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Population ecology

Increased sea ice concentration worsens fledging condition and juvenile survival in a pagophilic seabird, the snow petrel

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Polar sea ice is changing rapidly, threatening many taxa in the Arctic and the Antarctic. Little is known about the effects of sea ice on early life-history traits of sea ice specialist species, although juvenile stages are a critical component of population dynamics and recruitment. We examined how annual variation in sea ice concentration (SIC) affects juvenile survival and body condition at fledging in the snow petrel *Pagodroma nivea* using long-term datasets encompassing 22 years for body condition and 37 years for juvenile survival. We show that SIC and southern annular mode (SAM), the principal mode of variability of the atmospheric circulation in the Southern Hemisphere, have strong nonlinear effects on juvenile survival and body condition. Below *ca* 20–30% SIC, body condition remained stable, but decreased almost linearly for higher SIC. Juvenile survival was negatively related to SIC and to SAM during the chick rearing period. We suggest that the base of the sea ice food web would be directly affected by sea ice conditions, thus acting locally on the abundance and structure of prey communities.

1. Introduction

In contrast to Arctic sea ice, which has decreased markedly over the last four decades [1] with major consequences for Arctic ecosystems and species [2], Antarctic sea ice extent has increased over the same period, although with large and contrasting regional variations [3,4]. Links between ice, food availability and demography were shown for some Arctic species [5], but the response of ice-associated seabirds in the Antarctic is likely to differ between regions, depending on projected increases or decreases in sea ice cover [6]. Recently, the Antarctic sea ice extent has decreased at a historical record rate [7] owing to a combination of atmospheric and oceanic conditions [8], and there is strong evidence that Antarctic sea ice will decrease by the end of the century [9]. Endemic Antarctic animals specialized on sea ice habitats and their associated ecosystems are expected to be impacted by these major changes [2]. Therefore, it is important to document and understand the demographic responses of pagophilic (sea ice-dependent) species to sea ice variations.

Among seabirds, the snow petrel (*Pagodroma nivea*) is endemic to Antarctica and is one of the most pagophilic species, foraging almost exclusively within the pack ice year round [10,11]. Snow petrels feed by dipping and surface-seizing [10,12], primarily foraging on sea ice-associated fishes (*Pleuragramma antarctica* and *Electrona antarctica*) and crustaceans (*Euphausia* spp.) [10,13]. Sea ice conditions are known to be correlated with demographic parameters of adult snow petrels [14–16], but our knowledge is fragmentary and incomplete about the effects of sea ice on the juvenile stages, although younger age classes have a strong influence on population dynamics in long-lived species [17].

To this end, we used 22 years of data from a study to estimate fledgling body condition and 37 years of data from a mark–recapture study to estimate

Table 1. Results of the GAMM model explaining fledging body condition in snow petrels. $n = 1165$ observations. The proportion of deviance explained by the model was 18%. edf, estimated degree of freedom.

variables	smoother edf	*F*-test	*p*-value	σ^2 (s.e.)
southern annular mode	1.87	19.867	<0.001	
sea ice concentration	1.76	48.283	<0.001	
adult body size	1.51	1.929	0.09	
laying date	1.00	0.002	0.96	
breeding success	1.00	0.373	0.48	
parent 1 (random)				463.82 (21.54)
parent 2 (random)				583.99 (24.17)

juvenile survival. Based on these unique datasets, we addressed the following questions: (i) do fledging body condition and juvenile survival show temporal trends?; (ii) are these life-history traits affected by sea ice and other climatic or intrinsic factors?

2. Material and methods

(a) Study area and species

Snow petrels were studied at Pointe Géologie (66°40 S, 140°01 E), Adélie Land, Antarctica (electronic supplementary material). After laying in December, both parents incubate the single egg alternately until hatching. Incubation of the egg lasts 44 days. Hatching takes place in January and the chick fledges in March, about 48 days after hatching [18]. After a juvenile stage of several years at sea, individuals tend to display both natal philopatry and breeding site fidelity [16,19].

(b) Environmental variables

Three environmental covariates were considered to explain interannual variations in fledging body condition and juvenile survival (electronic supplementary material): sea ice concentration (SIC), sea surface temperature (SST) and the southern annular mode (SAM). We considered two periods for the covariates: (i) the chick rearing period (January to March of year t) to test for an effect of climate conditions during development, (ii) the winter period (April to September of year $t-1$) to test for delayed effects of climate conditions due to the time of integration of the effects of climate conditions on the food web.

(c) Modelling fledging body condition and juvenile survival

To estimate fledging body condition, we used the scale mass index (SMI) as recommended by Peig & Green [20].

Interannual variations of SMI were tested using an ANOVA. Temporal trend and autocorrelation of SMI were tested using a generalized additive mixed model (GAMM) with an autoregressive moving average (ARMA) structure to characterize the trend and autocorrelations within the time series. We used the same method for environmental covariates. The effects of covariates on SMI were tested using a GAMM whose predictor depends on a smoothing function and where the SMI is a function of climatic, phenotypic, phenological and demographic covariates (electronic supplementary material).

Apparent survival (Φ) and probability of recapture (p) were estimated using an age- and time-dependent capture–mark–recapture model (electronic supplementary material). Once the best model structure on p was determined, we tested the effects of climatic covariates and of some intrinsic factors (breeding success) on the probability of juvenile survival.

3. Results

(a) Body condition

Owing to collinearity issues between covariates, we used only two climatic covariates: SIC during the chick rearing period and SAM of the year (electronic supplementary material, table S1). Fledging SMI varied between years (ANOVA, d.f. $= 1163$, $F = 77.85$, $p < 0.001$). Negative and positive temporal trends were detected for SMI (ARMA (1, 1), $p < 0.001$) and SIC (ARMA (0, 1), $p < 0.001$), respectively (electronic supplementary material, figure S1). No temporal trend was detected for SAM.

Two covariates affected fledging body condition: SIC and SAM (table 1 and figure 1). Below *ca* 20–30% SIC, the SMI remained relatively stable, but decreased almost linearly for higher SIC. Fledging SMI decreased as SAM increased up to a value of *ca* 2 and tended to be positively related to SAM for higher values. Information about fitting procedure are available in electronic supplementary material, figure S2. Note that similar results were obtained using another measure of body condition (electronic supplementary material, table S4, figures S3 and S4).

(b) Juvenile survival

Recapture probability was best modelled using 23 age classes (electronic supplementary material, table S3). It was low (less than 0.025) from age 5 to age 8, increased from age 9 to age 22 and was constant at 0.375 ± 0.012 from age 23. Starting with this model ($\Phi_{\text{juv.t,ad}}$ p_{23}), there was strong evidence for a year effect on juvenile survival (electronic supplementary material, table S3). Juvenile survival was negatively related to SIC (figure 2) during the chick rearing period (standardized slope: -0.223 ± 0.056) and to SAM (standardized slope: -0.397 ± 0.063). Although we found a quadratic effect of SAM, slope parameters were not all significant and the effect was also negative without optimum values. The additive effects of SIC and SAM explained 50% of the variation in juvenile survival (table 2).

4. Discussion

Based on multi-decadal time series, we showed that snow petrel body condition at fledging and juvenile survival were related to SIC and large-scale Antarctic atmospheric

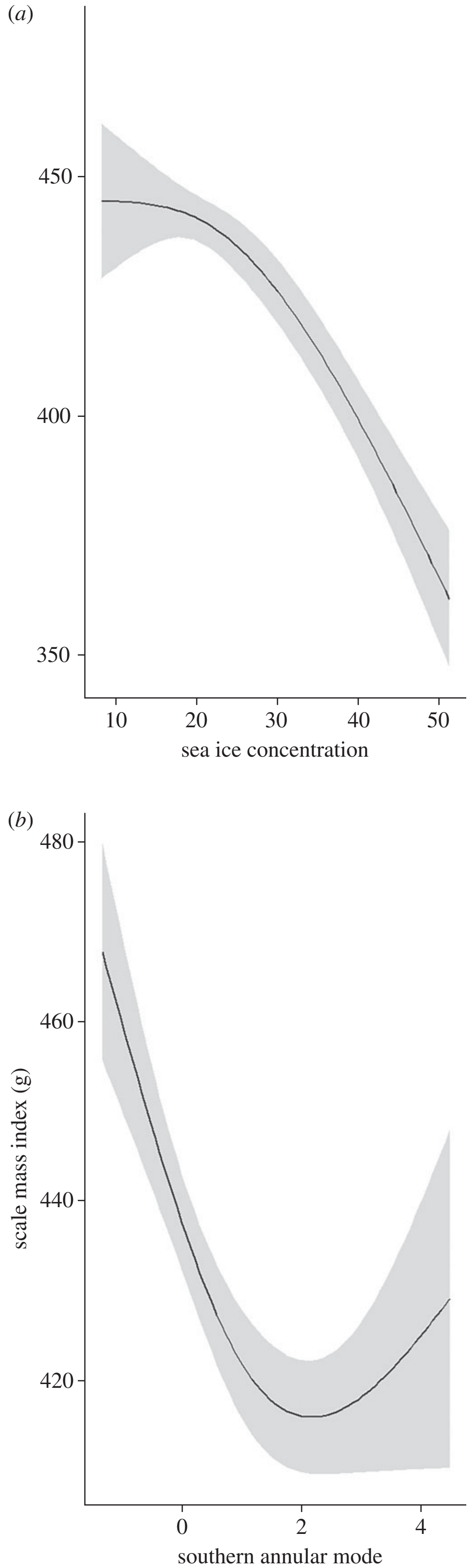

Figure 1. Estimated smoothing curves (s.e.) for sea ice concentration (SIC) (*a*) and southern annular mode (SAM) (*b*) in relation to fledging body condition (scale mass index, SMI).

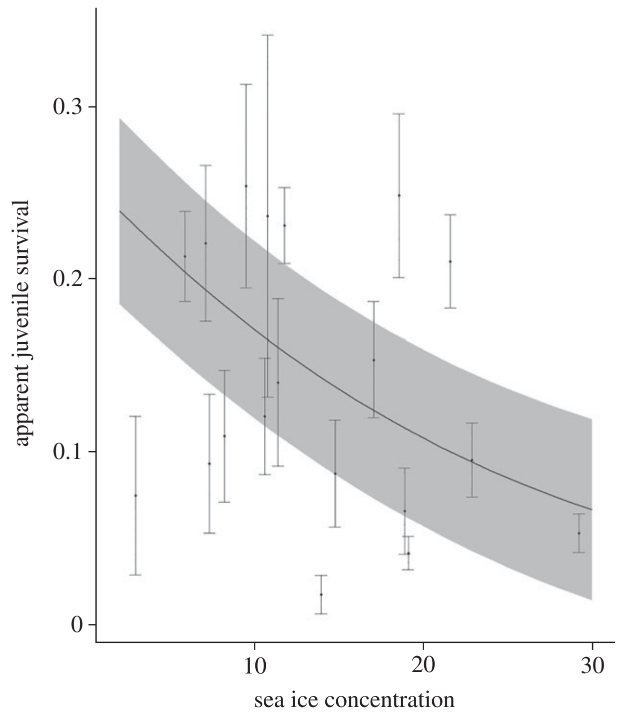

Figure 2. Juvenile survival modelled as a function of sea ice concentration SIC, (line) with 95% confidence intervals and annual estimates of juvenile survival obtained from the time-dependent model (filled circles). Error bars show s.e.

circulation. In the Arctic, sea ice conditions are known to affect diet of marine predators, and since sympagic fishes are expected to lose habitat due to sea ice decrease, this will affect their predators like seabirds and marine mammals [21]. Here, fledging body condition and juvenile survival decreased with increasing SIC and SAM, although nonlinearly for body condition. Studies indicate that, compared with adults, the diet of snow petrel chicks contains a higher proportion of Antarctic silverfish [22], which is associated with sea ice in various phases of its life-history stages [23]. The distribution of phytoplankton biomass is defined by the availability of light and nutrients [24]. SIC partly determines the amount of light to penetrate the water column which, together with other factors such as stratification of the water column, affects primary production, and therefore, food energy intake of fish such as Antarctic silverfish [25]. Warm and permeable sea ice is also more likely to provide food to Antarctic silverfish than colder and less porous ice [23]. Therefore, our results suggest that when SIC becomes higher than 20–30%, snow petrels have difficulties finding food for their chick, due to a decrease in prey abundance and/or accessibility since sea ice provides prey with shelter against predators. Juvenile survival may be affected through the same processes once fledglings go to sea. Alternatively, low juvenile body condition during heavy sea ice years may negatively affect juvenile survival, as shown for other seabird species [26,27].

The SAM induces a west wind anomaly in the Antarctic zone at the polar front, which generates an Ekman drift to the north and carries sea ice with it, thus increasing fast ice extension [28]. We suggest here that the extension of fast ice (in positive phase of SAM) decreases prey accessibility and has a negative effect on fledging body condition and juvenile survival. We do not know where juvenile individuals go in the months following fledging, but they are likely to move to the most productive areas along the ice shelf [29].

Recent increases in SIC seem to have negatively impacted fledgling snow petrel body condition and will likely have a negative impact on juvenile survival and population dynamics. These results contrast with positive effects found in other pagophilic species [5,30]. Thus, further long-term studies

Table 2. Testing for the effects of covariates on juvenile survival probability of snow petrels between 1964 and 2000. k = number of identifiable parameters; ANODEV = F statistic of the analysis of deviance (d.f.); p-value = statistical significance; R^2 = proportion of variance explained.

covariate	hypothesis tested	k	deviance	ANODEV	p-value	R^2
	time reference model	57	6886.1			
SIC	linear effect of SIC	40	7019.5	6.00 (1,17)	0.025	0.26
	quadratic effect of SIC	41	7018.1	2.94 (2,16)	0.082	
	constant reference model	39	7066.6			
SAM	linear effect of SAM	22	7074.6	9.90 (1,35)	0.003	0.22
	quadratic effect of SAM	23	7066.0	5.85 (2,34)	0.007	0.26
	constant reference model	21	7127.9			
breeding success (BS)	linear effect of BS	22	7118.5	1.42 (1,35)	0.241	
	quadratic effect of BS	23	7116.0	0.88 (2,34)	0.424	
	constant reference model	21	7127.9			
SIC + SAM	additive effect of SIC and SAM	41	6975.9	8.08 (2,16)	0.004	0.50

documenting the effects of sea ice on life-history traits are needed to improve our understanding of the complex effects of sea ice on predator demographics.

Ethics. The Ethics Committee of IPEV and Comité de l'Environnement Polaire approved the field procedures.

Data accessibility. Datasets supporting this article were uploaded as part of the electronic supplementary material.

Authors' contributions. Study design: C.B. Data analysis and processing: C.S., K.D. Writing: C.S., C.B., K.D. All authors edited and revised the manuscript, gave final approval for publication and agreed to be held accountable for the content therein.

Competing interests. We declare we have no competing interests.

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