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**Abstract**

In a fast-changing world, polar ecosystems are threatened by climate variability. Understanding the roles of fine-scale processes, linear and non-linear effects of climate factors on the demography of polar species is crucial for anticipating the future state of these fragile ecosystems. While the effects of sea ice on polar marine top predators are increasingly being studied, little is known about the impacts of landfast ice on this species community. Based on a unique 39-year time-series of satellite imagery, *in situ* meteorological conditions and on the world's longest dataset of emperor penguin *Aptenodytes forsteri* breeding parameters, we studied the effects of fine-scale variability of landfast ice and weather conditions on this species reproductive success. We found that longer distances to the landfast ice edge (i.e. foraging areas) negatively affected the overall breeding success but also the fledging success. Climate window analyses suggested that chick mortality was particularly sensitive to landfast ice variability between August and November. Snowfall in May also affected hatching success. Given the sensitivity of landfast ice to storms and changes in wind direction, important future repercussions on the breeding habitat of emperor penguins are to be expected in the context of climate change.

## 1. Introduction

Polar ecosystems are subject to local and regionally contrasted sea ice trends due to climate change [1,2]. Given the complexity of these trends, which are tightly linked to the atmosphere and the ocean dynamics, there is an urgent need to measure and forecast how polar marine populations will respond to sea ice habitat changes [3,4]. Among the studies that have investigated the impacts of climate change and variability on population dynamics in the Southern Ocean [5,6], a thorough understanding of the fine-scale processes by which climate affects the population dynamics of polar organisms is still lacking, thereby preventing the scientific community from improving model projections to correctly assess the future states of polar populations and ecosystems. Given that population dynamics are driven by several demographic components whose sensitivities to climatic factors vary [7,8], it is important to investigate the links between climate and each demographic component. Determining the spatial and temporal scales at which climate variability affects biological parameters is also of prime importance [9]. Also crucial for improving projections, long-term multi-decadal biological series are required to detect non-linear effects of climate on populations [10–13]. The obtention of such long time-series is however often limited by logistical challenges associated with conducting long-term studies in these remote and extreme areas.

Many Antarctic marine top predators, such as seals and seabirds, are intricately linked to landfast ice (LFI), i.e. the narrow band of coastal, compact sea ice held in place by ice shelves and grounded icebergs [14], throughout their breeding period [15–17]. Therefore, LFI variability, such as extreme extent or early break up, can profoundly impact their breeding areas and breeding success [19,20]. However, functional relationships between LFI variability and demographic parameters of polar marine predators remain poorly known due to the scarcity of biological datasets and the difficulty to characterize LFI variability over long time periods.

To improve our understanding of how polar species will respond to future climate changes, we explored the role LFI variability and *in situ* meteorological conditions have on the overall breeding success, but also the fledging and hatching success of a unique sea ice sentinel species [20], the emperor penguin (*Aptenodytes forsteri*). We used the longest historical time-series of Antarctic LFI collected by the Advanced Very High

Resolution Radiometer (AVHRR) and the Moderate-Resolution Imaging Spectroradiometer (MODIS), covering the years 1979 to 2017, i.e. since the inception of modern satellite monitoring. We also used the world's longest time-series of emperor penguin breeding parameters, collected at Pointe Géologie, Adélie Land, since 1952. The novelty of this research, while relying on previous studies (e.g. [21–26]), lies in i) assessing the climate effect on different components of the reproduction, ii) using the longest time-series available for LFI and emperor penguin reproduction, iii) taking into account the relative contribution of fine-scale processes (local LFI and *in situ* meteorological conditions), iv) exploring different time windows of these effects, and v) testing non-linear effects.

## 2. Material and methods

### (a) Landfast ice data

Three sources of satellite imagery were used to cover the 1979-2017 period and aggregate LFI data (electronic supplementary material; see figure S1 for examples):

1) 1979–1991: visible (when available) or thermal infrared images from AVHRR's Global Area Coverage (GAC) mode (spatial resolution of 4 kilometres per pixel; km/px).
2) 1992–1999: visible (when available) or thermal infrared images from the AVHRR Coastal Atlas of East Antarctica [27] (resolution of 1.1 km/px).
3) 2000–2017: LFI maps from Moderate-Resolution Imaging Spectroradiometer (MODIS) images (resolution of 1 km), classified by Ref. [28].

Distances between the penguin colony location and the nearest landfast ice edge (LFIE) (i.e., proxy for access to the ocean) and landfast ice areas (LFIA) were extracted from the images.

### (b) Meteorological data

Meteorological data were obtained from the French weather station of Dumont D'Urville. Three parameters were used in this study: the number of days per month with i) temperatures under -10°C, ii) winds above 28 m/s, and iii) snowfall. We hypothesised that egg loss during incubation and chick mortality could be enhanced during cold and windy conditions caused by katabatic winds and winter storms [15]. Heat loss due to cold temperatures and strong winds, which could be enhanced by snowfall, may increase chick morality.

### (c) Reproductive data

Data are similar to those used by Refs. [21,29] with updated estimates (electronic supplementary material). From count data we estimated 'breeding success' as the number of fledged chicks divided by the number of breeding pairs; 'hatching success' as the number of breeding pairs minus the number of dead eggs divided by the number of breeding pairs; and 'fledging success' as the number of fledged chicks divided by the number of breeding pairs minus the number of dead eggs. Breeding success was estimated over the period 1979–2017; hatching and fledging success over the period 1983–2017.

### (d) Climate window analysis

We performed a ‘climate window analysis’ using the R package *climwin*, following the steps described in Ref. [30]. Climate window analyses determine, without any *a priori* hypothesis, the best climate window(s) (i.e. candidate models) that identify potential climate signals between biological and climate data. Two datasets were analysed: one that contained our monthly climate data, i.e. landfast ice or meteorological data covering the 1979—2017 period, and one that contained information on the response variable, i.e. breeding, hatching, and fledging success. For each climate window, a model was computed. Akaike Information Criteria (AICs) were used for ranking and comparing different candidate climate windows, and then for assessing the best models, their uncertainty, explanatory power, and applicability. Details on the analysis and outputs of the analysis are provided in the electronic supplementary material. The full dataset and codes can be found on Dryad [31].

## 3. Results

(a) Reproduction time-series

Hatching success was the most stable reproductive parameter (mean ± SD = 0.82 ± 0.07, CV = 8.3 %), while fledging success (0.65 ± 0.30) and breeding success (0.53 ± 0.25) were more variable (CV = 46.4 % and 46.5 %, respectively; figure 1a). Hatching success increased during the study period (slope = 0.051 ± 0.007 (SE), $p < 0.001$), while fledging success (slope = -0.003 ± 0.052, $p = 0.96$) and breeding success (0.026 ± 0.040, $p = 0.52$) remained stable (figure 1a). Variations in both fledging and breeding successes seemed to co-vary with the LFIA, but even more so with the distance to the nearest LFIE (figure 1b-c).

(b) Climate window analysis

Breeding success was higher for shorter distances to the LFIE between August and November ($p_{randomization} = 0.006$; adjusted $R^2 = 0.4$), while the LFIA did not have a significant influence (i.e. based on the randomization test; table 1, figure 2a). The number of days per month with temperatures under -10° C, with winds above 28 m/s, and with snowfall did not influence the breeding success (table 1). Neither the LFIA nor the number of days per month with winds above 28 m/s or temperature below -10° C had an influence on the hatching success (table 1). However, the hatching success appeared to be influenced by the number of days with snowfall in May ($p_{randomization} = 0.0003$, adjusted $R^2 = 0.3$; table 1, figure 2c). This relationship was non-linear, with hatching success increasing with the proportion of days with snowfall per month up to 37% and remaining stable or decreasing slightly for higher proportions. Finally, fledging success was higher for shorter distances to the LFIE in November ($p_{randomization}= 0.035$, adjusted $R^2 = 0.5$; table 1, figure 2b), while the LFIA, the number of days per month with temperature below -10° C, with winds above 28 m/s, and with snowfall did not have a significant influence (table 1). Fledging success declined non-linearly with the nearest distance to the LFIE, with an accelerated decline for distances greater than ca. 50 km.

## 4. Discussion

We showed that, over 39 years, different components of the reproduction of an Antarctic seabird were affected by fine-scale LFI and *in situ* meteorological conditions at different times of its breeding season, and, importantly, these relationships were non-linear.

Adult emperor penguins during the breeding season forage and hunt by diving at the edge of the LFI in cracks, flaw leads, and polynyas [32]. Longer distances between the colony and foraging grounds accessed by the LFIE imply lower chick-feeding frequency, and thus lower chick growth with negative consequences on fledging and breeding success. Using historical AVHRR and recent MODIS images, our study brings important and novel results. First, we identified that distance to nearest LFIE particularly affected fledging success in November (and the second-best model identified a window between August and November), indicating that chick mortality was the main cause of declining breeding success with increasing distance to LFIE. Second, this relationship was nonlinear, with over 50% chick mortality when the distance to LFIE exceeded ca. 65 km. Non linearity could be detected by extending the time series from 8 years in a previous work [26] to nearly 40 years in our study. Third, we identified that the best climate window explaining the relationships between distance to LFIE (i.e. foraging grounds) and breeding success was between August and November, suggesting chicks were particularly sensitive to environmental variability during this period of high energetic demands for body growth [33,34].

Reproduction has been monitored at extremely few other emperor penguin colonies. Surprisingly, no relationship was found between LFI and breeding success of emperor penguins at Taylor Glacier colony [35]. Although this may depict the complex interactions between environment and penguin foraging behaviour and their consequences for breeding performances, ref. [35] used distance to LFIE in April and September, and our time windows analysis indicated that these months did not represent the full critical period for fledging and breeding success. Nevertheless, this highlights the need to monitor multiple sites in order to understand how sea ice variability, and especially LFI, is affecting the global emperor penguin population.

Our study supports previous findings that it is crucial to consider both fine-scale climate processes and fine-scale temporal windows when investigating the relationships between climate variability and demographic traits [9,36]. Despite the diversity of studies that have investigated the effect of climate change on polar species, there is a strong need to account for the factors that control population dynamics at local/regional scales in order to understand how they may modulate the effects of large-scale environmental variations on long-term population trend [13]. For example, ref. [37] compared the influence of environmental factors on the breeding success of snow petrels (*Pagodroma nivea*) at Casey station with the colony of Adélie Land, and showed that despite similarities in the biological processes controlling snow petrel breeding success, the correlation of large-scale environmental factors with breeding success differed substantially between the two colonies, likely due to the effects of the environmental factors at the local/regional scale.

Landfast ice variability may have important indirect effects that we did not consider in this study. For example, LFI break-ups could contribute to the phytoplankton seeding process (e.g. [38–40]) and may drive a phytoplankton bloom associated with trophic cascades. This could in turn benefit emperor penguins through bottom-up processes with a temporal lag depending on the timing within the breeding period. In the Arctic, longer temporal lags between sea ice melting and phytoplankton bloom resulted in rapidly decreasing breeding performance for little auks (*Alle alle*) and Brünnich's guillemots (*Uria lomvia*) [41]. Thus, considering local to regional-scale phenology in the development of potential phytoplankton blooms in responses to LFI variability may help understand climate-driven environmental impacts on seabirds.

During breeding, individual emperor penguins do not use a fixed nest site as do other penguins. Therefore, the colony is mobile during the breeding season and can move several hundred meters or even a few kilometers. Therefore, the selection of nest site (and experience to nest site) is not relevant for this species. However, there might be selection for sites where colonies are situated, as these sites are generally occupied for long time periods (several decades at least), as our results suggest a strong selection pressure form environmental factors such as LFIE. Nevertheless, the environmental factors affecting colony site selection have not been investigated and quantified to date.

Finally, none of the meteorological variables, except snow falls for the hatching success, had an influence on reproductive parameters. The positive relationship between the number of days with snowfall in May and the hatching success may be associated with the hydration of males during their long fasting period of ca. four months. We speculate that important snowfalls in May allow males to supplement their water intake by eating snow, thus decreasing dehydration potentially leading to the abandonment of the egg before it hatches. Indeed, field observations during winter indicate that male emperor penguins eat snow all along the incubation period ([42]; CB, pers. obs.).

Our results bring new insights on the proximate mechanisms through which a poorly known polar habitat feature, LFI, affects demographic parameters of polar top predators. We note that, although we might be able to better predict the future state of polar populations once such fine-scale processes are fully understood, population projections based on sea ice models (e.g. [43]) remain hampered by the fact that these models project sea ice extent but do not provide information on LFI dynamics yet. Important future repercussions on the breeding habitat of emperor penguins and ultimately their persistence are to be expected in the context of climate change [2] given the sensitivity of LFI to storms and changes in wind direction [44], as well as the recently observed strong and opposed LFI trends in adjacent regions [45]. Given the demographic sensitivity of emperor penguins associated with postglacial warming leading to a major southward expansion [46], major shifts such as decline or extinction of emperor penguin populations are expected under anthropogenic climate change.

## Figures and table

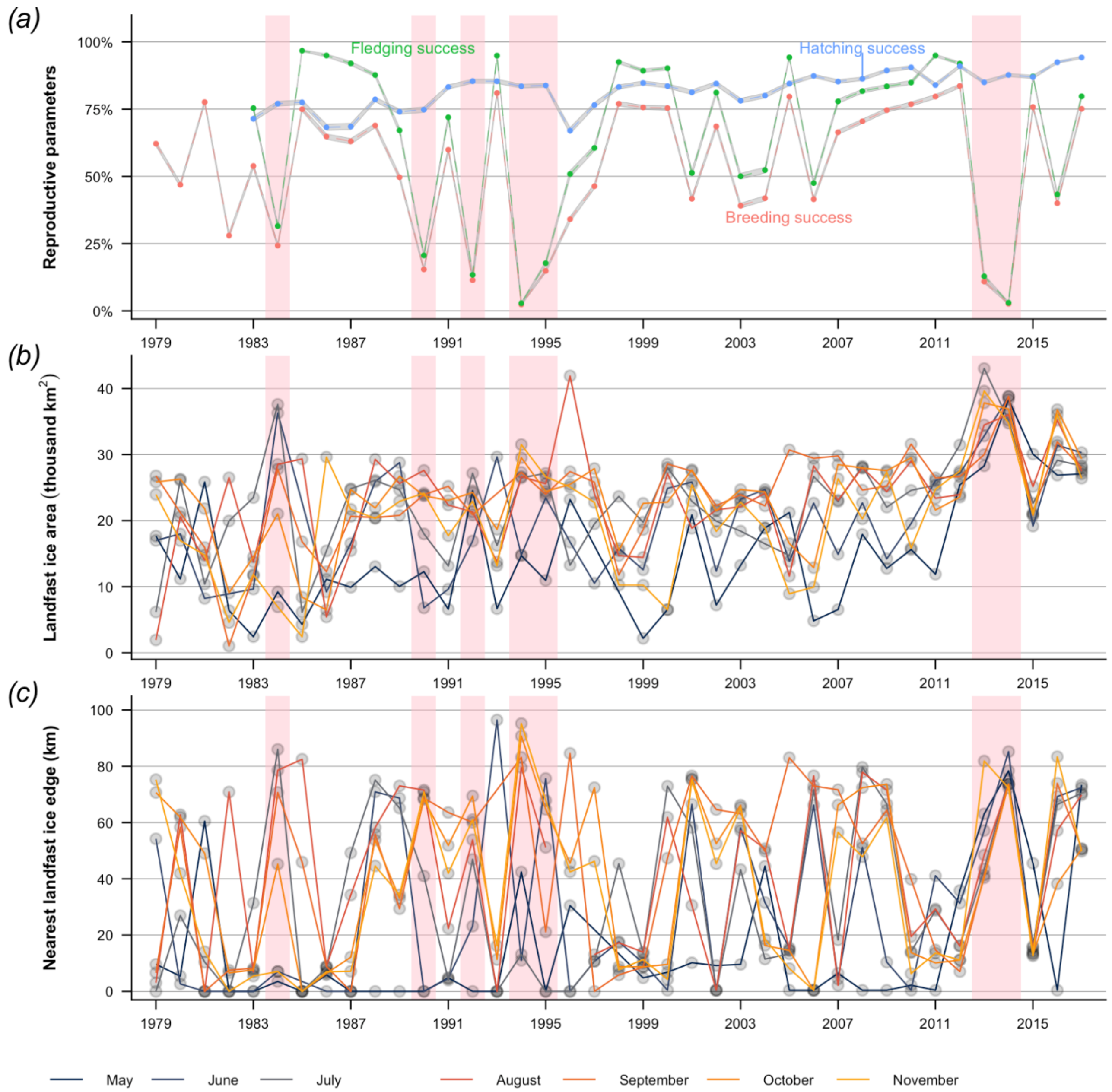


**Fig. 1** Times-series of the emperor penguin reproductive parameters (panel a; 95% confidence intervals in grey) and LFI conditions (LFIA, panel b; nearest distance to LFIE, panel c) at Pointe Géologie, 1979-2017. Pink rectangles highlight years for which breeding success was below 25%.

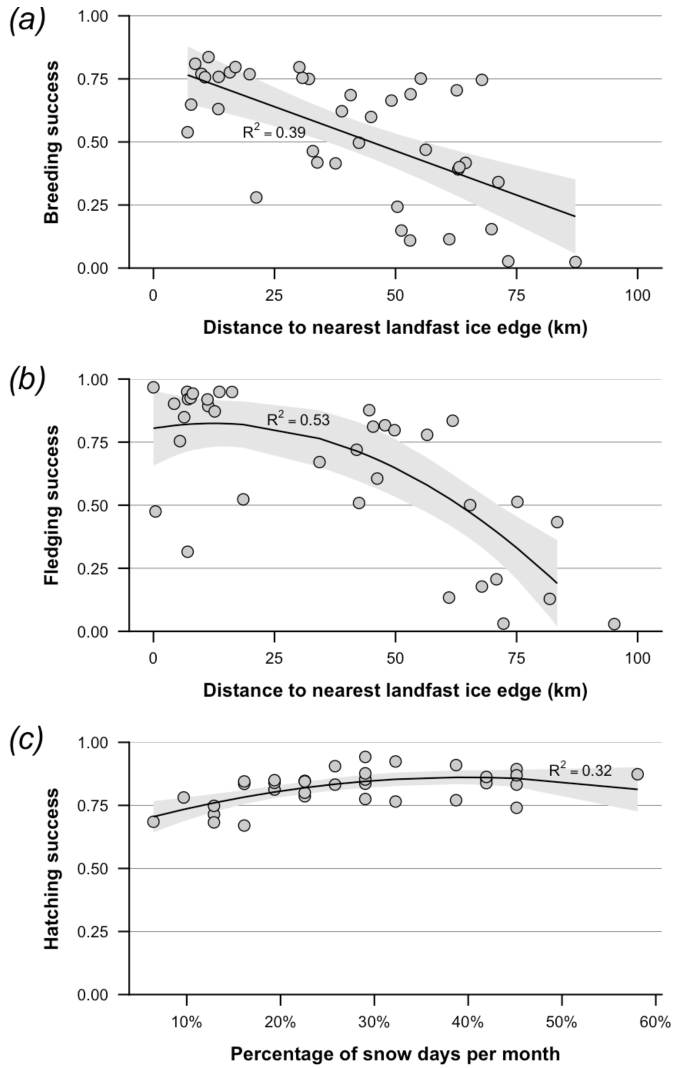


**Fig. 2** Relationships between emperor penguin reproductive parameters (breeding, fledging, and hatching successes, panels a, b, and c respectively) and climate variables from 1979 to 2017 at Pointe Géologie obtained from the climate window analysis. The best climate window was August to November for (a), November for (b), and May for (c).

**Table 1.** Summary of the climate window analysis.

| Climate variables | Biological variable | Period considered | Years | Best climate window | *p-value* best model[1] | *p-value* after randomisation | Fit selected [alternative fit] | Sign of the relation | $R^2$ after randomisation (k = 10) |
|---|---|---|---|---|---|---|---|---|---|
| **Nearest open water (LFIE)** | Breeding success | May-Nov. | 1979-2017 | Aug.- Nov. | 1.48e-05 | 0.006 | linear, AIC = -125.8826<br>[quadratic, AIC = -125.082] | - | 0.386 |
| | Hatching success | May-Aug. | 1983-2017 | | | | | | |
| | Fledging success | May-Nov. | 1983-2017 | Nov. | x = 0.500<br>$x^2$ = 0.025 | 0.035 | quadratic, AIC = -107.642<br>[linear, AIC = -105.3069] | - | 0.530 |
| **Landfast ice area (136°-146° E)** | Breeding success | May-Nov. | 1979-2017 | NS | 0.003 | 0.499 | | NS | |
| | Hatching success | May-Aug. | 1983-2017 | NS | 0.007 | 0.715 | | NS | |
| | Fledging success | May-Nov. | 1983-2017 | NS | 0.0001 | 0.266 | | NS | |
| **Nb. of days/month with temperatures under -10° C** | Breeding success | May-Nov. | 1979-2017 | NS | NS | / | | NS | |
| | Hatching success | May-Aug. | 1983-2017 | NS | NS | / | | NS | |
| | Fledging success | May-Nov. | 1983-2017 | NS | NS | / | | NS | |
| **Nb. of days/month with winds above 28 m/s** | Breeding success | May-Nov. | 1979-2017 | NS | NS | / | | NS | |
| | Hatching success | May-Aug. | 1983-2017 | NS | NS | / | | NS | |
| | Fledging success | May-Nov. | 1983-2017 | NS | NS | / | | NS | |
| **Nb. of days/month with snowfall** | Breeding success | May-Nov. | 1979-2017 | NS | 0.044 | 0.926 | | NS | |
| | Hatching success | May-Aug. | 1983-2017 | May | x = 0.003<br>$x^2$ = 0.017 | 0.0003 | quadratic, AIC = -198.8435<br>[linear, AIC = -194.5369] | + (bell shape) | 0.321 |
| | Fledging success | May-Nov. | 1983-2017 | NS | NS | / | | NS | |

[1] For quadratic relationships, *p*-values for the linear and quadratic terms are given as x and $x^2$ respectively.

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