This data set was obtained from the International Comprehensive Ocean–Atmosphere Data Set, ICOADS, from 1978 to 1997 and from the NCEP-GTS from 1998 to the present. HadSST2 is produced by taking in situ measurements of SST from ships and buoys, rejecting any measurements which fail quality checks. Measurements are converted to anomalies by subtracting climatological values from the measurements, and calculating a robust average of the resulting anomalies on a 5° by 5° degree monthly grid (Rayner et al. 2006). In particular, we used those cells located both west and east of the Ardley Island (Fildes Peninsula, King George Island), where our focal penguins populations are located.

Total ice-covered area (ICE) was obtained from the National Snow and Ice Data Center (NSIDC, <http://www.nsidc.org>) from 1978 to 2007. Total ice-covered area is defined as the area of each pixel with at least 15 percent ice concentration multiplied by the ice fraction in the pixel. In particular, we used cells located west (Bellingshausen and Amundsen Seas) and east (Weddell Sea) of the Ardley Island (Fildes Peninsula, King George Island). To assess

potential effects of ice seasonality on penguin populations. Ice cover data sets were divided in two seasons: winter (June–November) and summer (December–May) total ice-covered area.

Annual southern annular mode (SAM) index was obtained from <http://www.nerc-bas.ac.uk/icd/gjma/sam.html>. This index is calculated as described by Marshall (2003), using real sea-level pressure from six stations; the SAM is a pattern of tropospheric circulation variability centered on Antarctica, whose influence affects several atmospheric and oceanographic conditions.

Penguin data

Data on breeding population size was collected annually at every Adélie-, Chinstrap- and Gentoo-breeding colony on Ardley Island (Fildes Peninsula, King George Island; Fig. 1) from 1980 to 2006 (Fig. 2a–c). The index of abundance used was the count of active breeding pairs collected by observers during the month of December.

Krill data

Data representing krill (*E. superba*) abundance was obtained from aggregated catch and effort data aggregated over a fine-scale rectangle (0.5° latitude by 1.0° longitude) and by month by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) secretary. The area used corresponds to the rectangle located between latitude 60°S–64°S and longitude 54°W–65°W, (Subarea 48.1, Fig. 1). The catch data is given in tons (T), and the effort data represent total hours fished during a month in each rectangle. We transformed this data to catch per unit

of effort by adding the total tons of catch in the area and season (from October to April) and then dividing the resulting sum by the total hours fished (Fig. 2d).

Diagnosis and statistical models of population dynamics

To determining the endogenous structure of the penguin and krill populations, we first determined the order of the feedback structure of these time series. Hence, we carried out an autoregressive analysis using the partial rate correlation function (PRCF), according to Berryman and Turchin (2001). In all cases the populations were dominated by first-order feedback (Fig. 3); therefore, we used a nonlinear version of the simple Ricker's (1954) equation as a starting point to model the reproductive function or *R*-function (Berryman 1999). This allowed us to model the basic influence of endogenous and exogenous forces on these dynamics.

Theoretical models of population dynamics

Population dynamics of penguins and krill appear to be the result of intra-population processes that cause a first-order feedback structure in population fluctuations. To understand how these processes determine penguin and krill dynamics, we used a simple model of intra-specific competition, the exponential form of the discrete logistic model (Ricker 1954; Royama 1992):

$$N_t = N_{t-1} \times r_m \times \exp[-c \times N_{t-1}^a] \quad (1)$$

where N_t represents the population abundance at time t , r_m is a positive constant representing the maximum finite reproductive rate, c is a constant representing competition and resource depletion, and a indicates the effect of interference on each individual as density increases (Royama 1992); $a > 1$ indicates that interference intensifies with density and $a < 1$ indicates habituation to interference. By defining Eq. 1 in terms of the *R*-function, $R_t = \log_e(N_t/N_{t-1})$, log-transforming Eq. 1, and defining the population density in logarithm $X_t = \log_e(N_t)$, we obtain

$$R_t = R_m - \exp[a \times X_{t-1} + C] \quad (2)$$

where R_t is the realized per capita growth rate $R_t = \log_e(N_t/N_{t-1})$, $R_m = \log_e(r_m)$, a is the same parameter as in Eq. 1, $C = \log_e(c)$, and $X = \log_e(N)$. This model represents the basic feedback structure determined by intra-population processes. Because in this model the three parameters R_m , a , and C have an explicit biological interpretation, we can include climatic perturbations in each parameter using the framework of Royama (1992). In this manner, we may build mechanistic

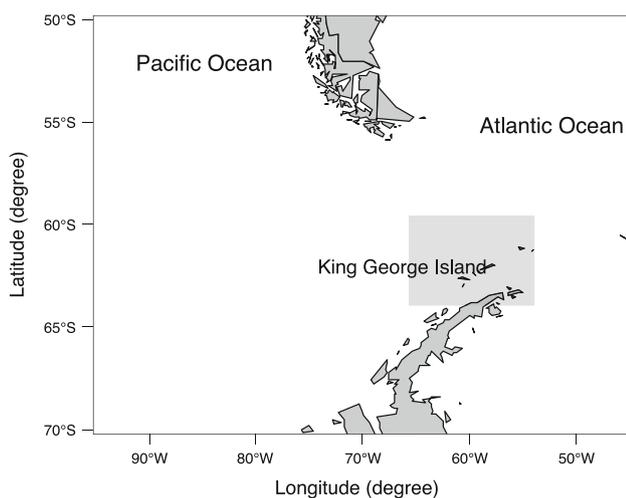


Fig. 1 Antarctic Peninsula region, where the King George Island is located. The grey shaded area corresponds to the subarea 48.1 where data of krill CPUE were obtained

Fig. 2 Logarithm of the annual counts of breeding pairs at Fildes Peninsula, King George Island, **a** The Chinstrap penguin (*P. antarctica*), **b** the Adélie penguin (*P. adeliae*), **c** the Gentoo penguin (*P. papua*) and **d** logarithm of the krill biomass estimated from CPUE data at subarea 48.1

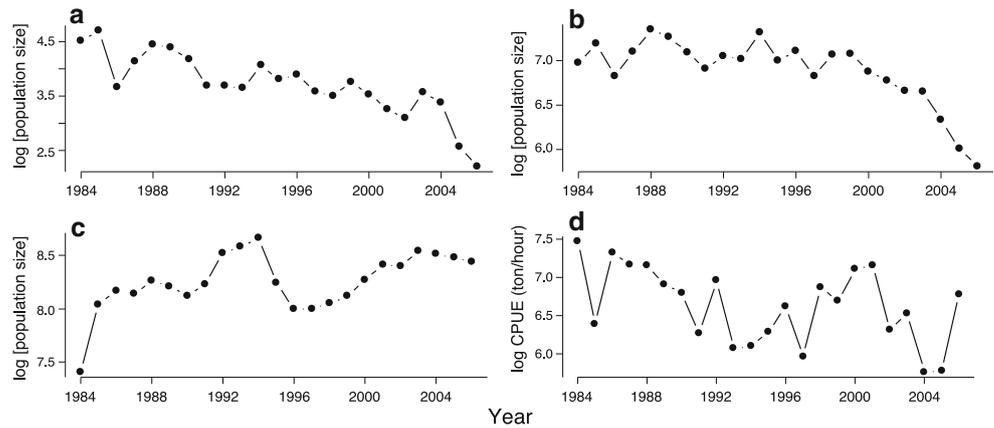
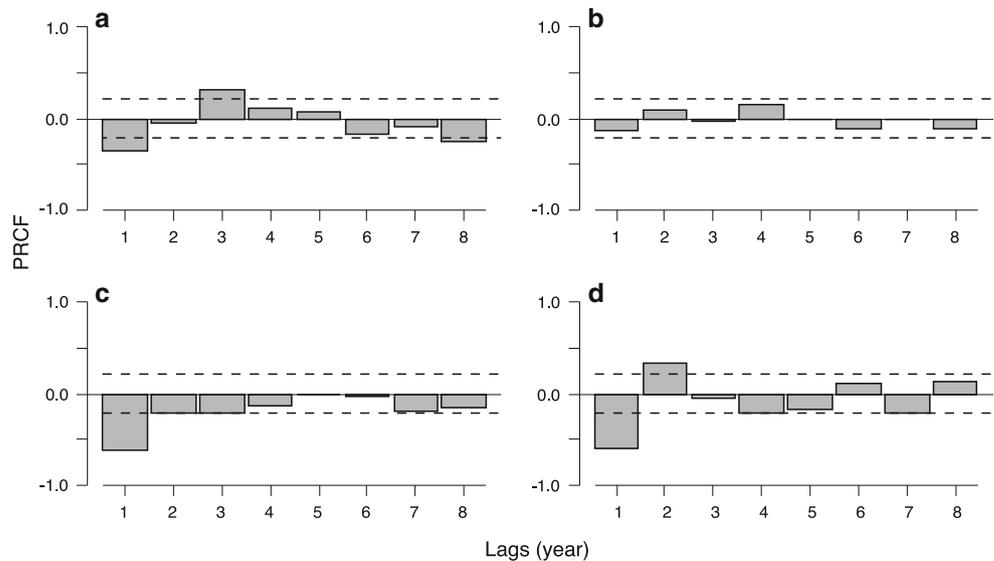


Fig. 3 PRCF plots for penguin and krill time series data. **a** The Chinstrap penguin (*P. antarctica*), **b** the Adélie penguin (*P. adeliae*), **c** the Gentoo penguin (*P. papua*) and **d** krill (*E. superba*) biomass estimates. The major influence of first-order feedback structure is clear. Dashed lines represent a 23-year time series Bartlett band, which is a rough approximation to the 95 % confidence interval



hypotheses about the effects of climate in these three penguin populations. For example, a simple additive climatic perturbation effect may be represented as a “vertical” effect that shifts the relative position of the *R*-function by changing *R_m* on the *y*-axis (Royama 1992). This may be expressed as;

$$R'_m = R_m + g(\text{Climate}) \tag{3}$$

where *g* is a simple linear function (positive or negative) of the different exogenous variables at different lags (e.g., SST or SAM). Another kind of climatic perturbation may occur when the equilibrium point of the population is influenced by the climate. This is the case when climate influences a limiting factor or resource such as food or shelter. The correct model structure in this scenario is that the carrying capacity (equilibrium point) is affected by the exogenous variable. In this case the climatic factor shifts the *R*-function curve along the *x*-axis without changing the slope at the equilibrium, which represents a “lateral” perturbation in Royama’s (1992) framework:

$$C' = C + g(\text{Climate/krill}) \tag{4}$$

In addition, we may include also in the logistic Eq. 1 a term representing inter-specific competition. In this ecosystem, the three penguin species showed similar ecological roles and food preferences (Lynnes et al. 2002), but they seem to exploit food resources at different areas and depths (Wilson 2010). Hence, a logistic model including intra- and inter-specific competition may be used to test this hypothesis.

$$N_t = N_{t-1} \times r_m \times \exp[-c \times N_{t-1}^a - c_1 \times P_{t-1}^b] \tag{5}$$

As in Eq. 1, *N_t* represents the penguin abundance at time *t*, *r_m* is a positive constant representing the maximum finite reproductive rate, *c* is a constant representing competition and resource depletion, and *a* indicates the effect of interference on each individual as density increase (Royama 1992). In addition, *P_t* is the density of the inter-specific competitor with *c₁* representing a constant inter-specific effect on the resource depletion and *b* indicating

the effect of interference on each inter-specific individuals. We defined Eq. 5 in terms of the R -function by defining $R_t = \log_e(N_t/N_{t-1})$, log-transforming Eq. 5, and defining the population density in logarithm $X_t = \log_e(N_t)$ and $Y_t = \log_e(P_t)$, resulting in the following equation:

$$R_t = R_m - \exp[a \times X_{t-1} + b \times Y_{t-1} + C_1] \quad (6)$$

where R_t is the realized per capita growth rate $R_t = \log_e(N_t/N_{t-1})$, $R_m = \log_e(r_m)$, a and b are the same parameters as in Eq. 5, and $C_1 = \log_e(c + c_1)$. This model represents the basic feedback structure determined by intra- and inter-population processes.

We fitted Eqs. 4, 6 by means of nonlinear regression analyses (Bates and Watts 1988) using the nls library in the program R (R Development Core Team 2011). In addition, we included the climatic variables in the parameters R_m , C , and a as linear functions (Eqs. 5, 6). All of the models were fitted and ranked according to the Bayesian information criterion (BIC) (Schwarz 1978). For clarity, BIC weights were also included in the results. Minimum BIC was selected to determine the best model. We used the data for the period between 1984 and 2000 to fit the models and data from the period between 2000 and 2006 to test the model predictions. To assess the predictive performance of the models we calculated the values of the root-mean-square prediction error (rmse; Sheiner and Beal 1981). Smallest rmse values represent the best predictive performance. In addition, we used Pearson's correlation coefficient between the observed and predicted numbers to assess model predictions. We used biological criteria to fix the R_m parameter (maximum per capita growth rates) (see Royama 1992). Observed maximum per capita growth rates in all three penguin species were between 0.40 and 0.65; which is consistent with the life history of these species.

Results

The numerical fluctuations of the three penguin species showed contrasting patterns. Chinstrap (*P. antarctica*) and Adélie (*P. adeliae*) penguins populations were characterized by irregular oscillations and a sudden decrease during the last years (Fig. 2a, b). In contrast, Gentoo penguins (*P. papua*) showed a positive trend during the last years in the study site (Fig. 2c). First-order negative feedback, PRCF (1), was the most important component of per capita growth rates in all the species analyzed (Fig. 3a–c). These results suggest that intra-specific competition is the most important component of these three feedback structures. The population fluctuation of the krill (*E. superba*) showed large irregular oscillations and a negative trend (Fig. 2d), similar to the penguin time series data. The krill

fluctuations were also characterized by a first-order negative feedback (Fig. 3d).

According to our analyses the logistic model without exogenous effects accounts for 24, 39, 44 and 44 % of the observed variation in R values of *P. antarctica*, *P. adeliae*, *P. papua* and *E. superba*, respectively (Table 1). The addition of krill abundance as a lateral effect in *P. antarctica* logistic models increased explained variance from 24 to 49 %. Also, the BIC criteria and the BIC weights indicated a strong support for the role of food (krill) as the main factor affecting chinstrap fluctuations (Table 1). Model 5 which includes krill as a lateral perturbation was 6.09 times more likely than model 1 ($w_1/w_5 = 6.09$). In addition, the second best model suggests a positive effect of the one year-lagged summer sea-ice cover (Table 1). These two models showed almost no differences in their predictive ability (Table 1), further suggesting the importance of krill biomass in determining the population decrease observed during the 2000–2006 period (Fig. 4a).

The addition of west side winter sea-ice cover seems to be the most important exogenous factor for *P. adeliae*, increasing explained variance from 39 to 50 % (Table 1). Similar models using east side winter sea-ice cover, or summer sea-ice cover also showed a good fit to the data, but their empirical support based on the BIC and BIC weights was weak (Table 1; $w_1/w_4 = 1.40$). Moreover, models using sea-ice cover as a lateral effect captured the negative trend of the observed data during the period 2000–2006 (Fig. 4b; Table 1). Nevertheless, it is important to note that the best models predicted higher values than the observed data for the years 2000–2006.

The Gentoo penguins (*P. papua*) showed positive effects of warming, the inclusion of one year-lagged positive effects of summer sea surface temperature (east side) and the negative effects of one year-lagged east side winter sea-ice cover increase the explained variance from 44 to 70 % (Table S1 in Electronic supplementary material). The evidence ratio showed that this model has 11.7 times more empirical support than the pure endogenous model ($w_1/w_5 = 11.74$). A close model was one with winter sea-ice cover and west side summer sea surface temperature effects, according to the BIC and BIC weights (Table 1). In both cases, model predictions appear to capture the increasing trend in this penguin species during the 2000–2006 period (Fig. 4c; Table 1).

The models including west side summer sea-ice cover as an exogenous lateral perturbation effect in the krill (*E. superba*) increased the explained variance from 44 to 59 % (Table 1). The addition of the lagged west side summer sea-ice cover also had some level of support according to the BIC and BIC weights values (Table 1). Although the model selection procedure was not able to distinguish a simple best model, the first best five models always include

Table 1 Optimal population dynamic models for penguin species and krill using the exponential ($R_t = R_m - e^{[aX_{t-1}+C]}$) form of logistic growth (Royama 1992); parameter values are given in the equations

	Log-likelihood	BIC	P	ΔBIC	w_i	R^2	rmse	r_p
Models for <i>Pygoscelis antarctica</i>								
1. $R_t = 0.5 - \exp(1.09 X_{t-1} - 0.82 - 0.62 Krill_t)$	-1.09	13.51	4	0.00	0.25	0.49	0.43	0.69
2. $R_t = 0.5 - \exp(1.18 X_{t-1} - 1.32 - 0.52 Krill_{t-0.88} Ice-sw_{t-1})$	-0.86	15.92	4	2.41	0.075	0.50	0.41	0.74
3. $R_t = 0.5 - \exp(1.16 X_{t-1} - 3.90 - 2.27 Ice-sw_{t-1})$	-2.71	16.73	4	3.22	0.050	0.37		
4. $R_t = 0.5 - \exp(0.21 X_{t-1} + 0.11) + 0.30 Krill_t$	-2.80	16.93	4	3.42	0.045	0.37		
5. $R_t = 0.5 - \exp(0.82 X_{t-1} - 3.84)$	-4.30	17.12	3	3.61	0.041	0.24		
6. $R_t = 0.5 - \exp(0.48 X_{t-1} - 1.65) + 1.29 Ice - sw_{t-1}$	-3.08	17.51	4	4.00	0.034	0.34		
7. $R_t = 0.5 - \exp(0.42 X_{t-1} - 1.46) + 1.10 Ice-sw_t$	-3.13	17.59	4	4.08	0.033	0.34		
8. $R_t = 0.5 - \exp(1.03 X_{t-1} - 4.71 + 0.40 SST-e_{t-1})$	-3.16	17.64	4	4.14	0.032	0.34		
9. $R_t = 0.5 - \exp(0.97 X_{t-1} - 4.49) - 0.28 SST-e_{t-1}$	-3.26	17.85	4	4.34	0.029	0.33		
Models for <i>Pygoscelis adeliae</i>								
1. $R_t = 0.4 - \exp(2.45 X_{t-1} - 14.50 - 0.77 Ice-we_t)$	7.79	-4.24	4	0.00	0.081	0.50	0.32	0.93
2. $R_t = 0.4 - \exp(1.30 X_{t-1} - 9.45) + 0.63 Ice-sw_{t-1}$	7.55	-3.77	4	0.47	0.063	0.49		
3. $R_t = 0.4 - \exp(2.40 X_{t-1} - 19.39 + 1.03 Ice-ww_t)$	7.54	-3.74	4	0.50	0.061	0.48		
4. $R_t = 0.4 - \exp(1.96 X_{t-1} - 14.79)$	6.10	-3.70	3	0.54	0.061	0.39		
5. $R_t = 0.4 - \exp(2.19 X_{t-1} - 15.95) - 0.034 SAM_{t-2}$	7.50	-3.67	4	0.57	0.061	0.49		
6. $R_t = 0.4 - \exp(2.38 X_{t-1} - 17.08 - 1.20 Ice-sw_{t-1})$	7.40	-3.47	4	0.77	0.062	0.48		
7. $R_t = 0.4 - \exp(1.95 X_{t-1} - 14.72 + 0.07 SAM_{t-2})$	7.27	-3.21	4	1.03	0.048	0.47		
8. $R_t = 0.4 - \exp(3.25 X_{t-1} - 16.65 - 1.12 Ice-we_{t-0.28} Krill_{t-1} + 0.27 SST-w_{t-2})$	10.06	-3.11	6	1.13	0.045	0.62	0.34	0.90
Models for <i>Pygoscelis papua</i>								
1. $R_t = 0.65 - \exp(0.49 X_{t-1} - 7.80 + 0.36 SST - e_{t-1} + 0.66 Ice-we_{t-1})$	12.42	-10.67	5	0.00	0.54	0.70	0.04	0.69
2. $R_t = 0.65 - \exp(0.54 X_{t-1} - 7.69 + 0.27 SST-w_{t-1} + 0.54 Ice-we_{t-1})$	12.26	-10.35	5	0.32	0.46	0.69	0.05	0.62
3. $R_t = 0.65 - \exp(0.72 X_{t-1} - 6.50 + 0.22 SST - w_{t-1})$	9.82	-8.30	4	2.37	0.16	0.59		
4. $R_t = 0.65 - \exp(0.75 X_{t-1} - 6.66) - 0.20 SST - e_{t-1}$	9.58	-7.53	4	3.14	0.11	0.58		
5. $R_t = 0.65 - \exp(0.85 X_{t-1} - 7.52)$	7.14	-5.77	3	4.90	0.046	0.44		
6. $R_t = 0.65 - \exp(0.78 X_{t-1} - 7.00) - 0.15 SST-w_{t-1}$	9.40	-7.46	4	3.21	0.11	0.57		
7. $R_t = 0.65 - \exp(0.72 X_{t-1} - 6.45 + 0.25 SST-e_{t-1})$	9.36	-7.38	4	3.29	0.10	0.57		
8. $R_t = 0.65 - \exp(0.75 X_{t-1} - 11.51 + 0.68 X Pad_{t-1})$	8.53	-5.72	4	4.95	0.045	0.52		
9. $R_t = 0.65 - \exp(0.70 X_{t-1} - 7.49 + 0.59 Ice-se_{t-1})$	8.45	-5.56	4	5.11	0.042	0.52		
10. $R_t = 0.65 - \exp(0.85 X_{t-1} - 7.51) + 0.002 Krill_t$	7.94	-4.54	4	6.13	0.025	0.49		
11. $R_t = 0.65 - \exp(0.42 X_{t-1} - 3.10) + 0.16 Ice-we_t$	7.91	-4.48	4	6.19	0.024	0.49		
12. $R_t = 0.65 - \exp(1.06 X_{t-1} - 9.51) - 0.75 Ice-se_{t-1}$	7.26	-3.20	4	7.47	0.024	0.49		
13. $R_t = 0.65 - \exp(0.83 X_{t-1} - 7.37 + 0.015 SST-w_t)$	7.15	-2.96	4	7.71	0.011	0.44		
Models for <i>Euphasia superba</i>								
1. $R_t = 3 - \exp(0.25 X_{t-1} - 0.22) + 2.39 Ice-sw_t$	-6.78	24.90	4	0.00	0.14	0.59		
2. $R_t = 3 - \exp(0.36 X_{t-1} - 0.91 - 0.73 Ice - sw_t)$	-6.78	24.90	4	0.00	0.15	0.59	0.28	0.86
3. $R_t = 3 - \exp(0.32 X_{t-1} - 0.49 - 0.43 Ice - sw_t) + 1.58 Ice - sw_{t-1}$	-5.55	25.27	5	0.37	0.12	0.64	0.30	0.82
4. $R_t = 3 - \exp(0.40 X_{t-1} - 0.98 - 0.58 Ice - sw_t - 0.46 Ice - sw_{t-1})$	-5.78	25.72	5	0.82	0.10	0.63	0.22	0.78
5. $R_t = 3 - \exp(0.25 X_{t-1} - 0.25) + 2.26 Ice - sw_{t-1}$	-7.19	25.72	4	0.82	0.10	0.56		
6. $R_t = 3 - \exp(0.35 X_{t-1} - 0.88 - 0.70 Ice - sw_{t-1})$	-7.46	26.25	4	1.35	0.080	0.55		
7. $R_t = 3 - \exp(0.30 X_{t-1} - 2.10 + 0.24 Ice - we_{t-1})$	-8.02	27.37	4	2.47	0.040	0.52		
8. $R_t = 3 - \exp(0.27 X_{t-1} - 0.75)$	-9.44	27.39	3	2.49	0.043	0.44		
9. $R_t = 3 - \exp(1.00 X_{t-1} - 6.98) - 0.44 Ice - we_{t-1}$	-8.29	27.72	4	2.82	0.036	0.51		

The best population dynamic models were chosen by using the Bayesian information criterion (BIC) or Schwarz (1978) criterion

For clarity, BIC weights were also included in the results. Model parameters were estimated by nonlinear regression analysis in R-program using the nls (nonlinear least squares) library R Development Core Team (2011). The model notations are: R_m , maximum per capita growth rate; a , effect of interference on each individual as population size increases; C , a constant representing competition and resource depletion; X_{t-1} , \log_e (population size); $Krill_t$, \log_e krill abundance; SAM , Southern Annular; $Ice-ww$, ice cover during winter western to Antarctic peninsula; $Ice-we$, ice cover during winter eastern to Antarctic peninsula; $Ice-sw$, ice cover during summer western to Antarctic peninsula; $Ice-se$, ice cover during summer eastern to Antarctic peninsula; $SST-w$, sea surface temperature western to the Antarctic peninsula and $SST-e$, sea surface temperature eastern to the Antarctic peninsula. Model predictions are evaluated through root-mean-square prediction error (rmse) and the Pearson's correlation coefficient r_p . The best models are shown in bold face

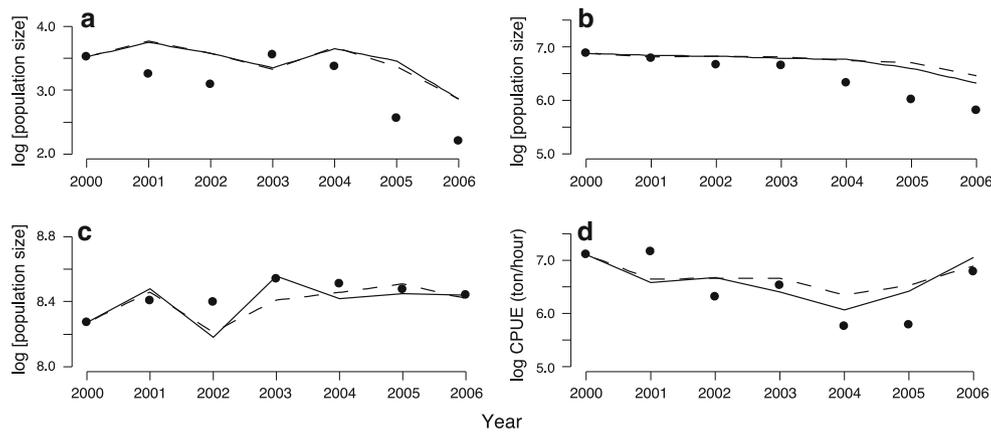


Fig. 4 Comparison of observed penguin abundance and krill biomass (solid circles) for the period 2000–2006 with predictions from models fitted to the data until the year 2000 (both solid and broken lines), **a** predictions from model 1 (solid line) and 2 (broken line) (Table 1) to the observed Chinstrap penguin data, **b** predictions from model 1

(solid line) and 2 (broken line) (Table 1) to the observed Adélie penguin data, **c** predictions from model 1 (solid line) and 2 (broken line) (Table 1) to the Gentoo penguin data and **d** predictions from model 2 (solid line) and 3 (broken line) (Table 1) to the krill biomass data

the sea-ice cover variable (Table 1). However, using only the positive effects of summer sea-ice cover as the main exogenous factor, we were able to predict the observed dynamics of krill quite accurately (Fig. 4d; Table 1). In fact this simple model has good empirical support compared with the pure endogenous model ($w_1/w_8 = 3.26$).

Discussion

Our results suggest that the relevant processes underlying the population dynamics of these penguin species at King George Island (Antarctic Peninsula) are intra-specific competition and the combined effects of krill abundance and sea-ice cover. Although the influence of krill and sea-ice cover have been widely reported elsewhere (Fraser et al. 1992; Trathan et al. 1996; Croxall et al. 2002; Fraser and Hofmann 2003; Atkinson et al. 2004; Murphy et al. 2007; McClintock et al. 2008; Trivelpiece et al. 2011), most of these studies were based on statistical correlation between estimates of population size and climatic variables (but see Murphy et al. 2007). We think that using simply logistic models (Ricker 1954) with few ecological parameters and good predictive ability provides a new perspective on penguin and krill dynamics at Western Antarctic Peninsula. Our results offer a slightly different hypothesis about the role of sea-ice cover and krill abundance on population trends of three species of penguins. Moreover, we will discuss how simple models can be used to interpret ecological hypotheses and to predict putative ecological mechanisms.

Several studies have reported the relationships between sea-ice cover, krill abundance and penguin trends (Fraser and Hofmann 2003; Trivelpiece et al. 2011; Lynch et al.

2012), while some support the “sea-ice hypothesis” (Fraser et al. 1992), others proposed that penguin populations trends are caused by changes in their main prey, the Antarctic krill (Trivelpiece et al. 2011). The “sea-ice hypothesis” proposes that the negative trend of sea-ice cover in several regions of Antarctica have affected the winter habitat of “ice-loving” species, such as, the Adélie penguins, but have been beneficial to populations of “ice-avoiding” species like the Chinstrap penguins (Trivelpiece et al. 2011). In particular, Chinstrap penguins at King George Island appear to be limited by food (krill) availability and regulated by intra-specific competition. The strong dependency of this penguin species on krill availability has been widely reported (Fraser and Hofmann 2003; Lynnes et al. 2004; Polito et al. 2011). In agreement with these studies, our results support the hypothesis that Chinstrap penguins are limited by food (krill availability) at the WAP ecosystem. Hence, due to its restricted distribution and the observed decreasing trend in krill recruitment, this species appears to be more threatened than others (Forcada et al. 2006; Trivelpiece et al. 2011). Chinstrap penguins conform to the typical case where food limitation is clearly expressed as a lateral perturbation effect arising in a logistic model (Royama 1992). As expected by population dynamic theory, the main factor limiting Chinstrap penguins is the demand/supply ratio between the population size and krill abundance. The high explanatory power of this form of interaction between limiting factors and intraspecific competition has been widely reported in other organisms (Berryman and Lima 2006; Lima et al. 2006, 2008a, b; Previtali et al. 2009; Lima and Naya 2011).

Regarding the other two species, our results seem to support the “sea-ice hypothesis” and they are consistent

with the contrasting population trends that both species exhibited at the Western Antarctic Peninsula (Forcada et al. 2006; Carlini et al. 2009; Lynch et al. 2010). Adélie penguins appear to be mainly influenced by the direct positive effects of sea-ice cover and intra-specific competition. However, the empirical support for the role of sea-ice cover in the fitted models for this species was weak, but the sign of the effect was consistent with previous findings (Forcada et al. 2006). In fact, there is substantial evidence that this species exhibited a high preference for habitats dominated by pack ice (Forcada et al. 2006; Trivelpiece et al. 2011). In particular, Adélie penguins on the Antarctic Peninsula are highly dependent on the year to year variations in sea-ice cover due to their habitat requirements during breeding (Forcada et al. 2006). Because the main food item in this area is the krill (Fraser and Hofmann 2003; Lynnes et al. 2004), which is closely related to sea-ice cover, we expected both variables (krill and sea-ice cover) to be important drivers of the population fluctuations. Nevertheless, model predictions underestimate the negative trend showed by this species. We think that some other factors not considered in our models may explain this bias, such as strong competition in the area with other top predators like seals, fur seals and whales (Trivelpiece et al. 2011). Also, environmental factors related to winter dispersal and/or juvenile overwinter survival can explain our biased predictions and the weak support for the positive effect of sea-ice cover (see Carlini et al. 2009; Lynch et al. 2010). In contrast, models for Gentoo penguins support the hypothesis that the observed positive trend of this species at WAP is a consequence of a niche expansion due to global warming (Forcada et al. 2006; Lynch et al. 2012). This species prefers ice-free areas to breed, in contrast to Adélie penguins (Forcada et al. 2006; Lynch et al. 2012). There is strong evidence that the southernmost breeding colonies of this species at WAP are increasing (Carlini et al. 2009; Lynch et al. 2010), which seems to be caused by the colonization of new breeding sites and foraging areas facilitated by climate warming. In addition, Gentoo penguins seem to exploit a slight different food niche than the other two species. They are deep divers and seem to forage in other prey items than krill (Carlini et al. 2009), although they are still highly dependent on krill during the breeding season.

Population dynamic models for krill supported the hypothesis that sea-ice cover and lagged sea surface temperature are key variables to understand krill fluctuations. Previous studies have reported a strong association between years of extensive winter sea ice and krill recruitment and density (Fraser and Hofmann 2003; Atkinson et al. 2004; Murphy et al. 2007). The mechanistic explanation for the relationship between ice and krill dynamics seems to be related to the importance of sea-ice

algae for adult spawning and larvae survival (Atkinson et al. 2004). There is a general consensus on the relationship between the fast rate of warming of the WAP and the shortening trend in winter sea-ice duration (Parkinson 2002). Therefore, we think that the use of simple logistic models to describe and predict krill dynamics represents a very important and interesting finding of this study. Fitted logistic models that use the demand/supply ratio between the krill abundance and sea-ice cover as a proxy of limiting factors capture the essential component of krill dynamics in the WAP ecosystem.

In summary, our results using population theoretical based models support the idea that global warming represents a major driver of avian predator populations and its major prey at the WAP ecosystem. At our study site, penguins showed species-specific responses to climate change. First, Chinstrap penguins were only influenced by krill abundance (food limitation) and are represented quite well by a simple logistic model with carrying capacity as a function of krill population size. Second, the contrasting population trends of Adélie and Gentoo penguins appear to be better explained by the “sea-ice hypothesis” (Fraser et al. 1992; Trivelpiece et al. 2011), but the models including sea-ice effects on Adélie penguins showed weak empirical support. Interestingly, none of the selected models included inter-specific competition suggesting that neither space nor food does inter-specific competition seem to be important for explaining the population trends. Despite the fact that several statistical relationships between climate, krill and penguins numbers have been reported (Croxall et al. 2002; Atkinson et al. 2004; Forcada et al. 2006; Murphy et al. 2007), we think that proper population dynamic modeling is essential to decipher the ecological mechanisms behind the dynamics of these penguin populations. In other words, this study is an example of applied ecological theory, in particular, the application of theories pertaining to nonlinear population dynamics, exogenous perturbations, and resource partitioning.

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