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ARTICLE

Bottom-up effects drive the dynamic of an Antarctic seabird predator–prey system

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Abstract

Understanding how populations respond to variability in environmental conditions and interspecific interactions is one of the biggest challenges of population ecology, particularly in the context of global change. Although many studies have investigated population responses to climate change, very few have explicitly integrated interspecific relationships when studying these responses. In this study, we aimed to understand the combined effects of interspecific interactions and environmental conditions on the demographic parameters of a prey–predator system of three sympatric seabird populations breeding in Antarctica: the south polar skua (*Catharacta maccormicki*) and its two main preys during the breeding season, the Adélie penguin (*Pygoscelis adeliae*) and the emperor penguin (*Aptenodytes forsteri*). We built a two-species integrated population model (IPM) with 31 years of capture–recapture and count data and provided a framework that made it possible to estimate the demographic parameters and abundance of a predator–prey system in a context where capture–recapture data were not available for one species. Our results showed that predator–prey interactions and local environmental conditions differentially affected south polar skuas depending on their breeding state of the previous year. Concerning prey–predator relationships, the number of Adélie penguin breeding pairs showed a positive effect on south polar skua survival and breeding probability, and the number of emperor penguin dead chicks showed a positive effect on the breeding success of south polar skuas. In contrast, there was no evidence for an effect of the number of south polar skuas on the demography of Adélie penguins. We also found an important impact of sea ice conditions on both the dynamics of south polar skuas and Adélie penguins. Our results suggest that this prey–predator system is mostly driven by bottom-up processes and local environmental conditions.

KEYWORDS

Adélie penguin *Pygoscelis adeliae*, emperor penguin *Aptenodytes forsteri*, integrated population model (IPM), interspecific relationships, intrinsic and extrinsic factors, prey–predator relationships, south polar skua *Catharacta maccormicki*

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INTRODUCTION

Marine ecosystems are difficult to study and quantify due to the large number of species involved, their complex interactions (interspecific and intraspecific), the diversity of environmental factors involved, and intricate mechanisms that interact together (Godfray & May, 2014). Fluctuations and changes in environmental conditions could interact with the different processes driving marine ecosystems (Stenseth et al., 2002) and even more so in polar marine ecosystems, which are highly sensitive to global change (Doney et al., 2012). Seabirds are excellent indicator species by which to study the state of marine ecosystems and the impact of global changes (Velarde et al., 2019). As upper-trophic-level long-lived predators, their dynamics reflect the impacts of climate change on lower trophic levels, which are often difficult to assess (Piatt et al., 2007), although the increasingly recognized role of terrestrial factors in seabird dynamics can be conflated or confounded with marine influences (Descamps et al., 2014; Sauser et al., 2021) and need to be accounted for. They are easier to study over the long term than other upper-trophic-level marine predators and highly visible and nest in large colonies in generally the same locations, which allows for efficient data gathering and can be used as a proxy to better understand some ecological processes on large spatial and temporal scales (Hazen et al., 2019; Velarde et al., 2019). Moreover, numerous studies have shown that bottom-up (Cairns, 1988) and top-down processes (Hipfner et al., 2012) affect simultaneously and differentially the demographic parameters of seabird populations (Horswill et al., 2016; Sauser et al., 2021). Thus, understanding the roles and importance of intrinsic and extrinsic factors for the dynamics of seabird populations is crucial in the context of global change. Quantifying the relative importance of environmental conditions, density dependence, and interspecific relationships, such as prey–predator effects, for the dynamics of seabird populations could help us to better understand the relative importance of bottom-up and top-down processes for marine ecosystems (Qu erou e et al., 2021) and better predict the future of species.

However, to better understand the dynamics of communities such as prey–predator systems, we need to consider not only the abundance of populations but also the underlying demographic processes (Horswill et al., 2016; Perkins et al., 2018), as well as the structure of the populations, including the different ages and states of individuals (Miller & Rudolf, 2011). Species responses to fluctuations of extrinsic factors like climatic conditions or food availability also differ depending on the species (Jenouvrier, 2013) or on the individual ontogenetic stage (Miller & Rudolf, 2011). This could lead to

modifications to a given population's structure, species interactions, or the diversity within communities (Thomas et al., 2004). Assessing, species by species, the responses to environmental fluctuations could cause one to overlook the role played by the different interspecific interactions. Furthermore, intrinsic factors such as density-dependence effects or individual characteristics (ontogenetic stage, age, size) could also influence the structure and dynamics of populations (Kramer et al., 2009).

Integrated population models (IPMs) are a powerful framework that allows us to estimate the state-dependent demographic parameters and the abundance of individuals within populations using different sources of information (e.g., count data, capture–recapture [CR] data) in a single analysis, simultaneously considering the various sources of uncertainty related to each type of data (Schaub & K ery, 2021). Recently, IPMs have been extended to multiple species for competition/parasitism (P eron & Koons, 2012) or for predator–prey interactions (Barraquand & Gimenez, 2019). Qu erou e et al. (2021) developed a multispecies IPM to assess the dynamics of a seabird predator–prey system using CR data for a predator (the brown skua, *Catharacta l onnbergi*) and its main prey (the blue petrel, *Halobaena caerulea*). However, obtaining CR data requires a substantial sampling effort and is not always possible to achieve for all species involved in predator–prey systems for logistical or technical reasons. Thus, multispecies IPMs are needed for cases where CR and count data are available for only one species of the predator–prey system, the data concerning the other species being only time series of counts.

The aim of our study was to assess the effect of interspecific relationships, as well as environmental conditions, on the demographic parameters within a predator–prey system of seabirds in Antarctica. To this end, we developed a two-species IPM combining 31 years of capture–mark–recapture (CMR) and count data for the south polar skua (*Catharacta maccormicki*) and count data for one of its main preys during the breeding season, the Ad elie penguin (*Pygoscelis adeliae*). We also include, as a covariate in the model, emperor penguin dead chicks (*Aptenodytes forsteri*), another major prey of the south polar skua.

The main strengths of our approach are that it (1) efficiently combines multiple different sources of data within a unified framework and (2) allows for the estimation of demographic parameters of a predator–prey system while assessing the impact of intrinsic and extrinsic factors on these demographic parameters in order to better understand the contribution of predator–prey interactions to population dynamics.

MATERIALS AND METHODS

Study site and species

We studied south polar skuas and Adélie penguins on major islands of the Pointe Géologie archipelago (Le Mauguen, Pétreils, Rostand, Bernard, Lamarck, and Nunatak), located near Dumont d'Urville Station (DDU), Terre Adélie (66°40' S, 140°01' E), representing 90% and 78% of the total populations of the archipelago for both species, respectively. We also used the number of dead emperor penguin chicks as a covariate to test its effect on the skua demographic parameters. Carcasses of dead emperor penguin chicks are counted every day from the end of July to December until the sea ice breaks up. Changes in the population sizes of the two species and on the number of dead emperor penguin chicks observed during the study period are shown in Appendix S1.

South polar skuas are medium-sized seabirds breeding all around the coast of Antarctica. Breeding pairs form in late October; generally two eggs are laid in November and hatch around mid-December (Barbraud & Weimerskirch, 2006). Chicks fledge about 50 days later. The parents feed their chicks until their departure from the breeding sites, around late March. At the end of the breeding season, skuas from the Pointe Géologie archipelago migrate to the east coast of Japan (35–45° N) for winter (Weimerskirch et al., 2015). Juveniles will return to Pointe Géologie 4–7 years after their departure to breed for the first time (Pacoureaux et al., 2019). The breeding cycle of skuas is synchronized with that of penguins (Appendix S2). At Pointe-Géologie during the breeding season, south polar skuas feed almost exclusively on penguins' chicks and eggs, as scavengers or as predators: From their arrival until the sea ice breaks up in December or January, skuas feed on dead chicks of emperor penguins, and from November until the end of the breeding season they mainly feed on the eggs and chicks of Adélie penguins (Ainley et al., 1990). Skuas breed on 17 islands of the archipelago, and the breeding population size has increased from 35 breeding pairs to 63 between 1988 and 2018.

Adélie penguins are medium-sized penguins living around the Antarctic coast. During the breeding season (October–late February), Adélie penguins form dense colonies on rocky ridges on the Antarctic coast or on islands (Ainley, 2002). In general, females lay two eggs. After hatching, the parents make numerous trips between the colony and the pack ice to forage for food for the chicks (Widmann et al., 2015). Highly dependent on sea ice conditions for their food, they feed mainly on crustaceans (in particular different species of krill, including the Antarctic krill, *Euphausia superba*; Cherel, 2008).

Outside the breeding period, Adélie penguins from Pointe Géologie migrate to the northwest, pursuing the pack ice edge within an area spanning around the colony of 1,900,000 km² (Thiebot et al., 2019). Adélie penguins breed on all islands of the archipelago, and the breeding population size has increased from 26,100 breeding pairs to 41,600 between 1988 and 2018.

Emperor penguins are large penguins living around the Antarctic coast and are the only birds to breed directly on sea ice during the austral winter. They are highly dependent on sea ice for their food (fish, crustacean, cephalopods) and as a breeding platform (Barbraud et al., 2011). Each breeding season they form colonies of thousands of individuals (Fretwell et al., 2014). Each pair will raise one chick. From hatching, the parents make numerous trips between the colony and the sea ice edge to forage for food for their chicks (Zimmer et al., 2008). Survival of emperor penguin chicks during the breeding season is highly sensitive to sea ice conditions between September and November and is negatively affected by longer distances between colony and fast ice edge (Labrousse et al., 2021). In December, all adults leave the colony, and the chicks follow them shortly thereafter. A single colony of emperor penguins breeds in the archipelago, and the breeding population size has increased from 3000 to 3400 breeding pairs between 1988 and 2018.

Count and CR data

We used demographic data for both skuas and Adélie penguins collected during the breeding season from 1988/1989 to 2018/2019 (thereafter referred to as 1988–2018). For emperor penguins, we used a time series data providing information on the annual number of dead chicks, which was used as a covariate in the IPM.

For skuas, three types of data were used: count data corresponding to the number of breeding pairs (Y_s), CR data of adult individuals observed in the monitored area, and the number of immigrants, that is, new individuals observed for the first time (not ringed) at the colony (N_{im}). Every year, the locations of the different nests were spotted during the laying period. Since the monitored area occupied was relatively small (about 80 ha), with no vegetation, and given the conspicuous behavior of the breeding skuas when defending their territories, we assumed that all active nests were detected each year (Pacoureaux et al., 2018). A major part of the population is marked using stainless steel and plastic bands engraved with a unique alphanumeric code. Every year during the breeding season, from mid-October to mid-April, nesting territories, as well as a zone where nonbreeding individuals are known to roost, were visited every 2 weeks on

average to determine the breeding status of each bird (Pacoureaux et al., 2019). The breeding status of each individual was defined as follows: breeder (B) for individuals seen at a nest with at least one egg, nonbreeder (NB) for individuals not seen at a nest with eggs or chicks, failed breeder (FB) for breeding individuals whose eggs did not hatch and/or chicks did not survive until fledging, successful breeder with one chick (SB1) for breeding individuals with one chick fledged, and successful breeder with two chicks (SB2) for breeding individuals with two chicks fledged. We also defined an uncertain state (C) for individuals that could not be assigned with certainty to one of the five breeding states described above. We did not have observation data available for juveniles after their fledging until they returned to the colony at Pointe Géologie at breeding age (at least 4 years old). The annual number of breeding pairs of skuas, that is, count data (Y_S), was defined as the number of nests identified and occupied by breeding individuals (Pacoureaux et al., 2018).

For Adélie penguins, two types of count data were used: the number of breeding pairs (Y_A) and the number of chicks ready to fledge (Y_P). Breeding pairs were visually counted every year, between 15 and 18 December, during the laying period. Live chicks ready to fledge were counted before their departure at sea, between 3 and 6 February. See Barbraud et al. (2020) for more information on monitoring protocols.

Integrated population model

We built a two-species IPM that combines count and CR data that makes it possible to estimate the abundance and demographic rates of south polar skuas and Adélie penguins. More specifically, we connected one IPM for the skuas and a state-space model for Adélie penguins through explicit predator–prey relationships (Barraquand & Gimenez, 2019). We incorporated the effects of species-specific demographic parameters such as survival and breeding parameters. The two models used are structured according to life-history traits (Figure 1). We used Poisson (Po) and binomial (Bin) distributions to account for demographic stochasticity. The details of the model are presented in Appendix S3.

Demographic parameters of south polar skuas and Adélie penguins could be affected by different covariates including interspecific predator–prey relationships, intraspecific density dependence, and environmental covariates such as temperature or sea ice conditions. To estimate those effects, we used logit linear regressions on the demographic parameters within the IPM. An example is shown in Appendix S3: Section S3.

In our IPM, we assessed the different demographic parameters (φ , β , Θ , δ) of skuas according to their breeding state during the previous breeding season. Nonbreeders were individuals that reached sexual maturity but do not reproduce (Penteriani et al., 2011) or skipped breeding due to poor body condition or because they could not find a partner or a territory to breed in (Ashmole, 1963). We assumed the demographic parameters of skuas could have different values depending on their breeding state in the previous year and different responses to environmental factors and intra- and interspecific relationships.

All covariates were standardized to compare the relative contribution of the effects. We calculated the 95% credible intervals (CRIs) for the regression coefficients α and the probabilities of having a negative slope value (PN) or of having a positive slope value (PP). A regression coefficient was considered significant when its probability of being negative (PN) was greater than 90% or less than 10% (equivalent to a probability of being positive [PP] at 90%). Bayesian posterior distributions of the multispecies IPM were approximated with Markov chain Monte Carlo (MCMC) algorithms. Two independent MCMCs of 30,000 iterations were used, with a burn-in period of 10,000 iterations. Gelman–Rubin convergence diagnostics (Brooks & Gelman, 1998) were below 1.1 for each parameter, and the mixing of the chains was satisfactory. The analyses were performed using JAGS (Plummer, 2003; version 4.3.0) and R (version 4.0.5).

Covariates and hypotheses

In what follows, we detail the covariates used (summarized in Appendix S4) and how we hypothesize they may affect the dynamics of skuas and Adélie penguins.

Predator–prey interactions

To estimate the effect of interspecific predator–prey relationships between skuas and Adélie penguins, that is, the dependence of demographic parameters of one species on the abundance of another species, we used the following state variables: number of adult (breeder and nonbreeder) skuas (N_{skua}) and the number of Adélie penguin breeding pairs (N_{AB}) estimated by the multispecies IPM. We hypothesized that a high availability of prey (number of Adélie penguin breeding pairs and dead emperor penguin chicks) would favor the survival, breeding probability, and breeding success of south polar skuas (Newton, 1998). As the carcasses of dead emperor penguin chicks are available at the beginning

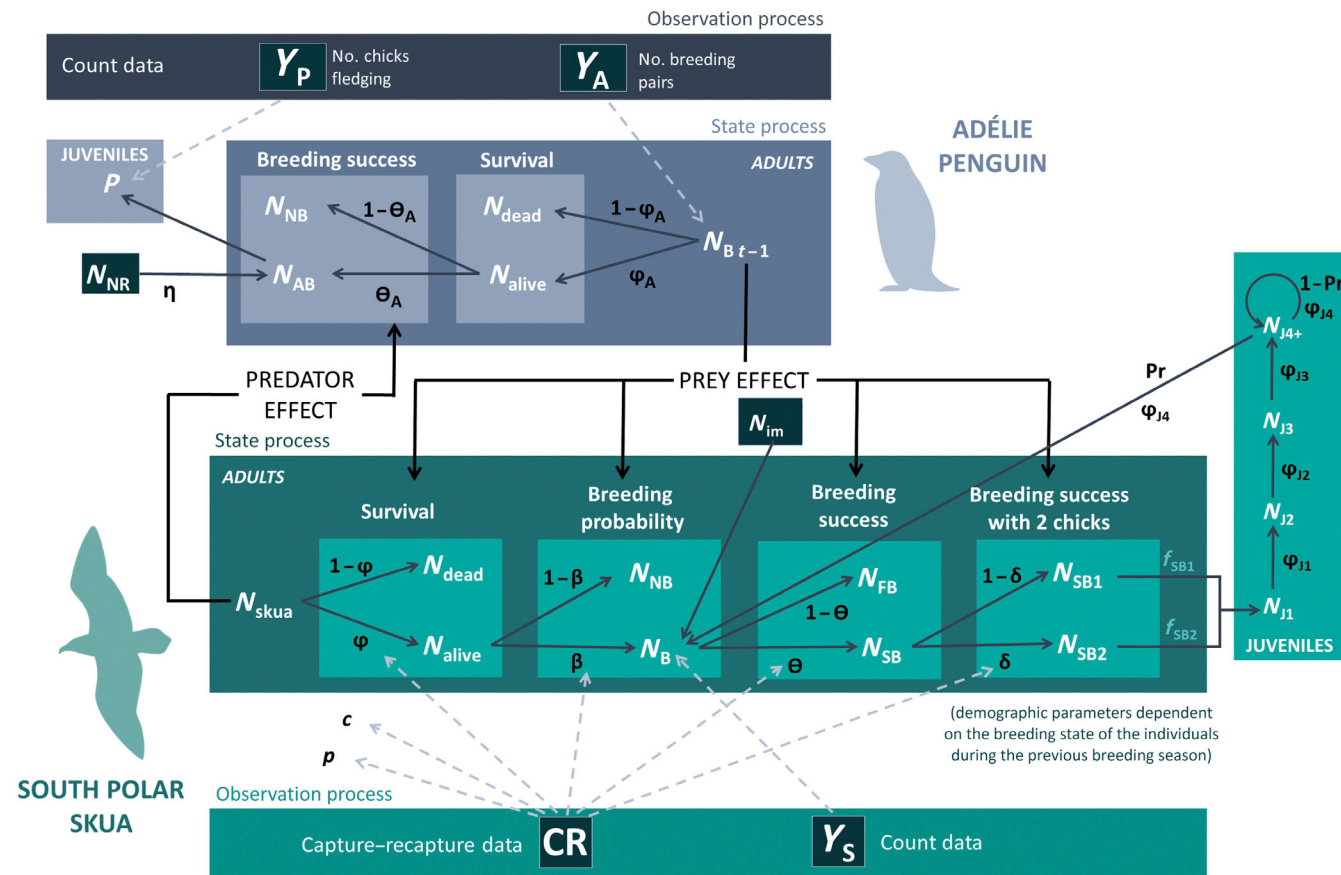


FIGURE 1 Structure of multispecies integrated population model for south polar skuas and Adélie penguins. Writing in white indicates different states, and writing in black indicates demographic parameters. Four types of data were used: capture–recapture (CR) data, counts of breeding pairs of skuas (Y_S), counts of breeding pairs of Adélie penguins (Y_A), and the number of Adélie penguin chicks just before fledging (Y_P). For skuas, the parameters estimated by the model were the apparent adult survival (φ), the apparent juvenile survival ($\varphi_{J1}-\varphi_{J4}$), the probability of first breeding (Pr), the breeding probability (β), breeding success (Θ), breeding success with two chicks (δ), detection probability (p), and the probability of assigning an individual to its real state (c). The demographic parameters for skuas were estimated depending on the breeding state of the individuals in the previous breeding season, either breeder or nonbreeder. The skua fecundity parameters (f_{SB1} and f_{SB2}) were fixed according to the breeding states (with one chick: SB1 or two chicks: SB2). For Adélie penguins, the parameters estimated by the model were the adult apparent survival (φ_A) and the breeding success (Θ_A). The Adélie penguin recruitment rate (η) was fixed. For skuas, the state variables estimated by the model were the total number of adults (N_{adtot}), dead (N_{dead}), alive (N_{alive}), breeders (N_B), nonbreeders (N_{NB}), failed breeders (N_{FB}), successful breeders with one chick (N_{SB1}), successful breeders with two chicks (N_{SB2}), and the number of juveniles 1–4 years old or older ($N_{J1}-N_{J4+}$). The number of immigrants, that is, new individuals observed for the first time (not ringed) at the colony (N_{im}), was a fixed vector. For the Adélie penguins, the state variables estimated by the model were the number of breeding pairs ($N_{A,B}$), alive (N_{alive}), dead (N_{dead}), adult nonbreeders ($N_{A,NB}$), and fledged chicks (P). N_{NR} corresponds to the number of Adélie penguin new breeders (local recruitment and immigration).

of the skua breeding season, we supposed that a large number of dead chicks would favor the breeding probability (β) of skuas. A large number of breeding Adélie penguins and emperor penguin dead chicks would ensure their accessibility to food resources during the breeding season and, thus, would increase their survival (φ) as well as the breeding successes (Θ and δ). In contrast, the predation on eggs and chicks of Adélie penguins by south polar skuas should have a negative effect on the breeding success (Θ_A) of Adélie penguins (Horswill et al., 2016).

Density dependence

We estimated intraspecific relationships for both species using the number of adult (breeder and nonbreeder) skuas (N_{skua}) and the number of Adélie penguin breeding pairs (N_{AB}) estimated by the IPM. We included the density dependence in our model, following the recommendation of Barraquand and Gimenez (2019), to produce a stable model with minimal complexity, as only considering interspecific links could lead to instability in the model. We supposed that an important number of

individuals of the same species within the colony could have a negative effect on the survival and breeding success by increasing competition for food resources and/or for high-quality nesting sites (Dhondt et al., 1992; Newton, 1998; Turchin, 1995) and adult predation on the eggs and chicks of other breeding pairs (Furness, 1987). At high densities, skuas and Adélie penguins would be less efficient to raise their chicks and thus would have lower breeding success (Θ , δ) than at low densities.

Environmental covariates

We considered several covariates suspected of affecting the populations of skuas and Adélie penguins, directly and through perturbations of the food web. For both Adélie penguins and south polar skuas, we supposed that local climatic conditions encountered by the parents and their offspring during the breeding season, as well as the climatic conditions encountered outside the breeding season by carry-over effects, would play a determining role in survival, breeding probability, and breeding success by affecting food availability and energy expenditure. Temporal variations for the environmental covariates considered over the study period (1988–2018) are represented in Appendix S1.

Air temperature

Air temperature (AT) was measured daily at the DDU station, located on Ile des Pétreles, Pointe Géologie archipelago. Data were downloaded from the British Antarctic Survey. Temperature data were averaged into two periods: spring (September–November) and summer (December–March). The first period corresponds to the breeding period when skuas arrive at the colonies, perform courtship rituals, form pairs, prepare a nest, lay eggs, and incubate the eggs. The second period corresponds to chick rearing from hatching until fledging. We assumed a negative effect of low ATs on demographic parameters (i.e., survival, breeding probability, and breeding success) of skuas. Low temperatures could cause an additional energetic cost due to thermoregulation and water loss, which could penalize parents and lead to a smaller number of eggs laid, and a higher mortality of chicks (Emmerson & Southwell, 2011; Spellerberg, 1969).

Sea ice concentration

Monthly sea ice concentration (SIC) data were averaged into three periods: late spring (September–November), summer (December–March), and winter (April–August). For spring and summer data, we considered the area around the DDU station (65°50′–66°50′ N, 139°50′–140°50′ E) corresponding to the area where emperor penguins,

Adélie penguins, and skuas forage during their breeding season (Pacoureaux et al., 2018). The winter data area was extended at 60°00′–66°50′ N, 100°00′–150°00′ E, corresponding to the foraging zone of Adélie penguins during their wintering period (Thiebot et al., 2019). The data came from the US National Oceanic and Atmospheric Administration (NOAA). As the abundance and distribution of their main prey (Antarctic krill or ice krill *Euphausia crystallographias*) depend entirely on sea ice (Flores et al., 2012), Adélie penguins are highly sensitive to changes in oceanic conditions and even more so during the breeding season, when the foraging area is limited (Weimerskirch, 2007). Numerous studies have shown a link between sea ice conditions near the colony, as a proxy of krill availability, and the breeding success of Adélie penguins (Barbraud et al., 2015; Barreau et al., 2019; Emmerson et al., 2011). We supposed that high SIC during winter and early in the breeding season (spring) would allow Adélie penguins to develop a better body condition and reduce the cost of reproduction and, hence, favor their breeding success (Dunn et al., 2020; Emmerson & Southwell, 2011; Graña Grilli et al., 2018). In contrast, a high SIC during summer would increase foraging trip lengths and energetic costs for Adélie penguins raising chicks (Emmerson & Southwell, 2008), which could lead to a decrease in breeding success (Barbraud et al., 2015; Ropert-Coudert et al., 2014). We thus hypothesized that sea ice conditions would affect the breeding success of Adélie penguins, as well as the south polar skua dynamics through bottom-up processes (Frederiksen et al., 2006). High SIC conditions in spring could favor the breeding probability and success of skuas as there would be more potential food resources available for the predator. Likewise, high SIC conditions in summer may increase the survival and breeding success of skuas due to the greater availability of penguin chick carcasses during the rearing period of their chicks.

Sea surface temperature anomalies

Sea surface temperature anomalies (SSTa) were used as a proxy of food availability in the wintering zone of south polar skuas, that is, east of the Sea of Japan (32°50′–44°50′ N, 139°50′–149°50′ E). Data were averaged between May and June and came from the NOAA. A high SSTa generally reflects poor local environmental conditions for zooplankton development and so potentially a lower availability of food for skuas, as a repercussion in the food web (Barbraud et al., 2012; Frederiksen et al., 2006; Hazen et al., 2019; Weimerskirch et al., 2015). We supposed a negative effect of high SSTa during the winter on the survival of skuas (μ) but also on their breeding parameters through carry-over effects, that is, events encountered by an individual before the breeding

season that will influence its breeding performance during the following season (Harrison et al., 2011).

RESULTS

Demographic parameters

The number of south polar skua breeders and the number of Adélie penguin breeding pairs obtained from model estimates and observed are shown in Figure 2. Variation in the demographic parameters for skuas and Adélie penguins over the years is shown in Figure 3. Estimates of the capture probability of skuas and the variation of the estimated number of skuas for the different breeding states between 1998 and 2018 are shown in Appendix S5.

The mean apparent adult survival (φ) for skuas was 0.936 ± 0.029 , with a survival for breeder skuas (0.914, 95% CRI [0.847, 0.963]) 4.4% lower than for nonbreeder skuas (0.958, 95% CRI [0.892, 0.994]; Figure 3). Survival of the two breeding states showed similar interannual variation. However, the survival of breeder skuas increased by 3.3% during the study period, while the survival for nonbreeder skuas decreased by 4%. Adélie penguin apparent survival (μ_A) was 0.724 (95% CRI [0.685, 0.764]). The breeding probability (β) for breeder skuas (0.842, 95% CRI [0.753, 0.913]) was 73% higher than that for nonbreeder skuas (0.107, 95% CRI [0.065, 0.159]). The

breeding success (Θ) for breeder skuas (0.662, 95% CRI [0.544, 0.77]) was 12.9% higher than for nonbreeder skuas (0.532, 95% CRI [0.323, 0.736]), and the breeding success with two chicks (δ) was 6.9% higher for breeder skuas (0.251, 95% CRI [0.145, 0.383]) than for nonbreeder skuas (0.182, 95% CRI [0.032, 0.446]). The two breeding success parameters for both breeding states showed similar variations through time and decreased by 31.6% for breeding success and by 14.9% for breeding success with two chicks. Adélie penguin breeding success (Θ_A) was 0.751 (95% CRI [0.748, 0.754]).

Effect of environmental covariates and population densities

All results obtained when estimating the effects of the different environmental covariates and population densities on the demographic parameters of skuas and Adélie penguins are shown in Appendix S5 and summarized in Table 1. Only the significant effects will be interpreted here.

Density dependence

We estimated a positive density dependence for the relationship between the apparent survival of breeder skuas (φ_B) and the number of adult skuas (slope = 0.882, 95%

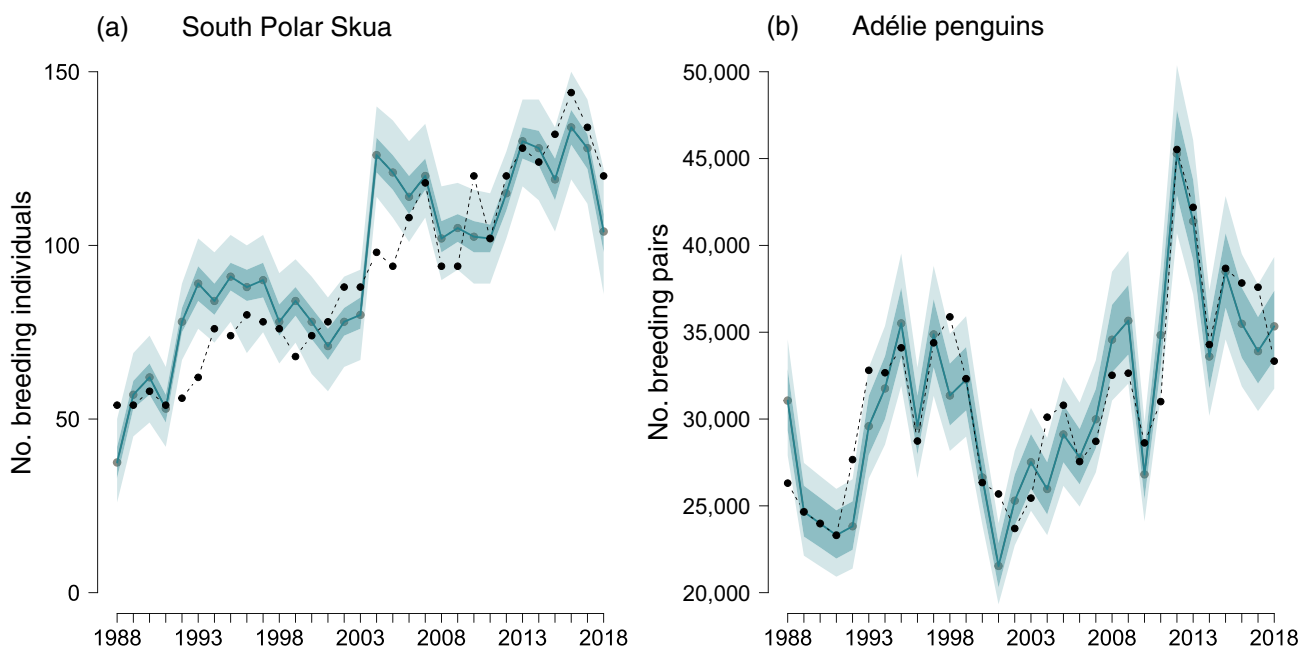


FIGURE 2 Estimated number of south polar skua breeding individuals (a) and Adélie penguin breeding pairs (b) at Pointe Géologie from 1988 to 2018. Solid blue line and blue dots represent the means of marginal posterior distributions. Shaded areas are the 50% and 95% credibility intervals. Black dots and dashed line represent the observed number of breeding skuas and penguins (count data).

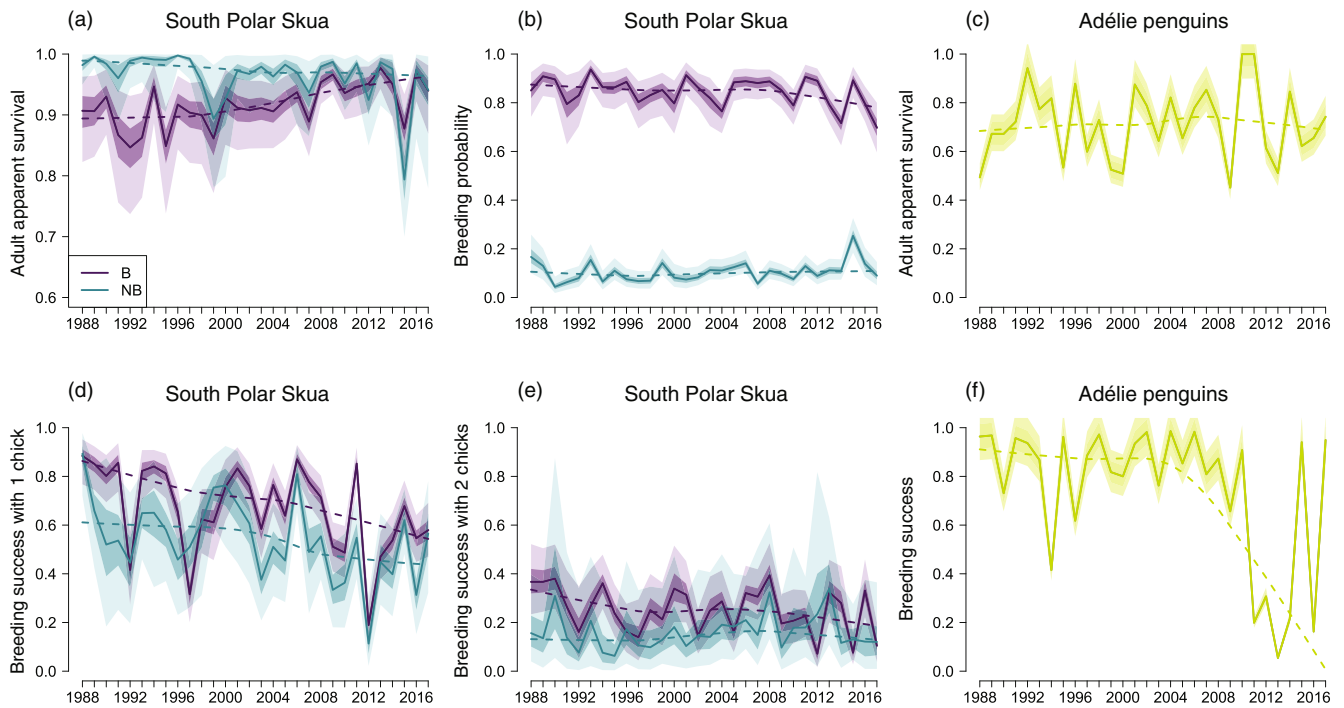


FIGURE 3 Estimated demographic parameters for south polar skuas—apparent adult survival (a), breeding probability (b), breeding success with one chick (d), and breeding success with two chicks (e)—by year, depending on their breeding state at the previous breeding season (B: breeder, in purple, and NB: nonbreeder, in blue) and for Adélie penguins—apparent adult survival (c) and breeding success (f), in green—from Pointe Géologie from 1988 to 2018. Solid lines represent means of marginal posterior distributions and dashed lines the marginal posterior distributions smoothed by the lowest function in R. Shaded areas are the 50% and 95% credibility intervals.

TABLE 1 Estimates of effects of environmental covariates and population densities on demographic parameters of south polar skuas depending on their breeding state in previous breeding season (B: breeder, and NB: nonbreeder) and of Adélie penguins.

Parameter	Breeding state	Effect of covariates	
		Positive	Negative
South polar skuas			
Adult apparent survival ϕ	B	AT spring, APB, DD	
	NB	AT spring, SIC spring	SSTa
Breeding probability β	B		EPC
Breeding success Θ	B	AT spring	SIC summer
	NB	AT spring	SIC summer
Breeding success with 2 chicks δ	B	EPC, AT spring	
Adélie penguin			
Breeding success Θ_A		SIC spring, SIC winter	SIC summer

Note: Only the significant effects (i.e., estimated effect with a probability of being negative greater than 90% or less than 10%) are shown.

Abbreviations: APB, number of Adélie penguin breeding pairs; AT, air temperature during spring (AT_{spring}) and summer (AT_{summer}); DD, intraspecific density dependence; EPC, number of emperor penguin dead chicks; SB, number of adult skuas; SIC, sea ice concentration during spring (SIC_{spring}), summer (SIC_{summer}), and winter (SIC_{winter}). Spring corresponds to the period September–November, summer corresponds to the period December–March, and winter corresponds to the period April–August; SSTa, sea surface temperature anomaly encountered by skuas while wintering (May–June).

CRI [0.687, 0.996]), as well as a positive density dependence between the breeding success of Adélie penguin (Θ_A) and the number of Adélie penguin breeding pairs (slope = 0.999, 95% CRI [0.998, 1]).

Predator–prey relationships

We estimated several interspecific relationships between the number of prey (Adélie penguin breeding pairs and

emperor penguin dead chicks) and the demographic parameters of the predator, the south polar skua. The apparent survival (φ_B , slope = 0.76, 95% CRI [0.351, 0.993]) for breeder skuas increased with Adélie penguin breeding pairs. Even though the effects were less clear (95% CRI including zero), there was evidence of a negative relationship between the number of emperor penguin dead chicks and the breeding probability for breeder skuas (β_B , slope = -0.206, 95% CRI [-0.458, 0.016]). On the other hand, we also detected that the probability of having two chicks (δ_B , slope = 0.309, 95% CRI [-0.038, 0.695]) for breeder skuas was positively linked to the number of emperor penguin dead chicks. No significant relationship was found between the number of skuas and the breeding success of Adélie penguins. However, the number of adult skuas was positively correlated with the number of Adélie penguin breeding pairs (Pearson correlation index = 0.62).

Environmental factors

We found positive relationships between AT in spring and the breeding success of skuas. The breeding success of breeder skuas (Θ_B , slope = 0.251, 95% CRI [-0.168, 0.615]) and nonbreeder skuas (Θ_{NB} , slope = 0.289, 95% CRI [-0.085, 0.691]), as well as the probability of raising two chicks for breeder skuas (δ_B , slope = 0.262, 95% CRI [-0.047, 0.615]) were higher when ATs between September and November increased. Higher temperatures in spring increased the apparent survival of breeder skuas (φ_B , slope = 0.225, 95% CRI [-0.08, 0.539]) and of nonbreeder skuas (φ_{NB} , slope = 0.435, 95% CRI [-0.131, 0.942]). We found no significant effect of AT in summer on the apparent survival or breeding probability and success of skuas.

Higher SIC during the breeding season was correlated with several demographic parameters of south polar skuas and Adélie penguins (Figure 4). The breeding success of Adélie penguins (Θ_A) was negatively related to SIC in winter (slope = -0.981, 95% CRI [-0.999, -0.954]) and in spring (slope = -0.643, 95% CRI [-0.663, -0.618]). The breeding success of Adélie penguins (Θ_A , slope = -0.378, 95% CRI [-0.404, -0.353]), as well as the breeding success of both breeder skuas (Θ_B , slope = -0.462, 95% CRI [-0.882, -0.044]) and nonbreeder skuas (Θ_{NB} , slope = -0.525, 95% CRI [-0.916, -0.121]) decreased with higher SIC conditions in summer. We also found positive relationships between the apparent survival of nonbreeder skuas (φ_{NB} , slope = 0.482, 95% CRI [-0.199, 0.956]) and higher SIC in spring. On the other hand, when nonbreeder skuas encountered higher SSTa in their wintering area (May–June), their

apparent survival was lowered (φ_{NB} , slope = -0.544, 95% CRI [-0.972, 0.251]).

DISCUSSION

Effect of breeding state of previous year

As predicted, our results showed differences in estimates and relationships between demographic parameters of skuas, environmental factors, and prey–predator relationships as a function of their breeding state during the previous year (Figure 3), which could reflect different foraging strategies and behaviors.

Both breeder and nonbreeder skuas showed similar demographic responses (survival, breeding success, and probability to fledge two chicks) to AT and SIC during spring and summer. This suggests that these environmental parameters similarly affected adult individuals regardless of their previous breeding status. However, nonbreeder skuas seemed to be more sensitive to the conditions during wintering than breeder skuas, as their survival was negatively affected by higher sea temperature anomalies. During the study period there was an increase in sea SSTa in the east of Japan, where skuas spent the nonbreeding season. High SSTa generally reflect lower availability of food for seabirds through bottom-up effects (Barbraud et al., 2012; Frederiksen et al., 2006; Hazen et al., 2019; Weimerskirch et al., 2015). We therefore suspect an increase in mortality due to decreased food abundance during wintering when sea surface temperature is warmer. Nonbreeder skuas may be more sensitive to such environmental conditions than breeder skuas since they might be mostly individuals in poorer body condition or with less experience. In contrast, breeder skua demographic parameters (survival, breeding probability, and probability to fledge two chicks) seemed to be more sensitive to prey availability (abundance of Adélie penguins and number of dead chicks of emperor penguin) than nonbreeder skuas. This could be a consequence of the higher energetic costs due to chick rearing compared to nonbreeder skuas (Drent & Daan, 1980; Weimerskirch, 1990).

Breeder skuas had higher breeding probability, higher breeding success, and higher probability to fledge two chicks but lower survival than nonbreeder skuas. This could indicate the existence of a survival cost of reproduction for breeder skuas. The large differences that we observed between the breeding probability of nonbreeders and that of breeders could be a consequence of a limited number of high-quality nesting sites. Because skuas are faithful to their nesting sites, it might be more difficult for a nonbreeder to find a place to breed than for

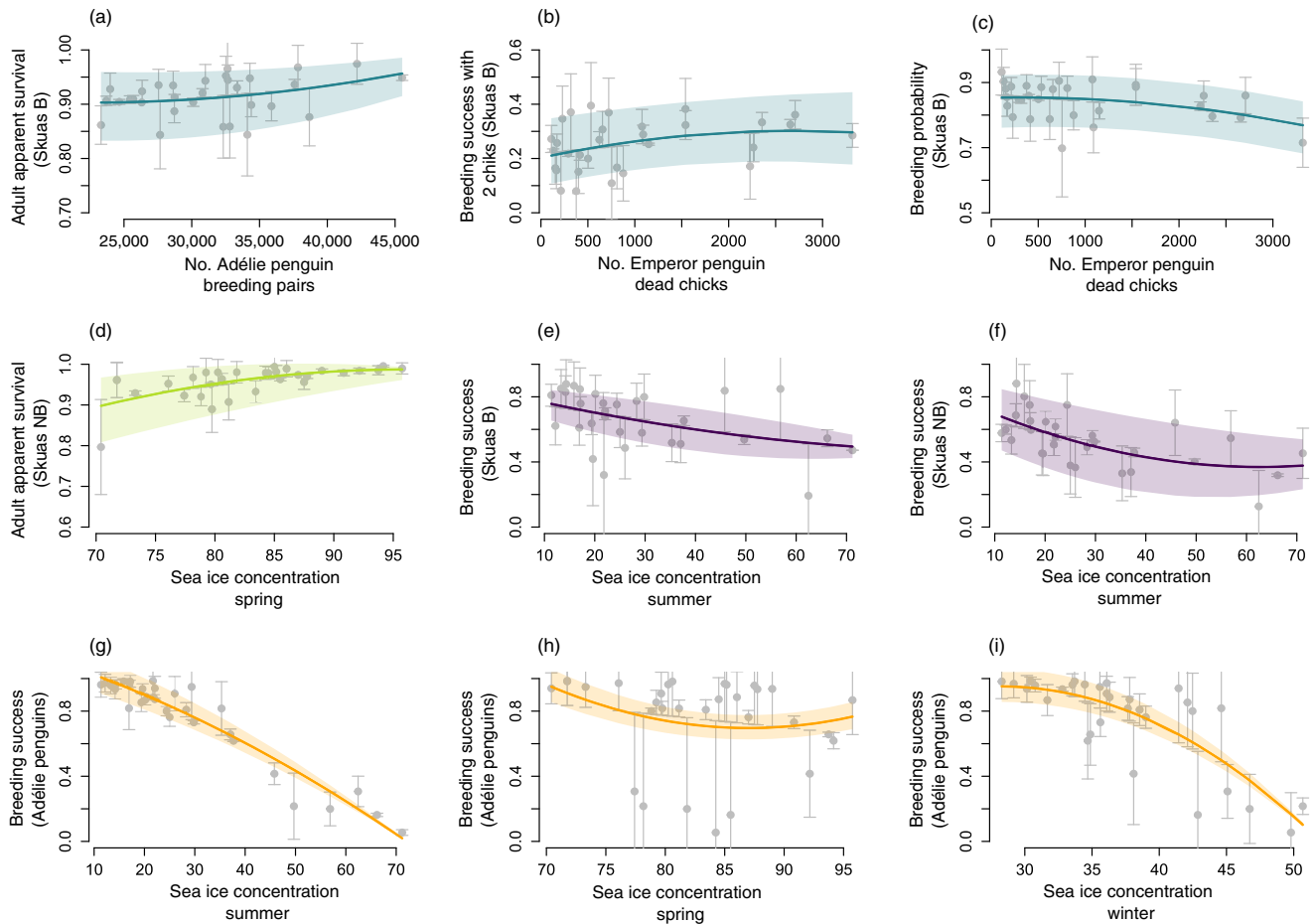


FIGURE 4 Effects of prey abundance and sea ice concentration (SIC) on demographic parameters of south polar skua. (a) Effect of estimated number of Adélie penguin breeding pairs on survival of breeder skuas, effect of number of emperor penguin dead chicks on (b) breeding success with two chicks of breeder skuas (skuas B) and (c) breeding probability of breeder skuas. Effect of SIC during austral spring (September–November) on (d) adult apparent survival of nonbreeder skuas and of SIC during austral summer (December–March) on breeding success of (e) breeder skuas and (f) nonbreeder skuas. Effects of SIC on breeding success of Adélie penguins during (g) austral summer, (h) austral spring, and (i) austral winter (April–August). Solid line represents modeled relationship obtained from covariate model, and shaded areas represent 95% credibility intervals. Points represent demographic parameter estimates each year plotted against covariate values, with standard deviations as errors bars.

a breeder skua (Pacoureaux et al., 2018; Young, 1972). Less experienced and often less competitive nonbreeder skuas could be relegated to poorer-quality sites and more exposed to wind, snow accumulation, and runoff from melting ice and snow (Dhondt et al., 1992; Kokko et al., 2004). This hypothesis is supported by the lower breeding success in nonbreeder compared to breeder skuas, but interpretation should be undertaken with caution since we found no effect of density dependence on the breeding probability of nonbreeder skuas.

Density dependence

Density dependence is a well-known factor influencing bird population dynamics (Newton, 1998; Turchin, 1995).

More individuals breeding at the same location increases intraspecific competition for food resources (Charnov et al., 1976) and breeding sites, territorial behavior (Rodenhouse et al., 1997), and the transmission of diseases or parasites (Schreiber & Burger, 2001). Several studies have shown negative effects of intraspecific density dependence on long-lived upper trophic bird species showing territorial behavior like the south polar skuas (Furness, 2015; Quéroué et al., 2021). We did not detect density-dependence effects of the number of skuas on the demographic parameters of nonbreeder skuas. However, contrary to our prediction, we found a positive effect of the number of adult skuas on the survival of breeder skuas. Likewise, we also observed a positive effect of the number of Adélie breeding pairs on the breeding success of Adélie penguins. Those positive relationships are likely

an indirect effect of environmental conditions on demographic parameters. When trophic conditions are good, it may favor the number of individuals that come back to the colonies to reproduce, as well as their survival and breeding success. In addition, the effect of density dependence on skuas should be treated with caution. Indeed, we used a covariate that was estimated by the model, that is, the total number of individuals (N_{tot}). This can create potential biases, as we do not know the exact number of nonbreeders. This can cause an overestimation of the effect of density dependence, particularly because of years with a very large number of individuals.

Interspecific relationships

The number of Adélie penguin breeding pairs, used as a proxy for the food available for skuas (i.e., Adélie penguins eggs and chicks), had a positive effect on the survival of breeder skuas (Figure 4). More Adélie penguins breeding likely increased the number of eggs and chicks available for skuas, which could minimize foraging effort and thus maximize survival of breeding individuals. Therefore, the increase in the number of Adélie penguin breeding pairs that we observed during this study at Pointe Géologie could partly explain the increase in the apparent survival of breeder skuas.

Contrary to our predictions, we did not find an effect of the number of Adélie penguin breeding pairs on the breeding success of skuas. Although Adélie penguin breeding pairs could be abundant early in the season (November–January), the extent and timing of egg failure and chick mortality may not match the period of highest energy demand for skuas, which occurs during chick rearing (December–March). This may explain the lack of relationship between skua breeding performance and numbers of Adélie penguin breeding pairs. Interestingly, we found a positive effect of the number of emperor penguin dead chicks on the probability of fledging two chicks in breeder skuas (Figure 4). Mostly consumed early in spring, before eggs and chicks of Adélie penguins become available (Pacoureaux et al., 2018), emperor penguin dead chicks will favor skuas to attain a good body condition so as to be able to afford the energetic costs due to the rearing of their chicks (Drent & Daan, 1980; Graña Grilli et al., 2018) and even more to raise two chicks. Thus, food availability early in the breeding season is likely a determinant of the breeding success of skuas.

However, unexpectedly, we observed a negative effect of the number of emperor penguin dead chicks on the breeding probability of breeder skuas. Greater food

availability early in the breeding season should allow more individuals to reach an adequate body condition to breed (Madsen & Shine, 1999). We suspect this effect is indirectly related to unmeasured environmental conditions, which could have a negative effect on both the mortality of emperor penguin chicks and the breeding probability of breeder skuas. For example, important fast ice extent during austral winter and early spring has a negative effect on the breeding success of emperor penguins (Labrousse et al., 2021) and may also negatively affect skua breeding probability.

We did not detect a top-down effect in this predator–prey system, that is, a negative effect of the number of adult skuas on the breeding success of Adélie penguins. As the Adélie penguin breeding population is around 340 times larger than the skua breeding population, the predation of skuas on Adélie penguin eggs and chicks is likely negligible. Since the beginning of the study (1988), the skua breeding population has doubled following a nearly twofold increase in the Adélie penguin breeding population (see *Materials and methods*). Thus, it seems that the skua population follows the growth of its main prey population and is not yet limited by the availability of nesting areas.

Environmental conditions

Local weather conditions during the breeding season influence the breeding success of seabirds directly via their effects on offspring growth (Hahn et al., 2007) and indirectly via the body condition of parents (Graña Grilli et al., 2018). In line with this, we found that the studied prey–predator system and the breeding success of both skuas and Adélie penguins was highly sensitive to local environmental conditions during the breeding season. To refine our results, it could be interesting in future studies to consider nonlinear relationships when assessing the effects of the covariates.

Air temperature

Warmer AT in spring had a positive effect on the survival and breeding success of skuas and on the probability of fledging two chicks in breeder skuas. Colder AT likely increases energetic costs and water loss due to thermoregulation and, hence, decreases the body condition of parents and their chicks (Pacoureaux et al., 2019; Spellerberg, 1969). Individuals in poorer conditions may lay smaller eggs of lower quality, with implications for chick quality and mortality until fledging (Furness, 1983; Hahn et al., 2007).

Sea ice concentration

The Adélie penguin is an ice obligate species (Ainley, 2002; Jenouvrier et al., 2006) and mainly feeds on Antarctic silverfish and krill (Cherel, 2008). Thus, as we predicted, Adélie penguin breeding success was strongly driven by sea ice conditions in winter, spring, and summer. High SIC in summer had a negative impact on the breeding success of Adélie penguins, as we hypothesized. Extreme sea ice cover during this period increases the distance between colonies and foraging areas, which reduces meal frequency for chicks and may cause nest abandonment and chick mortality (Barbraud et al., 2015; Ropert-Coudert et al., 2014). In line with this, we observed that the breeding success of Adélie penguins tended to decrease starting in 1988, which could be partly due to the increasing frequency of extreme summer SIC events and to an increase in the mean SIC in summer at Pointe Géologie (Appendix S1). The negative effect of important SIC in summer (Figure 4) seems to be most likely the result of summers with large expanses of fast ice (correlated to SIC; Massom et al., 2009), which are well known to have strong negative effects on the breeding success of Adélie penguins (Barbraud et al., 2015; Ropert-Coudert et al., 2014). Decreased winter sea ice is associated with lower densities during summer of krill (Loeb et al., 1997), one of the key resources for Adélie penguins during the breeding season. Furthermore, Emmerson and Southwell (2011) showed that the survival of subadult and adult penguins was higher when there was high SIC in winter. Contrary to our prediction, high SIC before the breeding season (in winter and spring) appeared to have a negative impact on the breeding success of Adélie penguins. Tracking studies have shown that Adélie penguins' preferred foraging habitats correspond to a SIC of 20%–30% (Le Guen et al., 2018). Medium sea ice cover seems to offer enhanced food availability and reduce the risk of predation (Langbehn & Varpe, 2017). During years when winter and spring SIC is higher, Adélie penguins may be forced to move farther away from the colony to find more favorable conditions for foraging. Thus, we can hypothesize that high SIC in winter and spring forces Adélie penguins to draw from their reserves in order to reach more favorable foraging areas, which may affect their body condition and contribute to decrease their breeding success.

Sea ice conditions also had an important effect on the demography of south polar skuas. High SIC in spring favored survival of nonbreeder skuas. This suggests that when high SIC conditions occurred in spring, more food resources were available. Higher food resources in spring may also favor nonbreeder skua survival through an increase in their body condition as these individuals are

negatively impacted by wintering conditions. Unexpectedly, we found a negative effect of high SIC in summer on the breeding success of skuas. Indeed, if high SIC summers coincide with an increased mortality of Adélie penguin egg and chicks, one might expect more food to be available for skuas and better breeding success. However, as observed in Adélie penguins, the breeding success of skuas decreased starting in 1988 while mean SIC in summer increased. Moreover, skuas experienced lower breeding success during years with extreme SIC (Barbraud et al., 2015). We thus suspect that, due to massive die-off of Adélie penguin chicks early in the breeding season, as has been observed during years with high summer SIC, skuas might not be able to correctly feed their chicks until fledging because of a lack of available food resources at the end of the rearing period.

CONCLUSION

Here, we reported on one of the most comprehensive studies on the factors impacting the demography of a predator–prey system, that of south polar skuas and Adélie penguins, while explicitly integrating interspecific relationships. We also proposed a new application of a multispecies IPM for a predator–prey system, in a context where CMR data are not available for one of the species. Estimating demographic parameters and abundance for both species simultaneously while assessing the effects of density dependence, climatic conditions, and intraspecific relationship in a unique model allows for better propagation of all sources of uncertainty, as well as a better understanding of joint population dynamics in predator–prey systems in the context of climate change. We highlighted that the dynamics of this predator–prey system over the past three decades was mostly driven by bottom-up processes and local environmental conditions. Our results reveal the complexity of the effects of environmental conditions on the demography of a predator–prey system, with several climate and oceanographic variables involved, in addition to several interspecific relationships. Overall, high SIC in spring and in winter, as well as high AT in spring, had positive effects on south polar skuas, while high SIC in summer had negative effects on both the predator and its prey. High SIC in spring and winter also had negative effects on the breeding success of Adélie penguins. This reveals the importance of sea ice before the breeding season for this predator–prey system, which is likely linked to the abundance of marine resources, such as krill and Antarctic silverfish, while high SIC in summer likely increased the costs of reproduction due to more highly constrained foraging conditions. During the past

30 years, populations of both the predator and its main prey have increased, suggesting that the overall net effect of environmental change experienced during the breeding and wintering periods was favorable to these species at this study site. As no negative density dependence was detected, both populations might continue to increase in future years if climatic conditions remain similar.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Viollat, 2024) are available in Zenodo at <https://doi.org/10.5281/zenodo.10953627>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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