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

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Abstract

Adult emperor penguins 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 days (from 86 to 344 days). After departing the colony in December/January, the juveniles travelled north up to 53.76°S before heading south in April/May to forage within the sea ice. The juveniles spent 49 ± 14 % of their total recorded trip (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 (i) a seasonal change in the krill distribution from surface to deep waters, and/or (ii) the presence of macrozooplankton at depth due to a reduced/absent nyctemeral migration. Furthermore, we showed for the first time that the diving behaviour 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.

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 distance 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 and Limpus, 1997; Weddell seals *Leptonychotes weddellii*: Hastings et al., 1999; king penguins *Aptenodytes patagonicus*: Orgeret et al., 2016; wandering albatross *Diomedea exulans*: De Grissac et al., 2017; emperor penguins *Aptenodytes 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, Adélie 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; Reid and Croxall, 2001; Brierley and Thomas, 2002; Tynan et al., 2010; Fraser and Hofmann, 2003). 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; Flores et al., 2012b; David et al., 2016; 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 and van Dijken, 2003; Labrousse et al., 2018).

Antarctic sea ice also plays a major role on 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 and 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 and 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 et al., 2003; Weddell seals, Heerah et al., 2013; minke whales *Balaenoptera bonaerensis*, Friedlaender et al., 2006; southern elephant seals *Mirounga leonina*, Labrousse 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).

The emperor penguin is 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 two key periods: after egg-laying, i.e. between autumn and mid-winter when females are rebuilding their body reserves (while the males incubate 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 and Robertson, 1997a, Kirkwood and Robertson, 1997b). 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 penguin’s diet).

Whether and how sea ice affects foraging and diving behavior during early life stages and how that compares with the adult behavior, remain open questions. The at-sea distribution of the juveniles outside sea ice has been relatively well described (Kooyman and Ponganis, 2007; Wienecke et al., 2010; Thiebot et al., 2013); in December, juvenile emperor penguins leave the colony and travel very far north (e.g. up to 57 °S; Kooyman and Ponganis, 2007), mostly in ice free waters. In early March the travelling north ends and the birds start to travel to, or remain near, the northern ice edge. Some studies 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 (Riotte-Lambert & Weimerskirch 2013; Burns et al., 1999; Orgeret et al., 2016); and sea ice may represent a constraint to breathe and feed in a patchy resource-distributed environment. 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 comprehend 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; Jenouvrier et al., 2012, 2014, 2017; Barbraud et al. 2011).

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 within the sea ice zone during the autumn and winter seasons in Thiebot et al. (2013), our first hypothesis (H1) is that juveniles use regions with sea ice more than previously reported (Kooyman and Ponganis, 2007; Wienecke et al., 2010). Furthermore, we posit (H2) that distance from the sea ice edge (from the inside or outside sea ice), season and time of day will impact diving behavior. Finally, we expect (H3) 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 distributions of resources (Jacobs, 1991).

Methods

Animal handling, deployment, data collected

Fifteen juvenile emperor penguins were equipped with SPLASH tags (Wildlife Computers, Redmond WA, USA) 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 cm^2 (< 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 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°N, 140.0302°E) in Terre Adélie, Antarctica. General information such as bird weight and biometrics before departure, trip duration and dive start and end date are reported in the Supplement, Table S1. 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 locations data on a 24 hours on/ 48 hours off cycle. Among the 15 individuals, an average of 18 ± 7 locations were transmitted per day of transmission. Three types of data were collected: (i) tracking data via the Argos position; (ii) diving behavior including a) dive profiles (maximum depth, dive duration and surface duration for all dives) and b) 4 hours dive duration, maximum depth and time-at-depth summary histograms (14 bins); (iii) temperature profiles including a) 4 hours time-at-temperature summary histograms (14 bins), and b) profiles of depth and temperature (i.e. PDT, including two profiles, one for the minimum and one 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 hours summary of time-at-depth histograms and temperature profiles (PDT) 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).

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, http://www.iup.physik.uni bremen.de:8084/amsr/amsre.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 and 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 are: (i) the sea ice concentration at the penguin location; (ii) the area covered by sea ice with a concentration of >90% within a 10 km and 25 km radius around the penguin location ($A_{90\%}$; as a measure of the spatial variability of concentrated sea ice patches); and (iii) the number of days with a sea ice concentration of >90% at a given location within a 30 day window ($T_{90\%}$; as a measure of the time variability of concentrated sea ice patches, Fig. S1).

The different sea ice zones may have various important consequences for seabirds (Stroeve et al. 2016). Three zones with distinct characteristics were used to define the sea ice cover in East Antarctica (Massom and Stammerjohn, 2010). These are (from north to south): (i) the highly-dynamic ‘‘marginal ice zone” (MIZ), extending 100 km or so south from the ice edge, and is composed of small floes and diffuse ice conditions (depending on wind direction); (ii) the ‘‘inner pack ice” zone (PIZ) comprising larger floes separated by leads; and (iii) a coastal zone comprising the band of compact ‘‘landfast (fast) ice” (FIZ) and persistent and recurrent areas of open water within sea ice in the form of polynyas and flaw leads.

Statistical analysis

We investigated the effect of sea ice on penguin diving behavior by modelling 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 kilometres from the sea ice edge (Massom and Stammerjohn 2010). To account for diel differences in diving behavior, we analyzed daylight (D) and twilight (T) 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 1997). To account for seasonal differences, we modelled 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 the Supplement, 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 results). 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 and 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:

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

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, $\beta_{oj}, \beta_{1j}, \beta_{2j}$ 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 $H_o\colon \beta_{oj} = B_o,\ j = 1,1, \dots, J$, of a common intercept against the alternative hypothesis $H_1\colon \beta_{oj} \neq \beta_{ok}$ for at least one pair of individuals j and k. We then tested the null hypothesis $H_o\colon \beta_{1j}, \beta_{2j} = \beta_1, \beta_2, j = 1, 2, \dots, J$, 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 $H_1\colon \beta_{1j}, \beta_{2j} \neq \beta_{1k}, \beta_{2k}$ for at least one 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, respectively, and comparing this quantity to the quantiles of a chi squared distribution with the appropriate degrees of freedom.

Oceanographic conditions

To investigate the linkages between penguin diving behavior and oceanographic conditions, we used the minimum temperature and depth profiles (PDT) 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 in average of 17 ± 10 m (based on 15 juveniles and a total of 3538 profiles). The criterion selected to define the mixed layer depth is a difference of 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 zero, we validated our approach using oceanographic data on mixed layer depth recorded by southern elephant seals over 10 years (see the Supplement and Fig. S2 for more information).

We then investigated the linkages between the mixed layer depth and bird's time at-depth. We used the time-spent by the juvenile 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 days) the vertical depth distance between the juvenile diving depth and the mixed layer depth, weighted by the time spent at-depth.

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 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.

Results

General diving behavior patterns and sea ice habitat

Data were obtained for 62,453 dives from the 15 juvenile penguins between December 2013 and December 2014. The penguins left the colony and started to dive between December 19th 2013 and January 12th 2014 (see the Supplement, Table S1). For two individuals, tags stopped recording dives after less than one day; and one individual's tag stopped after 31 days. For the remaining 12 individuals, tags recorded trips from 86 to 344 days and tags stopped between March 26th and December 22nd 2014. The maximum distance that a penguin traveled was 7794 km and the furthest distance from the colony was 3503 km.

All juveniles first travelled North reaching a maximum at 53.76 °S (Fig. 1a, c, see the Supplement, 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 MIZ and the PIZ, until the tags stopped transmitting (Fig. 1a, c, see the Supplement, Fig. S3). Penguins spent on average 49 ± 14 % (± Standard Error of Mean; SEM) of their time inside sea ice (n = 12; up to 73 % for one individual, see the Supplement, Table S1). Within sea ice, they were surrounded by highly covered concentrated sea ice areas (more than 75% of the area around them was covered by sea ice concentration above 90%, both in a 10 and 25 km radius; cf. $A_{90\%}$, see the Supplement, Fig. S4). Similarly, sea ice concentration at their position was above 90% and persisted above 90% for at least 20 days within a month; cf. $T_{90\%}$, see the Supplement, Fig. S4). The penguins' horizontal speed tended to be lower inside sea ice, i.e. 0.56 ± 0.12 km/h (± SEM, n = 12), compared to outside sea ice, i.e. 1.1 ± 0.98 km/h (n = 14; see the Supplement, Table S2).

Penguins only spent 2 ± 3 % (± SEM) of their time on the Antarctic shelf, 25 ± 12 % on the Antarctic slope and 72 ± 12 % of their trip in the deep ocean (with or without sea ice; Fig. 1b, see the Supplement, Table S1). They only visited one 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 (± SEM) 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 (see the Supplement, Table S2).

Penguins primarily dived when light, with 63 ± 11 % (± SEM) of their time diving during the day and 32 ± 10 % during twilight (Fig. 2a, see the Supplement, Table S1). Only 5 ± 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).

Change in the diving behavior within sea ice across seasons

We investigated the influence of sea ice on juvenile diving behavior by studying the relationship between the penguin diving depths and the distance from the sea ice edge using 2-components 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 dive for component 1 and deep dive 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, is presented in figure S5. Summary of the relations for the model suite *a*, *b & c* and the likelihood ratio tests to assess individual variability are presented in Table S3.

Summer season. 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 1*a*; Fig. 3a, red arrow; Table S3). Shallow dives were dominant in the distance bin [-101, 3 km) inside the sea ice (Fig. 3a). When penguins travelled 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 two 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.

Autumn season. During the daytime, penguins dived both to shallow (~20 m) and deep (~ 80-100 m) depths when they were inside sea ice far away from the edge (i.e. [-244, -135 km) and [-135, -92 km), Fig. 3c, red arrows 1 and 2). The distribution of each dive components (i.e. shallow and deep) were mainly constant across the different bin of distances but penguins dived to slightly deeper/shallower depths in the last bin respectively (i.e. [269, 496 km], model 2*a*, Fig. 3c, Table S3). 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 arrows 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 got significantly shallower as distance from the sea ice edge increased from inside to outside sea ice (Fig. 3d, red arrow 6, model 5*a;* Table S3).

Winter season. 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 3*a*; 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 distance from the sea ice edge (model 6*a*; Fig. 3f; Table S3).

Summary. In the summer when chicks departed the colony, they started diving near the sea ice and then travelled 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 (Supplement, Fig. S5). The presence of deep dives during daylight outside the slope and shelf regions far inside sea ice (i.e. ~ -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 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 the autumn season, 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 Supplement with Table S3, Fig. S6).

Change in the diving behavior relative to oceanographic conditions

From January to March (summer), all the penguins travelled north, encountering water masses with relatively warm temperatures sometimes above 3 °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 lower than 0.5 °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 above 0.5°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 on each PDT profile was qualitatively and quantitatively longer around the mixed layer depth, especially during the autumn and winter seasons (Fig. 4b and 5).

Discussion

There were two 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. Contrary to our expectation, juvenile emperor penguins did not exploit any coastal polynya; 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 the juvenile foraging behavior. Different habitats were used by the juveniles (open ocean versus sea ice) and these habitats were associated with different diving behaviours. However, it is still unclear if and how these changes were related to: (i) intrinsic factors such as the maturation of the juveniles' physiology (Ponganis et al., 1999), experience and foraging skills (Orgeret et al., 2016; Grecian et al., 2018); and to (ii) extrinsic factors such as changes in prey distribution (associated with the seasonality and/or habitat differences; Charrassin et al., 2001) and diet switch (Kirkwood & Robertson, 1997a), intra- and inter-specific competition (Burns and 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., 2017), and information about prey distribution and availability (prey field modelling; Courbin et al., 2018).

Travelling, diving and foraging beneath the sea ice

Our study contrasts with previous studies that hypothesised 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 the foraging ability (Zimmer et al., 2008; Wienecke et al., 2010). Juvenile emperor penguins spent 49 ± 14 % of their total recorded trip time inside sea ice and dived in high sea ice concentration areas, despite being unexperienced 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.

Summer and early autumn shallow dives. In summer and early autumn juvenile emperor penguins were within 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., 2016). 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-moult 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) under a strong influence of wind action and ocean wave-ice interaction processes (reviewed by Massom and Stammerjohn, 2010). Thus, juvenile emperor penguins may feed within the marginal ice zone, benefiting from this enhanced biological activity with concentration of krill and fishes throughout the year (Lancraft et al., 1991; Bost et al., 2004).

The 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 (i) a seasonal change in the krill distribution from surface to deep waters during daylight; and/or (ii) the presence of macrozooplankton at depth during twilight due to a reduced/absent nycthemeral migration in limited light. Wienecke and 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) also 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 such as basking *Cetorhinus maximus* and porbeagle *Lamna nasus* sharks (Francis et al., 2015; Braun et al., 2018) or king penguins (Charrassin et al., 2002), likely as a consequence of shifts in prey distribution.

The mixed layer depth: 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; i.e. 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 two 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 (Franck et al., 1992; Russell et al., 1999), making them easier to catch by penguins (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 of large macrozooplankton such as *E. 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.

The 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) were only occurring 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, 2000b). 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).

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 to use environmental cues such as temperature gradients to find food (Hays 2016). Foraging strategies are likely learned during individual exploratory behavior in early life (Grecian et al., 2018; Votier et al., 2017). This exploratory behaviour 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. our study; Kooyman et al., 1996; Wienecke et al., 2010; Thiebot et al., 2013; de Grissac et al., 2016). 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 behaviour 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 expected tag's 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 behaviour 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 and 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 behaviours and survival, hence their impact on population dynamics. We believe that our study 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.

Conclusion

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 is good enough 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 exhibit 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 remains to be answered. For example, how different foraging tactics (i.e. the different habitats exploited and the change in the diving behavior associated with) or how the physiology maturation (thermoregulation; Enstipp et al., 2017) may impact marine predator juvenile survival early in life.

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References

Abadi F, Barbraud C, Gimenez O (2017) Integrated population modeling reveals the impact of climate on the survival of juvenile emperor penguins. Global Change Biology 23:1353–1359

Ainley DG, Ballard G (2012) Non-consumptive factors affecting foraging patterns in Antarctic penguins: a review and synthesis. Polar Biology 35:1–13

Ainley DG, Fraser WR, Smith WO, Hopkins TL, Torres JJ (1991) The structure of upper level pelagic food webs in the Antarctic: effect of phytoplankton distribution. Journal of Marine Systems 2:111–122

Ardyna M, Claustre H, Sallée J-B, D'Ovidio F, Gentili B, Dijken G van, D'Ortenzio F, Arrigo KR (2017) Delineating environmental control of phytoplankton biomass and phenology in the Southern Ocean: Phytoplankton Dynamics in the SO. Geophysical Research Letters 44:5016–5024

Arrigo KR, Dijken GL van (2003) Phytoplankton dynamics within 37 Antarctic coastal polynya systems. Journal of Geophysical Research 108

Azzalini A (1996) Statistical Inference: Based on the likelihood, Chapman & Hall. London

Bannasch, R., Wilson, R.P., Culik, B., n.d. Hydrodynamic aspects of design and attachment of a back-mounted device in penguins 15.

Barbraud C, Gavrilo M, Mizin Y, Weimerskirch H (2011) Comparison of emperor penguin declines between Pointe Géologie and Haswell Island over the past 50 years. Antarctic Science 23:461–468

Barbraud C, Weimerskirch H (2001) Emperor penguins and climate change. Nature 411:183–186

Bost C-A, Charrassin J-B, Clerquin Y, Ropert-Coudert Y, Le Maho Y, others (2004) Exploitation of distant marginal ice zones by king penguins during winter. Marine Ecology Progress Series 283:293–297

Bost CA, Cotté C, Bailleul F, Cherel Y, Charrassin JB, Guinet C, Ainley DG, Weimerskirch H (2009) The importance of oceanographic fronts to marine birds and mammals of the southern oceans. Journal of Marine Systems 78:363–376

Boyer Montégut C de (2004) Mixed layer depth over the global ocean: An examination of profile data and a profile-based climatology. Journal of Geophysical Research 109

Bracegirdle TJ, Connolley WM, Turner J (2008) Antarctic climate change over the twenty first century. Journal of Geophysical Research 113

Braun CD, Skomal GB, Thorrold SR (2018) Integrating Archival Tag Data and a High-Resolution Oceanographic Model to Estimate Basking Shark (*Cetorhinus maximus*) Movements in the Western Atlantic. Frontiers in Marine Science 5

Brierley AN, Thomas DN (2002) Ecology of Southern Ocean pack ice. Advances in Marine Biology 43:171–276

Burns JM (1999) The development of diving behavior in juvenile Weddell seals: pushing physiological limits in order to survive. 77:11

Burns JM, Kooyman GL (2001) Habitat use by Weddell seals and emperor penguins foraging in the

Ross Sea, Antarctica. American Zoologist 41:90–98

Chapman EW, Ribic CA, Fraser WR (2004) The distribution of seabirds and pinnipeds in Marguerite Bay and their relationship to physical features during austral winter 2001. Deep Sea Research Part II: Topical Studies in Oceanography 51:2261–2278

Charrassin J-B, Bost C-A (2001) Utilisation of the oceanic habitat by king penguins over the annual cycle. Marine Ecology Progress Series 221:285–298

Charrassin J-B, Maho YL, Bost C-A (2002) Seasonal changes in the diving parameters of king penguins (*Aptenodytes patagonicus*). Marine Biology 141:581–589

Courbin N, Besnard A, Péron C, Saraux C, Fort J, Perret S, Tornos J, Grémillet D (2018) Short-term prey field lability constrains individual specialisation in resource selection and foraging site fidelity in a marine predator. Ecology Letters 21:1043–1054

Cox SL, Orgeret F, Gesta M, Rodde C, Heizer I, Weimerskirch H, Guinet C (2018) Processing of acceleration and dive data on-board satellite relay tags to investigate diving and foraging behaviour in free-ranging marine predators (RB O'Hara, Ed.). Methods in Ecology and Evolution 9:64–77

Daunt F, Afanasyev V, Adam A, Croxall JP, Wanless S (2007) From cradle to early grave: juvenile mortality in European shags *Phalacrocorax aristotelis* results from inadequate development of foraging proficiency. Biology Letters 3:371–374

David C, Schaafsma FL, Franeker JA van, Lange B, Brandt A, Flores H (2016) Community structure of under-ice fauna in relation to winter sea-ice habitat properties from the Weddell Sea. Polar Biology

Donnelly J, Sutton TT, Torres JJ (2006) Distribution and abundance of micronekton and macrozooplankton in the NW Weddell Sea: relation to a spring ice-edge bloom. Polar Biology 29:280–293

Eicken H (1992) The role of sea ice in structuring Antarctic ecosystems. Polar Biology 12:3–13

Enstipp MR, Bost C-A, Le Bohec C, Bost C, Le Maho Y, Weimerskirch H, Handrich Y (2017) Apparent changes in body insulation of juvenile king penguins suggest an energetic challenge during their early life at sea. The Journal of Experimental Biology 220:2666–2678

Flores H, Franeker J-A van, Cisewski B, Leach H, Van de Putte AP, Meesters E (H. WG., Bathmann U, Wolff WJ (2011) Macrofauna under sea ice and in the open surface layer of the Lazarev Sea, Southern Ocean. Deep Sea Research Part II: Topical Studies in Oceanography 58:1948–1961

Flores H, Franeker JA van, Siegel V, Haraldsson M, Strass V, Meesters EH, Bathmann U, Wolff WJ (2012) The association of Antarctic krill Euphausia superba with the under-ice habitat (S Thrush, Ed.). PLoS ONE 7:e31775

Francis MP, Holdsworth JC, Block BA (2015) Life in the open ocean: seasonal migration and diel diving behaviour of Southern Hemisphere porbeagle sharks (*Lamna nasus*). Marine Biology 162:2305–2323

Franks P (1992) Sink or swim, accumulation of biomass at fronts. Marine Ecology Progress Series 82:1–12

Freitas C, Lydersen C, Fedak MA, Kovacs KM (2008) A simple new algorithm to filter marine mammal Argos locations. Marine Mammal Science 24:315–325

Friedlaender AS, Halpin PN, Qian SS, Lawson GL, Wiebe PH, Thiele D, Read AJ (2006) Whale distribution in relation to prey abundance and oceanographic processes in shelf waters of the Western Antarctic Peninsula.

Goetz K, McDonald B, Kooyman G (2018) Habitat preference and dive behavior of non‑breeding emperor penguins in the eastern Ross Sea, Antarctica. Marine Ecology Progress Series 593:155–171

Grecian WJ, Lane JV, Michelot T, Wade HM, Hamer KC (2018) Understanding the ontogeny of foraging behaviour: insights from combining marine predator bio-logging with satellite-derived oceanography in hidden Markov models. Journal of The Royal Society Interface 15:20180084

Grissac S de, Bartumeus F, Cox SL, Weimerskirch H (2017) Early-life foraging: Behavioral responses of newly fledged albatrosses to environmental conditions. Ecology and Evolution 7:6766–6778

Grissac S de, Börger L, Guitteaud A, Weimerskirch H (2016) Contrasting movement strategies among juvenile albatrosses and petrels. Scientific Reports 6

Grün B, Leisch F (2007) Fitting finite mixtures of generalized linear regressions in R. Computational Statistics & Data Analysis 51:5247–5252

Grün B, Leisch F (2008) FlexMix Version 2: Finite Mixtures with Concomitant Variables and Varying and Constant Parameters. Journal of Statistical Software; Vol 1, Issue 4 (2008)

Hays GC, Ferreira LC, Sequeira AMM, Meekan MG, Duarte CM, Bailey H, Bailleul F, Bowen WD, Caley MJ, Costa DP, Eguíluz VM, Fossette S, Friedlaender AS, Gales N, Gleiss AC, Gunn J, Harcourt R, Hazen EL, Heithaus MR, Heupel M, Holland K, Horning M, Jonsen I, Kooyman GL, Lowe CG, Madsen PT, Marsh H, Phillips RA, Righton D, Ropert-Coudert Y, Sato K, Shaffer SA, Simpfendorfer CA, Sims DW, Skomal G, Takahashi A, Trathan PN, Wikelski M, Womble JN, Thums M (2016) Key Questions in Marine Megafauna Movement Ecology. Trends in Ecology & Evolution 31:463–475

Hastings KK, Testa JW, Rexstad EA (1999) Interannual variation in survival of juvenile Weddell seals (*Leptonychotes weddellii*) from McMurdo Sound, Antarctica: effects of cohort, sex and age. Journal of Zoology 248:307–323

Hazen E, Maxwell S, Bailey H, Bograd S, Hamann M, Gaspar P, Godley B, Shillinger G (2012) Ontogeny in marine tagging and tracking science: technologies and data gaps. Marine Ecology Progress Series 457:221–240

Heerah K, Andrews-Goff V, Williams G, Sultan E, Hindell M, Patterson T, Charrassin J-B (2013) Ecology of Weddell seals during winter: Influence of environmental parameters on their foraging behaviour. Deep Sea Research Part II: Topical Studies in Oceanography 88–89:23–33

Hobbs WR, Massom R, Stammerjohn S, Reid P, Williams G, Meier W (2016) A review of recent changes in Southern Ocean sea ice, their drivers and forcings. Global and Planetary Change 143:228–250

Horning M, Mellish J (2009) Spatially explicit detection of predation on individual pinnipeds from implanted post-mortem satellite data transmitters. Endangered Species Research 10:135–143

Hunt BPV, Pakhomov EA, Siegel V, Strass V, Cisewski B, Bathmann U (2011) The seasonal cycle of the Lazarev Sea macrozooplankton community and a potential shift to top-down trophic control in winter. Deep Sea Research Part II: Topical Studies in Oceanography 58:1662–1676

Jacobs SS (1991) On the nature and significance of the Antarctic Slope Front. Marine Chemistry 35:9–24

Jenouvrier S, Holland M, Stroeve J, Barbraud C, Weimerskirch H, Serreze M, Caswell H (2012) Effects of climate change on an emperor penguin population: analysis of coupled demographic and climate models. Global Change Biology 18:2756–2770

Jenouvrier S, Garnier J, Patout F, Desvillettes L (2017) Influence of dispersal processes on the global dynamics of Emperor penguin, a species threatened by climate change. Biological Conservation 212:63–73

Jenouvrier S, Holland M, Stroeve J, Serreze M, Barbraud C, Weimerskirch H, Caswell H (2014) Projected continent-wide declines of the emperor penguin under climate change. Nature Climate Change 4:715–718

Jenouvrier S, Desprez M, Fay R, Barbraud C, Delord K, Weimerskirch H, Caswell H (2018) Climate change and functional traits impact population dynamics of a long-lived seabird. Journal of Animal Ecology. in press

Kaufmann RS, Smith Jr KL, Baldwin RJ, Glatts RC, Robison BH, Reisenbichler KR (1995) Effects of seasonal pack ice on the distribution of macrozooplankton and micronekton in the northwestern Weddell Sea. Marine Biology 124:387–397

Kirkwood R, Robertson G (1997a) Seasonal change in the foraging ecology of emperor penguins on the Mawson Coast, Antarctica. Marine Ecology Progress Series 156:205–223

Kirkwood R, Robertson G (1997b) The foraging ecology of female emperor penguins in winter. Ecological Monographs 67:155–176

Kooyman GL, Kooyman TG, Horning M, Kooyman CA (1996) Penguin dispersal after fledging. Nature 383:397

Kooyman GL, Ponganis PJ (2007) The initial journey of juvenile emperor penguins. Aquatic Conservation: Marine and Freshwater Ecosystems 17:S37–S43

Kooyman GL, McDonald BI, Goetz KT (2015) Why do satellite transmitters on emperor penguins stop transmitting? Animal Biotelemetry 3

Kooyman G, Siniff D, Stirling I, Bengtson J (2004) Moult habitat, pre- and post-moult diet and post-moult travel of Ross Sea emperor penguins. Marine Ecology Progress Series 267:281–290

Labrousse S, Sallée J-B, Fraser AD, Massom RA, Reid P, Sumner M, Guinet C, Harcourt R, McMahon C, Bailleul F, Hindell MA, Charrassin J-B (2017) Under the sea ice: Exploring the relationship between sea ice and the foraging behaviour of southern elephant seals in East Antarctica. Progress in Oceanography 156:17–40

Labrousse S, Vacquié-Garcia J, Heerah K, Guinet C, Sallée J-B, Authier M, Picard B, Roquet F, Bailleul F, Hindell M, Charrassin J-B (2015) Winter use of sea ice and ocean water mass habitat by southern elephant seals: The length and breadth of the mystery. Progress in Oceanography 137:52–68

Labrousse S, Williams G, Tamura T, Bestley S, Sallée J-B, Fraser AD, Sumner M, Roquet F, Heerah K, Picard B, Guinet C, Harcourt R, McMahon C, Hindell MA, Charrassin J-B (2018) Coastal polynyas: Winter oases for subadult southern elephant seals in East Antarctica. Scientific Reports 8

Lancraft TM, Hopkins TL, Torres JJ, Donnelly J (1991) Oceanic micronektonic/macrozooplanktonic community structure and feeding in ice covered Antarctic waters during the winter (AMERIEZ 1988). Polar Biology 11:157–167

Lancraft TM, Torres JJ, Hopkins TL (1989) Micronekton and macrozooplankton in the open waters near Antarctic ice edge zones (AMERIEZ 1983 and 1986). Polar Biology 9:225–233

Lea M (2003) Fine-scale linkages between the diving behaviour of Antarctic fur seals and oceanographic features in the southern Indian Ocean. ICES Journal of Marine Science 60:990–1002

Leisch F (2004) FlexMix: A General Framework for Finite Mixture Models and Latent Class Regression in R. Journal of Statistical Software; Vol 1, Issue 8 (2004)

Marschall H-P (1988) The overwintering strategy of Antarctic krill under the pack-ice of the Weddell Sea. Polar Biology 9:129–135

Marshall J, Speer K (2012) Closure of the meridional overturning circulation through Southern Ocean upwelling. Nature Geoscience 5:171–180

Martinson DG (1990) Evolution of the Southern Ocean winter mixed layer and sea ice: Open ocean deepwater formation and ventilation. Journal of Geophysical Research: Oceans 95:11641–11654

Massom RA, Stammerjohn SE (2010) Antarctic sea ice change and variability – Physical and ecological implications. Polar Science 4:149–186

Meyer B, Freier U, Grimm V, Groeneveld J, Hunt BPV, Kerwath S, King R, Klaas C, Pakhomov E, Meiners KM, Melbourne-Thomas J, Murphy EJ, Thorpe SE, Stammerjohn S, Wolf-Gladrow D, Auerswald L, Götz A, Halbach L, Jarman S, Kawaguchi S, Krumpen T, Nehrke G, Ricker R, Sumner M, Teschke M, Trebilco R, Yilmaz NI (2017) The winter pack-ice zone provides a sheltered but food-poor habitat for larval Antarctic krill. Nature Ecology & Evolution 1:1853–1861

Moteki M, Fujii K, Amakasu K, Shimada K, Tanimura A, Odate T (2017) Distributions of larval and juvenile/adult stages of the Antarctic myctophid fish, *Electrona antarctica*, off Wilkes Land in East Antarctica. Polar Science 12:99–108

Moteki M, Koubbi P, Pruvost P, Tavernier E, Hulley P-A (2011) Spatial distribution of pelagic fish off Adélie and George V Land, East Antarctica in the austral summer 2008. Polar Science 5:211–224

Musick JA, Limpus CJ (1997) Habitat utilization and migration in juvenile sea turtles. In: Lutz P, Musick JA (eds) Biology of sea turtles. CRC Press, Boca Raton, FL, p137−163.

Nicol S, Pauly T, Bindoff N., Strutton P. (2000) “BROKE” a biological/oceanographic survey off the coast of East Antarctica (80–150°E) carried out in January–March 1996. Deep Sea Research Part II: Topical Studies in Oceanography 47:2281–2297

Nicol S, Pauly T, Bindoff NL, Wright S (2000) Ocean circulation off east Antarctica affects ecosystem structure and sea-ice extent. Science 260:1617–1623

Nicol S, Worby AP, Strutton PG, Trull TW (2005) Oceanographic influences on Antarctic ecosystems : Observations and insights from East Antarctica (0° to 150°E). In: Robinson AR, Brink KH (eds) The Sea ; Ideas and Observations on Progress in the Study of the Seas. Harvard University Press, Cambridge

Orgeret F, Weimerskirch H, Bost C-A (2016) Early diving behaviour in juvenile penguins: improvement or selection processes. Biology Letters 12:20160490

Orsi AH, Johnson GC, Bullister JL (1999) Circulation, mixing, and production of Antarctic Bottom Water. Progress in Oceanography 43:55–109

Pelletier L, Kato A, Chiaradia A, Ropert-Coudert Y (2012) Can Thermoclines Be a Cue to Prey Distribution for Marine Top Predators? A Case Study with Little Penguins (H Browman, Ed.). PLoS ONE 7:e31768

Pellichero V, Sallée J-B, Schmidtko S, Roquet F, Charrassin J-B (2017) The ocean mixed layer under Southern Ocean sea-ice: Seasonal cycle and forcing. Journal of Geophysical Research: Oceans 122:1608–1633

Ponganis PJ (1999) Development of diving in emperor penguins. :6

Raymond B, Lea M-A, Patterson T, Andrews-Goff V, Sharples R, Charrassin J-B, Cottin M, Emmerson L, Gales N, Gales R, Goldsworthy SD, Harcourt R, Kato A, Kirkwood R, Lawton K, Ropert-Coudert Y, Southwell C, Hoff J van den, Wienecke B, Woehler EJ, Wotherspoon S, Hindell MA (2015) Important marine habitat off east Antarctica revealed by two decades of multi-species predator tracking. Ecography 38:121–129

Reid K, Croxall JP (2001) Environmental response of upper trophic-level predators reveals a system change in an Antarctic marine ecosystem. Proceedings of the Royal Society B: Biological Sciences 268:377–384

Riotte-Lambert L, Weimerskirch H (2013) Do naive juvenile seabirds forage differently from adults? Proceedings of the Royal Society B: Biological Sciences 280:20131434–20131434

Russell R, Harrison N, Hunt G (1999) Foraging at a front:hydrography, zooplankton, and avian planktivory in the northern Bering Sea. Marine Ecology Progress Series 182:77–93

Stammerjohn SE, Smith RC (1997) Opposing Southern Ocean climate patterns as revealed by trends in regional sea ice coverage. Climatic Change 37:617–639

Stroeve JC, Jenouvrier S, Campbell GG, Barbraud C, Delord K (2016) Mapping and assessing variability in the Antarctic marginal ice zone, pack ice and coastal polynyas in two sea ice algorithms with implications on breeding success of snow petrels. The Cryosphere 10:1823–1843

Thiebot J-B, Lescroël A, Barbraud C, Bost C-A (2013) Three-dimensional use of marine habitats by juvenile emperor penguins Aptenodytes forsteri during post-natal dispersal. Antarctic Science 25:536–544

Tosh CA, Bruyn PJN de, Steyn J, Bornemann H, Hoff J van den, Stewart BS, Plötz J, Bester MN (2015) The importance of seasonal sea surface height anomalies for foraging juvenile southern elephant seals. Marine Biology 162:2131–2140

Tynan, C., Ainley, D., and Stirling, I. (2010). *Sea ice: a critical habitat for polar marine mammals and birds*.

Van de Putte AP, Jackson GD, Pakhomov E, Flores H, Volckaert FAM (2010) Distribution of squid and fish in the pelagic zone of the Cosmonaut Sea and Prydz Bay region during the BROKE-West campaign. Deep Sea Research Part II: Topical Studies in Oceanography 57:956–967

Van Franeker JA, Bathmann UV, Mathot S (1997) Carbon fluxes to antarctic top predators. Deep Sea Research Part II: Topical Studies in Oceanography 44:435–455

Votier SC, Fayet AL, Bearhop S, Bodey TW, Clark BL, Grecian J, Guilford T, Hamer KC, Jeglinski JWE, Morgan G, Wakefield E, Patrick SC (2017) Effects of age and reproductive status on individual foraging site fidelity in a long-lived marine predator. Proceedings of the Royal Society B: Biological Sciences 284:20171068

Weimerskirch H (2007) Are seabirds foraging for unpredictable resources? Deep Sea Research Part II: Topical Studies in Oceanography 54:211–223

Wienecke B, Kirkwood R, Robertson G (2004) Pre-moult foraging trips and moult locations of Emperor penguins at the Mawson Coast. Polar Biology 27:83–91

Wienecke B, Raymond B, Robertson G (2010) Maiden journey of fledgling emperor penguins from the Mawson Coast, East Antarctica. Marine Ecology Progress Series 410:269–282

Wienecke B, Robertson G (1997) Foraging space of emperor penguins Aptenodytes forsteri in Antarctic shelf waters in winter. Marine Ecology Progress Series 159:249–263

Zimmer I, Wilson R, Beaulieu M, Ancel A, Plötz J (2008) Seeing the light: depth and time restrictions in the foraging capacity of emperor penguins at Pointe Géologie, Antarctica. Aquatic Biology 3:217–226

Zimmer I, Wilson RP, Gilbert C, Beaulieu M, Ancel A, Plötz J (2007) Foraging movements of emperor penguins at Pointe Géologie, Antarctica. Polar Biology 31:229–243

Figures

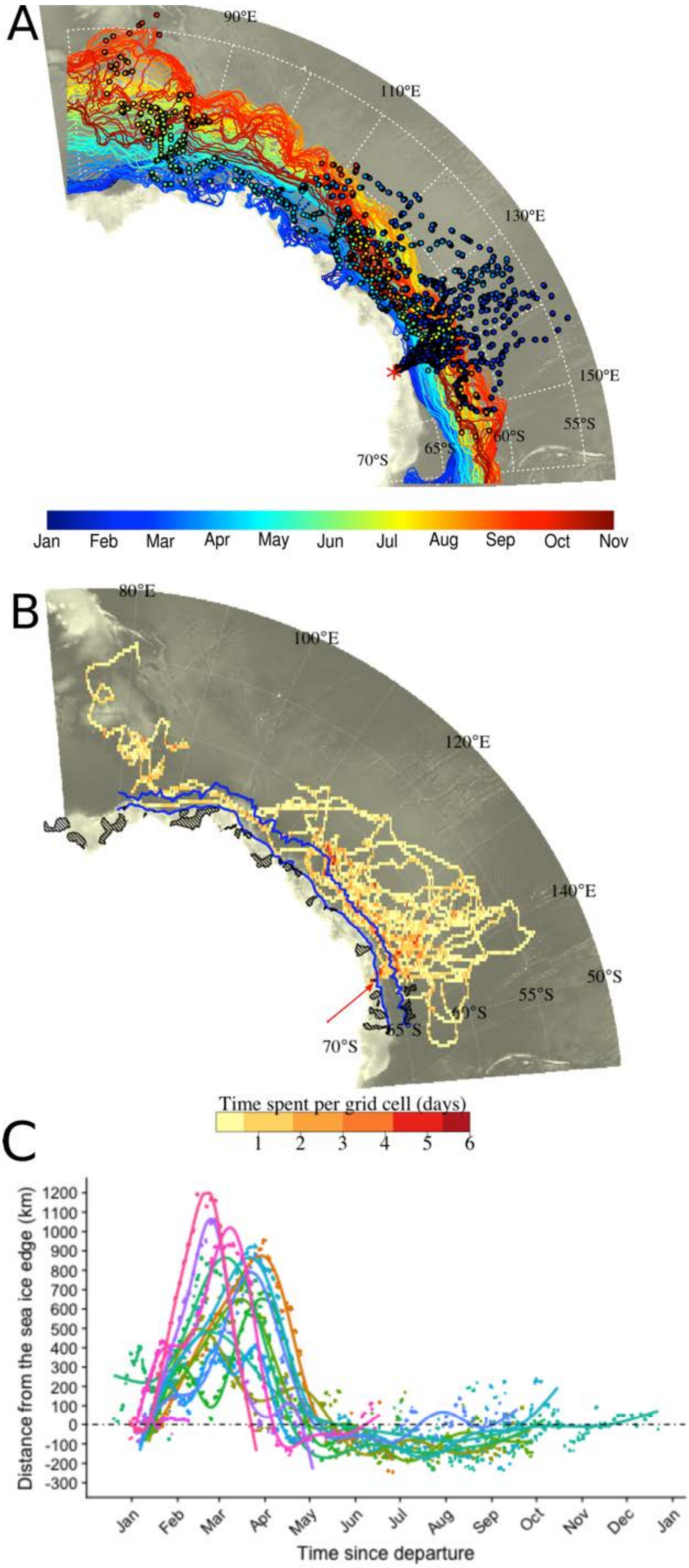
A
90°E
110°E
130°E
150°E
55°S
60°S
65°S
70°S
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
B
80°E
100°E
120°E
140°E
50°S
55°S
60°S
65°S
70°S
Time spent per grid cell (days)
1
2
3
4
5
6
C
Distance from the sea ice edge (km)
1200
1100
1000
900
800
700
600
500
400
300
200
100
0
-100
-200
-300
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Time since departure

Figure 1. At-sea distribution of the 15 juvenile emperor penguins equipped with SPLASH tags in 2013-2014. Panel (**a**) represents the tracks of the 15 juvenile emperor penguins linked with the seasonality of the sea ice in the East Antarctic region. The colour scale represents the time; the sea ice extent of a given day and associated penguin positions are colored in the same way. To simplify the figure, 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). The bathymetry contours represented are from ETOPO1, a 1 arc-minute global relief model of Earth's surface that integrates land topography and ocean bathymetry; http://www.ngdc.noaa.gov/mgg/global/global.html. The red star indicates the colony. Panel (**b**) represents a map of the sum of the time spent (days) across all individual penguins per grid cell (148.2 km × 296 km). The two 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 in Labrousse et al. (2018). The red arrow shows the small polynya close to the colony used by the penguins. Panel (**c**) represents a 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.

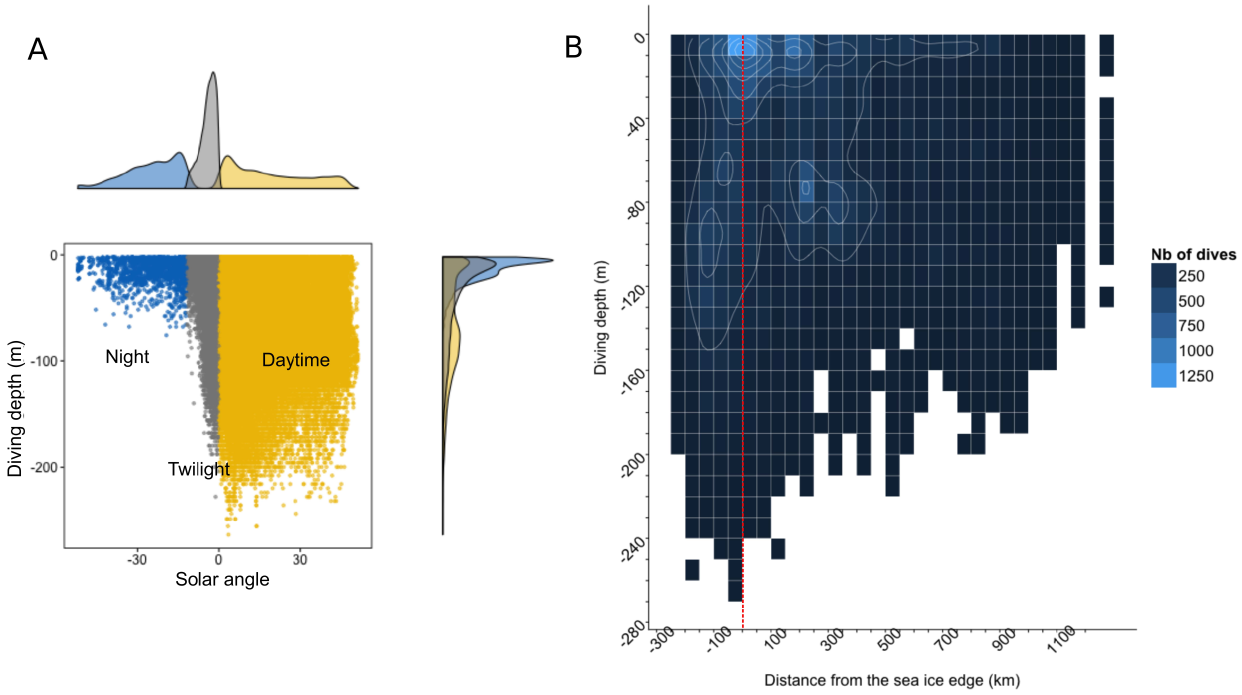

Figure 2. Diving depth distribution across time of the day and distance from the sea ice edge for the 15 juvenile emperor penguins. Panel (a) represents the diving depth (m) versus the solar angle (°). Day dives are coloured in yellow, twilight dives in grey, and night dives in blue. The density distribution of the solar angle and the diving depths for each group is represented on the top and right corner of the panel (a) respectively. Panel (b) represents diving depth (m) relative to the bird's distance from the sea ice edge (km) 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, from R Development Core Team). One contour is drawn every 250 dives. The red line represents the sea ice edge.

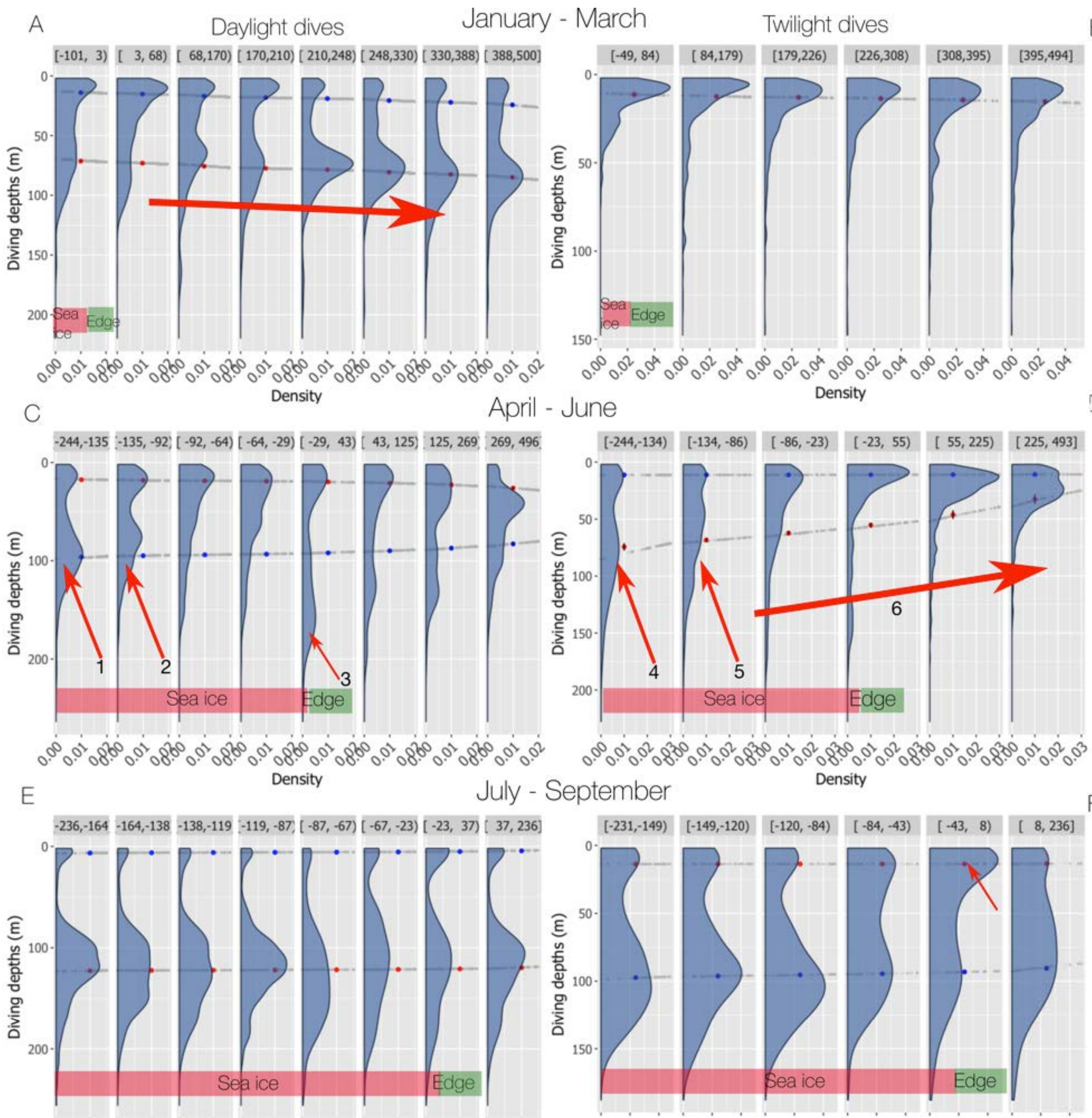

Figure 3. Density plots of the diving depth of juvenile emperor penguins relative to their distance from the sea ice edge for daytime and twilight respectively across summer (**a, b**), autumn (**c, d**) and winter (**e, f**). For illustration purposes, the distance from the sea ice edge was binned in 8 classes for daylight and 6 classes for twilight of equal number of observation. Fitted values from the 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 the Results section.

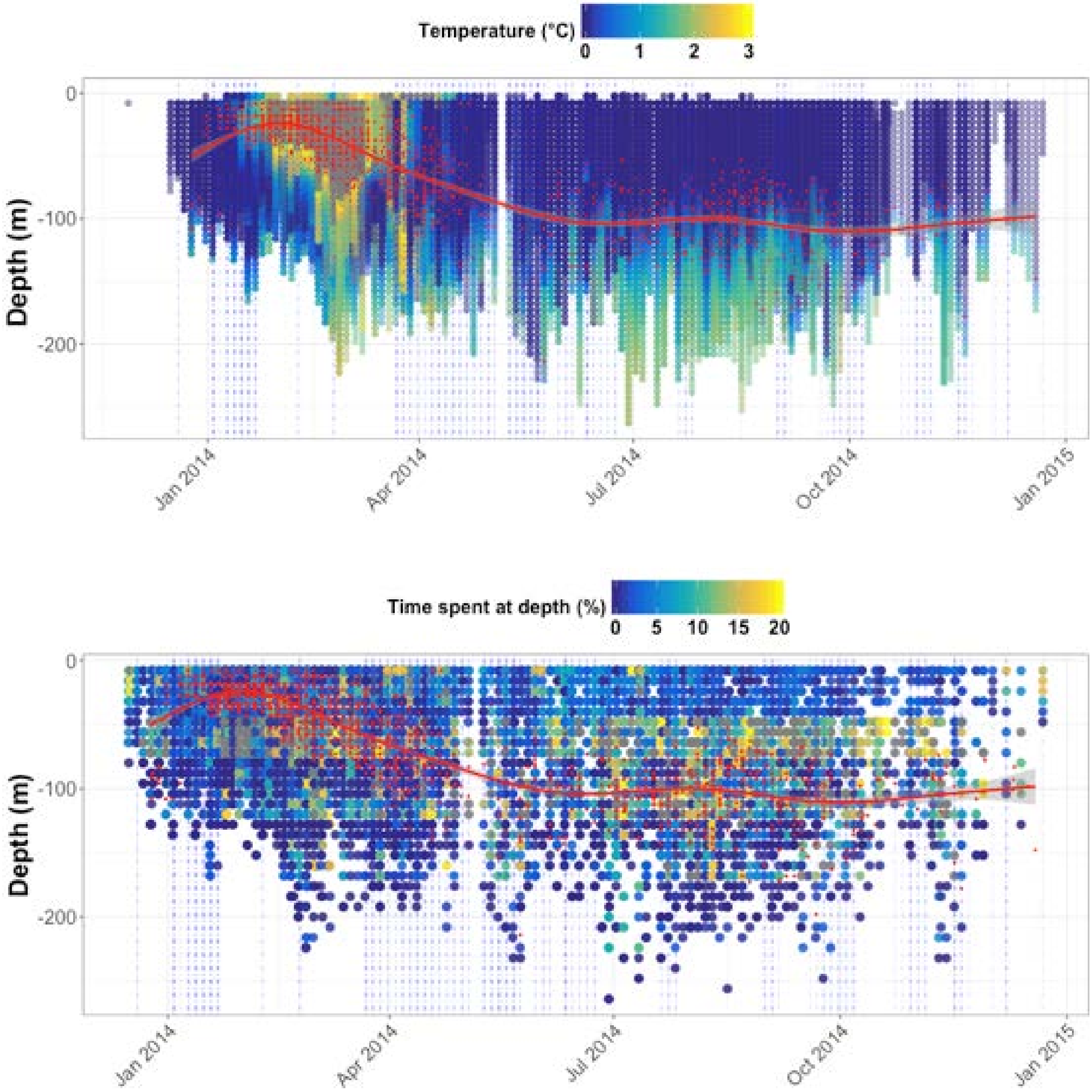

Figure 4. Times series of depth-temperature profiles and depth-time indexes for the 15 juvenile emperor penguins. Panel (a) represents the minimum temperature profiles (n=3538) collected by the birds along their trip at-sea and recorded as PDT. Panel (b) represents the time-spent at-depth along each PDT profile. For illustration purposes only, we linked the 4 hour-summary PDT profiles with the 4 hour-summary time-at-depth histograms. For each PDT profile, 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 profile. Red dots represent the mixed layer depth for each profile. The red curve corresponds to a smooth fitted line of the mixed layer depths (method generalised additive model). The dashed vertical red and blue lines correspond of profiles located on the upper and lower slope region respectively.

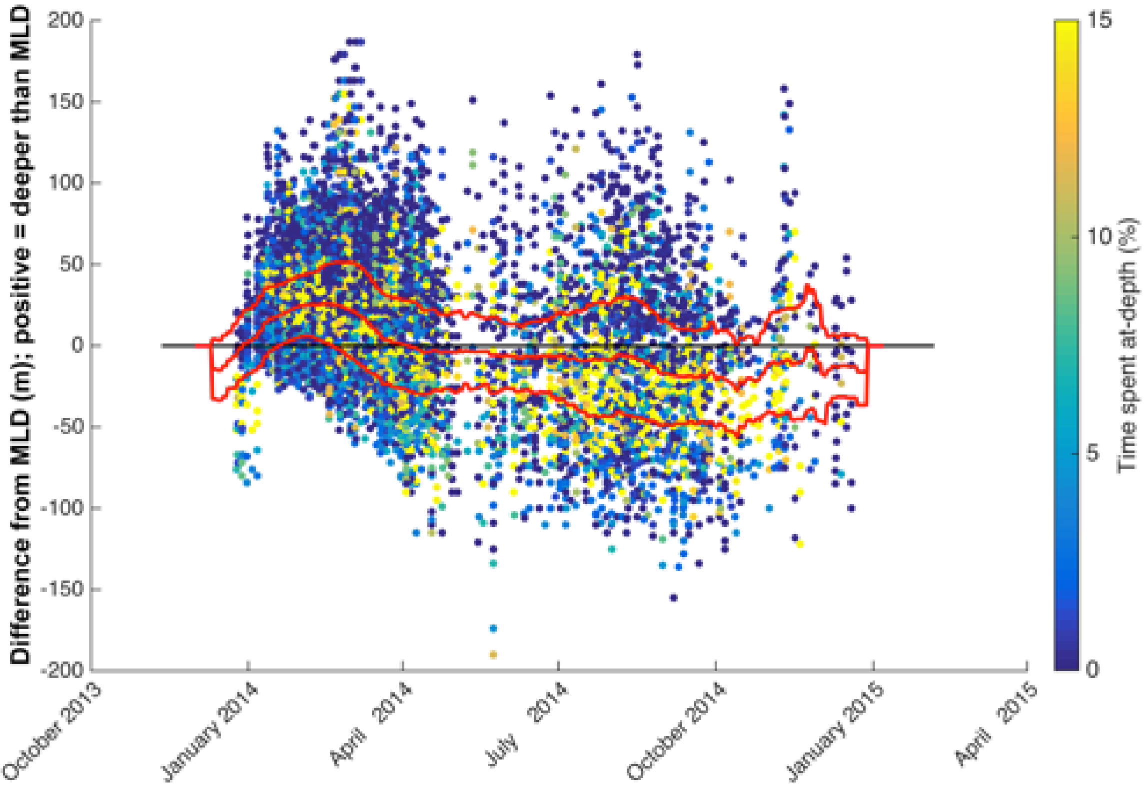

Figure 5. Times series of depth-difference between the 15 juvenile emperor penguin's depth and the mixed layer depth. The color scale represents the time spent at-depth. The middle red line corresponds to the average distance from the mixed layer depth (using a moving window of 30 days) weighted by the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