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FEATURE ARTICLE

First odyssey beneath the sea ice of juvenile emperor penguins in East Antarctica

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ABSTRACT: Adult emperor penguins *Aptenodytes forsteri* breed on fast ice and forage within sea ice in winter. However, it remains unknown whether juveniles exhibit similar foraging behavior during their early life at-sea movements, and how it links with the oceanographic conditions. We investigated the first at-sea odyssey of 15 juvenile emperor penguins from Terre Adélie in 2013–2014. The average tracking duration was 167 ± 110 d SD (range 86–344 d). After departing the colony in December/January, the juveniles traveled north up to 53.76° S before heading south in April/May to forage within the sea ice. The juveniles spent $49 \pm 14\%$ of their total recorded trips ($n = 12$) in the sea ice, over both the continental slope and deep ocean regions. The penguins dived primarily during daylight. Within sea ice, the juveniles performed both shallow and deep dives, with the proportion of each varying seasonally. The switch to primarily deep dives in the autumn and winter within sea ice may be a consequence of (1) a seasonal change in the krill distribution from surface to deep waters and/or (2) the presence of macrozooplankton at depth due to a reduced/absent diel migration. Furthermore, we showed for the first time that the diving behavior of juveniles was associated with the mixed layer depth. We suggest they feed on mesopelagic prey aggregating near the thermocline. This study provides insight into an important, but poorly understood, part of the emperor penguin life cycle, essential to predict their response to future climate change.

KEY WORDS: Emperor penguins · *Aptenodytes forsteri* · Juvenile behavior · Foraging ecology · Sea ice · Antarctic ecology · Oceanographic conditions · Thermocline · Diving behavior



Oceanographic and sea ice conditions affect the behavior of juvenile emperor penguin *Aptenodytes forsteri* during their first odyssey at-sea.

Photo: Vincent Munier

1. INTRODUCTION

The behavior and annual life cycle of many juvenile marine predators remains a mystery, because it is a challenge to monitor them at sea as they migrate over long distances for several years (Hazen et al. 2012). Oceanographic conditions may affect juveniles in different ways compared to adults because they are less experienced and they migrate over a wider range of different habitats (e.g. turtles: Musick & Limpus 1997; Weddell seals *Leptonychotes weddellii*: Hastings et al. 1999; king penguins *Aptenodytes patagonicus*: Orgeret et al. 2016; wandering albatross *Diomedea*

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exulans: de Grissac et al. 2017; emperor penguins *A. forsteri*: Kooyman et al. 1996, Kooyman & Ponganis 2007, Wienecke et al. 2010, Thiebot et al. 2013).

In Antarctica, the life cycles of many predators are closely associated with sea ice (e.g. crabeater seals *Lobodon carcinophaga*, leopard seals *Hydrurga leptonyx*, Weddell seals, Ross seals *Ommatophoca rossii*, emperor penguins, Adelie penguins *Pygoscelis adeliae* and snow petrels *Pagodroma nivea*; Tynan et al. 2010). Indeed, increased secondary production within the sea ice zone may be exploited by upper trophic levels (Eicken 1992, Van Franeker et al. 1997, Brierley & Thomas 2002). The under-ice habitat provides sheltered structures for zooplankton such as juvenile krill. These areas also accumulate organic material released from the ice during winter when productivity is low in the water column due to reduced light (Marschall 1988, Flores et al. 2011, 2012, David et al. 2017, Meyer et al. 2017). Finally, Antarctic coastal polynyas, areas of open water within the sea ice zone, are also thought to be key bio-physical features of the Antarctic ecosystem. They offer a recurrent and persistent open water access and often harbor high biological productivity in spring/late summer that may support productive ecosystems throughout the autumn and winter seasons (Arrigo & van Dijken 2003, Labrousse et al. 2018).

Antarctic sea ice also plays a major role in the oceanographic conditions of the underlying water column. By forming a high albedo on the ocean surface, sea ice seasonally modifies and affects exchanges between the ocean and the atmosphere, and the properties of the ocean surface (Massom & Stammerjohn 2010). Salt rejection and freshwater input from seasonal sea ice formation and melt are important determinants of the upper ocean stratification (Martinson 1990) and dense water formation, driving the global thermohaline ocean circulation (Orsi et al. 1999, Marshall & Speer 2012).

At different spatial and temporal scales, oceanographic features and processes such as thermal layers, eddies and upwelling zones, currents, frontal systems, seamounts and the edge of the continental shelf are known to affect the distribution of marine predators. By physically aggregating resources, these processes create areas where prey are abundant and foraging efficiency is increased (Chapman et al. 2004, Bost et al. 2009, Raymond et al. 2015). Many studies have linked the oceanographic conditions to marine mammal (e.g. fur seals, Lea & Dubroca 2003; Weddell seals, Heerah et al. 2013; minke whales *Balaenoptera bonaerensis*, Friedlaender et al. 2006; southern elephant seals *Mirounga leonina*, Labrous-

se et al. 2018) and seabird life cycles (reviewed by Weimerskirch 2007). Yet, the use of oceanographic conditions associated with sea ice remains poorly known during the juvenile cycle of marine mammals and seabirds (Hazen et al. 2012). The thermocline (or mixed layer depth) represents a key variable to investigate these questions; using animal-borne temperature sensors, the mixed layer depth can be tracked within the sea ice zone where eddies and upwelling are difficult to detect (Pellichero et al. 2017).

Emperor penguins are the only species to breed during the harsh Antarctic winter, during which they perform deep foraging dives under the sea ice (Kirkwood & Robertson 1997b). They are dependent upon sea ice as a platform for reproduction and laying eggs in late autumn and winter. They dive under winter sea ice at 2 key periods: after egg laying, i.e. between autumn and mid-winter when females are rebuilding their body reserves (while the males incubate the eggs), and during the chick-provisioning period, i.e. from mid-winter to December when both males and females alternate periods of foraging (Kirkwood & Robertson 1997a). From autumn to spring, breeding adult emperor penguins forage either in polynyas or open water areas over the continental slope (the slope polynyas), or in pack-ice regions further off-shore (Kirkwood & Robertson 1997a,b). The slope polynyas are thought to be prime foraging habitat because they provide the closest access to open water to the colonies and have high abundance of Antarctic krill *Euphausia superba*, Antarctic silverfish *Pleuragramma antarctica* and glacial squid *Psychroteuthis glacialis* in the vicinity of the slope (dominating the penguins' diet).

Whether and how sea ice affects foraging and diving behavior of emperor penguins during early life stages, and how that compares with the adult behavior, remain open questions. The at-sea distribution of juveniles outside sea ice has been relatively well described (Kooyman & Ponganis 2007, Wienecke et al. 2010, Thiebot et al. 2013); in December, juvenile emperor penguins leave the colony and travel far north (e.g. up to 57°S; Kooyman & Ponganis 2007), mostly in ice-free waters. In early March, the traveling north ends, and the birds start to travel to, or remain near, the northern ice edge. Some studies have suggested that juveniles probably avoid the sea ice habitat during winter (Zimmer et al. 2008, Wienecke et al. 2010). Juveniles may have lower foraging efficiency than adults due to lack of experience and physiological limitations (Burns 1999, Riotte-Lambert & Weimerskirch 2013, Orgeret et al. 2016), and sea ice may represent a constraint to breathing and feeding in an environment where resources are

patchily distributed. Juveniles are thus expected to increase their diving and foraging effort in order to compensate their lower foraging efficiency (Burns 1999, Daunt et al. 2007). Individuals that do not manage to compensate or increase their foraging effort above their physiological limits may perish at sea (Daunt et al. 2007, Orgeret et al. 2016). Thus, a mechanistic understanding of the diving behavior during the first year at sea and within sea ice is crucial to comprehending the effects of climate variability on juvenile vital rates (Abadi et al. 2017) and the persistence of emperor penguins under future climate change (Barbraud & Weimerskirch 2001, Barbraud et al. 2011, Jenouvrier et al. 2012, 2014, 2017).

Our aim was to fill this gap by investigating the foraging behavior of juvenile emperor penguins in relation to sea ice and oceanographic characteristics. We studied the foraging behavior of juvenile emperor penguins from the Pointe Géologie colony in 2013–2014. Our main objectives were to (1) identify the horizontal movements of juveniles within the sea ice zones/habitats (i.e. defined by sea ice zones, coverage and persistence); (2) investigate the influence of the distance from the sea ice edge, light and seasons on the diving depth; and (3) assess if and how oceanographic conditions such as the mixed layer depth influence penguins' diving behavior within sea ice, and consequently prey acquisition. Based on a single juvenile tracked by Thiebot et al. (2013) within the sea ice zone during the autumn and winter seasons, our first hypothesis (H_1) was that juveniles use regions with sea ice more than previously reported (Kooyman & Ponganis 2007, Wienecke et al. 2010). Furthermore, we posited (H_2) that distance from the sea ice edge (from the inside or outside sea ice), season and time of day will affect diving behavior. Finally, we expected (H_3) that juvenile emperor penguins may target prey associated with temperature or density gradients within the water column, similar to king penguins within sub-Antarctic areas (Bost et al. 2009), and forage extensively over the continental slope where the slope current and upwelling of nutrient-rich waters may control the distribution of resources (Jacobs 1991).

2. MATERIALS AND METHODS

2.1. Animal handling, deployment and data collected

Fifteen juvenile emperor penguins were equipped with SPLASH tags (Wildlife Computers) in December 2013 just before their first departure to sea. Tags

were attached to the middle-lower back to reduce drag (Bannasch et al. 1994), and fixed to the feathers using cyanoacrylate glue (Loctite 401) and cable ties. The tags had a cross-sectional area of 3.2 cm² (<1% of a bird's cross-sectional area) and weighed 62 g in air and 25.2 g in seawater (0.34–0.44% of a juvenile's body mass; Thiebot et al. 2013). The smooth and flexible antenna was 8 cm long, 1.6 mm thick and inclined 45° backwards. Deployments were conducted at the Pointe Géologie colony (Dumont d'Urville station, 66.665° S, 140.0302° E) in Terre Adélie, Antarctica. General information such as bird weight and biometrics before departure, trip duration and dive start and end dates are reported in Table S1 in the Supplement at www.int-res.com/articles/suppl/m609/p001_supp.pdf). SPLASH tags are data-archiving tags that transmit to the Argos system. These tags record both horizontal and vertical movements (i.e. diving data). They were programmed to record and transmit diving summary and location data on a 24 h on, 48 h off cycle. Among the 15 individuals, an average of 18 ± 7 SD locations were transmitted per day of transmission. Three types of data were collected: (1) tracking data via the Argos position; (2) diving behavior including (a) dive profiles (maximum depth, dive duration and surface duration for all dives) and (b) 4 h dive duration, maximum depth and time-at-depth summary histograms (14 bins); and (3) temperature profiles including (a) 4 h time-at-temperature summary histograms (14 bins) and (b) profiles of depth and temperature (PDTs, including 2 profiles, 1 for the minimum and 1 for the maximum temperature encountered by the penguins) observed at 8 depths chosen to include the minimum and maximum depths detected and 6 other depths arranged equally between them. For this study, the Argos locations, the dive profiles and the 4 h summary of time-at-depth histograms and temperature profiles (PDTs) were used to study penguins' habitat use relative to sea ice and oceanographic conditions. Erroneous locations were filtered out using a speed filter from the R package 'argosfilter' (Freitas et al. 2008). The maximum travel speed was fixed to 14 km h⁻¹ following Wienecke et al. (2010).

2.2. Sea ice data

Daily estimates of sea ice concentration were derived from satellite Advanced Microwave Scanning Radiometer (AMSR-2) data at 6.25 km resolution (University of Bremen, www.iup.uni-bremen.de:8084/amsr/amsre1.html; see Labrousse et al. 2017 for more

details). The distance of penguins from the sea ice edge was calculated as the minimum distance between penguin positions and the sea ice edge contour, as defined by the 15% sea ice concentration isocline (following Stammerjohn & Smith 1997). Contours corresponding to outlying floes or polynyas were removed to prevent bias in our sea ice edge distance computation. Three variables representing the sea ice concentration and its spatio-temporal variability were investigated at and around the bird's position (Labrousse et al. 2017), assuming that sea ice may become a constraint when the concentration is high and precludes birds from diving. These variables are: (1) the sea ice concentration at the penguin location; (2) the area covered by sea ice with a concentration of >90% within a 10 km and a 25 km radius around the penguin location ($A_{90\%}$; as a measure of the spatial variability of concentrated sea ice patches); and (3) the number of days with a sea ice concentration of >90% at a given location within a 30 d window ($T_{90\%}$; as a measure of the time variability of concentrated sea ice patches, Fig. S1 in the Supplement).

The different sea ice zones may have various important consequences for seabirds (Stroeve et al. 2016). Indeed, changes and variability in the marginal ice zone, the consolidated pack ice or the fast ice would likely lead to different resource distribution depending on each zone or different sea ice-scape, with consequences on prey availability and open water entries and exits for air-breathing animals. Three zones with distinct characteristics were used to define the sea ice cover in East Antarctica (Massom & Stammerjohn 2010). These are (from north to south): (1) the highly-dynamic marginal ice zone, which extends ~100 km south from the ice edge, and is composed of small floes and diffuse ice conditions (depending on wind direction); (2) the inner pack ice zone, comprising larger floes separated by leads; and (3) a coastal zone comprising the band of compact landfast (fast) ice and persistent and recurrent areas of open water within sea ice in the form of polynyas and flaw leads.

2.3. Statistical analysis

We investigated the effect of sea ice on penguin diving behavior by modeling the relationship between dive depth and distance from the sea ice edge. We restricted the analysis to dives within 500 km of the sea ice edge, as the influence of the marginal ice zone extends only a few hundred kilometers from the sea ice

edge (Massom & Stammerjohn 2010). To account for diel differences in diving behavior, we analyzed daylight and twilight dives separately. Night dives were excluded from the analysis, as they represented only 5% of the total number of dives, and did not include feeding dives (Kirkwood & Robertson 1997a,b). To account for seasonal differences, we modeled 3 seasons separately: (1) January–March (12 individuals), (2) April–June (11 individuals) and (3) July–September (6 individuals). The period October–December was excluded as it included observations for only 3 individuals. We also excluded 3 individuals with trip durations <30 d (see Table S1).

For each combination of season and time of day, the distribution of dive depth was bimodal, with a shallow component and a deep component (see Section 3). To account for this bimodal distribution, we analyzed the relationship between dive depth and distance from the sea ice edge using a 2-component Gaussian mixture regression model using the R package 'flexmix' (Leisch 2004, Grün & Leisch 2007, 2008). This model assumes that the distribution of the log of dive depth follows a 2-component Gaussian mixture with mean depending on distance from the sea ice edge. For each component, the general model is:

$$Y_{ij} = \beta_{0j} + \beta_{1j} x_{ij} + \beta_{2j} x_{ij}^2 + \varepsilon_{ij} \quad i = 1, 2, \dots, I_j; j = 1, 2, \dots, J \quad (1)$$

where Y_{ij} is the log of dive depth i for individual j , x_{ij} is the distance from the sea ice edge for this dive, β_{0j} , β_{1j} , β_{2j} are unknown regression parameters for individual j , and ε_{ij} is a normal error with mean 0 and unknown variance σ^2 . The quadratic term x_{ij}^2 is included in the model to allow for a nonlinear relationship between log dive depth and distance from the sea ice edge. Although our chief interest is in the existence of a consistent pattern across individuals in the relationship between dive depth and distance from the sea ice edge, we also tested for differences between the 12 individuals in both components of this relationship. To begin with, we tested the null hypothesis $H_0: \beta_{0j} = \beta_0, j = 1, 1, \dots, J$, of a common intercept against the alternative hypothesis $H_1: \beta_{0j} \neq \beta_{0k}$ for at least 1 pair of individuals j and k . We then tested the null hypothesis $H_0: \beta_{1j}, \beta_{2j} = \beta_1, \beta_2, j = 1, 2, \dots, J$, of a common effect of distance from the sea ice edge on log dive depth (i.e. the slope of the regression) against the alternative hypothesis $H_1: \beta_{1j}, \beta_{2j} \neq \beta_{1k}, \beta_{2k}$ for at least 1 pair of individuals. In both cases, we compared these models using a likelihood ratio test (Azzalini 1996). Briefly, this involved computing twice the difference in the log likelihood maximized under the alternative and null hypotheses, respec-

tively, and comparing this quantity to the quantiles of a chi-squared distribution with the appropriate degrees of freedom.

2.4. Oceanographic conditions

To investigate the linkages between penguin diving behavior and oceanographic conditions, we used the minimum PDTs recorded by the penguins following the method of de Boyer Montégut et al. (2004) to calculate the mixed layer depth for each profile. Each temperature profile was interpolated every 5 m from their original data points spaced on average 17 ± 10 m apart (based on 15 juveniles and a total of 3538 profiles). The criterion selected to define the mixed layer depth is a difference in temperature of 0.2°C from a near-surface value at 10 m depth. As the tags were programmed to record negative PDT temperature as 0, we validated our approach using oceanographic data on mixed layer depth recorded by southern elephant seals over 10 yr (see the Supplement and Fig. S2 for more information).

We then investigated the linkages between the mixed layer depth and the birds' time at-depth. We used the time spent by the juveniles in each depth bin, versus the distance of the depth bin from the mixed layer. We then quantified the seasonal variability of where the penguins spent most of their time relative to the mixed layer depth, by averaging over time (using a moving window of 30 d) the vertical depth distance between the juvenile diving depth and the mixed layer depth, weighted by the time spent at depth.

2.5. Ocean floor topography

To define the shelf area and the continental slope, we used the same criteria as in Labrousse et al. (2015). The inflection point in meridional bathymetric contours, which represents the shelf break, was identified for each half degree of longitude from 0 to 150° E. The boundary between the continental slope and the deep ocean was defined as the region where the influence of the Antarctic slope front stops. We used the pressure gradient on an isopycnal computed from historical Argo floats and ship observations of the region to dynamically define the influence of the slope front and associated it with, roughly, the 3500 m isobaths for our region. Each penguin dive position was attributed either to the shelf, slope or the deep ocean area.

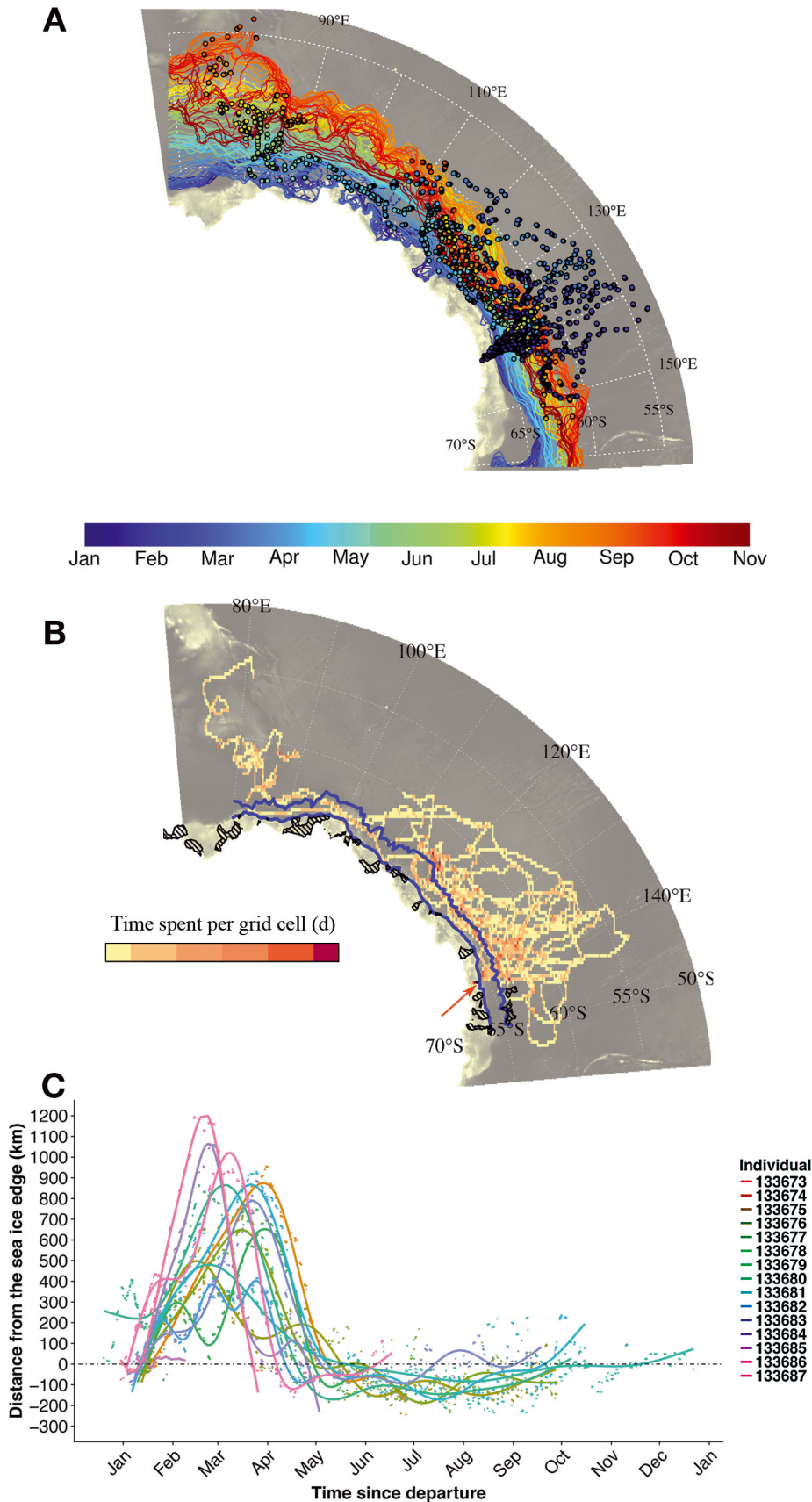
3. RESULTS

3.1. General diving behavior patterns and sea ice habitat

Data were obtained for 62453 dives from the 15 juvenile penguins between December 2013 and December 2014. The penguins left the colony and started to dive between 19 December 2013 and 12 January 2014 (Table S1). For 2 individuals, tags stopped recording dives after less than 1 d, and 1 individual's tag stopped after 31 d. For the remaining 12 individuals, tags recorded trips from 86 to 344 d, and tags stopped between 26 March and 22 December 2014. The maximum distance that a penguin traveled was 7794 km, and the furthest distance from the colony was 3503 km.

All juveniles first traveled north, reaching a maximum at 53.76° S (Fig. 1A,C, and see Fig. S3). In March/April, the penguins turned south, entering the sea ice in April/May. They remained in the sea ice, within 100–200 km of the ice edge, typically within the marginal and the pack ice zones, until the tags stopped transmitting (Fig. 1A,C, see Fig. S3). Penguins spent on average $49 \pm 14\%$ (\pm SE) of their time inside sea ice ($n = 12$; up to 73% for 1 individual, see Table S1). Within sea ice, they were surrounded by a high coverage of concentrated sea ice areas ($>75\%$ of the area around them was covered by sea ice concentration above 90%, both in a 10 km and a 25 km radius; cf. $A_{90\%}$, see Fig. S4). Similarly, sea ice concentration at their position was above 90% and persisted above 90% for at least 20 d within a month; cf. $T_{90\%}$, see Fig. S4). The penguins' horizontal speed tended to be lower inside sea ice, i.e. 0.56 ± 0.12 km h^{-1} ($n = 12$), compared to outside sea ice, i.e. 1.1 ± 0.98 km h^{-1} ($n = 14$; see Table S2).

Penguins only spent $2 \pm 3\%$ of their time on the Antarctic shelf, $25 \pm 12\%$ on the Antarctic slope and $72 \pm 12\%$ of their trip in the deep ocean (with or without sea ice; Fig. 1B, see Table S1). They only visited 1 small polynya near the colony. They tended to spend more time at the lower boundary of the slope area (Fig. 1B). Their diving depth increased from the shelf to the deep ocean, with average diving depths of 35 ± 19 m ($n = 11$, maximum = 180 m) on the shelf, 44 ± 13 m ($n = 12$, maximum = 232 m) on the continental slope and 64 ± 11 m ($n = 12$, maximum = 264 m) in the deep ocean. Similarly, the average dive duration across individuals ranged from 2.4 ± 0.5 min ($n = 11$, maximum = 7 min) over the shelf, 3.3 ± 0.5 min ($n = 12$, maximum = 32 min) over the continental slope and 3.6 ± 0.5 min ($n = 12$, maximum =



32 min) in the deep ocean. For all juvenile emperor penguins, approximately 0.07% of the dives exceeded the previous duration record for adult emperor penguins of 32.2 min (Goetz et al. 2018). Errors in the dive duration computation are likely due to non-detection of the surface at the end of dives. These dives were not included in the dive statistics (Table S2).

Penguins primarily dived when light, with $63 \pm 11\%$ of their time diving during the day and $32 \pm 10\%$ during twilight (Fig. 2A, Table S1). Only $5 \pm 3\%$ of dives were at night. Dives were deepest during the day and shallowest at night (Fig. 2A). Deep and shallow dives were observed both within and outside of the sea ice (Fig. 2B). Diving depths were very shallow at the sea ice edge (Fig. 2B).

Fig. 1. At-sea distribution of 15 juvenile emperor penguins equipped with SPLASH tags in 2013–2014 (dots). (A) Tracks of the 15 juveniles linked with the seasonality of the sea ice in the East Antarctic region. The color scale represents time; the sea ice extent of a given day and associated penguin positions are colored in the same way. For simplicity, sea ice extent is only shown for every third day. Sea ice extent was obtained from SSM/IS daily sea ice concentration (resolution 25 km). (B) Sum of the time spent across all individual penguins per grid cell (148.2×296 km). The 2 blue lines delineate the continental slope area. The black-hatched polygons represent the polynya areas computed using annual sea ice production from March to October 2014 as developed by Labrousse et al. (2018). The red arrow shows the small polynya close to the colony used by the penguins. (C) Time-series of the distance from the sea ice edge for each of the 15 individuals. Color scale corresponds to each individual. Smoothing lines were fitted for each individual observation

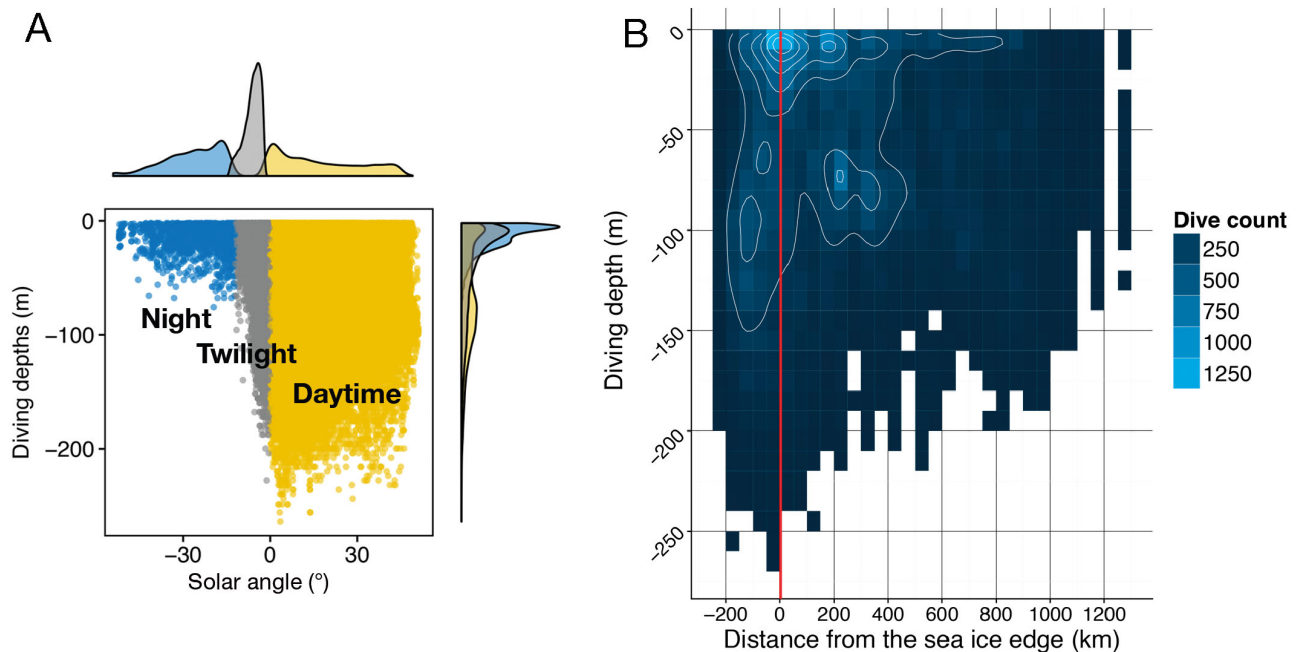


Fig. 2. Diving depth distribution across time of day and distance from the sea ice edge for 15 juvenile emperor penguins. (A) Diving depth versus the solar angle. Day dives are in yellow, twilight dives in grey and night dives in blue. The density distributions of the solar angle and the diving depths for each group are represented at the top and right side, respectively. (B) Diving depth relative to the bird's distance from the sea ice edge using a 2D kernel density estimation with a bandwidth of 50 m for the diving depth and 10 km for the distance from the sea ice edge (kde2D function from package MASS, R Development Core Team; Venables & Ripley 2002). One contour is drawn every 250 dives. The red line represents the sea ice edge

3.2. Change in diving behavior within sea ice across seasons

We investigated the influence of sea ice on juvenile diving behavior by studying the relationship between penguin diving depths and the distance from the sea ice edge using 2-component mixture models for summer, autumn and winter seasons for daytime dives (models 1–3) and for twilight dives (models 4–6). Here we refer to shallow dives for component 1 and deep dives for component 2. Negative distances from the sea ice edge are inside sea ice while positive distances are outside sea ice. Details about the distribution of the diving depths for each season and day/twilight times per zone, i.e. continental slope and shelf and deep ocean, are presented in Fig. S5. A summary of the relations for the model suites 'a,' 'b' and 'c' and the likelihood ratio tests to assess individual variability is presented in Table S3.

3.2.1. Summer

Most dives were outside of the sea ice. Dives were significantly deeper (for both shallow and deep dive

components) as they moved further away from the sea ice edge in open water during daytime (model 1a; Fig. 3A, red arrow; Table S3). Shallow dives were dominant in the distance bin $[-101, 3 \text{ km}]$ inside the sea ice (Fig. 3A). When penguins traveled further away from the sea ice edge, we observed an increase in the number of deep dives and a decrease in the shallow dives (Fig. 3A). Twilight dives during summer were almost exclusively shallow dives; the 2 components of the model were superimposed, as there were no deep dives (Fig. 3B), indicating that the diving depths were mostly constant across the different distances from the sea ice edge.

3.2.2. Autumn

During the daytime, penguins dived both to shallow ($\sim 20 \text{ m}$) and deep ($\sim 80\text{--}100 \text{ m}$) depths when they were inside sea ice far away from the edge (i.e. $[-244, -135 \text{ km}]$ and $[-135, -92 \text{ km}]$, Fig. 3C, red arrows 1 and 2). The distributions of each dive component (i.e. shallow and deep) were mainly constant across the different distance bins, but penguins dived to slightly deeper/shallower depths in the last bin (i.e. $[269, 496 \text{ km}]$, model 2a, Fig. 3C, Table S3).

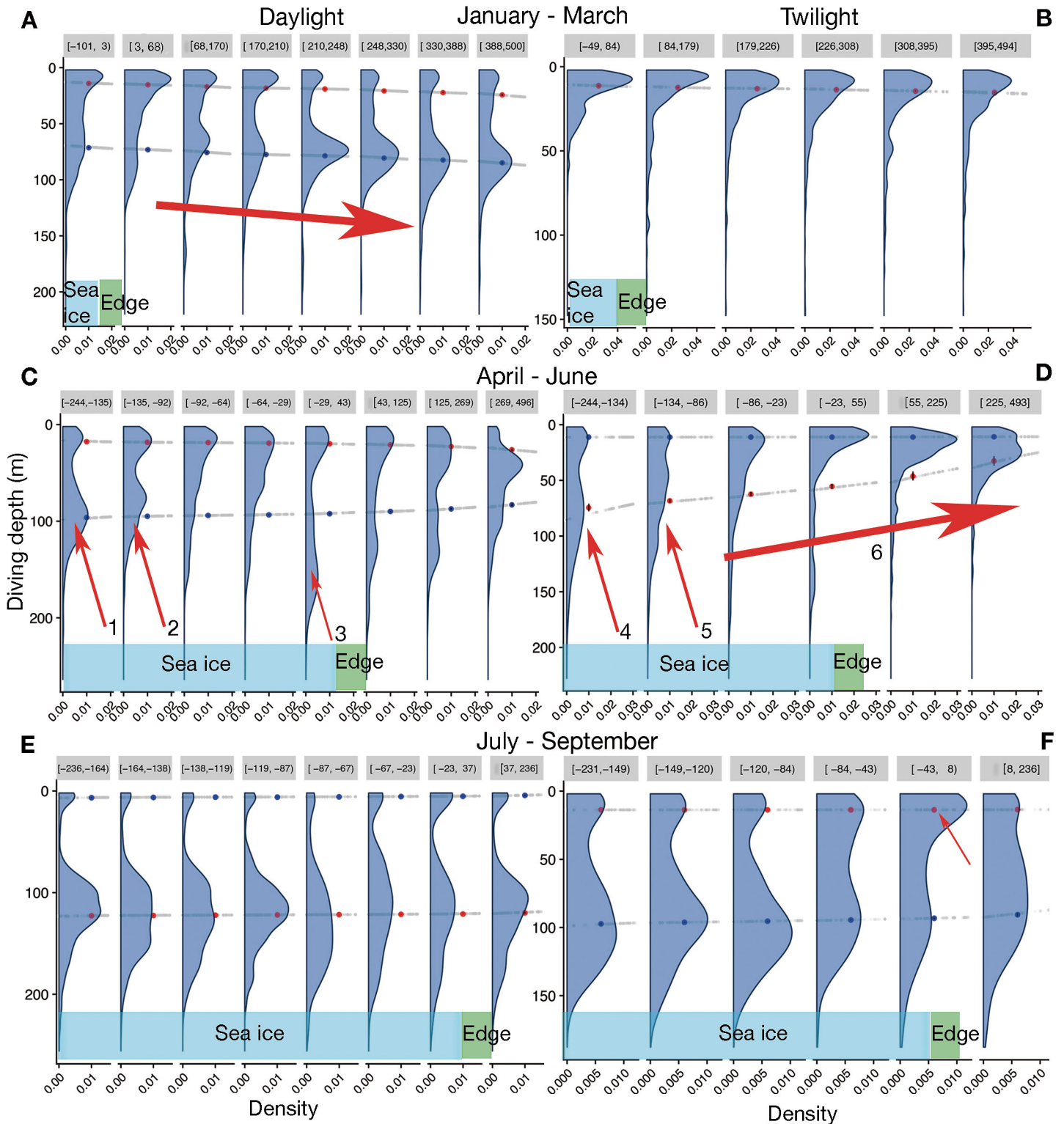


Fig. 3. Density plots of the diving depth of juvenile emperor penguins relative to their distance from the sea ice edge (grey boxes: distance bins, km) for daytime and twilight respectively across (A,B) summer, (C,D) autumn and (E,F) winter. For illustration purposes, the distance from the sea ice edge was binned in 8 classes for daylight (A,C,E) and 6 classes for twilight (B,D,F) of equal numbers of observations. Fitted values from mixture model 'a' are represented by grey dots, and the mean fitted value per bin of distance from the sea ice edge is represented in red or blue for each component. Red arrows correspond to comments in the main text of Section 3.2

These slight changes in the diving depths were statistically significant (Table S3). The density function highlights the presence of deeper dives (below ~150 m) at the sea ice edge (bin [-29, 43 km]; Fig. 3C, red arrow 3). At twilight, penguins performed both shallow and deep dives within the sea ice (Fig. 3D, red arrows 4 and 5); however, compared to day dives, shallow dives were dominant outside of the sea ice (Fig. 3D). There was no relationship between distance from the sea ice edge and the depth of shallow dives. In contrast, the deep dives became significantly shallower as distance from the sea ice edge increased from inside to outside sea ice (Fig. 3D, red arrow 6, model 5a; Table S3).

3.2.3. Winter

For daytime dives, both components remained almost constant across the different distances from the sea ice edge; only a slight significant decrease (i.e. shallower depths) in both components was observed (model 3a; Fig. 3E; Table S3). Interestingly, the deep dive component was dominant across the different distances from the sea ice edge (Fig. 3E). Penguins also performed deep dives at twilight except at the sea ice edge where shallow dives were dominant (Fig. 3F, red arrow). Both shallow and deep dive components remained mostly constant across the different distances from the sea ice edge (model 6a; Fig. 3F; Table S3).

3.2.4. Summary

In the summer when chicks departed the colony, they started diving near the sea ice and then traveled north into open water. During daylight, a transition from shallow to deep dives was recorded with increasing distance from the sea ice edge. However, twilight dives were exclusively shallow and mainly outside sea ice. In autumn during daylight, when juveniles came back to the sea ice zone after their northern trip, there was a dominance of shallow dives on the slope region (Fig. S5). The presence of deep dives during daylight outside the slope and shelf regions far inside sea ice (i.e. ca. -244 to -92 km) indicates a switch in penguin diving behavior through the autumn towards the winter. In autumn during twilight, deep dives only occurred inside sea ice. In winter, deep dives (~120 m) were dominant, and a change in diving depths was only observed in the slope region. No clear effect of the distance from the

sea ice edge was observed for the winter season during daylight and twilight. However, we observed an effect of the distance from the sea ice edge during autumn, principally for twilight dives. Finally, although there were differences between individuals in the details of these relationships, the overall pattern was consistent among individuals (see Table S3, Fig. S6).

3.3. Change in the diving behavior relative to oceanographic conditions

From January to March (summer), all penguins traveled north, encountering water masses with relatively warm temperatures sometimes $>3^{\circ}\text{C}$. In April, the penguins returned to the sea ice zone. In the sea ice zone during the autumn and winter, the water column started to be homogeneous from the surface to the mixed layer depth at ~100 m, with temperatures $<0.5^{\circ}\text{C}$, suggesting the penguins were foraging in Antarctic Surface Water (AASW) or Winter Water (WW; Fig. 4A). When penguins dived below the mixed layer depth, temperatures encountered were $>0.5^{\circ}\text{C}$, likely representing the relatively warm modified Circumpolar Deep Water (mCDW, Fig. 4A; see Labrousse et al. 2018). When birds returned within the sea ice region, they mainly dived closer to the beginning of the shelf break (i.e. upper part of the slope region) in April/May, while from June through October, they dived closer to the limit between the continental slope and the abyssal plain (i.e. lower part of the slope region; Fig. 4).

The mixed layer depth profile was shallow from January to March (summer), starting to deepen at the end of March/beginning of April during the autumn season and remained quasi-constant in winter from May to November (Fig. 4A). The time spent at depth reported in each PDT was qualitatively and quantitatively longer around the mixed layer depth, especially during the autumn and winter seasons (Figs. 4B & 5).

4. DISCUSSION

There were 2 distinct phases during the first year at sea for juvenile emperor penguins, as reported in previous studies (Wienecke et al. 2010, Thiebot et al. 2013). Juveniles first dispersed northward over large distances outside the sea ice ecosystem before turning back to the sea ice in April/May, where they remained through the winter. Our study demonstrates the close association of the juveniles with sea ice during the second part of their first trip at sea.

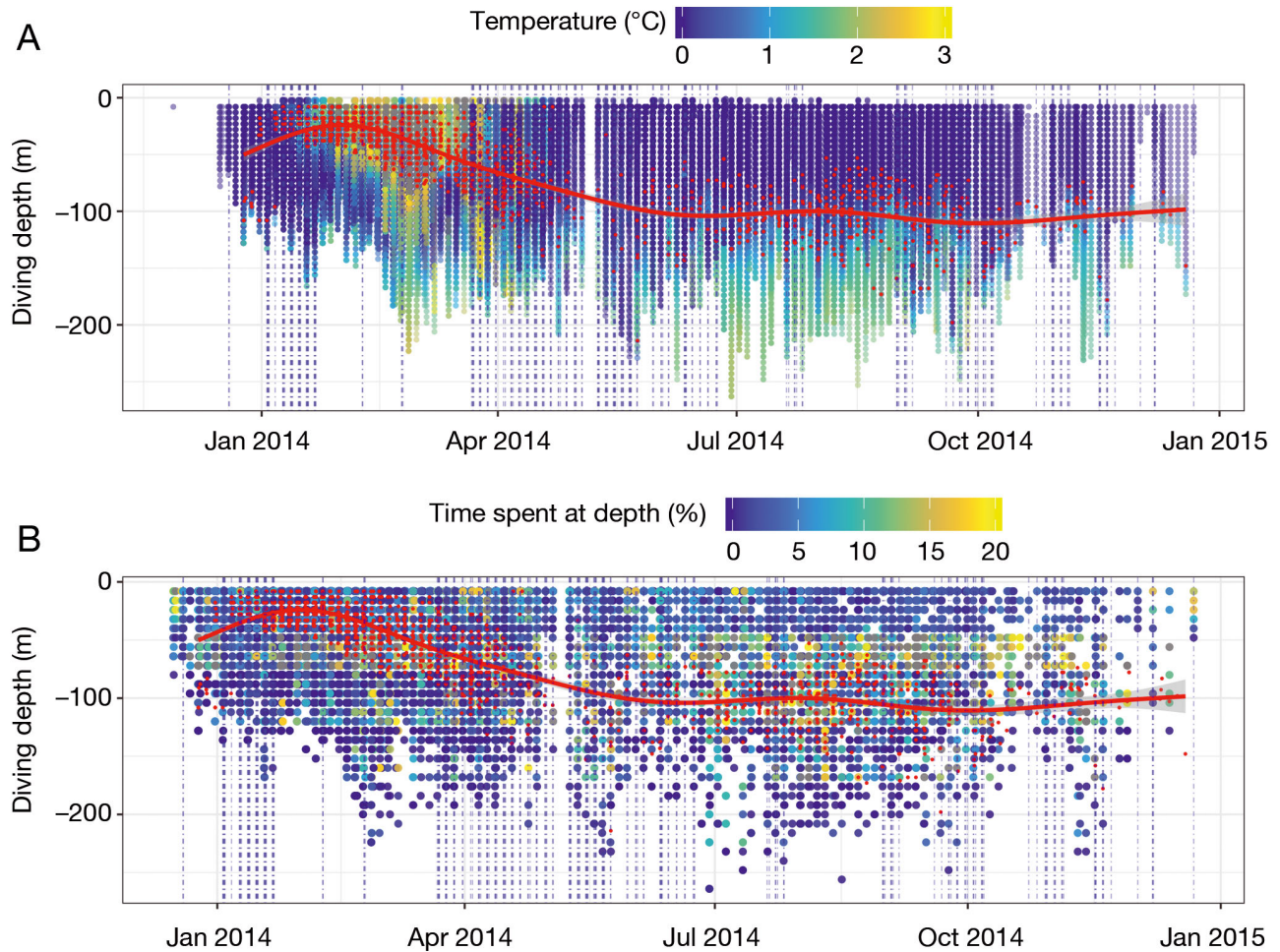
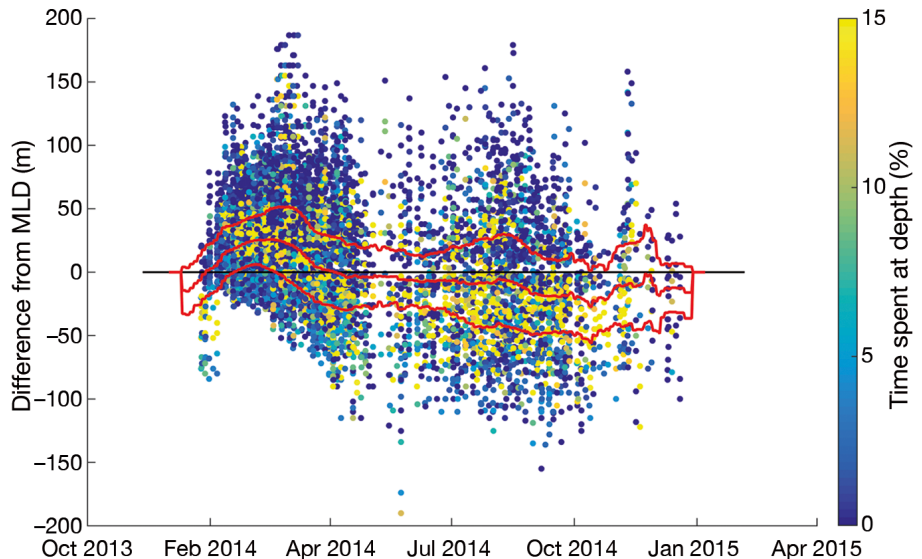


Fig. 4. Times series of depth-temperature profiles and depth-time indexes for 15 juvenile emperor penguins. (A) Minimum temperature profiles ($n = 3538$) collected during the birds' trips at sea and recorded as profiles of depth and temperature (PDTs). (B) Time spent at depth along each PDT. For illustration purposes only, we linked the 4 h summary PDTs with the 4 h summary time-at-depth histograms. For each PDT, we looked at the corresponding time-at-depth histogram based on the date, time and depth; we then attributed the time spent at depth to each depth of the PDT. Red dots represent the mixed layer depth for each profile. Red curve: predicted values of a smooth fitted line of the mixed layer depths (generalized additive model); grey shaded envelope: 95 %CI of the predicted values. The dashed vertical blue lines correspond to profiles located on the slope region

Contrary to our expectation, juvenile emperor penguins did not exploit any coastal polynyas; they remained in high sea ice covered areas in space and time within 100–200 km from the sea ice edge. We found that within sea ice, juvenile emperors dived both at shallow and deep depths during daylight, with changes in depth across seasons. Such a seasonal switch from shallow to deep dive dominance towards the winter has been poorly documented for adults and juveniles. In addition, we show for the first time that juveniles dived to the limit of the mixed layer depth, i.e. right to the thermocline, especially in winter. To our knowledge, the use of the thermocline below the mixed layer by adults is still an open question. To cope with the patchiness and heterogeneity

of marine resources, juveniles presumably learn along their trip to rely on specific environmental features in which prey availability might be predictable (Weimerskirch 2007). The strong association between the thermocline and emperor penguin juvenile foraging behavior emphasizes the role of this critical temperature gradient for aggregating prey during the autumn and winter seasons (see Charrassin & Bost 2001). Finally, these results raise questions about the ontogeny of juvenile foraging behavior. Different habitats were used by the juveniles (open ocean versus sea ice), and these habitats were associated with different diving behaviors. However, it is still unclear if and how these changes were related to: (1) intrinsic factors such as the maturation of the juveniles' phys-

Fig. 5. Times series of depth-difference between 15 juvenile emperor penguins' depth and the mixed layer depth (MLD). Positive values: deeper than MLD. The color scale represents the time spent at depth. The middle red line corresponds to the average distance from the MLD (using a moving window of 30 d) weighted by the time spent at depth (i.e. where the penguins spent most of their time relative to the MLD). The bottom and top red lines correspond to the standard deviation of this moving weighted average



iology (Ponganis et al. 1999), experience and foraging skills (Orgeret et al. 2016, Grecian et al. 2018); and (2) extrinsic factors such as changes in prey distribution (associated with the seasonality and/or habitat differences; Charrassin & Bost 2001) and diet switch (Kirkwood & Robertson 1997a), intra- and inter-specific competition (Burns & Kooyman 2001) and predation (reviewed by Ainley & Ballard 2012). Disentangling these factors is complex and would require further studies with time series of physiological measurements (such as body temperature, Enstipp et al. 2017), better proxies of foraging events (such as satellite-relayed accelerometry data, Cox et al. 2018) and information about prey distribution and availability (prey field modeling; Courbin et al. 2018).

4.1. Traveling, diving and foraging beneath the sea ice

Our study contrasts with previous studies that hypothesized that the sea ice habitat is probably avoided by penguins during winter due to complete ice cover and limited daylight at that time, hence restricting their foraging ability (Zimmer et al. 2008, Wienecke et al. 2010). Juvenile emperor penguins spent $49 \pm 14\%$ of their total recorded trip time inside sea ice and dived in areas of high sea ice concentration, despite being inexperienced in these environments. Thus, they are able to feed and survive in heterogeneous habitats ranging from lower latitudes (i.e. when they initially dispersed northward) to high latitudes with high sea ice concentration areas. This flexibility in foraging habitat use and diving behavior

may be important for the species' persistence over the long term when facing variable and changing sea ice conditions.

4.1.1. Summer and early autumn shallow dives

In summer and early autumn, juvenile emperor penguins passed the sea ice edge when they dispersed northward from the colony to open water or when they came back to the sea ice, respectively (Fig. 3). In these seasons, most shallow dives are observed within sea ice during daylight and twilight. The ice supports abundant (under-ice) food resources because it provides both a substrate for the growth of ice algae and a refuge for herbivorous zooplankton such as juvenile krill and other crustaceans (Marschall 1988, Flores et al. 2011, 2012, David et al. 2017). In summer, krill postlarvae are associated with the melting sea ice, while in autumn they are more abundant outside sea ice than inside. In winter, they are found at depth during the day and beneath sea ice at night (Flores et al. 2012). The dominance of shallow dives observed during summer and early autumn seasons may be associated with a diet based on Antarctic krill during daylight or on mesopelagic Antarctic lanternfish *Electrona antarctica* from their vertical migration at twilight. This diet was also reported for adults during their pre-molt trips for the colonies of Pointe Géologie, Taylor and Auster, and the Ross Sea (Kooyman et al. 2004, Wienecke et al. 2004, Zimmer et al. 2007). These shallow dives were numerous within the marginal ice zone. The marginal ice zone is characterized by melting sea ice and

breakdown, releasing a high quantity of food resources (i.e. ice algae) particularly when under a strong influence of wind action and ocean wave-ice interaction processes (reviewed by Massom & Stammerjohn 2010). Thus, juvenile emperor penguins may feed within the marginal ice zone, benefiting from this enhanced biological activity, and a relatively high concentration of krill and fishes throughout the year (Lancraft et al. 1991, Bost et al. 2004).

4.1.2. Autumn–winter transition, deep dives beneath sea ice

A switch towards dominant deep dives was observed during both daylight and twilight times in the winter. In autumn at twilight, sea ice had a strong effect on the diving depths; juveniles dived to deep depths far inside sea ice and then switched to shallow depths outside sea ice. Hence, we hypothesize that the switch to primarily deep dives in the autumn and winter within sea ice occurred because of (1) a seasonal change in the krill distribution from surface to deep waters during daylight; and/or (2) the presence of macrozooplankton at depth during twilight due to a reduced/absent diel migration in limited light. Wienecke & Robertson (1997) and Zimmer et al. (2008) found similar diving behavior in adult emperor penguins during winter. For example, deep diving in winter was correlated with higher prey densities likely being predominantly Antarctic krill, distributed at depth in winter during daylight. Thiebot et al. (2013) also reported this behavior for juveniles spending much more time deeper than 50 m, especially at depths greater than 100 m, with dives reaching 200–250 m during winter. Goetz et al. (2018) suggested that a change in diving depths for adult non-breeders might be associated with a change in diet from krill at shallow depths to squid and fish at deeper depths. Broadly, a seasonal shift with deeper dives in winter was also observed in other predator species, such as basking sharks *Cetorhinus maximus* and porbeagle sharks *Lamna nasus* (Francis et al. 2015, Braun et al. 2018) or king penguins (Charrassin et al. 2002), likely as a consequence of shifts in prey distribution.

4.2. Mixed layer depth as a cue to prey distribution for juveniles

Interestingly, juvenile emperor penguins' time spent at depth was strongly associated with the

mixed layer depth in autumn and winter. In this study, the mixed layer base likely coincides with the boundary between cold surface waters (likely AASW or WW) and warmer waters (likely CDW–mCDW; Fig. 4a). Mesopelagic fauna such as zooplankton, finfish and squid may aggregate near the thermocline (Van de Putte et al. 2010, Pelletier et al. 2012, Moteki et al. 2017) due to increased nutrients from the nutrient-rich CDW (Nicol et al. 2005) concentrating at the boundary layer between the 2 water masses. Moreover, the thermocline may act as a physical barrier, preventing prey from dispersing, or slowing down the escape speed of the ectothermic prey by the sudden change in temperature (Francks et al. 1992, Russell et al. 1999), making them easier to catch (Charrassin & Bost 2001). A similar association with thermoclines was previously reported for king penguins in sub-Antarctic regions (Bost et al. 2009).

We therefore posit that the association between the juvenile emperor penguins and the mixed layer base in winter may be linked with the distribution of their prey. The myctophid fish *E. antarctica* is likely the dominant prey available to penguins in the upper 200 m of the water column (Lancraft et al. 1991) along with squids in the autumn and winter (Ainley et al. 1991). Indeed, in high-latitude Antarctic pelagic waters, about 24–70% of the biomass of the myctophid *E. antarctica* from 0–1000 m depth was found to occur in the upper 200 m at night (Lancraft et al. 1989, Donnelly et al. 2006). Hunt et al. (2011) indicated a seasonal migration and/or increased residence time in the epipelagic during the winter months for large macrozooplankton such as *Electrona antarctica*.

The boundary of the winter mixed layer constitutes predictable and reliable foraging areas in time and space. In terms of thermoregulation, it may confer an advantage to spend time foraging in winter at the interface of warm, mesopelagic waters. Thus the combination of favorable energetics associated with warmer overwintering habitat and food availability (Braun et al. 2018) likely explains the amount of time juveniles spent near the mixed layer depth.

4.3. Ecological relevance of the Antarctic slope region

Shallow dives were mainly on the slope region in autumn, and in winter, changes in diving depths (through the season) only occurred within the slope

region. The continental slope region and the Antarctic slope current form a cold, dynamic and topographically constrained structure, which constitutes a deep ocean source region for nutrients (Jacobs 1991). This may result in higher productivity and enhanced and concentrated resources with a role in the distribution of sea ice, chlorophyll, krill and juvenile emperor penguins (Nicol et al. 2000a,b). Wienecke et al. (2010) found similar results, with juvenile emperor penguins from the Auster and Tayler glacier drifting passively with the westward pack ice motion within the Antarctic slope current. Adult emperor penguins were also found foraging over the continental slope in winter and spring (Kirkwood & Robertson 1997a,b). The Antarctic slope front also separates the oceanic mesopelagic fish communities from the neritic notothenioid communities (Moteki et al. 2011). Hence, mesopelagic prey may be one of the dominant prey of juveniles, while the notothenoid Antarctic silverfish is the major prey item of the adults during winter (e.g. Wienecke & Robertson 1997).

4.4. Future directions

The importance of the oceanographic features during the first trip at-sea of different bird and marine mammal species is still poorly documented (reviewed by Hazen et al. 2012; e.g. Thiebot et al. 2013, Tosh et al. 2015, Grecian et al. 2018). We still lack a full understanding of the role of learning and sensory capacities involved in using environmental cues such as temperature gradients to find food (Hays et al. 2016). Foraging strategies are likely learned during individual exploratory behavior in early life (Votier et al. 2017, Grecian et al. 2018). This exploratory behavior could also be under genetic control; juveniles often follow a directive dispersion just after their departure from the colony, despite their complete lack of knowledge of their new environment (i.e. Kooyman et al. 1996, Wienecke et al. 2010, Thiebot et al. 2013, de Grissac et al. 2016, this study). Another possible explanation of such dispersive behavior is that juveniles avoid intra-specific competition and are relayed in other habitats because of their lower foraging efficiency compared to the adults (Thiebot et al. 2013).

We found that juveniles were able to perform deep dives within a few weeks of fledging (see also Thiebot et al. 2013). This rapid initial improvement in dive capacity suggests that the subtle changes in diving behavior in autumn and winter reflect

changes in prey availability and distribution. A recent study on juvenile king penguins also showed this rapid change in the diving behavior after fledging (Enstipp et al. 2017). The authors concluded that juvenile king penguins should be more constrained by their insulation performances (their fat deposit at the periphery layer) and thus by their ability to successfully forage enough, rather than by the maturation process of their diving physiology (Enstipp et al. 2017).

The juvenile period of the life cycle can represent an important demographic pathway by which climate variability can impact population dynamics, particularly because juveniles are often more sensitive to environmental factors than adults (Jenouvrier et al. 2018). Nevertheless, this critical life cycle transition remains poorly understood for many seabird species. An improved understanding of the factors that influence juvenile emperor penguin survival is therefore a research priority (Hazen et al. 2012, Abadi et al. 2017). In our study, 9 tags stopped before the end of the expected battery life, due to either early juvenile mortality or tag failure (Kooyman et al. 2015). Further studies are needed to better understand and describe the changes in behavior just before the tags stop, potentially leading to deeper insights into the causes of these mortality events (Orgeret et al. 2016). The use of transmitters that provide data on time and location of death (Horning & Mellish 2009) will make it possible to link precise oceanographic and behavioral parameters to juvenile survival. It would then be possible to separate death by starvation (Daunt et al. 2007) from predation (Ainley & Ballard 2012), and to quantify their relative importance.

Comparing the foraging behaviors of emperor penguins during their first year at sea across several years and several sites (e.g. Ross Sea, Weddell Sea) would be necessary to draw general conclusions on the effects of sea ice and oceanographic conditions on early life foraging behaviors and survival, hence their impact on population dynamics. We believe that our analysis of the results revealed some robust conclusions, as the seasonal shift in diving depths within sea ice was consistent among individuals. While we have accounted for individual variation in the relationship between dive depth and distance from the sea ice edge through fixed individual effects, an approach based on random effects is also possible. Such an approach would need to account for non-normality in the random effects and, in our judgment, the additional model complexity is not justified by a gain in biological understanding.

5. CONCLUSIONS

The first trip at sea is critical for penguins, since food has to be acquired at a high rate to ensure that body condition and insulation are sufficient to allow survival and increased diving capabilities (Orgeret et al. 2016). Here we found that juvenile emperor penguins spent a significant amount of time foraging within sea ice, and exhibited seasonal differences in diving behavior, likely in response to changes in prey distribution. For the first time for this species, we reveal that juvenile diving activity was strongly associated with the thermocline, likely indicating a reliable signal of resource availability at this depth. To better understand and predict emperor penguin population changes, many questions remain; for example, how different foraging tactics (i.e. the different habitats exploited and the associated changes in diving behavior) or physiological maturation (thermoregulation; Enstipp et al. 2017) may impact marine predator juvenile survival early in life.

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