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SHORT NOTE

Scale matters: sea ice and breeding success of Adélie penguins

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Abstract
Southern Ocean ecosystems are extremely vulnerable to sea-ice changes occurring at different spatial and temporal scales. Variability in the sea-ice conditions strongly influence the survival and reproduction of animals that are synchronized with the seasonality of sea ice. Although the linkages between Adélie penguins (*Pygoscelis adeliae*) and sea-ice conditions are well established, the spatial and temporal scales at which sea ice affects individuals and populations are poorly known. Using 23 years of penguin breeding success and remote-sensing data of sea ice, we investigate the spatial and temporal scales at which sea-ice changes best explain variations in the reproductive success of Adélie penguins at Pointe Géologie, East Antarctica. The best spatial scale encompassed all foraging areas exploited and all the sea-ice conditions encountered by penguins over a breeding season. There was a consistent influence of sea-ice concentration during the guard stage on the overall breeding success. We demonstrate the importance of considering sea ice at a fine temporal scale rather than using an average value over the breeding season to best explain reproductive success in Adélie penguins.

Keywords East Antarctica · *Pygoscelis adeliae* · Time series · Sea-ice concentration · Spatial and temporal scales

Introduction

Polar species have evolved to be synchronized with the seasonality of sea ice. For instance, it is widely accepted that sea-ice variability affects the physiology, behaviour, demography and dynamic of polar populations and species (Constable et al. 2014). Indeed, sea ice can be a primary factor determining seabird survival and reproduction (Croxall et al. 2002; Jenouvrier et al. 2005; Barbraud and Weimerskirch 2006; Forcada et al. 2006). The relationship between the Adélie penguin (*Pygoscelis adeliae*) and sea ice is now well established with influence on foraging and on breeding ecology through a variety of processes operating at different spatial and temporal scales (Watanuki et al. 1997; Ainley et al. 1998; Ainley 2002; Croxall et al. 2002; Kato et al. 2002, 2003; Forcada et al. 2006; Emmerson and Southwell 2008). Adélie penguins are often considered a proxy for the ecological effects of changes in sea ice (Ainley 2002). It has been suggested that there is an optimal range of sea-ice cover during the breeding season that maximizes the foraging and the breeding success (Ainley 2002; Lescroël et al. 2010; Barbraud et al. 2015; Le Guen et al. 2018). However, none of these studies have tested different temporal and spatial scales on foraging parameters or breeding success, despite the scale-specific response of species to sea-ice changes. Determining the spatial and the temporal scales at which sea-ice characteristics should have an effect is thus of prime importance for studies of climatic impact on demographic parameters of pagophilic species. Our study aims to investigate the sea-ice spatial and temporal scales that best explain the reproductive success of Adélie penguins in a colony of Terre Adélie, Antarctica (Fig. 1). Over the recent years, this location experienced unprecedented changes in sea-ice conditions leading to extreme variations in breeding success of this species and even episodic complete breeding failures (Barbraud et al. 2015; Ropert-Coudert et al. 2015, 2018). This high variability, together with long-term observations, offers a good study system to investigate this question.

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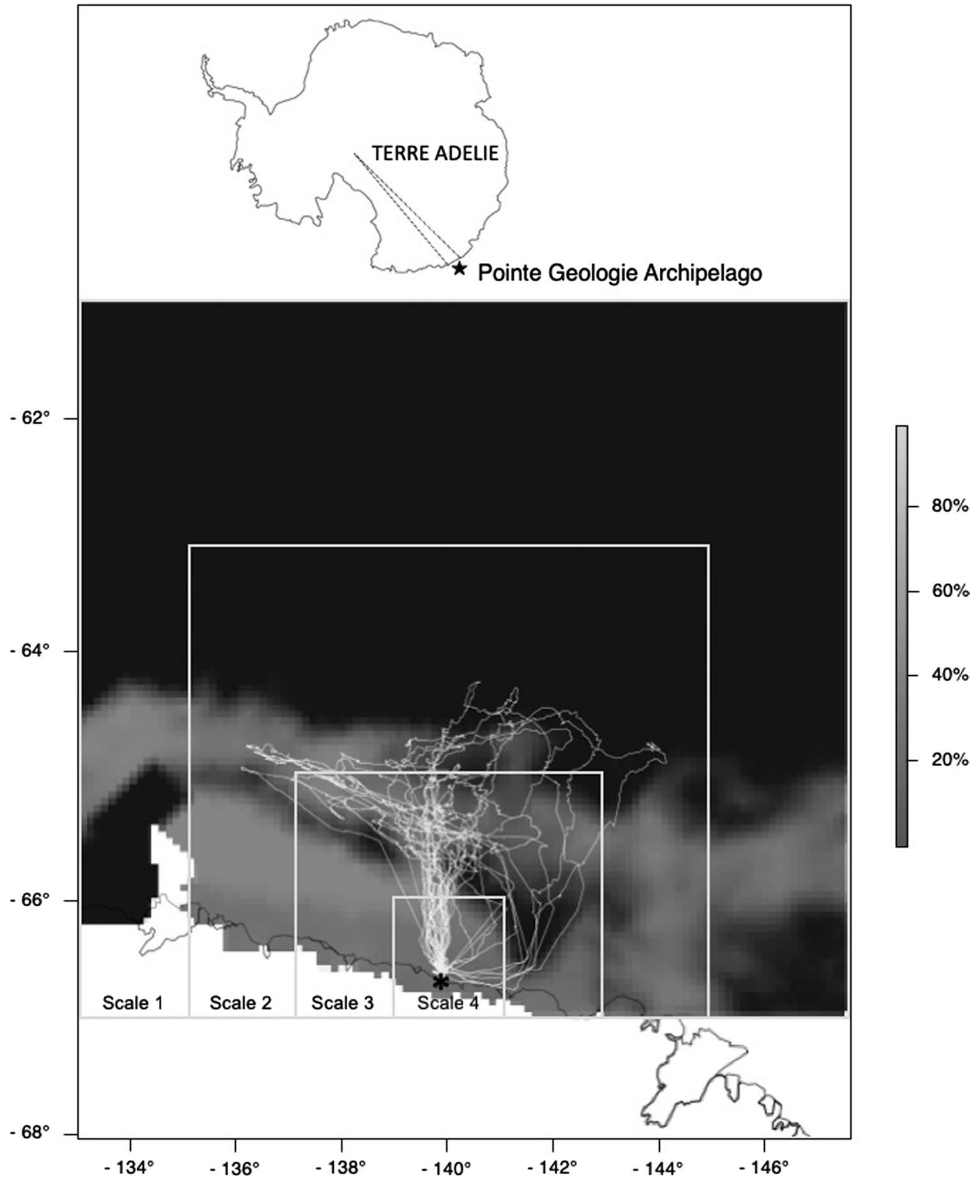

Fig. 1 Areas considered for the study of the influence of sea-ice concentration on the annual breeding success of Adélie penguins at Ile des Pétrels. Sea-ice concentration in light grey gradation (ftp://ftp.ifremer.fr/ifremer/cersat/products/gridded/psi-concentration/data/antarctic/monthly/netcdf/), GPS tracks of foraging trips undertaken by Adélie penguins in white and their colony (black star) are shown for December 2016. Scale 1 (133°E–148°E and 61°S–67°S), scale 2 (135°E–145°E and 63°S–67°S), scale 3 (137°E–143°E and 65°S–67°S) and scale 4 (139°E–141°E and 66°S–67°S) are indicated (see text for explanations)

Material and methods

Study area and species

Adélie penguin breeding colonies of Ile des Pétrels (66°40′S, 140°01′E), Pointe Géologie archipelago, Terre Adélie, Antarctica, have been monitored every year since 1990. Here, we used the data from Ile des Pétrels over 23 breeding seasons from 1993 to 2016 for which breeding success was recorded. Adélie penguins arrive at their breeding sites on land around October and the peak of laying occurs mid-November (Barbraud and Weimerskirch 2006). Males and females alternatively incubate 1–2 eggs during 30 to 39 days until hatching, and brood the chicks on average 22 days until the end of the guard stage. When the chicks become thermally independent around mid-January, they gather in crèches. At this stage, parents forage simultaneously and feed their chicks every 1 to 2 days until they fledge at the age of 50–60 days in late February (Barbraud and Weimerskirch 2006). The number of breeding pairs was counted in mid-November and the number of chicks was counted in early February. We calculated the annual breeding success as the number of chicks divided by the number of breeding pairs (see Jenouvrier et al. 2006 for details).

Sea-ice concentration

We used passive-microwave estimates of monthly sea-ice concentration (SIC) from October to February and from 1993 to 2016 obtained from the Institut Français de

Recherche pour l' Exploitation de la Mer (ftp://ftp.ifremer.fr/ifremer/cersat/products/gridded/psi-concentration/data/antarctic/monthly/netcdf/). The monthly SIC is calculated as the mean percentage of an area (12.5 km grid resolution) covered by sea ice with 0% being open water and 100% being full ice cover.

A recent study showed the area between 134°E–142°E and 63°S–66°S to be exploited by Adélie penguins during their foraging trips off Ile des Pétrels (Widmann et al. 2015). However, this spatial scale does not encompass the temporal modifications of the sea ice as it recedes throughout the breeding season (Jenouvrier et al. 2006). To address this, we extracted monthly sea-ice data at four spatial scales (Fig. 1) using "raster" package (Hijmans 2017) on R 3.4.3 (R Core Team 2019). Scale 1 (S1: 133°–148°E, 61°–67°S; area = 487,292 km^2) includes the maximum sea-ice extent recorded for the studied period and is larger than scale 2 (S2) for including variability that may occur just outside the maximum foraging range of penguins. S2 (135°–145°E, 63°–67°S; area = 213,557 km^2) encompasses the maximal extent ever recorded for foraging trips of adults during incubation (Widmann et al. 2015). Scale 3 (S3: 137°–143°E, 65°–67°S; area = 61,295 km^2) is an intermediate scale (Fig. 1). Finally, Scale 4 (S4: 139°–141°E, 66°–67°S; area = 10,007 km^2) corresponds to the area encompassing feeding trips during the chick rearing period. Correlation between each monthly values of SIC from October to February and at all spatial scales was tested with correlation matrix and checked visually using correlogram from "corrplot" package (Wei and Simko 2017).

Modelling analyses

Generalized additive models (GAMs) can describe complex non-linear relationships between a response variable and the predictors (Zuur et al. 2009). GAM with a Gaussian distribution and identity link function were fitted to the data using the "mgcv" library in R. The smoothing parameter estimation was by generalized crossed validation (Wood 2006). The relationship of the breeding success and SIC was investigated at a monthly scale from October to February. The four scales defined previously were associated with each month of the breeding season in our models. Taking into account over-dispersion, our models were compared and selected using the corrected quasi-likelihood adjusted Akaike information criterion (QAIC$_c$) (Akaike 1981; Burnham and Anderson 2004). Akaike weights (W_{AIC}) were calculated for each covariate to select the best spatial scale and months affecting breeding success (Wagenmakers and Farrell 2004). Therefore, the model was:

$$E(\text{breeding success}_i) = \beta_0 + f_k\ (\text{ScaleJ\_MonthK}_i),$$

where $E(\text{breeding success}_i)$ is the expected value of the breeding success of year i as a function of the predictors, β_0 is an intercept, $f_k = 1,\ldots,4$ are nonparametric smoothing functions, and $\text{Scale}_J\text{\_Month}K_i$ is the value of the sea-ice covariate for scale J ($J = 1,\ldots,4$) during month K ($K = \text{October},\ldots,\text{March}$) and year i.

The quadratic aspect of the relationship between the reproductive success and SIC was tested comparing a GAM with and without a quadratic term (using the quasi-likelihood Akaike information criterion QAIC$_c$).

Results and discussion

Results indicated a significant influence of SIC in January ($F_{3.4,4.3} = 8.4$, adjusted $R^2 = 0.61$ and $p < 0.001$) and in February ($F_{3.5,4.3} = 9.37$, adjusted $R^2 = 0.63$ and $p < 0.001$) on the annual breeding success (Fig. 2). However, the relationship of SIC to the time series of breeding success was not quadratic. S2 best explained the relationship between the annual breeding success and SIC in all models (Tables 1, 2). Considering both temporal and spatial scales, the effects of SIC during January ($W_{AIC} = 0.45$) and February ($W_{AIC} = 0.51$) were equally, yet independently, high (Table 2). We found high correlation between January and February SIC at each spatial scale. Correlation coefficients ranged between 0.8 and 0.94. Nonetheless, every month was modelled separately as both months have important weights and corresponded to a critical period of the chick rearing.

Our results indicate that Adélie penguins breed successfully under an optimal range of sea-ice conditions corroborating previous studies (Smith et al. 1999; Ainley 2002; Barbraud et al. 2015; Le Guen et al. 2018). Large sea-ice extent and/or high cover prohibit penguins to access their foraging grounds and increase the amount of time spent travelling (Ainley 2002; Emmerson and Southwell 2008; Ropert-Coudert et al. 2015). During chick rearing—the temporal scale selected by our models—a large SIC extent could decrease the frequency of provisioning chicks and have a strong impact on breeding success. Conversely, krill (*Euphausia* spp.), the main prey of Adélie penguins, feed on under-ice communities (e.g. microalgae; Nicol et al. 2000), and thus low sea-ice cover could reduce the amount of food available to krill and, by cascading effect, to the penguins (Quetin et al. 1996; Massom and Stammerjohn 2010) leading to a lower breeding success. The timing at which the sea ice retreats can amplify a negative effect on the reproductive success if an important sea-ice cover persists during the chick rearing (Emmerson and Southwell 2008). The optimal SIC also depends on the spatial and temporal scales at which SIC is examined and can vary from 5 to 30% in the literature (Ballard et al. 2010; Barbraud et al. 2015; Le Guen et al. 2018). At Ile des Pétrels, our spatial S2 best explaining

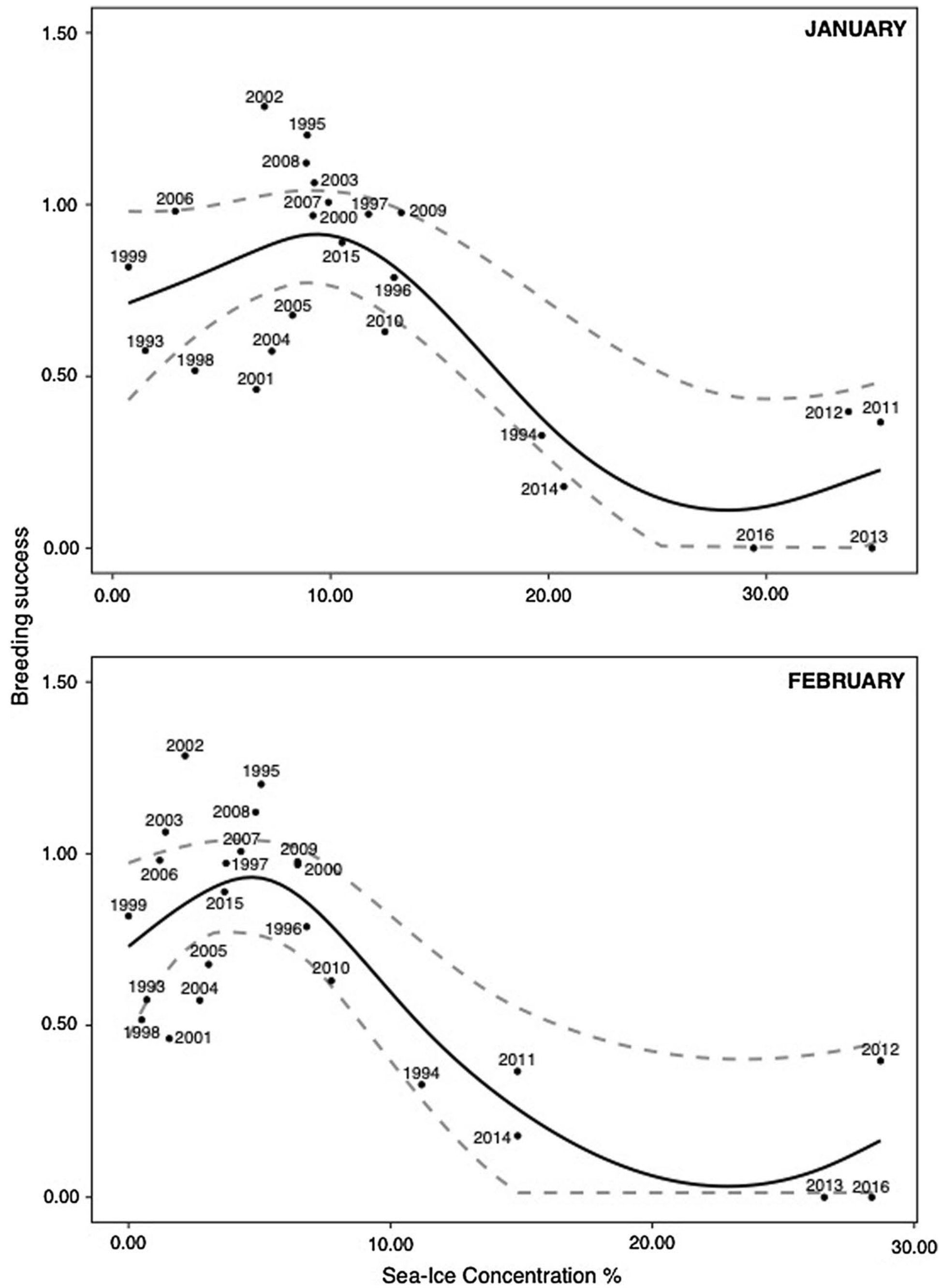

Fig. 2 Fitted GAM results (black line) on Adélie penguins breeding success measured (black dots) over 23 years from 1993 to 2016, with the percentage of sea-ice concentration extracted at scale 2 in January and February. Broken lines indicate 95% confidence intervals

variations in breeding success was larger than the one used by Barbraud et al. (2015) and slightly smaller than that of Le Guen et al. (2018). While one could expect the spatial S3 or S4 to be selected, as they correspond to the foraging area during chick rearing, S2 was selected probably because it encompassed foraging areas from all the breeding season. Indeed, this spatial scale was probably more integrative of the trophic conditions encountered during breeding. In parallel, January and February are critical months, as parents have less flexibility to adjust their trip duration while they have to regularly and rapidly provision their chicks.

Although mechanisms underlying the link between sea ice and Adélie penguin breeding success are complex, the choice of the spatio-temporal scale at which sea ice is extracted is important to project population responses (Jenouvrier 2013). Our results suggest that a specific combination of spatial and temporal scales plays a crucial role in explaining breeding success over a breeding season. Downscale SIC extraction both spatially and temporally allowed us to investigate its effect on reproductive success at a finer scale. Moreover, monthly resolution appeared advantageous in explaining variations of the breeding success rather than

Table 1 Model selection for GAMs of the annual breeding success of Adélie penguins as a function of different spatial and temporal scales (S1–S4, see text for definition) of sea-ice concentration

Month	Scale	$QAIC_c$	$\Delta QAIC_c$	W_{AIC}
February	**S2**	**1.90**	**0.00**	**4E−01**
January	**S2**	**3.51**	**1.61**	**1.65E−01**
January	**S4**	**3.62**	**1.72**	**1.57E−01**
January	S1	5.25	3.35	6.93E−02
February	S1	5.64	3.74	5.70E−02
All	S1	5.87	3.97	5.09E−02
February	S3	5.99	4.09	4.79E−02
January	S3	6.95	5.05	2.96E−02
December	S1	7.90	6.00	1.84E−02
December	S2	8.64	6.74	1.27E−02
All	S2	9.03	7.13	1.05E−02
All	S4	11.26	9.36	3.43E−03
All	S3	11.33	9.43	3.32E−03
February	S4	11.41	9.51	3.19E−03
November	S2	14.40	12.5	7.15E−04
November	S1	14.96	13.06	5.40E−04
December	S4	19.01	17.11	7.13E−05
December	S3	20.13	18.23	4.07E−05
October	S2	23.01	21.11	9.65E−06
November	S3	23.22	21.32	8.69E−06
November	S4	23.72	21.82	6.76E−06
October	S3	24.36	22.46	4.91E−06
October	S1	24.42	22.52	4.77E−06
October	S4	24.68	22.78	4.19E−06

Models are ranked by $QAIC_c$; models with substantial support ($\Delta QAIC_c < 2$) are shown in bold

$\Delta QAIC_c$ difference between the model and the minimum $QAIC_c$ score, W_{AIC} Akaike weights

Table 2 Temporal and spatial variables best explaining the relationship between the annual breeding success of Adélie penguins and sea-ice concentration

Variables	W_{AIC}
S2	**0.59**
S4	0.20
S3	0.16
S1	0.08
October	0.00
November	0.00
December	0.03
January	**0.42**
February	**0.51**

Models with the highest Akaike weights (W_{AIC}) are shown in bold. W_{AIC} is calculated on all the models tested

considering it over all the breeding season. We suggest a similar approach to be conducted for other sites and colonies across the Antarctic to examine if similar scales are selected under different environmental conditions. Indeed, the responses of populations to climate changes are likely to differ regionally or even locally (Forcada et al. 2006). Thus, improving our understanding of the influence of sea ice on breeding outcomes in both space and time scale is a key to better evaluate and anticipate how future sea-ice changes will affect populations and species around Antarctica.

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Authors' contributions Study design: A.K., C.B., Y.R–C. Breeding success data management: K.D. Data analysis and processing: E.B. Writing: E.B., A.K., C.B., Y.R.-C., K.D. All authors edited and revised the manuscript, gave final approval for publication and agreed to be held accountable for the content therein.

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Compliance with ethical standards

Conflict of interest We have no competing interests.

Ethical approval Ethics Committee of the Institute Paul Emile Victor (IPEV) and Comité de l' Environnement Polaire approved the field procedures.

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