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RESEARCH ARTICLE

Sea ice and local weather affect reproductive phenology of a polar seabird with breeding consequences

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ABSTRACT

Breeding at the right time is essential for animals living in seasonal environments to ensure that energy requirements for reproduction, especially the nutritional needs for rearing offspring, coincide with peak food availability. Climate change is likely to cause modifications in the timing of maximum food availability, and organisms living in polar environments where the breeding period is heavily contracted may be particularly affected. Here we used a 26-year dataset to study the phenological response of a pagophilic species, the Snow Petrel (*Pagodroma nivea*), to climate change and its demographic impact. First, we investigated the trends and relationships between climate variables and hatching dates measured in three neighboring colonies. In a second step, we examined the impact of the hatching date and environmental covariates on the fledging probability. Our results showed that sea ice, a climate-related variable, showed a positive temporal trend. We found that hatching date was delayed when sea ice concentration was greater and local weather conditions were worse (i.e., increase in the number of windy days or the number of snow days). Hatching date had a negative effect on fledging probability, and fledging probability showed a bell-shaped temporal trend. We suggest that Snow Petrels can delay breeding phenology in response to environmental conditions. However, this plasticity may be limited as fledging success decreased with delayed hatching, potentially making the Snow Petrel vulnerable to a mismatch between resource availability and nutritional needs.

Keywords: climate change, fledging success, hatching date, laying date, seabird, sea ice, snowfall, Snow Petrel, wind

LAY SUMMARY

- Timing of reproduction is essential for wild animals to ensure that reproductive requirements, including nutritional requirements for rearing offspring, coincide with peak food availability.
- Climate change can affect the timing of food availability, and organisms living in polar environments, where the timing of reproduction is highly contracted, may be particularly affected. We analyzed whether a sea ice dependent species, the Snow Petrel (*Pagodroma nivea*), would breed earlier or later in response to climate change, as measured by changes in sea ice and weather conditions. Then, we looked at the impact that a shift in reproduction might have on breeding success.
- Our results showed that hatching date was delayed when sea ice increased and local weather conditions worsened. Secondly, we showed that the shift in hatching date had a negative effect on breeding success.
- Snow Petrels adjusted the onset of reproduction in response to environmental changes. However, this adjustment had limits since late reproduction likely leads to a mismatch between the availability of resources and nutritional needs, and thus to a decrease the breeding success.

La glace de mer et le climat local affectent la phénologie de la reproduction d'un oiseau marin polaire avec des conséquences sur la reproduction

RÉSUMÉ

La reproduction au bon moment est essentielle pour les animaux vivant dans des environnements saisonniers afin que les besoins énergétiques pour la reproduction, et surtout les besoins nutritionnels pour l'élevage, coïncident avec le pic de disponibilité alimentaire. Le changement climatique est susceptible d'entraîner des modifications dans le calendrier de la disponibilité maximale de la ressource, et les organismes vivant dans des environnements polaires où la période de reproduction est fortement contractée peuvent être particulièrement affectés. Nous avons utilisé ici 26 ans de données pour étudier la réponse phénologique d'une espèce pagophile, le pétrel des neiges (*Pagodroma nivea*), au changement climatique et à son impact démographique. Dans la zone d'étude, la glace de mer, une variable liée au climat, montre une tendance temporelle positive qui peut avoir un impact sur les populations d'oiseaux marins. Dans un premier temps, nous avons étudié les tendances et les relations entre les variables climatiques et les dates d'éclosion mesurées dans trois colonies voisines. Dans un deuxième temps, nous avons examiné l'impact de la date d'éclosion et des covariables environnementales sur la probabilité d'envol. Nos résultats ont montré que la glace de mer, une variable liée au climat, présentait une tendance temporelle positive. Nous avons constaté que la date d'éclosion était retardée lorsque la concentration de glace de mer était plus importante et que les conditions météorologiques locales étaient plus mauvaises (c'est-à-dire augmentation du nombre de jours de vent ou du nombre de jours de neige). La date d'éclosion a eu un effet négatif sur la probabilité d'envol, et la probabilité d'envol a montré une tendance temporelle en forme de cloche. Nous suggérons que les pétrels des neiges peuvent retarder la phénologie de reproduction en réponse aux conditions environnementales. Cependant, cette plasticité peut être limitée car le succès de l'envol diminue lorsque l'éclosion est retardée, ce qui peut rendre le pétrel des neiges vulnérable à une inadéquation entre la disponibilité des ressources et les besoins nutritionnels.

Mots clés: changement climatique, succès à l'envol, date d'éclosion, date de ponte, oiseau marin, glace de mer, chute de neige, vent, Pétrel des neiges

INTRODUCTION

In the current context of unprecedented climate change and biodiversity crisis (Ceballos et al. 2017) it is important to understand how species adapt to environmental changes. Today we know that Earth is warming up, and this climate change is already having significant ecological consequences for terrestrial and marine ecosystems (Walther et al. 2002). In particular, changes in the synchronization of cyclic biological events have been observed. For example, phenological events of spring and summer generally occur earlier in the year (Root et al. 2003, Thackeray et al. 2010, 2016, Brown et al. 2016, Cohen et al. 2018). Seasonal synchronization processes are critical for species because they may have an impact on breeding performance, juvenile survival or migration (Verhulst and Nilsson 2008). Thus, for individuals of many species, the synchronization of their phenological cycle with their environment is crucial for maximizing their fitness (Martin 1987).

Organisms living in seasonal habitats are exposed to regular changes in the quality and abundance of food resources (Gili and Petraitis 2009). Many also have a limited breeding season, which corresponds to peak food availability. Several mechanisms enable organisms to respond to these seasonal alterations in the abundance of food resources, for example by changing their phenology or qualitatively changing their diet (Visser and Both 2005). In addition to matching with the food resource, the breeding season generally corresponds to the season with the mildest weather. Wind, rainfall and snowfall, that characterize this local weather, can also influence breeding performance of birds (Rodriguez and Bustamante 2003, Dunn and Møller 2019, Huchler et al. 2020).

Polar environments are characterized by a very short summer season where there is maximum food availability and less severe weather conditions than normal, conducive to breeding (Arrigo et al. 2008). As a result, many polar organisms have developed specific adaptations favoring a short breeding cycle (Smetacek and Nicol 2005). However, polar ecosystems are particularly sensitive to climate change and small differences in temperature can have significant effects on the availability of food resources such as the extent and thickness of sea ice (Fossheim et al. 2015, Frainer et al. 2017). Thus, polar organisms such as seabirds which are heavily time-constrained in their phenology may be particularly sensitive to changes in the timing of peak food availability, which may have demographic and population consequences (Croxall 2002, Chambers et al. 2013, Descamps et al. 2017). Contrary to terrestrial organisms, relatively few studies have investigated the impact of climate on breeding phenology and the consequences on fitness parameters of marine polar species. In particular, there is a clear lack of knowledge in the Southern Hemisphere concerning the phenological responses of polar seabirds to sea ice and climate changes (but see: Barbraud and Weimerskirch 2006, Hahn et al. 2007, Chambers et al. 2013, Descamps et al. 2016).

Here we investigated the change in breeding phenology of a sea ice-obligated seabird, the Snow Petrel (*Pagodroma nivea*), over a 26-year period. From data collected in three nearby colonies, we studied the impact of several environmental covariates on the variation of the hatching date and the consequences on fledging probability. Snow Petrels breed during the austral summer and feed exclusively in pack ice areas (Ainley et al. 1984). Sea ice is suspected to affect the phenology and breeding phenology of several polar seabirds including petrels (Barbraud and Weimerskirch 2006, Moe et al. 2009, Chambers et al. 2013, Ramírez et al. 2017, Descamps et al. 2019). During incubation and rearing periods, sea ice concentration may affect the abundance or accessibility of food resources that may in turn influence the incubation duration and the hatching date or the chick feeding frequency, and the fledging success. Therefore, we expected to find a delay in breeding phenology related to an increase in sea ice concentration.

Despite the fact that previous studies suggested that the phenological adjustments observed in seabirds are relatively small (Chambers et al. 2013, Keogan et al. 2018), changes in breeding phenology can result in a mismatch between peak food availability and the breeding season (Arrigo et al. 2008), so we predicted that changes in breeding phenology in Snow Petrels would have demographic consequences. More specifically, we predicted that a delay in breeding phenology would have negative effects on fledging probability, a pattern described in other bird species (Morrison et al. 2019). In addition, we hypothesized that increasing the number of snow days early in the breeding season could affect breeding phenology. Snow Petrel nests may be blocked by snow or ice (Chastel et al. 1993), which may affect the onset of reproduction by making access to the nest more complicated for egg laying.

MATERIALS AND METHODS

Study Species

Snow Petrels are small Procellariiformes (200–500 g, 80–90 cm wingspan) breeding on rockscape of the coastline and within the Antarctic continent and some sub-Antarctic islands (Brooke 2004). Adults arrive in late October to early November at their breeding site and lay a single egg in early December that hatches in January. The chick fledges in March. Snow Petrels forage over Antarctic waters partly covered by sea ice, preying on sea ice-associated species, mainly small fish (Antarctic silverfish *Pleuragramma antarcticum*) and crustaceans (Antarctic krill [*Euphausia superba*], ice krill [*E. crystallorophias*] and amphipods such as *Themisto gaudichaudii*), whose proportions vary according to locality (Ainley et al. 1984, Ridoux and Offredo 1989, Rau et al. 1992).

Snow Petrels were studied at Ile des Pétrels (66°40′S, 140°01′E), Pointe Géologie archipelago, Terre Adélie, Antarctica. On average 550 pairs of Snow Petrels breed on Ile des Pétrels and 800–1,000 pairs breed in the entire archipelago (Micol and Jouventin 2001; CEBC-CNRS unpublished data). Nearly 300 breeding pairs were monitored annually from the breeding season of 1992/1993 in three colonies until 2017/2018 (Colony 1: ~72 pairs; Colony 2: ~77 pairs; Colony 3: ~140 pairs) in which nest sites were individually marked. The colonies are close to each other (<1 km) but present differences in breeding performance (C. Sauser et al. personal communication). In each colony, hatching date was recorded yearly for each nest. The egg-laying date was collected only for colony 3 from the breeding season 2009/2010 until 2017/2018. Adults and chicks were leg-banded with a stainless-steel band. Adults were sexed by vocalization and relative size (Barbraud et al. 2000). Hatching dates are recorded by daily inspections of nest contents, and a final nest visit in mid-February was made to ring the chicks just before fledging and to determine the breeding success (i.e., failed if no chick was present, successful if a chick was present). More details about the study species and the monitoring methodology are provided in Chastel et al. (1993) and Barbraud and Weimerskirch (2001).

Environmental Covariates

Selection of environmental covariates was based on previous knowledge of seabirds and Snow Petrel ecology. First, we used a large-scale climatic index, the southern annular mode (SAM). SAM is the dominant mode of atmospheric variability in the Southern Hemisphere and is characterized by the displacements of atmospheric masses between polar and mid-latitudes (Marshall 2003). SAM is related to temperature changes in the Antarctic, sea-surface temperature of the Southern Ocean, and the distribution of sea ice around Antarctica. A positive phase of SAM is associated with an amplification of westerly winds at the surface around 60°S. This induces an Ekman drift that increases the extent of Antarctic sea ice, increases upwelling activity near Antarctica and therefore primary productivity in Antarctic marine ecosystems (Thompson et al. 2011). Thus, one might hypothesize that through bottom-up processes, high SAM may have a positive effect on the abundance of food resources for Snow Petrels and may favor earlier breeding. SAM data were from the British Antarctic Survey database (http://www.nerc-bas.ac.uk/icd/gjma/sam.html).

Second, we used a local oceanographic covariate on different temporal (i.e., during the incubation period and rearing period) scales: the sea ice concentration (SIC). Sea ice concentration describes the relative amount of surface covered by sea ice compared to a reference area. SIC data available from satellite products (OI.v2 analysis, Reynolds et al. 2002) describes the proportion of a 25.0 × 25.0 km area covered by sea ice. Sea ice is the main foraging habitat of Snow Petrels both during the breeding and nonbreeding periods (Ainley et al. 1984, Delord et al. 2016, Barbraud et al. 2019). Sea ice contributes to annual primary productivity in the seasonal ice zone and plays an important role in the life cycle of krill and Antarctic silverfish (Vacchi et al. 2012), two essential food resources for Snow Petrels. The link between sea ice and the associated food resources for seabirds such as Snow Petrels is hypothesized to follow a nonlinear relationship (Wilson et al. 2001, Ballerini et al. 2009, Barbraud et al. 2012). A low SIC can decrease the abundance of food resources by reducing the prey habitat of Snow Petrel, and a high SIC can limit the amount of light entering the water column and reduce primary production. Moreover, a high SIC can constitute a less favorable foraging habitat (Barbraud et al. 2019) and can decrease the accessibility of food resources by providing shelter for the prey of Snow Petrels. Accordingly, several demographic parameters and foraging behaviors of

Snow Petrels are related to SIC; for example, the survival of male is negatively affected by sea ice concentration in summer (Jenouvrier et al. 2005) and females feed less than males in areas with higher sea ice concentration (Barbraud et al. 2019). In addition, SIC shows a general negative but nonlinear effect on the body condition of juvenile Snow Petrels (Sauser et al. 2018).

Sea ice concentration was extracted during the incubation and rearing periods (in two distinct periods) for the sector 66°S–67°S/138°E–142°E, corresponding to the Dumont d'Urville Sea where Snow Petrels forage during the breeding season (Delord et al. 2016, Barbraud et al. 2019). During the winter period (from April to October) SIC was extracted from the sectors 66°S–67°S/119°E–149°E and 66°S–67°S/49°E–68°E, where Snow Petrels are known to distribute during the nonbreeding period (Delord et al. 2016).

Third, to characterize the effect of local weather on hatching date we used meteorological data recorded at the study site (Ile des Pétrels). Strong winds during incubation may increase the energy demands of parents incubating the egg. This can enhance the frequency of egg neglect (i.e., interruption of a day or more of incubation) if parents must leave the nest unattended for feeding at sea, and thus increase the length of the incubation period (Boersma 1982). Therefore, over the period 1993–2018, we used the number of days of wind >100 km hr^{-1} as a covariate. Snowfall can have a significant impact on the reproductive conditions of polar seabirds. Snowstorms may have a negative impact on the body condition of chicks or incubating parents (Kuepper et al. 2018). In the Arctic, when snowmelt is delayed, breeding success is greatly reduced (Martin and Wiebe 2004). Snowfalls causing flooding of nests during the breeding season are a major cause of the death of eggs in Snow Petrels (Chastel et al. 1993) and may have negative consequences on embryonic development. We, therefore, used the number of days with snowfall during incubation over the period 1993–2018 as a covariate. In the same way, local weather may affect fledging success. We thus used the same covariates during the rearing period to test their effects on fledging success. Meteorological data were obtained from the Dumont d'Urville station weather station of Météo France public administrative institution.

To detect collinearity between covariates we used variance inflation factors with a threshold value of 3 (Zuur et al. 2009). Covariates used to test the effect of environmental variation on fledging success and hatching date showed no collinearity (variance inflation factors < 3).

Modeling Temporal Trends in Environmental Covariates

Using generalized additive models (GAM) we tested for temporal trends in covariates. To account for temporal autocorrelation of the residuals we built an optimal error structure (ARMA) in the GAM models (Zuur et al. 2009). We assessed the best optimal structure by comparing models with all potential ARMA structures with p and q smaller than 3 to a model without ARMA structure. Model selection was done using the Akaike Information Criterion (AIC). The best model was the lowest AIC model, and we considered that two models i and j were different when the ΔAIC was >2, where $\Delta AIC = AIC_i - AIC_j$ (Burnham and Anderson 2002).

Modeling Phenological Response to Environmental Changes

The phenological dataset included hatching date measured during 26 years (1993–2018) at the three study colonies, while egg-laying date was only available for 8 years (2010–2018) at a single colony. We therefore used the hatching date to measure the phenological response because the time series was longer. We modeled the effect of environmental variables on the hatching date using a two-step approach.

First, using GAMMs we tested for temporal trends in hatching date (Zuur et al. 2009). Hatching date recorded by nest in the three study colonies was used as a response variable and year as continuous predictor. Given that there are differences in breeding success between colonies (C. Sauser et al. personal communication) and that the same nests contributed multiple times in the data set, nest and colony were used as random factors.

Second, we analyzed the effect of covariates on the hatching date. To do so, we redesigned the previous model that tested for the temporal trends, to which we added the covariates as continuous predictors. To account for nonlinear relationships between hatching date and covariates and to limit model over-fitting, we chose an optimal amount of knots (k) based on a visual comparison of the smoothers. The smooth term was set to a maximum of $k = 3$.

Modeling Hatching Date and Environmental Effects on Fledging Probability

We used observation of nests ($n = 289$) individually monitored on 3 colonies during the period 1993–2018 to model the probability of fledging success. We used two states to describe nests where a chick fledged (coded 1) and nests where a chick died during the rearing period (coded 0). Using GAMM with a binomial distribution, we tested for a temporal trend in fledging success. Nest status was the response variable, the year a continuous predictor, nest and colony were random factors. Then, we analyzed the effects of hatching date and environmental covariates. To do so, we redesigned the previous model that tested for the temporal trend to which we added hatching date and environmental covariates as continuous predictors. To account for nonlinear relationships between hatching date and

TABLE 1. Results of the GAMM model testing for a temporal trend in hatching date for Snow Petrels breeding at Ile des Pétrels, Terre Adélie, Antarctica, in 1993–2018. Total deviance explained by the model: 41.1%. Deviance explained by random effects: 24.1%. Standard deviation (SD) = estimated variance components. 95% CI = 95% confidence interval. edf = estimated degrees of freedom.

	Smoother edf	*F*-test	*P*-value	SD (95% CI)
Hatching date	1.93	40.02	<0.001	
Random effect				
Nest				1.79 (1.58, 2.04)
Colony				0.51 (0.14, 1.72)

covariates and to limit model over-fitting we chose an optimal amount of knots (k) based on a visual comparison of the smoothers. The smooth term was set to a maximum of $k = 3$.

We assess the statistical significance of each covariate by making inferences based on the P-values on the slope parameters of the model. All analyses were performed in R (R Core Team 2020) with the package *mgcv* (Wood 2011).

RESULTS

Temporal Trends

There was a nonlinear temporal trend in the hatching date (Table 1, Figure 1). The mean hatching date was delayed by ~3 days in 26 years. There was also a nonlinear temporal trend in fledging success (Table 2, Figure 2). Fledging success increased from 1993 to 2005 and decreased afterwards.

The number of days with snowfall during rearing and the SIC (during incubation and rearing) showed positive temporal trends. The number of days with snowfall during rearing was increased by ~7 days in 26 years. SIC was increased by ~30% during incubation and by ~35% during rearing in 26 years. The number of windy days during incubation and the number of days with snowfall during incubation showed negative temporal trends. The number of days with snowfall during incubation was decreased by ~6 days in 26 years. The number of windy days was decreased by ~3 days during incubation and by ~7 days during rearing in 26 years (Table 3, Supplementary Material Figure S1).

Effect of Environmental Covariates on Hatching Date

The model indicated positive relationships between 3 covariates and hatching date: 2 local covariates (number of days of wind, number of days of snowfall) and 1 oceanographic covariate (sea ice concentration during incubation) (Figure 3, Table 4, Supplementary Material Figure S2). Hatching date was delayed in years with high SIC during incubation up to thresholds of ~40% and remained stable for higher SIC. Hatching date was also delayed in years with a high number of windy days and of days with snowfall up to thresholds of 15 days and 25 days, respectively, and remained stable thereafter.

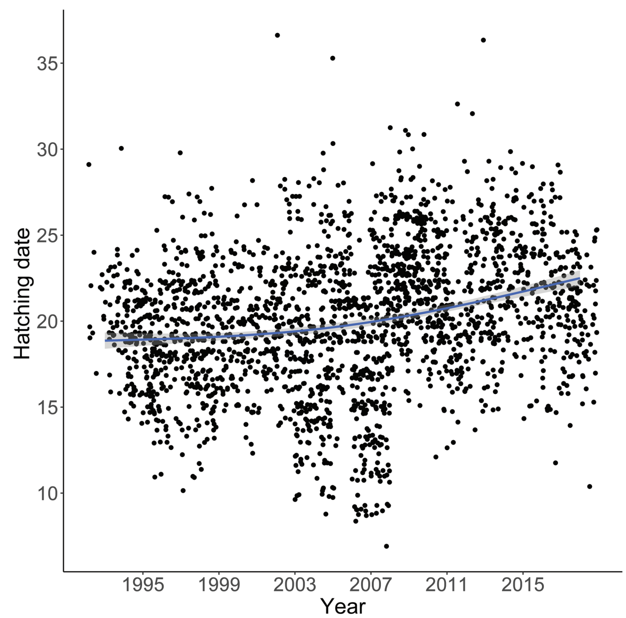

FIGURE 1. Snow Petrel delayed their hatching date over the time series of data. Observed (n = 2330) and modeled hatching date expressed in annual Julian day for Snow Petrels breeding at Ile des Pétrels, Terre Adélie, Antarctica, 1993–2018. Plain line corresponds to estimated smoother from the GAMM model. Gray shading indicates 95% confidence interval.

Effect of Hatching Date and Environment on Fledging Success

The model indicated a negative effect of hatching date on fledging success (Figure 4, Table 5, Supplementary Material Figure S3). There was also a negative effect of the number of days with snowfall on fledging success (Figure 4B , Table 5), and a positive effect of sea ice concentration during rearing on fledging success (Figure 4C, Table 5).

DISCUSSION

We found a clear phenological response (delayed breeding) of a long-lived polar seabird to climate change. First, the hatching date of Snow Petrels was delayed during the study period. Second, SIC, the number of windy days and the number of days with snowfall increased during the incubation period and delayed Snow Petrel hatching date. In addition, we found that delayed breeding, as well as SIC

TABLE 2. Results of the GAMM model testing for a temporal trend in fledging success probability for Snow Petrels breeding at Ile des Pétrels, Terre Adélie, Antarctica, in 1993–2018. Total deviance explained by the model: 6.5%. Deviance explained by random effects: 5.6%. Standard deviation (SD) = estimated variance components. 95% CI = 95% confidence interval. edf = estimated degrees of freedom.

	Smoother edf	χ^2	*P*-value	SD (95% CI)
Fledging probability	1.94	15.01	<0.001	
Random effect				
Nest				0.46 (0.29, 0.73)
Colony				0.15 (0.03, 0.87)

TABLE 3. Results of GAMM models testing for temporal trends in covariates during the period 1993–2018. ARMA corresponds to the selected ARMA structure. edf = estimated degrees of freedom.

Variable	Smoother edf	*F*-test	*P*-value	ARMA
Southern Annular Mode	1	0.45	0.511	0,0
Number of days with snowfall during incubation	1	1.48	0.235	0,0
Number of days with snowfall during rearing	1	67.48	<0.001	2,1
Number of windy days during incubation	1	4.98	<0.05	0,2
Number of windy days during rearing	1	2.81	0.107	0,0
Sea ice concentration during incubation	1	3.87	0.061	0,2
Sea ice concentration during rearing	1.653	6.65	<0.01	0,0

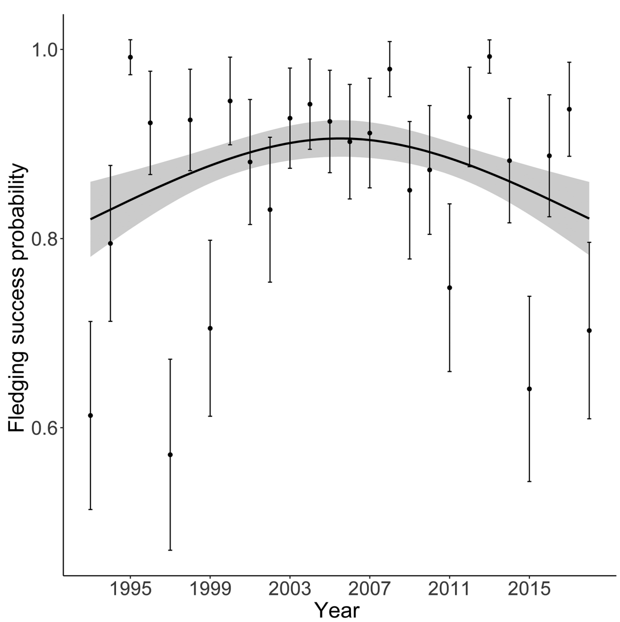

FIGURE 2. Fledging success of Snow Petrel increased from 1993 to 2005 and decreased afterwards. Observed and modeled fledging success probability for Snow Petrels breeding at Ile des Pétrels, Terre Adélie, Antarctica, 1993–2018. Plain line corresponds to estimated smoother from the GAMM model. Gray shading indicates 95% confidence interval.

and the number of days with snowfall, had a negative impact on fledging probability.

Results suggest that Snow Petrels delayed breeding during the study period. This corresponds with previous findings showing delayed breeding in this Antarctic seabird community (Barbraud and Weimerskirch 2006). However, our results improve our knowledge since Barbraud and Weimerskirch (2006) did not find a trend in Snow Petrel phenology using the date of first laying date as a phenological parameter. The study by Barbraud and Weimerskirch (2006) used a shorter data set (between 1993 and 2005). In our model, the trend between 1993 and 2005 seems relatively stable, suggesting that the phenological shift started after 2005. Furthermore, Barbraud and Weimerskirch (2006) used the first date of egg-laying while in our study we used the average hatching date which allowed us to limit the noise generated by possible outliers. Thus, our results showed a clear trend in the breeding phenology.

In our study, Snow Petrel breeding phenology was delayed by ~3 days over 26 years. This appears to be faster than the delay found in Barbraud and Weimerskirch (2006), which was 2.1 days between the early 1950s and 2005 for the community of species breeding in Terre Adélie. This suggests that environmental changes over the past two decades may have been more intense or faster, resulting in a more pronounced shift in phenology. Although Keogan et al. (2018) did not observe a change in phenology on average across 145 seabird populations between 1952 and 2015, our study clearly demonstrates a phenological response to environmental changes in Snow Petrels. This highlights the importance of fine-scale studies for understanding the processes impacting seabird phenology. As expected, the breeding phenology of Snow Petrels was affected by sea ice characteristics. Results showed a delayed hatching date in relation to increasing SIC during the incubation period. This suggests that Snow Petrels started breeding later when SIC was high during the breeding period. This is consistent with results from Descamps et al. (2019) showing delayed breeding of surface feeding Arctic seabirds with delayed spring onset, highlighting the key

TABLE 4. Results of the GAMM when testing for environmental effects on hatching date of Snow Petrels breeding at Ile des Pétrels, Terre Adélie, Antarctica, in 1993–2018. Total deviance explained by the model: 52.6%. Deviance explained by random effects: 29.0%. Standard deviation (SD) = estimated variance components. 95% CI = 95% confidence interval. edf = estimated degrees of freedom.

Covariate	Smoother edf	*F*-test	*P*-value	SD (95% CI)
Southern annular mode	2	1.34	0.261	
Number of windy days during incubation period	1.993	72.88	<0.001	
Number of snow days during incubation period	1.967	164.60	<0.001	
Sea ice concentration during incubation period	1.001	33.94	<0.001	
Random factor				
Nest				1.78 (1.57, 2.00)
Colony				0.47 (0.14, 1.61)

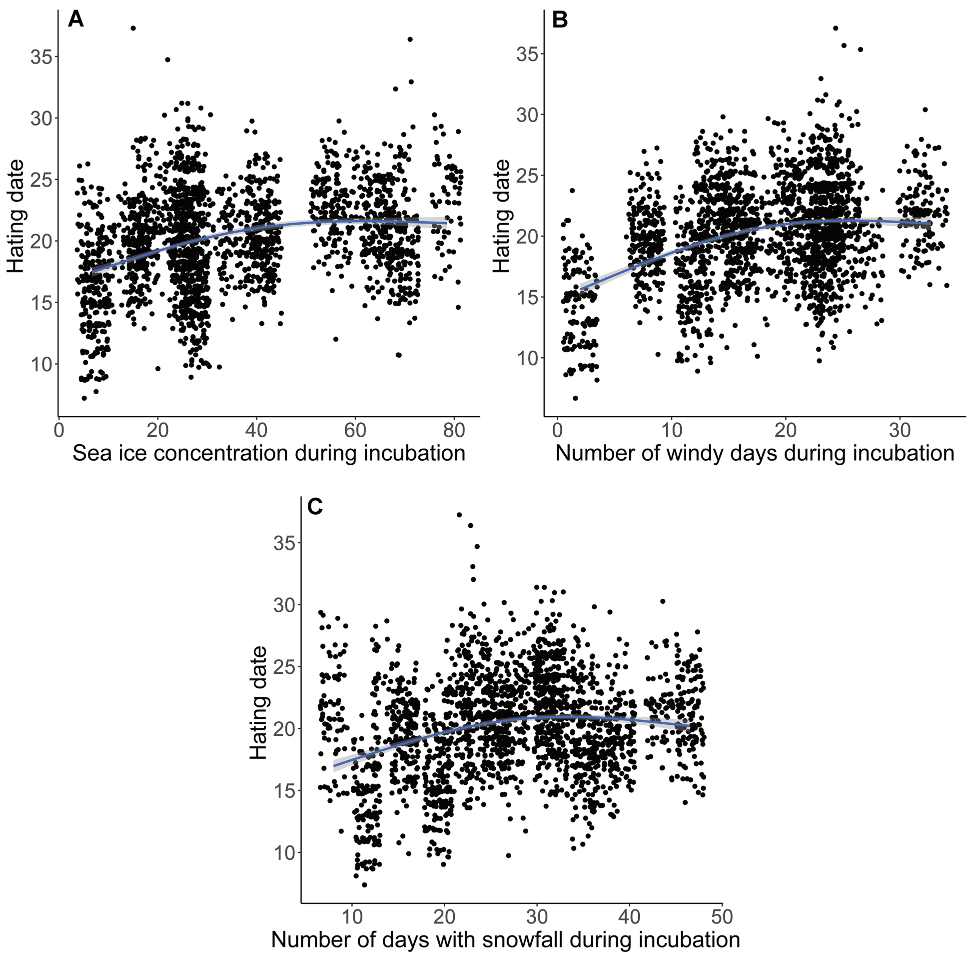

FIGURE 3. Poor local weather conditions and high sea ice concentration during incubation delayed hatching date of Snow Petrel. Relationships between sea ice concentration during incubation (A), number of windy days during incubation (B), number of days with snowfall during incubation (C) and hatching date of Snow Petrels breeding at Ile des Pétrels, Terre Adélie, Antarctica, 1981–2018. Plain line corresponds to the estimated smoother from the GAMM models. Gray shading indicates 95% confidence interval.

role of foraging behavior and habitat in the phenological responses of polar seabirds to climate change. The link between sea ice and reproductive phenology has been demonstrated for several organisms in the Arctic (i.e., Kerby and Post 2013, Ramírez et al. 2017). Sea ice plays a key role in the primary production of the polar seas by driving the rhythm of the two impulses of marine autotrophs that form the basis of Arctic food webs: sea ice algae and phytoplankton (Ji et al. 2013). Changes in the timing of these productivity surges can result in a mismatch between resource needs and availability, thereby affecting the transfer of biomass and energy to higher trophic levels, such as seabirds (Moe et al. 2009, Mallory et al. 2010, Ramírez et al. 2017). In Antarctica, the links between breeding phenology and sea ice are less well understood (Barbraud and Weimerskirch

TABLE 5. Results of the GAMM model testing for environmental effects on fledging probability of Snow Petrels breeding at Ile des Pétrels, Terre Adélie, Antarctica, in 1993–2018. Total deviance explained by the model: 13.9%. Deviance explained by random effects: 6.9%. Standard deviation (SD) = estimated variance components. 95% CI = 95% confidence interval.

Covariate	Smoother edf	*F*-test	*P*-value	SD (95% CI)
Hatching date	1.259	14.25	<0.001	
Number of days with snowfall during rearing period	1.904	32.97	<0.001	
Number of windy days during rearing period	1.385	0.38	0.632	
Sea ice concentration during rearing period	1.814	31.87	<0.001	
Southern annular mode	1	1.41	0.236	
Random factor				
Nest				0.53 (0.35, 0.80)
Colony				0.18 (0.04, 0.89)

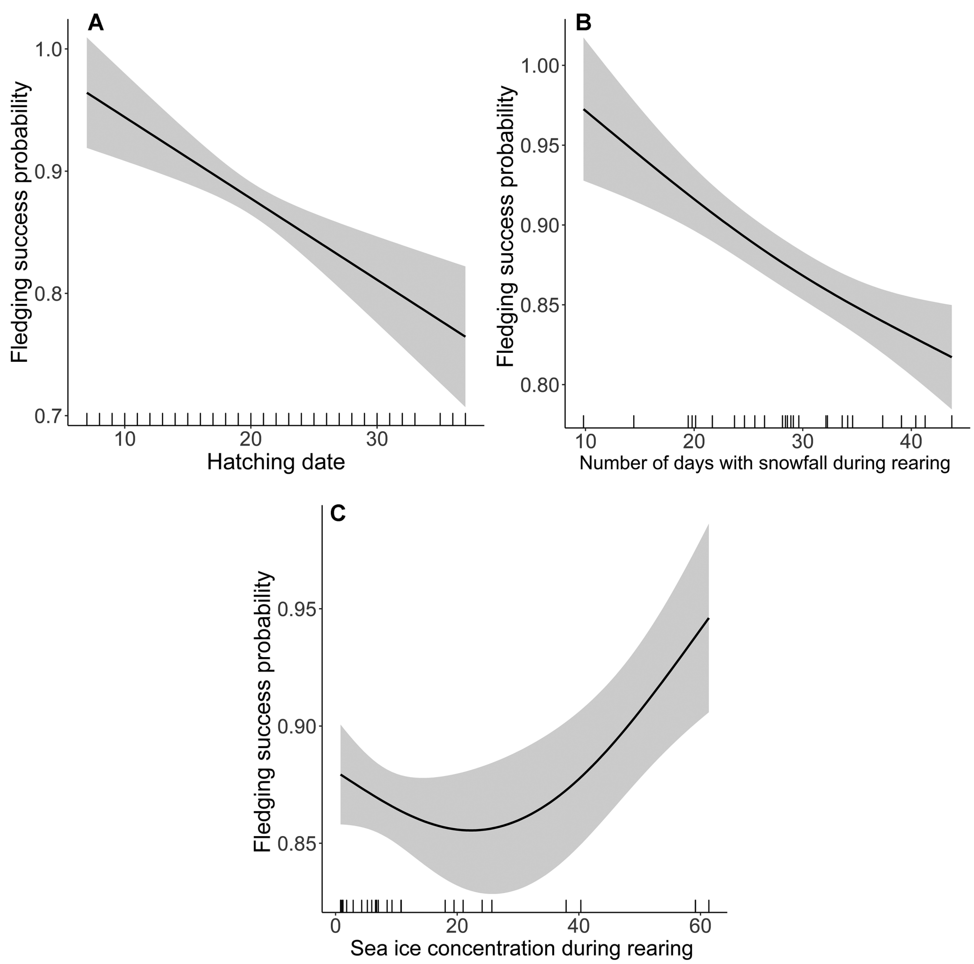

FIGURE 4. Delayed hatching date and high number of days with snowfall during rearing period decreased fledging success of Snow Petrel but high sea ice concentration during rearing period increased fledging success of Snow Petrel. Relationships between hatching date (A), number of days with snowfall during rearing (B), sea ice concentration during rearing (C) and fledging success probability of Snow Petrels breeding in Terre Adélie, Antarctica, 1981–2018. Plain line corresponds to the estimated smoother from the GAMM models. Gray shading indicates 95% confidence interval.

2006). Although some studies have found relationships between climate change and the phenology of seabirds, the responses differ according to the regions studied (Emmerson et al. 2011, Chambers et al. 2013, Youngflesh et al. 2017). Here, we speculate that high SIC may negatively impact the abundance and accessibility of Snow Petrel food resources. Since SIC partly determines the amount of light entering the water column, combined with other factors such as water column stratification, a high SIC may provide a suboptimal habitat for krill and Antarctic silverfish (Meyer et al. 2017), the main prey of Snow Petrels, through a decrease in primary productivity. In addition to decreasing abundance, high SIC may also reduce access to prey by providing protective shelter from aerial predators (Meyer et al. 2017).

We also found a positive relationship between the hatching date and local weather conditions (number of windy days and number of days with snowfall) during the incubation period. Snow Petrels hatched their egg later when conditions were windier. A greater exposure of incubating individuals to wind may increase their energy expenditure through increased thermal loss (Hilde et al. 2016). Therefore, individuals may be forced to leave the nest for foraging at sea, which could (1) increase the frequency of egg neglect and thus the length of the incubation period resulting in a delay in hatching date, and (2) slow down the embryonic development during incubation.

The associations between phenology, breeding success and specific environmental factors are poorly known for Antarctic seabirds, although this is critical to understand the mechanisms by which seabirds respond to climate change (Reed et al. 2009). Late hatching can cause a mismatch between the high energetic demands during chick-rearing and peak food availability. In Antarctica, sea ice retreat in early spring generates an increase in primary productivity during the austral summer with a peak in December and January, then a decrease in February and March (Arrigo et al. 2008, Smith and Comiso 2008). The chick-rearing period of Snow Petrels takes place from the end of January to the beginning of March, thus towards the end of the peak in primary productivity. Consequently, during years when chicks hatch late, food availability may be lower during the chick-rearing period, which may negatively affect chick growth, body condition and their survival at the nest. This corresponds with results from a recent study on Snow Petrels showing that high SIC had a negative impact on the body condition of fledglings (Sauser et al. 2018). The literature describes the influence of phenological changes on the breeding performance of individuals (Both et al. 2006, Møller et al. 2008, Thackeray et al. 2010). Specifically in seabirds, it is documented that early breeding improves breeding performance (Frederiksen et al. 2004, Sauve et al. 2019) as opposed to late breeding that decreases breeding performance. In the Arctic, earlier warming is causing changes in the phenology of melting sea ice, a key driver of primary production, and breeding consequences have been shown for some seabird species (Moe et al. 2009, Descamps et al. 2019).

Fledging success probability showed a bell-shaped temporal trend, with fledging success increasing before 2005 and decreasing thereafter. Our results suggest that several mechanisms may affect fledging success. On the one hand, fledging success was negatively affected by delayed breeding (induced by increased SIC and worsened local weather conditions) suggesting an indirect effect of climate on fledging success. On the other hand, fledging success was positively affected by SIC and negatively affected by the number of snow days, suggesting a direct effect of climate (independent of the effect on hatching date) on fledging success. Based on our assumptions and observed trends, it is likely that the decrease in fledging success since 2005 was due to delayed breeding. Given the negative relationships detected between SIC (during the incubation period) and hatching date, it is likely that the decrease in fledging success was indirectly related to the increase in SIC during the incubation period since 2005. The causes of increase in fledging success before 2005 are less clear, since SIC remained relatively stable from 1993 to 2005 as well as hatching date. However, the number of days with snowfall during the rearing period was lower during 1993–2005 compared to 2005–2018, and may partially explain the increase in fledging success.

Our model does not fully explain the variation in fledging success, which suggests that other unknown covariates may influence fledging success and could possibly explain the increase before 2005. It is also possible that some effects are interacting, making the relationships more complex. On days with snowfall and wind, the snow may be blown away from the nests causing other effects on breeding. We found that the hatching date showed a positive temporal trend; in other words, it was delayed in later years. This suggests that individuals showed some level of phenotypic plasticity in the timing of breeding, which appears to be relatively common among birds (Charmantier and Gienapp 2013) including polar seabirds (Sauve et al. 2019). Indeed, the generation time of Snow Petrels (~25 years, Péron et al. 2016) is too long to have allowed a micro-evolutionary change in the timing of breeding during the study period (26 years). Therefore, we speculate that individuals were able to adjust their breeding date to changes in environmental conditions such as SIC. This plasticity in the timing of breeding may involve changes in diet (e.g., Pierotti and Annett 1991), foraging habitat selection (Paiva et al. 2010, Pettex et al. 2012), and migratory behavior (Pulido 2007), as observed in other seabird species (Grémillet and Charmantier 2010). For an ice-obligate Arctic species such as the Mandt's Black Guillemot (*Cepphus grylle mandtii*), an earlier laying date was associated with an increase in the number of fledglings, but this was an individual response (some individuals advanced their laying date and increased their success and others did not). This suggests that phenotypic plasticity allows some individuals to cope with environmental changes (Sauve et al. 2019). However, the overall breeding success of this population is declining (Divoky et al. 2015), suggesting that despite the ability of some individuals to adapt, this species has a limited capacity to respond to environmental change through phenotypic plasticity. Similarly, our results suggest that, although Snow Petrels showed some plasticity in their breeding phenology in response to environmental changes, they were not able to cope with these changes, since fledging success decreased when the hatching date was delayed and SIC increased since 2005. Late hatching date induces a late fledging date, which may increase the exposure of chicks to poor weather conditions towards the end of the austral summer (such as more frequent snowfalls and more windy conditions). Indeed, we found that the number of days with snowfall affected fledging probability.

So far, climate change in Antarctica has been variable from place to place, particularly regarding sea ice (the region around the Antarctic Peninsula has shown a significant retreat of sea ice that is less pronounced in other regions of Antarctica, Maksym 2019). Similar to our study area, SIC showed a positive trend during the austral summer in East Antarctica since the late 1970s (Parkinson and Cavalieri 2012), and our results suggest that this may have impacted the breeding phenology and fledging success of Snow Petrels in this region. Climate projections indicate major changes in sea ice characteristics in the coming decades (Turner et al. 2013), highlighting the need for further fine-scale studies on the phenological responses of Antarctic seabirds to environmental changes and fitness consequences in order to fully understand the ecological consequences of climate change.

Our study has some limitations in understanding the mechanisms involved in the relationship between the environment and breeding phenology of Snow Petrels, which could be the focus of future studies. A more detailed study of incubation and rearing periods could provide a better understanding of the different mechanisms involved, for example by linking hatching date or fledging success to the body condition of adults, the duration of foraging trips and environmental conditions.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Ornithological Applications* online.

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Author contributions: C.B. and C.S. conceived the ideas and designed the methodology; K.D. managed the data; K.D. and C.S. checked the quality of the data; C.S. analyzed the data; C.S. and C.B. led the writing of the manuscript. All authors collected part of seabird data, contributed critically to the drafts and gave final approval for publication.
Data depository: Analyses reported in this article can be reproduced using the data provided by Sauser et al. (2021).
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