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Reproductive performance and diving behaviour share a common sea-ice concentration optimum in Adélie penguins (*Pygoscelis adeliae*)

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Graphical abstract

Multiple tools for assessing the effects of sea-ice conditions
on the foraging activity and breeding success of Adélie penguins
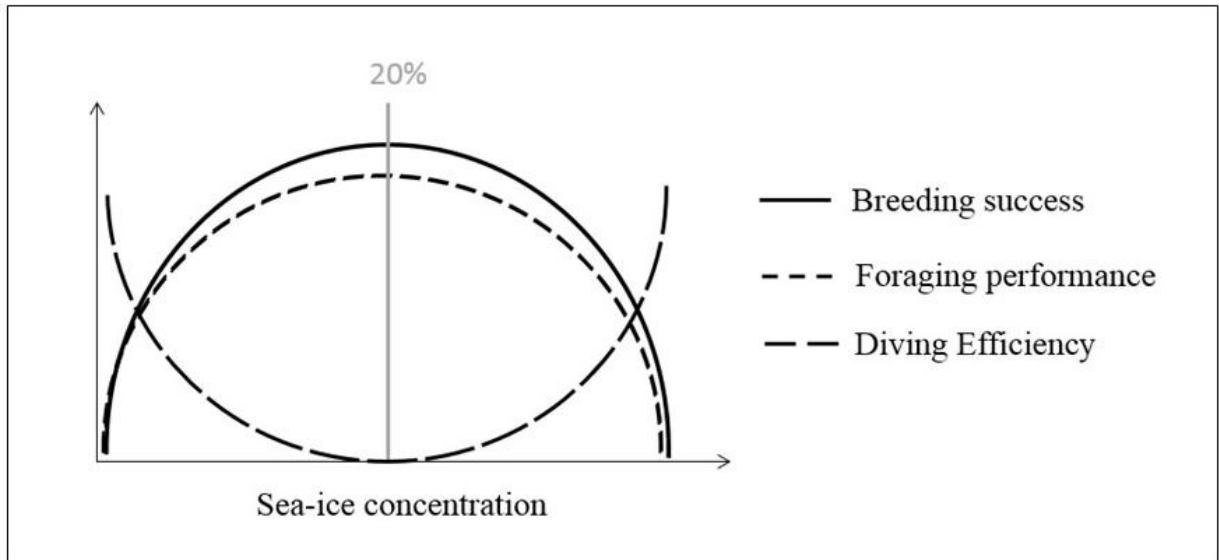
Highlights

When sea ice covers approximately 20% of the Adélie penguins' foraging area, we found that breeding success reaches a peak, and that most diving parameters reach an optimum for similar sea-ice conditions, suggesting that sea ice affects the reproductive performance of Adélie penguins through its effects on diving activity.

Abstract

The Southern Ocean is currently experiencing major environmental changes, including in sea-ice cover. Such changes strongly influence ecosystem structure and functioning and affect the survival and reproduction of predators such as seabirds. These effects are likely mediated by reduced availability of food resources. As such, seabirds are reliable eco-indicators of environmental conditions in the Antarctic region. Here, based on nine years of sea-ice data, we found that the breeding success of Adélie penguins (*Pygoscelis adeliae*) reaches a peak at intermediate sea-ice cover (*ca.* 20%). We further examined the effects of sea-ice conditions on the foraging activity of penguins, measured at multiple scales from individual dives to foraging trips. Analysis of temporal organisation of dives, including fractal and bout analyses, revealed an increasingly consistent behaviour during years with extensive sea-ice cover. The relationship between several dive parameters and sea-ice cover in the foraging area appears to be quadratic. In years of low and high sea-ice cover, individuals adjusted their diving effort by generally diving deeper, more frequently and by resting at the surface between dives for shorter periods of time than in years with intermediate sea-ice cover. Our study therefore suggests that sea-ice cover is likely to affect the reproductive performance of Adélie penguins through its effects on foraging behaviour, as breeding success and most diving parameters share a common optimum. Some years, however, deviated from this general trend, suggesting that other factors (*e.g.* precipitation during the breeding season) might sometimes become preponderant over the sea-ice effects on breeding and foraging performance. Our study highlights the value of monitoring fitness parameters and individual behaviour concomitantly over the long term to better characterize optimal environmental conditions and potential resilience of wildlife. Such an approach is crucial if we want to anticipate the effects of environmental change on Antarctic penguin populations.

Introduction

Marine ecosystems are experiencing various disturbances (Richardson and Poloczanska, 2008), such as climate change (IPCC, 2007; Doney *et al.*, 2012), overfishing (Jennings and Kaiser, 1998) and invasion of exotic species (Elton, 1958; Katsanevakis *et al.*, 2014). Determining how and to what extent organisms are able to cope with environmental changes is fundamental to understand and protect marine ecosystems. This is especially needed in the Antarctic, parts of which have shown rapid change in recent decades (Clarke and Harris, 2003). In these marine ecosystems, the seasonal and inter-annual sea-ice dynamics are the main drivers of biogeochemical cycles (Sedwick and DiTullio, 1997; Wang *et al*., 2014). Seasonal changes in sea-ice cover alter nutrient cycling and induce seasonal variation in nutrient availability (Wang *et al*., 2014). These seasonal changes also control phytoplankton blooms, which occur after sea ice locally breaks up (Smith and Nelson, 1985; Wang *et al*., 2014). Importantly, sea ice provides a favourable habitat for microalgae and bacteria (Thomas & Dieckmann, 2010) that are able to cope with variable salinity conditions and to photosynthesize even under low light conditions (Knox, 2006). In turn, some krill species (*e.g.* the Antarctic krill, *Euphausia superba*) feed on these microalgae (Brierley *et al*., 2002), and predators can take advantage of this association to feed on concentrated prey (Knox, 2006). Sea ice therefore shapes the structure and functioning of the Antarctic ecosystem, from grazers to the highest trophic levels, and changes in its dynamics are likely to disrupt this interplay.

At a time when climatic conditions are changing rapidly, the Antarctic ecosystem requires close monitoring. However, monitoring an entire ecosystem is logistically challenging. To circumvent this difficulty, meso- and top-predators like seabirds and marine mammals can be used as eco-indicators of changes in their respective ecosystems (Furness and Camphuysen, 1997; Boyd and Murray, 2001; Frederiksen *et al*., 2007), as they integrate

and amplify the perturbations occurring at lower trophic levels (Hindell *et al*., 2003). Seabirds are widely used as eco-indicators because they are sensitive to environmental variability in marine ecosystems (Smith *et al.*, 1999; Croxall *et al.*, 2002; Bost *et al*., 2009). This logic formed the basis of the Conservation of Antarctic Marine Living Resources (CCAMLR) Ecosystem Monitoring Program (CEMP) (CCAMLR, 2014). In addition, seabirds are central-place foragers (Orians and Pearson, 1979), meaning that individuals return regularly to their nesting site during the breeding season, which makes them easily accessible to researchers (Piatt *et al*., 2007). In Antarctica, changes in sea-ice cover are major determinants of seabird survival and reproduction (Croxall *et al*., 2002; Barbraud and Weimerskirch, 2003; Jenouvrier *et al.*, 2014). Sea ice can be a primary factor affecting the foraging patterns of breeding adults, the provisioning of chicks, the breeding success, and ultimately the population dynamics (Fraser *et al*., 1992; Kato *et al*., 2002). This highlights the need to investigate the relationship between sea-ice conditions and seabird foraging behaviour if we are to use such species as indicators of changes in this polar ecosystem. Developments in bio-logging technology have greatly facilitated advances in our state of knowledge about seabird foraging behaviour and indicators of prey availability (Bost *et al.,* 2009). Indeed, seabirds can now be tracked at increasingly finer scale and higher resolution, enhancing their value as eco-indicating species (Ropert-Coudert and Wilson, 2005; Ropert-Coudert *et al*., 2012).

Among seabirds, penguins represent up to 90% of the total avian biomass in the Southern Ocean (Knox, 2006). Adélie penguins (*Pygoscelis adeliae*) are predators that need to dive to forage, as they mostly feed on Antarctic krill (*E. superba*), ice krill (*E. crystallorophias*), Antarctic silverfish (*Pleuragramma antarcticum*) (Volkman *et al*., 1980; Croxall and Lishman, 1987; Libertelli *et al.*, 2003; Cherel, 2008) and to a lower extent on jellyfish (Thiebot *et al.*, 2016). With its typically ice-associated prey and its circumpolar distribution,

the Adélie penguin is a relevant candidate as an indicator of the state of sea-ice ecosystem (Woehler and Johnstone, 1991; Ainley, 2002; CCAMLR, 2014). Few studies have previously investigated the relationship between Adélie penguin diving behaviour and sea-ice dynamics. Among them, Emmerson and Southwell (2008) investigated the breeding and foraging performance of Adélie penguins in relation to annual sea-ice conditions. However, detailed information on their foraging behaviour, especially regarding the diving activity, which is required to genuinely link such responses to sea-ice conditions, remains rare, as does any understanding of the associated mechanisms. Other studies have typically compared only two or three penguin breeding sites for a given year (Watanuki *et al.*, 1997; 2002) and/or seasons with contrasting sea-ice conditions at a given site (Ainley *et al.*, 1998; Kato *et al.*, 2003; Beaulieu *et al.*, 2010), thereby limiting the generality of their results. Some studies have also investigated the relationship between sea-ice concentration and foraging efficiency (Lescroël *et al.*, 2014) or breeding success and survival (Lescroël *et al.*, 2009; Dugger *et al.*, 2014) over the long term, but none have included analyses of fine-scale diving activity. However, all these studies converged towards the conclusion that sea ice plays a fundamental role in determining foraging strategies, and it was suggested that there may be an optimal range of sea-ice cover during the breeding season that leads to maximal foraging and breeding success (Smith *et al.*, 1999; Ainley, 2002; Ballard *et al.*, 2010; Barbraud *et al.*, 2015). In this context, long-term monitoring of the foraging activity and breeding performance of Adélie penguins covering a wide array of sea-ice conditions is required to better understand and predict how these predators will respond to the forthcoming environmental changes in the Southern Ocean, especially given that the total extent of Antarctic sea-ice showed a counterintuitive, small increase of 1.5% per decade over the past 34 years, with strong regional differences around the Antarctic (Vaughan *et al.*, 2013).

In this study, we investigate how changes in sea-ice characteristics at a given location affect the breeding success and diving activity of Adélie penguins. We aimed to test the robustness of the conceptual model of Smith et al. (1999) and determine whether an optimal sea-ice concentration is indeed observable for this species not only in relation to breeding success but also to fine-scale metrics characterizing foraging activity, namely diving activity. Towards this end, we monitored the breeding success and diving behaviour, at multiple measurement scales, of chick-rearing Adélie penguins from a single colony in Adélie Land, East Antarctica, over nine austral summers with variable sea-ice conditions. The last aim of our study was to assess the relevance of Adélie penguins as eco-indicators of the Southern Ocean ecosystem, a key step towards addressing question 65 of the 1st Antarctic and Southern Ocean Science Horizon Scan of SCAR (Scientific Committee on Antarctic Research), *i.e.* "What will key marine species tell us about trophic interactions and their oceanographic drivers such as future shifts in frontal dynamics and stratification?" (CCAMLR, 2014; Kennicutt *et al.*, 2014).

Materials and methods

An Adélie penguin breeding colony located near the Dumont d'Urville station (66°40'S, 140°01'E), Adélie Land, Antarctica (Fig. 1) was studied over nine non-consecutive austral summers (October-March) between 1995 and 2014. To reduce variability due to differences in foraging strategies across the breeding cycle (Widmann *et al.*, 2015), we focused on the guard stage (end of December - beginning of January), during which one parent guards the chicks on the nest while the other is foraging at sea to bring food back to its offspring. A total of 121 birds (with one foraging trip for each individual) were monitored (Table S1 for details).

Sea-ice characteristics

We used satellite-derived passive microwave measurements of daily sea-ice concentration (SIC) (Cavalieri *et al.,* 1996) to characterize the sea-ice conditions encountered by the studied individuals in every considered year. Other studies have shown that foraging trips of Adélie penguins at the Dumont d'Urville colony extend from 63.7°S to 66.6°S and from 134.7°E to 142.3°E across the breeding season, corresponding to an area of 119,389 km^2 or a foraging distance (maximum distance from the colony) of 392 km (Cottin *et al*., 2012; Widmann *et al*., 2015). Hence, we considered a slightly larger area from which we extracted sea-ice data to ensure complete cover of their foraging domain (62-67°S and 134-144°E) (Fig. 1). Sea-ice data were processed using R (R version 3.2.3, R Core Team, 2015) and the package 'raster' (Hijmans *et al*., 2016) with a resolution of 25 km, which was the smallest common resolution for all years. Daily maps were created with a single value of SIC in each pixel of the raster (62°-67°S, 134°-144°E) (Fig. 1). SIC describes what percentage of a 25 x 25 km box is covered with ice, 0% being open water and 100% being full ice cover. For each day, the mean value of SIC was calculated over all pixels. The overall SIC value was calculated as the mean of the daily SIC values extracted within the area between the 1st of November (beginning of the season) and the 15th of January (end of diving data).

Adélie penguin breeding success

Breeding success of Adélie penguins in Dumont d'Urville was monitored annually from 1995 to 2014 (see Jenouvrier *et al.*, 2006 and Barbraud *et al*., 2015 for further details). Breeding success is defined here as the ratio of the number of chicks counted in the area in early February (just before fledging) to the number of incubating pairs in late November (just after laying). A generalized additive model (GAM), which is a non-parametric smoothing regression technique, specified with a Gaussian error distribution, was fitted on the data

available (20 years from 1995 to 2014) to investigate the relationship between breeding success and the overall SIC. The quadratic aspect of the relationship between these two variables was tested comparing a GAM with and without including a quadratic term (models compared using the Akaike Information Criterion, AIC). We used the 'mgcv' package in R (version 3.2.3) to fit the GAM to our data (Wood, 2006), using a cubic regression spline. We used three knots as there were less than 30 observations, following the optimal amount of smoothing recommended by Zuur *et al*. (2009).

Adélie penguin foraging activity

Diving behaviour was recorded by miniature data loggers attached to the birds. Birds were captured while, or just before, leaving their nest for a foraging trip and equipped with data-loggers. These devices recorded time series of depth readings taken regularly at pre-determined intervals (1 or 5 seconds) (Supplementary Table 1). Loggers were attached to the lower back of penguins using waterproof tape (Wilson and Wilson, 1989), except the LUL loggers used in 2014 which, given their small size, were attached to a leg band (Ratcliffe *et al.*, 2014). After one or several foraging trips, birds were recaptured upon their return to the colony and the loggers were retrieved. Upon recovery, depth data were downloaded onto a computer and analysed using IGOR Pro (WaveMetrics, Version 6.3, Oregon, USA). A total of 180,050 dives were analysed over the nine-year period.

Each dive deeper than 1 m was identified, and different metrics were automatically calculated with a purpose-written macro in IGOR Pro. Among the parameters automatically extracted by the macro, we principally investigated dive depth and duration, the bottom phase duration, the number of undulations during the bottom phase in a dive and the post dive duration (see Ropert-Coudert *et al*., 2007 for parameter definitions). Two indices were also

calculated: diving efficiency (Ydenberg and Clark, 1989) (Eq. 1) and ACPUE (Attempts of Catch Per Unit Effort) (Zimmer *et al*., 2010) (Eq. 2).

$$\text{Diving efficiency} = \frac{\text{Bottom duration}}{\text{Dive duration+Surface duration}} \qquad \text{(Eq. 1)}$$

$$\text{ACPUE} = \frac{\text{Number of undulations}}{\text{Bottom duration}} \qquad \text{(Eq. 2)}$$

Differences in sampling intervals (5 s in 1995 and 2007 and 1 s for all other years, Appendix 1), introduce a bias in the analysis of diving parameters. Therefore, data collected in 1995 and 2007 were excluded from most of the analyses presented, except when conducting the analysis of the maximum dive depth (considering deep dives only (>15 m, see below)) and the fractal analysis on diving time series, as the method is robust to such changes in sampling interval (MacIntosh *et al*., 2013). Concerning the maximum dive depth, all nine years were compared using only dives deeper than 15 m. This threshold was extracted from the relationship between the maximum dive depth and the dive duration applied to all years and corresponds to a breakpoint dividing the distribution in two main portions (one concerning deep dives and one concerning surface dives). The technique assumes that these two categories of dives emerge from two different processes: shallow dives reflecting transit movements and deeper dives reflecting foraging movements (Ropert-Coudert *et al.*, 2001). We have used the 'segmented' package in R (Muggeo, 2015) to identify this threshold.

Student t-tests were used to compare the means of each diving parameter when sample variances were equal (F-test for equality of variances: p-value > 0.05) and Welch tests were used in case of non-equal variances. The Bonferroni correction was applied to correct the level of significance because multiple comparisons were performed simultaneously.

Dive metrics were also modelled as a function of sea ice and bird ID, where SIC was modelled as a fixed effect and bird ID as a random effect. Linear Mixed Models (LMMs) combining fixed (SIC) and random (bird ID) effects were performed using the lme function of the R package 'nlme' (Pinheiro *et al*., 2016) and Generalized Linear Mixed Models (GLMMs) were applied using the glmer function of the R package 'lme4' (Bates *et al*., 2015). Dive duration and bottom duration were excluded from the analyses, as they were highly correlated to the dive depth and the number of undulations, respectively (with a Pearson correlation coefficient of 0.854 and 0.751, respectively). Diving efficiency and ACPUE (response variables) were analysed in a LMM with a normal error distribution in relation to SIC (fixed effect) and bird ID (random effect). To investigate the relationship between both maximum dive depth and post-dive duration (response variables) and sea ice using a LMM, the values of maximum dive depth and post-dive duration were log_{10}-transformed, while keeping SIC and bird ID as fixed and random predictors. The number of undulations was analysed as the response variable in a GLMM specified with a Poisson error distribution, with SIC as a fixed effect and bird ID as a random effect. The residuals from the chosen statistical models were visually inspected to ensure that the assumptions of residual homogeneity and homoscedasticity were met. For all diving metrics, we identified the best distribution to use (Normal, log_{10}, Poisson, etc.) using the AIC. Then, a random intercept and slope model was performed assuming that the relationship between each diving metric and sea ice is different for each bird, and this model structure was always preferred compared to a simple intercept model (model selection still performed using the AIC). When a hump-shaped curve was observed, models specified with and without a quadratic term were compared (using the AIC) to investigate whether or not the relationship between the diving metric and SIC is statistically quadratic. For mixed models, the R^2 can be divided in two components: the marginal R^2 (R^2m) describes the proportion of variance explained by the

fixed factor (SIC), while the conditional R^2 (R^2c) describes the proportion of variance explained by both the fixed and random factors (SIC and bird ID). This permits to identify the part of the variance that is due to the fixed external effect (*i.e.* sea ice) and the part that is due to internal factors (*i.e.* the individual "quality", characterised by the bird ID).

Penguins dive in foraging bouts, which correspond to sequences of multiple dives in succession over a certain period of time (Naito *et al.*, 1990). Between two foraging bouts, individuals can rest at the surface, on land, on sea ice or transit to other foraging areas (Le Boeuf and Laws, 1994). Bout metrics are expected to reflect prey availability, as greater numbers of dives in a bout should coincide with larger prey patches (Boyd, 1996; Sommerfeld *et al*., 2015). Similarly, small delays between dives within a bout likely reflect a higher prey patch density, while the distance between bouts (*i.e.* the distance between two prey patches) can be linked to the prey encounter rate of the bird (Boyd, 1996; Watanabe *et al*., 2014; Sommerfeld *et al*., 2015). Here, foraging bouts were defined using the log survivorship analysis, which corresponds to a graphical method to specify the minimum surface interval between two dives belonging to separate bouts, also called the Bout Criterion Interval (BCI) (Martin and Bateson, 1993). A single BCI value was calculated per year, based on the average BCI values of all birds in each year. We used the 'segmented' package in R (Muggeo, 2015) to find BCIs (i.e. the "breakpoint" of the post-dive duration distribution). Following the definition of bouts, we calculated, for days with complete records only (24 hours), the number of dives per day, the number of dives per bout, the number of bouts per day, the bout duration and the mean bottom duration per bout for each bird. Mean comparisons between years were performed on the number of dives per day and the number of bouts per day using Student t-tests and Welch tests applied with the Bonferroni correction. Because of the small amount of observations for each bird concerning these two parameters, the quadratic aspect of the relationship between both the number of dives and the number of

bouts per day and SIC was tested comparing a GAM with and without a quadratic term. However, bout duration and bottom duration per bout were analysed using LMMs. Post-dive duration within bouts (post-dive duration < BCI) and post-dive duration between bouts (inter-bout duration, post-dive duration > BCI) were investigated separately. Mean comparisons between years were also performed on these parameters using Student t-tests and Welch tests applied with the Bonferroni correction. To investigate the relationship between both post-dive duration within bouts and inter-bout duration (response variables) and sea ice using a LMM, the values were $\log_{10}$-transformed, while keeping SIC and bird ID as fixed and random predictors. When a hump-shaped curve was observed, the chosen model specified with and without a quadratic term were compared (using the AIC) to investigate whether the relationship between the diving metric and SIC is statistically quadratic or not.

Finally, we also used fractal analysis (Mandelbrot, 1977) to investigate how the temporal organisation of dive sequences changes in relation to sea ice (see review in MacIntosh, 2014). Fractal time series analyses of animal behaviour aim to describe the structure of behaviour as it occurs through time, and to measure through a simple index the level of complexity observed in behavioural sequences (Asher *et al*., 2009; MacIntosh, 2014). Interactions between the behavioural strategies of an animal and the prevailing environmental conditions lead to the emergence of observed complexity signatures, which might reflect behavioural adaptations to environmental changes (Cribb and Seuront, 2016). Based on previous research (Sims *et al.*, 2008; MacIntosh *et al*., 2011; Meyer *et al*., 2017), we hypothesized that foraging sequences would display greater complexity (here decreased long-range dependence and thus increased stochasticity) under more challenging and/or heterogeneous environmental conditions related to sea-ice cover. Following the method described by MacIntosh *et al*. (2013) and applied to Adélie penguins in Cottin *et al.* (2014) and Meyer *et al.* (2015), we

used Detrended Fluctuation Analysis (DFA; Peng *et al*., 1992) to measure long-range dependence in the sequential distribution of dives and surface times as an indicator of complexity in individual diving sequences. We performed DFA using the 'fractal' package (Constantine and Percival, 2011) in R to estimate the scaling exponents (α_{DFA}) of these sequences (Peng *et al*., 1992), which measures the degree to which time series are long-range dependent and statistically self-similar (Taqqu *et al*., 1995). This scaling exponent is also theoretically inversely related to the fractal dimension of a time series, which is a classical index of structural complexity (see Mandelbrot, 1977 for details). As α_{DFA} increases from 0.5 to 1, diving sequences are increasingly persistent and long-range dependent, and the patterns as they occur over time are increasingly consistent/invariable (i.e. dives and surface times of a given length will be followed by dives and surface times of a similar length) (Peng and Havlin, 1995). A GAM was performed to investigate variations in α_{DFA} values (one value per individual) in relation to the overall SIC. The GAM was specified with a Gaussian family and five knots as there were more than 100 observations (121 values of $\alpha_{DFA)}$, following the optimal amount of smoothing recommended by Zuur *et al*. (2009). The GAM provides evidence of a quadratic relationship between α_{DFA} and the overall SIC, GAMs with and without a quadratic term were compared using AIC.

The alpha level for all significance tests was set at 0.05. Results are generally presented as mean ± standard errors (SE).

Results

Breeding success and sea ice

A significant effect of the overall SIC on breeding success was found by fitting a GAM specified with a quadratic relationship to the time series of breeding success (F-test = 7.277, adjusted R^2 = 0.39 and p-value = 0.015) (Fig. 2a). Breeding success was the highest in

intermediate years, around 20% of SIC. The breeding season in 2014 had intermediate SIC values, but sea-ice retreat was so slow in that year that the distance between the colony and the open water was *ca*. 100 km in January. Birds had therefore to walk a very long way between feeding and nesting grounds, which likely explains the low breeding success in 2014. For this is reason, the GAM specified with a quadratic term was also performed excluding data from the year 2014, thereby improving the model and highlighting the quadratic relationship between breeding success and the overall SIC (F-test = 16.78, adjusted $R^2 = 0.578$ and p-value = $8.43*10^{-4}$) (Fig 2b).

Daily SICs varied across years for the days when diving data were recorded (Fig. 2). The years 1998 and 2001 were visually identified as low sea-ice cover years, while 2011 and 2012 corresponded to high sea-ice cover years (Fig. 2). Other years are subsequently referred to as "intermediate" years. For the entire study period (1995-2014), both breeding success and SIC varied substantially (Fig. 2).

Foraging activity and sea ice

During the chick-guard stage, foraging trips typically last 1-2 days (mean ± SE: 49 ± 51 hours). The overall SIC had a significant effect in all selected models that investigated diving parameters as a function of sea ice (all p-values < 0.05) (Table 1). In all models, the random effect (due to individual variability) largely contributed to explain the global variability (Table 1).

With the exception of 2011 showing a high overall sea-ice concentration, the maximum dive depth was significantly greater, on average, during intermediate years (around 20% of sea-ice concentration) than during years with high or low sea-ice cover (model considering only deep dives from all years) (Fig. 3; Table 1). The shallowest average diving depths were

observed in 2001 and 2012, with a mean of 13.93 ± 0.12 m and 13.83 ± 0.08 m, respectively. Linear mixed models performed on all years with log-transformed maximum dive depth as the response variable and SIC as the predictor with and without the specification of a quadratic term were statistically similar based on the AIC criterion (AIC=2441 and 2439, respectively) (Table 1). Therefore, according to this model, intermediate and high SIC years are not statistically different. The same models were performed excluding the year 2011. In this case, the quadratic aspect of the relationship between the maximum depth and SIC was statistically evidenced. Indeed, the model with the quadratic effect was significantly better (AIC=13163, F-value=17.192, R^2c=0.288, R^2m=0.042, p-value=0.0001) than the one without it (AIC=13170, F-value=9.931, R^2c=0.287, R^2m=0.026, p-value=0.0021).

Diving efficiency followed a roughly open upward quadratic function, though the differences between years seemed small, with lower diving efficiencies observed in intermediate years and higher efficiencies in high and low sea-ice cover years (Fig. 4). The linear mixed model applied with a normal distribution performed with diving efficiency as the response variable and SIC as the predictor specified with a quadratic effect was significantly better that the one without it (AIC=-10844 and -10826, respectively) (Table 1). Therefore, the model shows that a quadratic relationship exists between diving efficiency and the overall SIC (F-value=25.966, R^2c=0.15, R^2m=0.03, p-value<0.0001) (Table 1).

We also tried to simply relate yearly mean diving efficiencies to yearly mean breeding success by fitting a linear model on these variables and found that the relationship was significantly linear (F=8.97, adj-R^2=0.562, p-value=0.02011). Indeed, these variables are highly negatively correlated (with a Pearson correlation coefficient of -0.749). In contrast,

there was no significant effect of SIC on the number of undulations in a dive, ACPUE, mean bout duration and mean bottom duration per bout (Table 1).

Regarding the bout analysis, a total of 2,981 bouts were identified over the seven years with a sampling frequency of 1 second, for which the BCI averaged 207.7 seconds (range: 168.2 – 247.5 seconds). Both the average numbers of dives and bouts per day were the highest in 2001 and 2012 (649.9 ± 43.9 and 633.7 ± 50.3 dives per day and 13.2 ± 1.2 and 13.2 ± 0.9 bouts per day, for 2001 and 2012 respectively) (Fig. 5a, b). The lowest number of dives per day was found in 2014 (417.2 ± 50.8 dives per day) and the year 2010 showed the lowest number of bouts per day (7.0 ± 0.8 bouts per day) (Fig. 5a, b). GAMs were performed on all years using the number of dives per day as the response variable and the overall SIC as the predictor, with and without including a quadratic term. The model with the quadratic term was significantly better (AIC=1218, F-value=4.537, R^2-adj=0.079, p-value=0.0360) than the model without it (AIC=1224, F-value=1.997, R^2-adj=0.0505, p-value=0.108) even though it did not explain much variation. Years with intermediate SIC were characterized by lower numbers of dives per day and lower numbers of bouts per day, on average (Student's t-tests, p-values < 0.05) (Fig. 5a, b). In contrast, for the number of bouts per day, the model without the quadratic term was significantly better (AIC=521, F-value=3.096, R^2-adj=0.155, p-value=0.0142) than the model including it (AIC=531, F-value=2.631, R^2-adj=0.031, p-value=0.108), thereby suggesting the absence of a quadratic effect for the overall SIC.

The model performed with post-dive duration within bouts (post-dive duration < 207 seconds) as the response variable and SIC as the predictor, specified with a quadratic effect, was similar than the one without it (AIC=30603 and 30604, respectively) (Table 1), thereby not highlighting the existence of a quadratic relationship between post-dive duration within

bouts and overall SIC (F-value=7.622, R^2c=0.0916, R^2m=0.008, p-value=0.0069; Fig. 6a). Similarly, inter-bout durations appeared to be shorter in years of intermediate sea-ice conditions, on average (Welch test: p-value < 0.002), with the notable exception of 2014, compared with values obtained for high and low sea-ice cover years (Fig. 6b), but no quadratic relationship could be evidenced for this parameter.

Concerning the fractal analysis, values of αDFA were similar to those reported previously for Adélie penguins at 0.94 ± 0.005 (Meyer *et al.*, 2015), indicating that foraging time series were long-range dependent and persistent (αDFA > 0.5, *i.e.* dive and post-dive times of a given length were more likely to be followed by dive and post-dive times of similar lengths). The highest average value was recorded in 2011 (0.930 ± 0.004) and the lowest in 1998 (0.874 ± 0.009), with high and low SIC, respectively (Fig. 7). Multiple t-tests (applied with Bonferroni correction) comparing the year 2001 to other years have shown that the year 2001 significantly departed from this general trend (0.928 ± 0.006) (t-test: p-values < 0.001), considering the low SIC for this year. The αDFA tended to increase as SIC increased but with the year 2001 as an exception (Fig. 7). A linear regression was performed using αDFA as the response variable and the overall SIC as the predictor. Results suggested that the relationship between αDFA and the overall SIC was non-linear (linear model: F-test=6.4313, p-value=0.0125, adj-R^2=0.0433). Results depend significantly on whether or not we consider the year 2001 as an outlier. A GAM was performed on αDFA values according to the overall SIC for all years (Fig. 7a). Results show that the effect of the overall SIC is significant (F-test=10.09, adj-R^2=0.254, p-value=1.33*10^{-6}, AIC=-540.92) but we did not observe a significant quadratic relationship (GAM with quadratic effect: F-test=7.076, adj-R^2=0.0561, p-value=0.0089, AIC=-518.13). The same approach was applied to all years except 2001 (Fig. 7b). The effect of the overall SIC remained significant (F-test=17.04, adj-R^2=0.341, p-

value=1.26*10^{-8}, AIC=-459.42) but again, we did not observe a significant quadratic relationship (GAM with quadratic effect: F-test=16.68, adj-R^2=0.322, p-value=9.08*10^{-5}, AIC=-457.49).

In other words, because no quadratic trend could be evidenced in either scenario, it can only generally be assumed that the temporal organisation of diving behaviour is more consistent/less stochastic in the diving sequences (*i.e*. characterized by a higher degree of dependence on history) during high sea-ice cover years. Conversely, reduced sea ice concentration coincided with more complex/more stochastic diving sequences.

Discussion

Similar effect of sea-ice cover on breeding success and diving behaviour

The breeding success and some diving parameters of Adélie penguins at Dumont d'Urville varied quadratically with sea-ice cover, both reaching a peak − either upward or downward − when sea-ice cover is intermediate, around 20%. Our results confirm the existence of an "optimal" range of sea-ice cover for Adélie penguins, as suggested by Ainley (2002) and corroborated by Barbraud *et al*. (2015) for breeding success. Ballard et al. (2010) also found a quadratic effect of SIC on foraging parameters in Adélie penguins, showing an optimum SIC around 10-15%. The difference from our findings of an optimum around 20% is noteworthy and probably results from the fact that these authors studied trip duration and total food delivered, while we investigated the influence of SIC on diving activity. In addition, the similarity in the shape of the curve and the coincidence of the peaks around a given range suggest that sea ice may influence breeding success via prey availability (prey abundance and accessibility), which might affect diving behaviour. During the years of intermediate sea-ice cover, breeding success was generally maximized, suggesting that these

years offer enhanced food availability compared to years with high or low sea-ice cover. Indeed, as krill feed on under-ice communities (e.g. microalgae) (Nicol, 2006), low sea-ice cover would reduce the amount of food available to krill, therefore negatively affecting their abundance. Conversely, foraging costs for chick-rearing penguins increase when sea-ice cover is high, forcing parents to walk longer distances on ice to reach open foraging areas (Ropert-Coudert *et al*., 2015). This, in turn, increases body mass loss for parents and, as their foraging trips are longer, decreases the provisioning frequency to the chicks (Davis, 1982; Ballard *et al.*, 2010). A recent study has also shown that in low sea-ice cover conditions, the visual performance of predators is enhanced by increased light (Langbehn and Varpe, 2017). Consequently, intermediate sea-ice conditions seem to maximize prey availability and to minimize foraging costs for penguins, thereby resulting in enhanced foraging success. The 20% sea-ice concentration could correspond to a Marginal Ice Zone (MIZ), which is recognized as a concentration enhancing productivity in the trophic chains (Smith & Nelson, 1985; Smith IV *et al.*, 1988). However, our optimal SIC value is a mean calculated over the whole potential foraging area of the birds and over a season, and it would be surprising if this whole area was covered with MIZ all summer long.

Although inter-individual variability was high and, consequently, the quadratic trend in diving parameters was not as clear as it was for breeding success, the same pattern was found in some of the diving parameters investigated. More importantly, this trend was evident at various temporal scales: at the scale of the foraging trip and at the finer scale of individual dives. During years of intermediate sea-ice conditions (characterized by high breeding success and thus supposedly enhanced prey availability), Adélie penguins showed lower diving efficiencies but dove deeper than in years with high or low sea-ice cover; and at a lesser extent, spent less time commuting between prey patches while performing fewer bouts

per day and fewer dives per day. In other words, although located at deeper depths, these metrics strongly suggest that intermediate years are characterized by higher prey encounter rates and prey availability.

The decreasing complexity in foraging behaviour as sea-ice cover increases indicates that Adélie penguins become increasingly constrained (i.e. they do not have much flexibility) in their diving sequences with increasing sea-ice cover. Following Reynolds et al. (2015), we can postulate that birds in heavy ice would favour exploitation over exploration, while it would be the reverse when water becomes increasingly free of ice. This finding is also in accord with the fact that in intermediate sea-ice cover years, Adélie penguins exhibited high levels of plasticity in foraging efficiency (Lescroël *et al.*, 2014). Indeed, a greater heterogeneity in the vertical distribution of prey like that observed in open water (Ropert-Coudert *et al*., 2009; Pelletier *et al*., 2012) should force penguins to favour the exploration of their environment, which is more likely to lead to complex behaviour (Shimada *et al*., 1995; Kembro *et al*., 2009; MacIntosh *et al*., 2011). In contrast, the consistent/invariable diving sequences occurring during years with high sea-ice cover could be due to the fact that birds are more constrained in their foraging movements, targeting shallower prey patches for which the need for more exploratory dives is limited. The presence of polynyas under these conditions becomes crucial in explaining the foraging activity of penguins as the high predictability of prey in polynyas likely leads to more consistent/invariable diving sequences (Meyer, 2016; Meyer *et al.*, 2017).

Interestingly, some years clearly deviated from the norm regarding the relationship between sea-ice concentration and breeding success (2014) and the relationship between sea-ice concentration and diving parameters (depth in 2011 and 2014, post-dive duration in 2001, inter-bout duration in 2014, daily number of dives in 2011, daily number of bouts in 2011). As 2001 and 2011 were characterized by the lowest and highest sea-ice concentrations (14%

and 32%, respectively) in our study, it is possible that the effects of sea-ice concentration on certain characteristics of the diving behaviour of penguins are reversed over a certain threshold. However, 2014 was not characterized by such extreme sea-ice concentrations; this year showed a late sea-ice retreat and a distance between the colony and the open water around 100 km in January. This suggests that these environmental factors are able to disrupt the effects of sea-ice concentration on the foraging behaviour and the breeding performance of penguins. However, some diving parameters (diving efficiency, αDFA) were not affected by these environmental factors, and therefore better reflected sea-ice changes. To better anticipate how changes in sea-ice concentration will affect Adélie penguins in the coming decades, future studies should examine how it interacts with other environmental changes to modulate their foraging behaviour and breeding success.

The paradox of the diving efficiency index

If years with intermediate sea-ice cover correspond to profitable prey availability and higher breeding success, why was diving efficiency significantly lower during these years? This is indeed surprising as breeding success has been linked to foraging success (meal size provided to the chicks and their fledging mass) in Adélie penguins (Clarke *et al*., 2002). The explanation probably lies in the parameters involved in the calculation of this index. Besides the fact that undulations in the dive profiles may not always reflect prey capture (Watanabe and Takahashi, 2013; Watanabe *et al*., 2014), the index was initially designed for shallow, benthic feeders, for which prey items are predictably located at the bottom of the water column. Yet, the term "efficiency" has often been applied to species for which prey locations are not predictable in the water column (as in our case, but see also Zimmer *et al*., 2010), making variation in diving "efficiency" difficult to interpret. In fact, this index informs us about how birds deal with the different components of a dive (transit, hunting and resting)

within a limited time window. Furthermore, both the quality and the quantity of the encountered prey are necessary to understand the mechanisms underlying the different components of a dive. During periods of high sea-ice concentration, the shallow diving activity of penguins suggests that they search for prey just under the ice. Do penguins target young krill or are they switching to fish associated with sea ice? The question deserves further investigation. In contrast, in a year of low sea-ice cover, we hypothesize that prey might be less available, as their area of occurrence (the sea-ice edge) is less extensive and prey resources could be depleted quickly as birds concentrate on the ice edges. From the above, we can hypothesize that sea ice at moderate amounts is favourable to the prey itself and this optimal is reflected in the activity of the penguins. Adélie penguins probably forage on highly profitable albeit deeper prey fields during years of intermediate sea-ice conditions, which translates in an apparent lower diving efficiency during those years due to the metrics used in its calculation. Regardless of the mechanisms involved, we strongly advocate for the diving efficiency index to be renamed so as to better reflect the heterogeneous nature of the phenomenon it measures.

Perspectives

Our results suggest the existence of an optimal range of sea-ice cover that enhances the foraging success and subsequently the breeding success of Adélie penguins, peaking at approximately 20% cover in the foraging zone around DDU (Ainley, 2002; see also Barbraud *et al*., 2015). There may be other factors that can impact penguin breeding success. Optimal sea-ice conditions are likely to be a necessary but insufficient condition for high breeding success (Youngflesh *et al.*, 2017). For instance, the timing of phytoplankton blooms may influence the availability and quality of prey (Atkinson *et al.*, 2008; Saba *et al.*, 2014). In addition, climatic conditions such as low ambient air temperature or high levels of

precipitation can also affect the survival of the chicks (Boersma and Rebstock, 2014; Ropert-Coudert *et al.*, 2015), directly impacting breeding success. Delimiting precisely the extent of this optimal range will require further investigation but is an essential step in assessing the capacity of this species to buffer forthcoming changes in sea-ice conditions. One can hypothesize that the narrower the range of optimal sea-ice conditions, the more affected the eco-indicating species will be by environmental changes and other potential threats, such as marine pollution, expanding tourism or other anthropogenic activities, the increasing risk of competing with fisheries or introduced species exploiting krill resources (Kennicutt *et al*., 2014; Xavier *et al*., 2016). To better refine the limits of this range, including additional years in the monitoring effort is a prerequisite, but homogenising the protocol of data collection is also paramount. It would also be interesting to add a horizontal dimension (*e.g.* GPS tracking, see Widmann *et al*., 2015) to the monitoring of the foraging behaviour of penguins, to precisely assess the ice habitats used by penguins (polynyas, fast ice cracks, etc.).

Finally, it seems necessary to extend this approach to other colonies of Adélie penguins around Antarctica because changes in sea-ice conditions in some parts of Western Antarctica are opposite to what is currently being observed at Dumont d'Urville (*e.g.* Antarctic Peninsula, Lima and Estay, 2013; McClintock *et al.*, 2008; Stammerjohn *et al.*, 2012). If the situation observed in the Peninsula - less sea ice links to population decrease - becomes a general trend around the continent, the global Adélie penguin populations might soon be facing unprecedented challenges. Yet, penguins may be capable of greater flexibility than current knowledge suggests. Results of paleoecological studies show that Adélie penguins have not always been the creatures of the sea ice that they are considered to be today. Indeed, they have switched from eating fish to krill after humans began to hunt whales in the past (Emslie and Patterson, 2007). By removing krill predators from the environment, the penguins took advantage of an open niche to target and exploit krill surpluses. Such

flexibility indicates the complexity of investigating trophic links in the so-called simple Southern Ocean ecosystem. In the framework of the CCAMLR Ecosystem Monitoring Program (CCAMLR, 2014), this calls for the need to use collaborations among existing Adélie penguin monitoring sites to determine in real time the changes occurring in these contrasted environments (using tracking data among other variables), and to better evaluate the range of impacts these changes have on ecosystem functioning. At a time when the CCAMLR is considering the feasibility of developing a network of Marine Protected Areas around the continent, such monitoring sites would be particularly useful to test the efficiency of the MPA in protecting the resources and the species that depend on them.

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Tables

Table 1. Results of the main mixed effects models for each diving metric in relation to the overall SIC. The expression "n.s." stands for "non-significant" and hyphens stands for "non-calculated". δAIC represents the difference between AIC for the model without the quadratic effect and the one including it. For the maximum dive depth, models were performed on 49,411 deep dives (>15m) of 121 birds over the nine-year period. For the other parameters, all 167,672 dives (>1m) of 102 birds over the seven-year period (all years excluding 1995 and 2007) were analysed.

	Without	quadratic	effect	With	quadratic	effect	δAIC
	R^2c	R^2m	p-value	R^2c	R^2m	p-value	
Dive depth (>15m, 9 years)	0.46	0.06	0.0010	0.47	0.05	0.0010	2
Diving efficiency	0.17	0.02	<0.0001	0.15	0.03	<0.0001	18
Attempts of Catch Per Unit Effort	-	-	n.s.	-	-	n.s.	-
Number of undulations in a dive	-	-	n.s.	-	-	n.s.	-
Post-dive duration within bouts	0.11	0.01	0.0301	0.10	0.01	0.0177	1
Inter-bout duration	0.13	0.01	0.0027	-	-	-	-

Figure captions

Figure 1. Map showing the location of the Dumont d'Urville research station, along with maps of sea-ice concentration (SIC) for two different days within the same season 1995-1996, a) 15th December 1995 and b) 15th January 1996. White represents 100% sea ice covered and black represents open water. Black dot in a) and white dot in b) represent the studied penguin colony in Dumont D'Urville.

Figure 2. Fitted GAM results on Adélie penguins' breeding success using (a) all years (*i.e.* 20 years between 1995 and 2014) and (b) all years except 2014, in relation to the overall sea-ice concentration. Shades indicate 95% confidence intervals. Dark dots represent the studied years and light dots correspond to additional breeding success data concerning the period of interest 1995-2014.

Figure 3. Boxplots of dive depth according to years ordered by increasing overall sea-ice concentration (all years only considering dives deeper than 15m). Medians and the 25th and 75th percentiles are represented by the box. The dots represent outliers. In each box, the central mark indicates the median, and the bottom and top edges of the box indicate the 25th and 75th percentiles, respectively. The whiskers extend to the most extreme data points not considered outliers, and the dots represent outliers that are plotted individually.

Figure 4. Boxplots of diving efficiency according to years ordered by increasing sea-ice concentration. Only the years with a sampling frequency of 1 second are considered here. In each box, the central mark indicates the median, and the bottom and top edges of the box indicate the 25th and 75th percentiles, respectively. The whiskers extend to the most extreme data points not considered outliers.

Figure 5. Barplots of a) the mean number of dives per day and b) the mean number of bouts per day, according to years ordered by increasing sea-ice concentration. Error bars represent standard errors. The asterisks refer to a statistical difference between two groups defined with brackets. The letters refer to groups that are not statistically different. Results are given for the seven years with a sampling frequency of 1 second and considering all dives.

Figure 6. Barplots representing a) the post-dive duration within bouts (post-dive duration $\leq$ 207 seconds) and b) the post-dive duration between bouts (post-dive duration > 207 seconds, or inter-bout duration). Error bars represent standard errors. The asterisks refer to a statistical difference between two groups defined with brackets. The letters refer to groups that are not statistically different. Only seven years with a sampling frequency of 1 second are considered here.

Figure 7. Fitted GAM results of α_{DFA} performed on a) all years and b) all years except 2001, considering all dives according to years classed by increasing sea-ice concentration.

(a)

(b)

(a)

(b)

(a)

(b)