**HIGHLIGHTED STUDENT RESEARCH**

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# Population response of an apex Antarctic consumer to its prey and climate fluctuations

Nathan Pacoureau[1] · Matthieu Authier[2] · Karine Delord[1] · Christophe Barbraud[1]

## Abstract

A fundamental endeavor in population ecology is to identify the drivers of population dynamics. A few empirical studies included the effect of prey abundance when investigating simultaneously the effects of density-dependence and climate factors on marine top-predator population dynamics. Our aim was to unravel the mechanisms forcing population dynamics of an apex consumer seabird, the south polar skua, using long-term climatic and population time series of the consumer and its prey in Terre Adélie, Antarctica. Influences of density-dependence, climatic factors, and prey abundance with lag effects were tested on the breeding population dynamics with a Bayesian multi-model inference approach. We evidenced a negative trend in breeding population growth rate when density increased. Lagged effects of sea-ice concentration and air temperature in spring and a contemporary effect of prey resources were supported. Remarkably, results outline a reverse response of the south polar skua and one of its main preys to the same environmental factor (sea-ice concentration), suggesting a strong link between skua and penguin dynamics. The causal mechanisms may involve competition for food and space through territorial behavior as well as local climate and prey availability, which probably operate on breeding parameters (breeding propensity, breeding success, or recruitment) rather than on adult survival. Our results provide new insights on the relative importance of factors forcing the population dynamics of an apex consumer including density-dependence, local climate conditions, and direct and indirect effects of prey abundance.

**Keyword** Adélie penguin · Bayesian modeling · Density-dependence · Emperor penguin · South polar skua

✉ Nathan Pacoureau
 n.pacoureau@gmail.com

1 Centre d'Études Biologiques de Chizé, UMR-CNRS 7372, 79360 Villiers-en-Bois, France

2 Observatoire PELAGIS, UMS-CNRS 3462, Université de la Rochelle, allée 4 de l'Océan, 17000 La Rochelle, France

## Introduction

Determining the factors driving population abundance is a long-standing research program and one of the most debated topics in ecology (Nicholson 1933; Andrewartha and Birch 1954; May 1999; Berryman 2004; Lebreton 2009). With evidence from experiments in closed populations and complemented with empirical studies on open populations, most ecologists now agree that a range of dynamical components (density-dependence, environmental and demographic stochasticity, climate forcing, and prey abundance) and their complex interactions influence population dynamics (Bjørnstad and Grenfell 2001).

A population is regulated through negative density-dependence when its growth rate is negative above a certain carrying capacity. Regulation can occur through many mechanisms such as competition for space and food or disease (Murdoch 1994; Albon et al. 2002). Density-independence processes encompass demographic stochasticity and exogenous factors such as environmental variability (weather,

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food, etc) and predation (Berryman 1999; Grange et al. 2015). Detecting and disentangling the roles and relative importance of density-dependent and density-independent factors are crucial to understand population dynamics in the wild, especially in a world where species face one of the fastest global climate changes ever experienced before (IPCC 2014). Such an endeavor relies heavily on the statistical analysis of empirical time series on population abundance or of long-term detailed longitudinal data on marked individuals (Dennis and Taper 1994; Lande et al. 2002; Clutton-Brock and Sheldon 2010; Frederiksen et al. 2014).

Population dynamic models can provide reasonably accurate predictions and unravel the source of population change (Berryman 1999; Royama 2012). While time series analyses aiming at separating density-dependent and density-independent mechanisms involved in population trajectories are continuously documented in a slow–fast life-history continuum of terrestrial (Newton 1998; Aars and Ims 2002; Pasinelli et al. 2011; Rodríguez-Caro et al. 2016; Bonardi et al. 2016) and marine vertebrates (Fromentin et al. 2001; Lewis et al. 2001; Barbraud and Weimerskirch 2003; Zabel et al. 2006; Rotella et al. 2009), relatively, a few studies have explicitly included the effect of prey abundance on their consumer dynamics in marine ecosystems (Frederiksen et al. 2006; Furness 2007; Cury et al. 2011; Erikstad et al. 2013; Barbraud et al. 2017), mainly because prey abundance if often difficult to quantify.

In polar ecosystems, skuas are top predators and scavengers which play an important role in ecosystem functioning (Votier et al. 2007; Dawson et al. 2011; Schmidt et al. 2012; Barraquand et al. 2014). However, their demographic and population responses to fluctuations in climate and prey abundance remain poorly understood, especially in Antarctic ecosystems. South polar skuas (*Catharacta maccormicki* generic assignment follows Carlos 2016) feed exclusively on marine species such as other seabird species, fish, penguins, and seals (Davis and McCaffrey 1986; Norman and Ward 1990; Wang and Norman 1993; Baker and Barbraud 2001; Krietsch et al. 2016). They can be considered apex consumers, but, contrary to other meso- or top-predator Antarctic species, little is known about the factors affecting their population dynamics (Pezzo et al. 2001). However, predicting how populations and ecosystems react to changes in environmental variability requires population dynamics models with explicit functional relationships to environmental factors.

Here, we used a high-quality long-term study of the south polar skua to disentangle, with a Bayesian multi-model inference approach, the respective effects of density-dependent and density-independent factors, including prey abundance, on population dynamic. We first investigated for the presence of density-dependence in the population time series using an a priori set of two density-independent and one density-dependent population models commonly used to describe abundance time series. We expected to detect density-dependence in this breeding population due to the increasing number of potential breeders (Micol and Jouventin 2001) and the strong territorial behavior showed by this species as territories include both breeding and feeding grounds (Jouventin and Guillotin 1979; Ainley et al. 1990). Second, we tested for the effects of local climatic covariates and prey covariates during the breeding and the non-breeding seasons on the population dynamics. While the importance of environmental factors on breeding sites to the population regulation of long-distance migratory species, such as many seabirds, has long been acknowledged, conditions experienced during migration and on non-breeding sites may contribute as well but remain largely undocumented (Newton 2006; Norris and Marra 2007). A recent study identified the non-breeding ground of the studied population of south polar skuas (Weimerskirch et al. 2015), allowing us to integrate multiple spatial scales to our study. On breeding sites, south polar skuas are often associated with breeding colonies of other seabirds, especially penguins, and usually exploit them by predation, scavenging and kleptoparasitism. Our studied population mainly feeds on meso-predators, the Adélie penguin (*Pygoscelis adeliae*) and the emperor penguin (*Aptenodytes forsteri*), whose continuous monitor since 1976 allowed us to investigate the direct effects of their abundance on south polar skua population regulation. Finally, we tested for delayed effects of environmental factors on south polar skua population dynamics to shed light on underlying demographic mechanisms. Because delayed effects of climate and other environmental factors through cohort effects are important in both marine and terrestrial ecosystems (Albon et al. 1987; Lindström 1999; Forchhammer et al. 2001; Lindström and Kokko 2002; Jensen et al. 2006; Cam and Aubry 2011), we considered different time lags for the effects of covariates. First, environmental factors may affect the breeding propensity or survival of the adult age-classes, in which case one would expect current year effects or 1 year lag carry-over effects of covariates on abundance, respectively. Second, survival and recruitment of individuals born in a specific year may vary depending on the environmental conditions in the year of birth. We thus considered several time lags to take account of environmental factors affecting the quality of individuals resulting in varying delays in age at first reproduction. This record offers a unique opportunity to assess simultaneously the evidence for density regulation, climate regulation, and direct prey-mediated regulation for a wild species occupying one of the highest trophic levels of Antarctic food webs.

## Methods

### Study species

South polar skuas were studied at the Pointe Géologie archipelago, Terre Adélie, Antarctica (66°40′S, 140°01′E). The south polar skua is a long-lived species that breeds in Antarctica, and is highly territorial during breeding with strong site tenacity and mate fidelity (Young 1963a, 1972; Jouventin and Guillotin 1979; Ainley et al. 1990; Pietz and Parmelee 1994). Pair formation starts in October; usually, two eggs (one in late nesting pairs) are laid at intervals of 2–4 days in mid-November, hatching occurs in late-December, and chicks fledge 50 days after (Young 1963a). Parents feed their chicks till they leave the nesting territory (Spellerberg 1971a) at the end of the breeding season between late March and mid-April (Le Morvan et al. 1967). Individuals start to breed when 3 years old at the earliest, but most females start breeding between 5 and 7 years, and a little later for males (Ainley et al. 1990). Foraging effort during breeding depends on the distance between south polar skua nests and that of their prey: long distances prevent offspring predation by conspecifics and nest trampling by penguins, but may limit prey accessibility (Hagelin and Miller 1997). After the breeding season, adults from Pointe Géologie migrate directly to winter off eastern Japan at latitudes of 35–45°N, without marked stopovers (Weimerskirch et al. 2015).

The total south polar skua population in Terre Adélie was greatly reduced by shooting during the first years following the settlement of the research station in 1956. Shortly after, this population had a sustained increase (3–4 times), foraging heavily on human refuse on the dump site until its closure in 1988. However, the breeding population on the main islands increased at a much slower rate than the total population for the same period (from around 20 breeding pairs to 30), probably reflecting that the dumpsite mainly benefited to non-breeders (Prévost 1963; Le Morvan et al. 1967; Micol and Jouventin 2001).

### Field methodology

Breeding pairs have been monitored annually since 1968/1969 (named the 1968 breeding season) on the main islands of the Pointe Géologie archipelago forming the Core Area (Ile des Pétrels, Ile Bernard, Ile Lamarck, Ile Rostand, Ile Le Mauguen, and Nunatak du Bon Docteur; Fig. 1). Every year, the entire Core Area was searched for nests during the laying period at regular intervals of 8–10 days. The location of each detected nest was reported on a map and the content of the nest noted. Due to the

relatively small size of the core area ($\approx 80$ ha), with ~50 breeding pairs annually, the absence of vegetation, and the conspicuous behavior of south polar skuas during breeding with agonistic behavior towards territory intruders, we assumed that all active nests were detected each year given the monitoring effort deployed.

### Modeling population dynamics

We used an a priori model set of two density-independent and two density-dependent (direct and delayed) population dynamics models. Models were built in discrete time and were fitted within a Bayesian framework. Let $N_t$ denote the true abundance in year $t$ and $x_t = \ln(N_t)$, the density-independent models incorporated non-directional population fluctuations at each time step ('random walk'; Foley 1994):

$$x_{t+1} = x_t + \varepsilon_{xt},$$

and the standard geometric Malthusian growth model ('exponential'; May 1975) with a normally distributed error term:

$$x_{t+1} = r + x_t + \varepsilon_{xt},$$

where $r$ is the logarithm of the average growth rate of the population.

The density-dependent model was a stochastic Gompertz model, allowing to test for density-dependence and to estimate its intensity, and was defined through the equation for direct density-dependence:

$$x_{t+1} = r_{max} + (1 - DD) \times x_t + \varepsilon_{xt},$$

and for direct and delayed density-dependence:

$$x_{t+1} = r_{\max} + (1 - DD) \times x_t + \beta \times x_{t-1} + \varepsilon_{xt},$$

where $r_{\max}$ is the logarithm of $\lambda$ (finite rate of increase of the population in one time step), DD is a constant parameter measuring the strength of direct density-dependence, $\beta$ is a parameter measuring delayed density-dependence, and $\varepsilon_{xt}$ is a normally distributed process error with mean zero and process variance $\sigma_N^2$ (Lebreton and Gimenez 2013).

We linked $x_t$ with the true population size using the following equation:

$$Y_t = \exp(x_t).$$

We assumed, given the intensive effort deployed in the core area, that the observation variance was null: nominal abundance was equal to true abundance. We used uniform priors for the process scale $\sigma_\varepsilon \sim \text{unif}(0, 100)$, and for parameter DD, we used a Student-$t$ prior distribution with mean 0, degrees-of-freedom parameter $\nu$, and scale $\kappa$ ($\sim t$-distribution$(0, \nu = 7, \kappa = 5)$, with $\nu$ and $\kappa$ chosen to provide weak prior information. Several authors (Delean et al. 2013; Lebreton and Gimenez 2013) recommended the choice of a reasonable prior for $r_{\max}$ based on
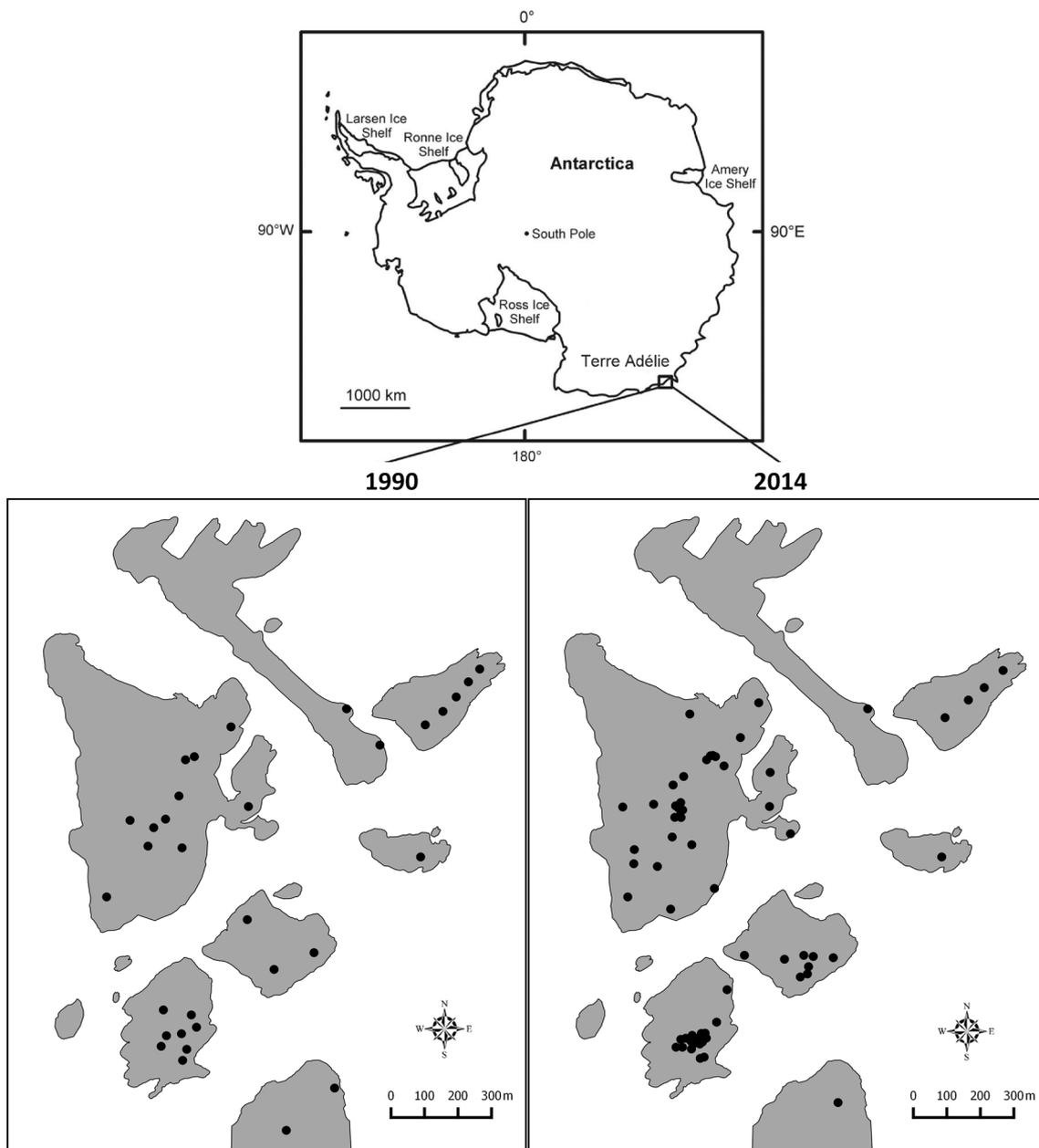
**Fig. 1** Map indicating the location of Terre Adélie in Antarctica and south polar skua nests on the islands of the core area indicated by dots for 1990 (left) and 2014 (right)

external comparative information. We used the comparative demographic approach (Niel and Lebreton 2005) to estimate priors for $r_{max}$ for the south polar skua (see ESM Appendix 1). The resulting prior distribution for $r_{max}$ was $N(0.0788, 0.005)$. We used uniform prior for $r$ bounded between $-0.10$ and an upper bound constrained to be the upper 95% limit following a normal distribution centered on $r_{max}$. Sensitivity analyses were conducted to check results' robustness: a range of different prior for $r_{max}$ were tested (see ESM Appendix 1).

Three Monte Carlo Markov chains were run for each model with different initial values. Each Markov chain was initiated by assuming a prior distribution on the initial condition $x_1$ equal to the first observation of abundance $x_1 = \ln(Y_1)$. Between 20,000 and 80,000 first iterations were discarded ("warm-up"), and in the remaining 200,000 iterations, 10,000 were selected for posterior inference. Thus, parameter posterior distributions were estimated from 30,000 values. Convergence of each parameter was checked with the Gelman and Rubin diagnostic (Gelman and Rubin 1992).

Plots of fitted value versus residuals were checked to informally assess goodness-of-fit.

Analysis were performed using R Statistical Software v3.2.3 (R Core Team 2015) and via the interface from R ('rjags' package v4-5; Plummer 2016 to JAGS ('Just Another Gibbs Sampler' v4.0.0; Plummer 2015).

## Covariates

We used previous knowledge on seabirds and south polar skua ecology to select candidate prey and environmental covariates. We limited the time series to the period 1988–2014 (Fig. 2), because some covariates were not available before. Two prey covariates were selected corresponding to Antarctic meso-predators regularly consumed by south polar skuas in Pointe Géologie: the emperor penguin and the Adélie penguin. We used the number of dead chicks of emperor penguins and the number of

Adélie penguin breeding pairs as a measure of food availability for south polar skuas during their breeding season. Selected environmental covariates included two local climate variables for the breeding period in Pointe Géologie: the air temperature recorded at the Dumont d'Urville station and the sea-ice concentration (SIC), and one local climate variable for the non-breeding period in eastern Japan Sea: the sea surface temperature anomaly (SSTa). Monthly SIC data and air temperatures were, respectively, averaged into two separate periods: late winter–spring (September–November) and summer (December–March). We used SSTa as a proxy of food abundance for skuas in their wintering area.

As interpreting individual coefficients of a model in which collinearity between predictors exists is a long-standing problem in ecological modeling (Graham 2003), we also checked collinearity of selected covariates after each selection step. We used for this purpose the vif (Variance Inflation
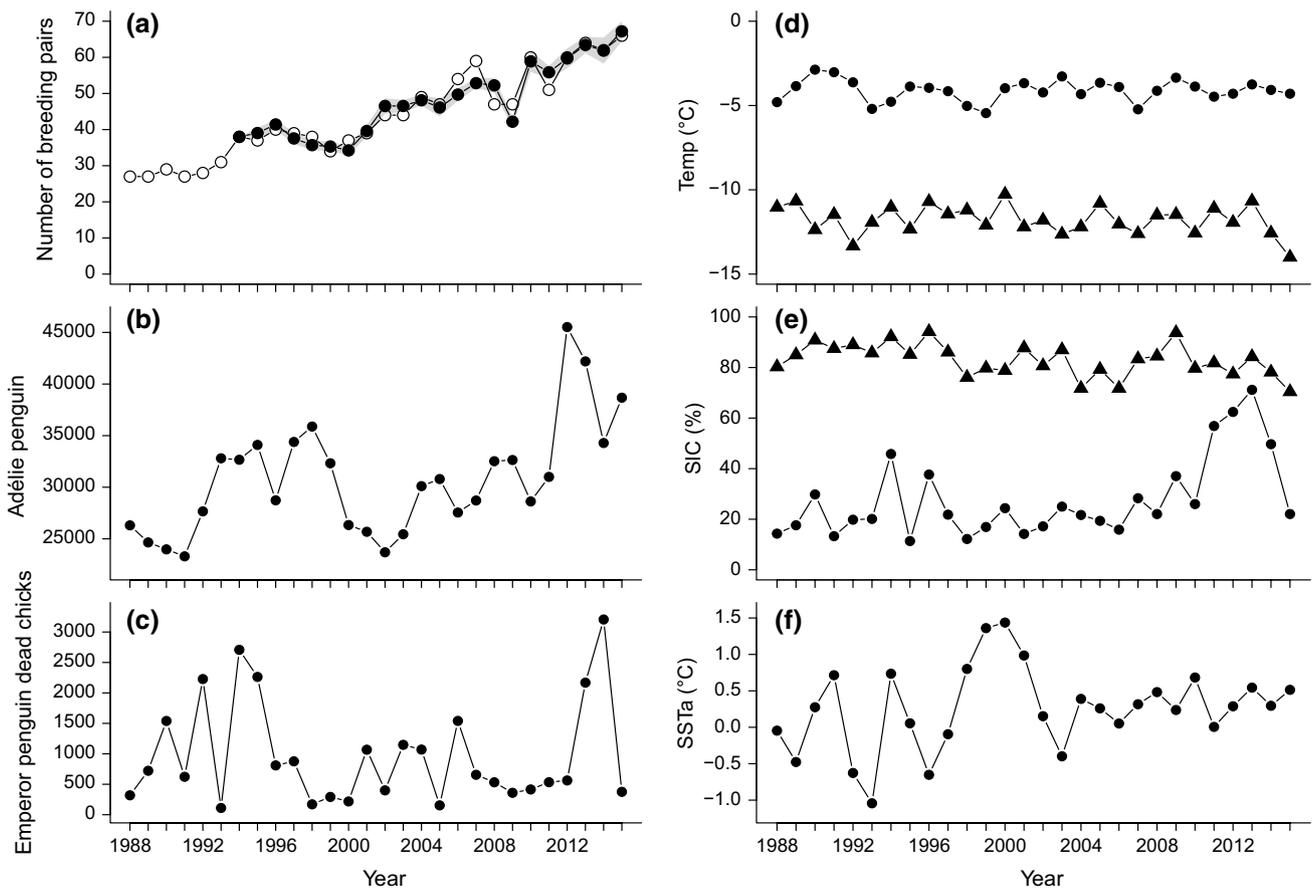


**Fig. 2** Time series showing the variation of the number of south polar skua breeding pairs, climate, and prey covariates from 1988 to 2015. **a** Observed (empty circle) and modeled (solid circle; from 1994 to 2015) abundance of breeding pairs of south polar skua within the core area obtained from the selected Gompertz model. Gray area represents the standard deviation. **b** Number of Adélie penguin breeding pairs. **c** Number of dead chicks of emperor penguin. **d** Air temperature (Temp) recorded at the Dumont d'Urville station in winter–spring (triangle) and summer (circle). **e** Sea-ice concentration (SIC) for the Dumont d'Urville Sea area in winter–spring (triangle) and summer (circle). **f** Sea surface temperature anomaly (SSTa) in the wintering area

Factor) function in the usdm package ('usdm' package v1.1-15; Naimi 2015) and took a vif of 2 as an upper limit.

More details on covariates and the forward stepwise model selection by PSIS-LOO (Pareto Smoothed Importance Sampling Leave One Out; Vehtari et al. 2016) are available in ESM Appendix 2. Model with the smallest PSIS-LOO value has a better predictive performance. Highest Posterior Density (HPD) Interval was used as the interval estimator of credible interval.

## Results

### Evidence for density-dependence and influence of environment and prey

The number of breeding pairs of south polar skua increased between 1994 and 2015 (Fig. 2) from 38 to 66. Direct density-dependent and density-independent model fits were relatively similar (see ESM Appendix 3: Table A3, Step 1). The posterior probability of the density-dependence parameter constraining population growth [Pr(DD > 0)] in the initial direct density-dependent model was superior to 98%. A one sample $t$ test on the density-dependence parameter was significant ($t = 363.34$, $df = 29,999$, $P < 0.005$), indicating that the true mean of this parameter was greater than 0. These results support a strong negative density-dependent regulation of the breeding population. The final model fit was good as indicated by the residuals and correlations between posterior and prior distributions (ESM Appendix 4: Fig. A4-1 and Fig. A4-2). The posterior probability of the density-dependence parameter constraining population growth [Pr(DD > 0)] in the final model was superior to 99% (Table 1).

The first covariate selected was a quadratic effect of SIC with a 6-year lag on the number of breeding pairs (see

**Table 1** Parameter estimates of the selected model of south polar skua population dynamics including the effects of density (DD), sea-ice concentration in winter–spring with a quadratic and 6-year lag effect (SIC_winter-spring$_6$), number of dead chicks of emperor penguin with a quadratic effect during the current year (Emp$_0$), and temperature in winter–spring with a 5–years lag (Temp_winter-spring$_5$)

| Parameter | Mean | HPD | % |
|---|---|---|---|
| DD | 0.0268 | 0.012 to 0.040 | 99.96 |
| SIC_winter-spring$_6$ | 0.0321 | − 0.005 to 0.068 | 96.00 |
| SIC_winter-spring$_6^2$ | 0.0900 | 0.055 to 0.121 | 99.99 |
| Emp$_0$ | 0.1109 | 0.044 to 0.183 | 99.80 |
| Emp$_0^2$ | − 0.0409 | − 0.074 to 0.009 | 99.16 |
| Temp_winter-spring$_5$ | 0.0391 | 0.002 to 0.076 | 97.90 |

%: percentage of positive (or negative) values in the posterior distribution if parameter mean is positive (or negative)

*HPD* highest posterior density interval

ESM Appendix 3: Table A3, Step 2). The second covariate selected was a quadratic effect of the contemporary number of dead emperor penguin chicks (see ESM Appendix 3: Table A3, Step 3). The 'best' final model evidenced a density-dependent effect, a quadratic effect of late winter–spring SIC with a 6-year lag, a quadratic effect of the number of dead emperor penguin chicks, and a linear effect of late winter–spring temperature with a 5-year lag (see ESM Appendix 3: Table A3, Step 4; model in bold). Sensitivity analyses and examination of residuals suggested a good fit and robustness to prior choice (not shown). Models including interactions between density-dependent and covariate effects did not have better cross-validation scores compared to the final model (see ESM Appendix 3: Table A3, Step 5). Density-dependence and environmental and prey covariates parameters are shown in Table 1 for the best fitting model selected with leave-out-one cross validation.

### Relationships between covariates and population dynamics

Figure 3a, b shows the predicted relationships between late winter–spring SIC, late winter–spring temperature, and,
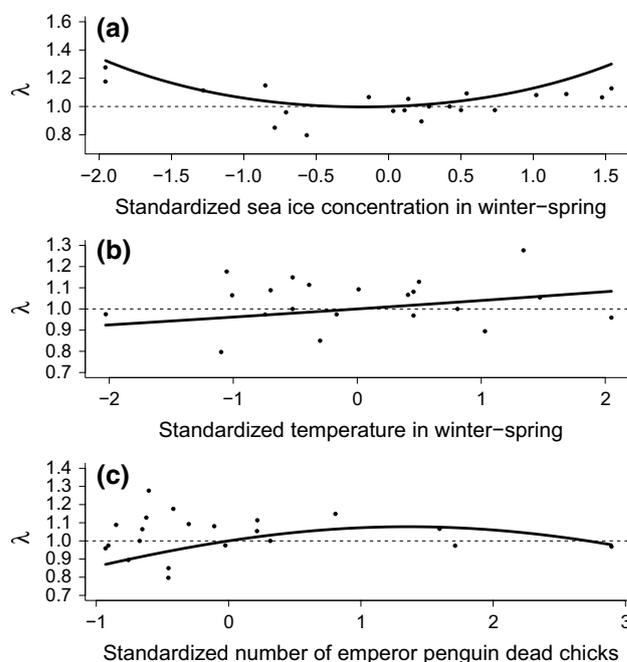
**Fig. 3** Rate of increase (λ) of the number of south polar skua breeding pairs as a function of **a** sea-ice concentration in winter–spring 6 years earlier, **b** temperatures in winter–spring 5 years earlier, and **c** number of emperor penguin dead chicks of the current year. The black line was calculated based on the exponential of the mean parameter estimates of each covariates of the final selected model. Black points represent the λ calculated from the observed time series of the number of breeding pairs of south polar skua from 1994 to 2015

respectively, the number of skua breeding pairs 6 and 5 years later. The number of breeding pairs increased strongly when late winter–spring SIC was low or high 6 years before. Breeding pairs of skuas increased strongly with warm temperatures during late winter–spring 5 years earlier. Figure 3c shows the predicted relationships between the number of dead emperor penguin chicks and the current number of breeding pairs of skuas. When prey availability was low, the number of breeding pairs decreased. The number of breeding pairs increased at the intermediate values of prey availability and moderately increased when prey availability was very high.

## Discussion

This empirical study clearly evidenced joint effects of endogenous and exogenous factors, including prey covariates, on population dynamic of a long-lived marine apex consumer. Our results demonstrated an interplay of local climate factors and prey availability affecting the number of breeding pairs. In addition, we found a negative feedback loop on population abundance of an apex consumer.

### Effect of sea-ice concentration

We found that low or high sea-ice concentrations during late winter–spring had a positive effect on the breeding population, with no effect at intermediate concentrations. Climatic factors can directly affect populations and indirectly through prey (i.e., prey abundance, quality, and availability). A direct effect of sea-ice concentration is unlikely here, because south polar skuas do not depend on sea ice as a foraging habitat in Terre Adélie. For all pairs breeding on the rocky archipelago, foraging areas were restricted to penguin colonies within the archipelago (R. Phillips, unpublished GPS tracks from 2012). Observational and isotopic data suggest Adélie and emperor penguins are the main prey of south polar skuas (Jouventin and Guillotin 1979; Cherel 2008; Goutte et al. 2014; Weimerskirch et al. 2015; Carravieri et al. 2017). Therefore, sea-ice cover was probably not affecting this south polar skua population directly via Antarctic silverfish *Pleuragramma antarctica* availability as observed in the more productive Ross Sea (Young 1963b). Adélie penguins, one of the main preys of south polar skuas, are known to be ice obligate (Croxall et al. 2002; Ainley et al. 2005; Forcada and Trathan 2009), and mainly feed on Antarctic silverfish and crustaceans such as *Euphausia superba* and *E. crystallorophias* (Cherel 2008). We, therefore, strongly suspect that the relationship between SIC and the skua breeding population size was actually mediated by Adélie penguin foraging ecology, although we cannot entirely exclude that a few breeding pairs with limited access

to penguins could rely more on fish or crustaceans. Interestingly, the relationship between Adélie penguin breeding success and summer SIC follows a bell shape with lower success at low or high SIC (Barbraud et al. 2015), whereas south polar skuas showed a U-shape relationship with SIC. This result outlines a remarkable reverse response of a top predator and its prey to the same environmental factor, suggesting that their dynamics are closely linked due to a direct dependence of the predator dynamics to its prey, and that sea-ice cover variations affect south polar skuas indirectly via their prey dynamics.

During heavy ice years, a distant sea-ice edge and consolidated ice (with fewer polynyas) delayed the return of females Adélie penguin during the incubation period and impacted the duration of foraging trips during incubation and the guard phase (Spée et al. 2010; Ropert-Coudert et al. 2014). Foraging trips of breeding Adélie penguins during the incubation and the guard phase are thus prolonged to reach foraging areas and due to decreased prey accessibility (Spée et al. 2010; Ropert-Coudert et al. 2014). This results in (i) an increased abandonment of eggs and young chicks by the nest-attending, but fasting, parent if its partner spends too much time foraging at sea, or (ii) in an increase of chick mortality due to undernourishment; thus in a decrease of breeding success (Wilson et al. 2001; Emmerson and Southwell 2008, 2011; Lescroël et al. 2009; Spée et al. 2010; Ropert-Coudert et al. 2014; Le Guen et al. (in press). The likely consequence for south polar skuas is a food surplus during these heavy ice years.

Low sea-ice concentration and a close ice edge during late-winter and spring led to more readily available foraging areas for Adélie penguins (Cottin et al. 2012). However, during such years, Widmann et al. (2015) suggested that resources can be consumed earlier potentially leading to a local depletion of prey abundance and to a stronger competition pressure in prey patches. In addition, winters and springs with less sea-ice coverage are associated with lower Antarctic krill densities, an important food resource for Adélie penguins (Loeb et al. 1997; Flores et al. 2012a, b). Thus, food abundance may be limited for Adélie penguins to feed their chicks during years with low sea-ice coverage, which may increase chick mortality and provide additional food resources for their main predators on land: south polar skuas. Finally, for breeding Adélie penguins, a lower sea-ice concentration can outline a lack of stable ice platforms from which to forage, escape predators, and to rest, potentially increasing adult mortality and, by consequence, egg or chick mortality.

All these elements coalesce to suggest a positive effect of low or high sea-ice coverage on the apex consumer population considered here due to an increase of their available food (Adélie penguins), through facilitated predation on weaker individuals and unguarded eggs or chicks (Davis and

McCaffrey 1986) and scavenging of dead chicks or individuals dead ashore.

The 6-year lag found in the SIC effect on the south polar skua breeding population suggests a higher proportion of individuals joining the breeding population 6 years later. This could be due to a higher fledging rate and/or a better body condition of yearlings and thus a higher survival of individuals during early life and an earlier age of sexual maturity (Metcalfe and Monaghan 2001; Monaghan 2008; Cam and Aubry 2011). Indeed, several studies on *Stercorariidae* reported positive relationships between breeding performance and prey availability (Phillips et al. 1996, 2004; Gilg et al. 2006, 2009; Hahn et al. 2007; Meltofte and Høye 2007; Furness 2007; Dawson et al. 2011). Increase in food supply also reduces sibling rivalry observed in many long-lived species (Viñuela 1999; Hofer and East 2008; Trillmich and Wolf 2008), and particularly in south polar skuas where one chick, older by 2–4 days, often kills the second chick during food shortage conditions (Procter 1975; Young and Millar 2003).

### Direct effect of prey

Our study also evidenced a direct effect of the abundance of an important prey resource on a marine apex consumer. The absence of a lag effect of the prey covariate suggests that adult survival and/or the proportion of breeders were the most likely demographic mechanisms involved. Dead emperor penguin chicks account for nearly all the prey items available for skuas from their arrival on the breeding sites and before Adélie penguins start to breed. Later in spring and in summer, dead chicks of emperor penguin become unavailable after sea ice breaks up and skuas rely on Adélie penguins for food. We thus suspect an impact of the number of dead emperor penguin chicks on the proportion of skuas that engage in reproduction. Skipped breeding during critical years is known to be an important strategy in long-lived birds to maximize their residual fitness (Erikstad et al. 1998). During years with reduced quantity of food, a higher proportion of the birds may not be able to build up the energy reserves necessary for breeding and could decrease their current reproductive effort to ensure their maintenance costs (Nager 2006). Conversely, abundant food at the beginning of the breeding cycle of skuas could increase breeding propensity with more birds reaching a sufficient body condition to start breeding, as observed in other capital breeders (Guinet et al. 1998; Madsen and Shine 1999; Toïgo et al. 2002; Reed et al. 2004). Schmidt et al. (2012) found a decline in breeding propensity of long-tailed jaegers (*Stercorarius longicaudus*) when their prey (Arctic lemming *Dicrostonyx torquatus*) were scarce, while the number of birds arriving on the breeding ground remained relatively stable.

Contrary to emperor penguins, we failed at identifying a relationship between the abundance of Adélie penguins and the number of skua breeding pairs. This may result from the different nature of the covariates. Indeed, dead emperor penguin chicks directly represented the abundance of food for skuas, whereas the number of Adélie penguin breeding pairs was an indirect estimate, since skuas do not feed on adult Adélie penguins but on their eggs and chicks. This is further supported by the reverse response of Adélie penguins and skuas to sea-ice concentration as discussed above. However, the number of Adélie penguin dead chicks or eggs was not available.

### Temperature effect

Warmer air temperatures during the beginning of a breeding season correlated with an increased number of skua breeding pairs 5 years forward. This lag effect suggests an influence of warmer temperatures on reproductive success and subsequent recruitment of skuas with a probable effect on survival of young individuals and an advanced maturity. Thompson and Ollason (2001) found a similar lag effect of temperature on the population response of northern fulmars (*Fulmarus glacialis*) and suggested an influence through age at sexual maturity.

Colder temperatures during spring can increase the energetic cost of thermoregulation and water losses of adults (Spellerberg 1969). Since egg size is sensitive to maternal investment and individuals in poorer condition may lay smaller eggs and of lesser quality with repercussion on chick quality, smaller eggs may result in the production of smaller and lighter chicks which may have a disadvantage in terms of survival, particularly during the early stages of growth, as found in south polar skua and some other *Stercorariidae* (Furness 1983; Ratcliffe et al. 1998; Phillips et al. 2004; Hahn et al. 2007) and in other avian species (Williams 1994; Saino et al. 2004; Rubolini et al. 2006). A lower ambient temperature could also directly increase egg losses. Spellerberg (1969) described the negative effect of the exposure of eggs of south polar skuas to a low ambient temperature (around $-3$ °C) on calm days and the heat loss rate of eggs measured was of $-2.3$ °C/min when there was no incubating parent.

### Density-dependence

Our study clearly evidenced a negative feedback in breeding population dynamics when the number of breeding pairs increased. Lande et al. (2002) showed that the age structure of this population could explain a part of the density-dependence observed and suspected density-dependence stemming from the strong territorial behavior

displayed by the breeding individuals. Territorial behavior is a regulating social system found in many animal populations, and is fundamentally determined by food availability and interference for territory establishment and copulation (Maher and Lott 2000; Adams 2001). Many animal species are characterized as territorial due to their exclusive use of areas with no or low overlap by conspecifics (Maher and Lott 1995; Ferreras et al. 1997). To maximize their fitness, individuals should establish themselves in high "quality" sites and defend them against conspecifics (Rodenhouse et al. 1997). Due to the inclusion of both breeding and feeding grounds (Adélie penguin colonies) in skua territories and the relative promiscuity of nests in the area studied (~ 70 breeding pairs in a 2-km-diameter area), we suspect strong density-dependence through territorial behavior limiting the breeding population in Terre Adélie (Young 1972; Lande et al. 2002). Defending a territory against conspecifics is generally costly in terms of time and energy, potentially limiting energy investment in reproduction, or increasing mortality risks during fights. South polar skuas start defending a territory just a few days after arrival on a breeding site, and do not stop until the breeding season is over (Spellerberg 1971b). If the number of territories is limited, a proportion of sexually mature individuals may be unable to breed because of the intense competition and could form a floater component. This is a common feature of *Stercorariidae* colonies with club sites—small areas, where the immature and mature non-breeding skuas and the floaters gather in flocks to rest together or to display and practice social behavior (Furness 1987). A club site (~ 30–50 individuals) was found at the same place all years in the study area on the Piste du Lion Island in the core Area, and the non-breeder component reached up to nearly 50% in some years (Micol and Jouventin 2001). We suggest that direct disturbance and strife mainly by floaters, and in a lesser extent by neighbors, could prevent some birds to breed or to breed successfully. Contests for breeding space might also act as a density-dependent mechanism by increasing adult mortality during violent fights (Newton 1998). This was observed several times during a single breeding season at Terre Adélie with a member of a breeding pair holding a territory being killed by a contester (Barbraud personal observation). Evidence for site-dependent population regulation has been previously found for several territorial bird species (e.g., bald eagle *Haliaeetus leucocephalus*: Turrin and Watts 2014, brown skua *C. lonnbergi*: Phillips et al. 2004, common guillemot *Uria aalge*: Kokko et al. 2004, great skua *C. skua*: Furness 2015, osprey *Pandion haliaetus*: Bretagnolle et al. 2008) as well as in mammals (Gray wolf *Canis lupus*: Cubaynes et al. 2014), and

reptiles (side-blotched lizard *Uta stansburiana*: Calsbeek and Sinervo 2002).

## South polar skua population dynamics

Carneiro et al. (2016) highlighted the importance of understanding the underlying causes of skua population dynamics to assess the conservation status of these species as important top predators and scavengers in the Antarctic environment. Population trends of south polar skuas are poorly documented (Carneiro et al. 2016) and our study population is one of the few that were monitored during several decades. South polar skuas seem relatively resilient to environmental changes underway. Indeed, the breeding population in Terre Adélie has been increasing since the beginning of the study despite important variations in prey abundance and climate factors. Barraquand et al. (2014) showed a substantial role of the floaters in a long-tailed skua population dynamics, dampening the increasing environment fluctuations. Even if the ecological context of south polar skuas differs from the context described in Barraquand et al. (2014)—where long-tailed skuas rely on collared lemming (*Dicrostonyx groenlandicus*) which show strong cycles (3–5 years) in abundance—we believe that the population studied here benefited, after the closure of the dumpsite nearby the station, from the high number of potential reproducers in the area and from the increase in Adélie penguin colonies (Prévost 1963; Le Morvan et al. 1967; Micol and Jouventin 2001). Monitoring of the floater component of the population and inter-populations exchange (through biologging) should be undertaken in the future to investigate its importance on the population dynamic.

On King George Island (Antarctic Peninsula), Hahn et al. (2007) reported an impact of sea-ice conditions on south polar skua reproduction parameters through linear regression analysis, although negative. They suggested a reduced accessibility of their main prey, pelagic fishes, with sea-ice cover. Sympatric brown skuas were quite insensitive to sea-ice conditions probably due to a change in their prey community, with chinstrap (*Pygoscelis antarctica*) and gentoo penguins (*Pygoscelis papua*) being less sea-ice obligate than Adélie penguins and replacing them (Ducklow et al. 2007).

It should be noted that a few brown skuas (< 5 individuals) and giant petrels *Macronectes giganteus* (10–15 breeding pairs restrained to one island) make the south polar skua population in Terre Adélie free of predators and of competitors on Adélie penguin colonies. However, predators and competition with other species were shown to be strong drivers of two other *Stercorariidae* populations. Meltofte and Høye (2007) showed intra-guild predation in Northeast Greenland with arctic foxes *Vulpes lagopus* impacting the fledging success of long-tailed skuas. Inter-specific competition for territories, with great skuas, was found regulating

the arctic skua *Stercorarius parasiticus* populations, as well as prey availability (sandeels and whitefish discards from fishing vessels) (Votier et al. 2007; Dawson et al. 2011).

## Methodological considerations

While the covariates and the lags identified indicated significant relationships between density-independent factors and the population growth rate, some methodological aspects deserve mention. First, these relationships cannot be interpreted as the solely causal effects, in view of the approximate standard errors for model's LOO criterions. Second, and to depict more accurately cohort effects, alternative methods to single time lags (such as penalized regression including several lags, Sims et al. 2007) might be used in the future. Finally, although the quadratic relationships seemed to fit well the observed data and that there was no evidence for threshold effects in the quadratic relationships selected, splines or change points models were not used here. Quadratic relationships can sometimes overstate effects for extreme covariate values not sufficiently represented. That could be the case for some of the extreme values of the relationship between the skua breeding population, the number of emperor penguin dead chicks, and sea-ice concentration in spring–late winter).

## Conclusion

To conclude, our results suggest that the breeding population of an apex marine consumer was driven by a complex interplay of local climate (sea ice), prey abundance, and a density-dependent competition for territories. Evidence for lagged and unlagged influence of critical factors determining the fluctuation of the breeding population led us to suggest that demographic processes involved mainly breeding parameters (breeding propensity, breeding success, or recruitment) rather than adult survival. A better understanding of the demographic functioning of this and other skua populations requires capture–mark–recapture programs allowing disentangling the effects on demographic parameters. Our study supports the previous findings of a relationship between sea-ice conditions and top-predator populations in polar environments (Fraser and Trivelpiece 1996; Barbraud and Weimerskirch 2001; Jenouvrier et al. 2005, 2012; Ainley et al. 2005; Barbraud et al. 2011). Deciphering the demographic processes linking environmental covariates and population size proposed in this study, in addition to monitoring precisely the spatial variation in territories and modeling jointly predator and prey (as already achieved in the high-arctic tundra), would allow to build scenarios of population response to changes in climate and prey availability. For example, using sea-ice forecasts and a population projection models, Jenouvrier et al. (2012) predicted an 81% decline of the Terre Adélie emperor penguin population by the year 2100. Our results suggest that this could directly negatively affect the south polar skua population.

**Author contribution statement** CB and NP designed and coordinated the research. Data management and quality check were performed by KD and NP. Analyses were performed by NP with the support of MA and CB. NP, MA, KD, and CB wrote the manuscript

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