Dynamic fine-scale sea-icescape shapes adult emperor penguin foraging habitat in East Antarctica

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Keypoints

- Dynamic fine-scale sea-icescape in East Antarctica affects the foraging routes and effort of emperor penguins during the breeding season
- Emperor penguins used short-term ephemeral polynya openings to forage during the breeding season instead of using the persistent ones
- The breeding foraging habitat was consistent among months, years, sexes and sites despite the highly dynamic sea-ice environment

Keywords

emperor penguin; foraging ecology; polynya; fast ice; sea ice; icebergs

Abstract

The emperor penguin, an iconic species threatened by projected sea-ice loss in Antarctica, has long been considered to forage at the fast ice edge, presumably relying on large/yearly-persistent polynyas as their main foraging habitat during the breeding season. Using newly developed fine-scale sea-icescape data and historical penguin tracking data, this study for the first time suggests the importance of less-recognized small openings, including cracks, flaw leads and ephemeral short-term polynyas, as foraging habitats for emperor penguins. The tracking data retrieved from 47 emperor penguins in two different colonies in East Antarctica suggest that those penguins spent 23% of their time in ephemeral polynyas and did not use the large/yearly-persistent, well-studied polynyas, even they occur much more regularly with predictable locations. These findings challenge our previous understanding of emperor penguin breeding habitats, highlighting the need for incorporating fine-scale seascape features when assessing the population persistence in a rapidly changing polar environment.

Plain Language Summary

Polar ecosystems are threatened by future loss of sea ice. The availability of satellite sea-ice products has facilitated a better assessment of the impact of sea ice on polar species. Yet most studies have focussed on coarse spatial scale sea-ice products hampering an understanding of the mechanisms by which sea ice affects species. The development of fine-scale sea-ice products now provides an unprecedented opportunity to better understand the responses of sea-ice obligate species to climate change. The emperor penguin is an iconic species threatened by projected sea-ice loss in Antarctica. Here we used fine-scale satellite sea-ice observations to understand the emperor penguin's sea-ice habitat during the entire breeding and Antarctic winter season. Sea-ice characteristics affect both the foraging routes and effort of polar species, with consequences for their reproduction and survival, ultimately affecting population dynamics and species persistence. Emperor penguins dived at the edge of the landfast sea ice in cracks, flaw leads and open water areas called polynyas, formed by winds on both long and short time-scales. By using daily passive microwave observations, we identified that emperor penguins did not venture into the large/persistent polynyas but dived instead in the ephemeral polynyas associated with daily changes in wind direction.

1. Introduction

Antarctic sea ice extent has shown considerable inter-annual variability with marked regional variation (Zwally et al., 2002; Liu et al., 2004; Comiso and Nishio, 2008; Turner et al., 2009; Parkinson and Cavalieri, 2012; Hobbs et al., 2016; Meehl et al., 2019; Parkinson et al., 2019). Accordingly, Antarctic predator populations do not respond uniformly to changes in sea-ice coverage around the continent. In these populations, contrasting trends are observed that reflect regional differences in sea-ice conditions but also the variability in the species' ecology and biological requirements (Massom and Stammerjohn, 2010; Constable et al., 2014; Robertson et al., 2014; Southwell et al., 2015; Jenouvrier et al., 2017).

The availability of satellite sea-ice products has facilitated a better understanding of the impact of sea ice on polar species (e.g. seabirds: Jenouvrier et al., 2005; polar bears: Stern and Laidre, 2016; seals: Labrousse et al., 2018; whales: Herr et al., 2019). Yet most studies have focussed on coarse-resolution estimates of sea-ice concentration and extent at large spatial scales due to the limited resolution / availability of sea-ice products (e.g. emperor penguin: Barbraud and Weimerskirch, 2001; Jenouvrier et al., 2012). However, the sea-ice habitat that influences polar species is diverse at a fine scale (Ainley et al., 2010). Sea-ice characteristics affect both the foraging routes and effort of polar species (e.g. Le Guen et al., 2018), with consequences for their vital rates (reproduction: Massom et al., 2009; Ropert-Coudert et al., 2018; survival: Kooyman et al., 2007; Fretwell et al., 2019), ultimately affecting population dynamics (Ainley et al., 2010) and species persistence (Jenouvrier et al., 2014). Yet, we lack an understanding of these proximate mechanisms. The development of fine-scale sea-ice products now provides an unprecedented opportunity to better understand the responses of sea-ice obligate species to climate change within the sea-icescape.

Specifically, four broad habitat types can be distinguished within the seasonal sea-ice zone (from south to north) (Massom et al., 2010): (i) a coastal zone comprising a band of compact "landfast ice" in which persistent regions of open water (and/or thin ice or low sea-ice concentration) formed by dominant winds can be found that range from tens to tens of thousands of square kilometers in area, called coastal (i.e. latent heat) polynyas (Barber and Massom, 2007); (ii) the continental slope region and the Antarctic Slope Current, in East Antarctica near the boundary between fast ice and pack ice, which represent a cold, dynamic and topographically constrained structure where nutrient rich circumpolar deep water upwells onto the shelf (Jacobs, 1991); (iii) the "inner pack ice" zone comprising large floes separated by flaw leads; and finally (iv) the highly-dynamic "marginal ice zone", which typically extends hundreds of kilometers north to the ice edge (< 15% ice cover; Worby et al., 2013), and is generally made up of small floes and diffuse ice conditions. In the first two habitats, the presence of grounded icebergs is an important sea-icescape feature (e.g. Smith et al., 2007; Chambert et al., 2012; Joiris, 2018).

The emperor penguin (*Aptenodytes forsteri*) is an Antarctic circumpolar sea-ice obligate species that relies on sea ice throughout its life cycle. Emperor penguins forage under the winter sea ice at two key periods of their life cycle: after egg-laying (~late May until mid-July) when females are rebuilding their reserves while the males incubate eggs; and during the chick provisioning period from mid-July to December when both males and females alternate periods of foraging with periods caring for the chick (Prévost, 1961). Several studies hypothesized the use by emperor penguins of open water areas between the landfast ice and the inner pack ice and the importance of fast ice extent on penguin access to the water, which affects their performance at-sea as well as breeding success (Ancel et al., 1992; Kooyman et al., 1993; Kirkwood and Robertson, 1997a, 1997b, Wienecke and Robertson, 1997; Rodary et al., 2000; Zimmer et al., 2007; Massom et al., 2009). However, most of these studies covered only one to three of the six months of the breeding season, used coarse sea-ice concentration data or prevalent fast ice conditions, and did not quantify the sea-ice habitat use especially because of the lack of fine resolution satellite sea-ice products.

In this study, we assess how emperor penguins respond to fine scale sea-ice habitat over their entire breeding season (May-November) in two East Antarctic colonies. In the dynamic and changing seasonal sea-ice environment, we assess for the first time whether the habitat is consistent among months, years, and sites but also between sexes. Specifically, we investigate (i) whether penguins use large/yearly-persistent coastal polynyas or ephemeral (i.e. daily to monthly scale) polynya openings between the pack ice and the fast ice to forage; (ii) the effect of the fast ice extent distribution on their movements; (iii) whether they use the continental slope to forage; (iv) whether the presence of icebergs influences their travelling paths; and finally (v) whether patches with thin ice, a proxy of recent/future open water areas, are preferentially used. To do so, we used concomitant historical tracking data of 47 breeding emperor penguins in two different colonies in East Antarctica (previously published in Kirkwood and Robertson, 1997a, 1997b; Rodary et al., 2000; Wienecke and Robertson, 1997), with high-resolution fast ice satellite images and unique sea-ice production metrics to identify ephemeral polynyas.

The novelty of this research lies in using fine-scale sea-ice products only accessible through multidisciplinary approaches in order to understand how complex and changing sea-ice features affect an Antarctic predator foraging movements at sea (Meijers et al., 2019). Our study is the first to quantify the habitat use, and combines tracking data collected for emperor penguins raising chicks over two years at two colonies along the East Antarctic coast. In doing so, we provide more accurate information on the foraging habitat requirements for this key Antarctic species.

2. 2 Data and Methods

2.1 Logger deployments

A total of 56 breeding emperor penguins were instrumented with trackers at the Auster colony (67.38°S, 64.07°E) at the Mawson Coast in 1993 and 1994, and at the Pointe Géologie colony (Dumont d'Urville station, 66.67°S, 40.03°E) in Terre Adélie in 1996 and 1997 (see the supporting information, Tables S1, S2 and S3). After filtering the tracks, 47 penguin tracks (23 females, 15 males and 9 individuals of unknown sex; Table S1) were usable for further analysis. For more details about animal handling, logger deployment and the filtering process of the location data, see the supporting information.

2.2 Sea ice

Visible (when available) or thermal infrared images showing fast ice extent were obtained from the AVHRR Coastal Atlas of East Antarctica (Michael et al., 2003) with a 1.1 km resolution. Data in the Atlas are presented for five selected areas along the East Antarctic coastline and named according to the main Antarctic station in the region. In this study, we used the data from Mawson and Terre Adélie areas. The Atlas provides one image per month over an 8-year period (1992-1999). The months of July, August and September 1994 are missing in the Atlas, so, instead we used original AVHRR images from Global Area Coverage (GAC) with a resolution of 4 km. Images were sorted based on their cloud coverage and the best image within a month was selected. On each monthly image, the fast ice contour was drawn using the function *locator* in the R package graphics. From this, fast ice polygons were created using the functions *Polygon*, *Polygons* and *SpatialPolygons* from the R package sp (Pebesma and Bivand, 2005; Bivand et al., 2013). Occasionally, the thermal infrared image indicated that the fast ice was warmer (i.e. thinner) than in previous/upcoming images, suggesting some recent open water regions within the given month. We decided to exclude these regions to be as conservative as possible, i.e. open regions were categorized as "not fast ice". The distances between the penguin locations and the edge of the fast ice were then computed using the function *spDistsN1* of the R package sp. Rasters of distance to the fast ice extent and the upper continental slope were calculated using the function *distanceFromPoints* of the R package raster (Hijmans, 2017). Our analysis would have been improved by analyzing fast ice satellite images weekly instead of monthly. However, for the winter months, cloud cover did not allow regular clear images for a consistent weekly analysis. Thus, the time spent near the fast ice edge may have been underestimated by monthly fast ice delineations missing open water areas through the process of fast ice formation within a given month.

Coastal latent heat polynyas are regions of open water and/or thin ice or low sea-ice concentration (recurrent and/or persistent), ranging from tens to tens of thousands of square kilometers in surface extent (Barber and Massom, 2007). They are mechanically formed in shelf regions of divergent sea ice due to dominant winds, oceanic currents, and/or barriers (e.g. ice shelves, icebergs) blocking the passage of pack ice, and promoting the formation of new sea ice from the heat lost from the ocean to the atmosphere (Morales and Maqueda, 2004; Tamura et al., 2016). Here, we defined these latent heat polynyas at two temporal scales: a) at the scale of the year (i.e. March to October through the sea-ice season), large recurrent and persistent in time, well studied, found adjacent to the continental margin; b) at the daily to monthly scale, ephemeral openings found both close to the coast but also nearby the fast ice edge, close to the continental slope, that can be small openings or extended areas from persistent polynyas. These ephemeral polynyas forming in these locations are indeed latent-heat polynyas (and not bathymetry-driven warm water upwelling-associated sensible heat polynyas, e.g., Jacobs & Comiso (1989)) by observing the presence of frazil-ice streaks in recent Sentinel-1 Synthetic Aperture Radar imagery (not shown). We used thin ice thickness estimates from passive microwave polarization ratio (Tamura et al., 2007) to identify thin ice areas (< 0.2 m), as a proxy of recent/future open water areas. It is worth noting the uncertainty associated with thin ice thickness estimates - the spread around the line linking polarisation ratio to thickness is considerable. Moreover, this thin ice zone becomes at any time solid ice again due to sea-ice growth by cold air temperatures and sea ice rafting/ridging by ice convergence by wind. Thin ice patches and yearly polynya delineations were determined as detailed in Labrousse et al. (2018) using estimated thin ice thickness (expressed in m) and sea-ice production (expressed in m.y^{-1}). From Labrousse et al. (2018), we added daily polynya delineations. We used a sea-ice production threshold of 0.002 m.d^{-1} to identify any patch of open water. Thin ice thickness and sea-ice production data with a resolution of 12.5km were obtained from Tamura et al. (2007, 2008, 2011) and updated from Tamura et al. (2016).

Iceberg locations for both colonies were digitised from RAMP AMM-1 SAR Image Mosaic of Antarctica (Jezek et al., 2013).

Given the uncertainties associated with penguin locations before the filtering process (Table S4) and fast ice delineation, we investigated the time spent within 10 km of the fast ice edge and 3 km of the iceberg centroids.

2.3 Niche modelling

To model habitat suitability for breeding emperor penguins and explore their sea-ice niche with respect to colony sites, seasons and sexes, we used the "ecological niche factor analysis" (ENFA; Hirzel et al., 2002). Theoretically, the analysis of habitat selection corresponds to the comparison of environmental conditions of used sites (sites where the species is present) with environmental conditions of available sites (sites where the species could be present; Aarts et al., 2008). The study area is discretized into resource units (corresponding to pixels of a raster map). Each resource unit is characterized by several environmental variables; here we used four different rasters of 6.25 km resolution: the distance between a pixel and the fast ice extent (corresponding to the area where an open water area is observed between pack ice and fast ice); the distance to the upper part of the continental slope; the cumulative number of days within a month where a daily polynya was observed in a pixel (sea-ice production greater than 0.002 m.d^{-1}); and the cumulative number of days within a month where thin ice (sea ice with thickness less than 0.2 m) is present within a pixel. There are two units describing the availability and the utilization weights of the resource unit by the penguins. Here, we defined equal availability weights for all resource units, and the utilization weight was defined by the sum of the time spent per pixel by all the penguins (6.25 km resolution). We considered the habitat from May to October (although some tracking data lasted until December in 1996). November is considered the end of the breeding season and December could either correspond to remaining chick provisioning and/or the departure of chicks and adults from the colony; as such November and December tracking data may not be fully representative of the breeding foraging habitat (e.g. Rodary et al., 2000). Penguin tags were not always retrieved before the penguins returned to the colony, so some individual tracking data were recorded while the penguins were at the colony. To analyse the time spent out of the colony, a reliable proxy of foraging intensity and feeding success (Bost et al., 1997), we set to zero the time spent within a radius of 5 km around the colonies.

The principle of the ENFA analysis is to first compute the marginality vector. This vector gives the direction and the magnitude from which the distribution of habitat use differs from the distribution of the habitat available in average. Then the cloud of resource units is projected on the hyperplane orthogonal to the marginality vector. Next, the direction is found in this subspace where the specialization (minimizing the ratio between the variance of the distribution of availability weights and the variance of the distribution of utilization weights) is the largest, i.e. which proportion of the habitat available is used. Finally, a "Mahalanobis distance factor analysis" (MADIFA) was used in order to describe the monthly habitat selection for each site. The methods and results are presented in the supporting information.

3. Results

3.1 Summary of the tracking data

A total of 9962 locations from 47 breeding emperor penguins were recorded in 1993, 1994, 1996 and 1997. Detailed metrics of the tracking data are available in the supporting information, Table S1 and S2. Trackers recorded trips from 8 to 146 days (average ± sd of 55 ± 35 d). The maximum distance a penguin travelled was 5058 km (average ± sd of 1024 ± 903 km) and the furthest distance from the colony was 1643 km (average ± sd of 234 ± 325 km) (Figure 1).

3.2 Time spent in different habitats

Of the total time spent away from the colony (T_{oc}), penguins spent 27% crossing the fast ice to reach and return from open water and 33% of the T_{oc} within 10 km of the fast ice edge (on the fast ice walking or in the water). Once they reached water, they spent 23% of the T_{oc} inside ephemeral polynya openings adjacent to the fast ice edge (all individuals cumulatively between May and October; Figures 2, 3 and 4a; animations S1-S4); these were either small openings or extended areas of large coastal polynyas. Adult emperor penguins did not visit the large, yearly-persistent coastal polynyas adjacent to the continental margins except on one occasion, when one penguin (from Pointe Géologie colony) passed through the Mertz polynya (Figure 1b). Iceberg centroids were located within the fast ice, near the fast ice edge and in pack ice regions further offshore. The penguins spent 17% of the T_{oc} within 3 km of iceberg centroids (all individuals cumulatively between May and October).

3.3 Qualitative description of habitat use

Pointe Géologie colony. From May to July 1996, when females were at-sea, they mostly used the region northeast of the colony at the edge of the fast ice sometimes overlapping with the large polynya in the east of the region (Figures 2a, b, c; S2a, b, c). This region is of particular interest for its complex bathymetry, ranging from 200 to 500 m. In August 1996, when males and females started to alternate trips to sea, all individuals (n=5) spent most of their time in an open water region within the fast ice, not identified as a polynya by the sea-ice production data (Figures 2d and S2d; i.e. lighter colour of the fast ice indicating that this region was opened at the beginning of the month and closed in the month); from September to October 1996, they used a V-shaped inlet in the fast ice to the northwest of the colony, which lay over an oceanic trough (depth of ~700 to 1000 m) between the Adélie and Dibble banks and where ephemeral polynya openings formed (Figures 2e, f; S2e, f). This inlet cuts across the continental shelf to the northwest of Pointe Géologie and almost reaches the coast at the colony. This area is the site of ephemeral mid-season breakouts (see Massom et al., 2009). In September 1997, the penguins both used the open water region within the fast ice in front of the colony as in 1996 but also foraged at the edge of the fast ice in daily polynya openings (Figures 2h; S2h). The V-shaped ice break-out west of the colony in October 1996 was not present in 1997. In its absence, the penguins foraged mainly to the northeast of the colony at the edge of the fast ice sometimes overlapping with the large polynya on the east side of the region in October 1997 (Figures 2i and S2i).

Auster colony. The situation was different from the Pointe Géologie colony. From May to October in 1993 and 1994, penguins foraged at the edge of the fast ice and spread along the edge with a slight preference for the east side of the region where both small and large polynya openings occurred (Figures 3 and S3).

3.4 Quantitative modeling of habitat use

The ENFA identified a strong marginality (x-axis) / specialization (y-axis) pattern in the data (the two first axes represented 54.5% and 39.8% of the variance of the time spent per pixel), with a substantial contribution of the distance to the fast ice and continental slope edges and the number of days when polynyas were present (Figure 4b). However, the presence of thin ice patches had a weak influence. Penguins spent most of their time at the shortest distance from the fast ice edge and the upper edge of the continental slope (Figure 4d, e); this corresponds to the open water areas between the fast and pack ice, i.e., cracks, leads or the ephemeral polynya openings that showed a positive effect on the time spent. Overall, there was a clear difference between the habitat available and the habitat used by the penguins (Figure 4b-e). The distance to the fast ice and continental slope edges contributed to both the marginality and the specialization. Specifically, we observed a negative correlation for the marginality (i.e. penguins spent more time at shorter distances). For the specialization, only the absolute value is important: the variance of the habitat available is larger than the variance of the habitat used (i.e. the penguins target a narrow range of distances from the continental slope and the fast ice edge). The number of days when polynyas were present only influenced the marginality, i.e. penguin spent more time in areas with ephemeral polynya openings but did not show any preference for areas with a certain number of days the polynyas were open.

The habitat available differed slightly between months (see the supporting information, Figure S4a) as did the habitat used (Figure S4b). The ellipse of habitat used in May had the smallest area, restricted to the shortest distance to the fast ice and the upper continental slope edges. From June to October, the used habitat ellipses grew larger with months, with slightly longer distances from the fast ice and the continental slope edges. No strong difference was observed between the two sites and between sexes, neither in the habitat availability nor in the habitat use (see the supporting information, Figure S4c, d, e, f). Larger differences between the two colonies were observed in habitat availability compared to habitat use, meaning that foraging individuals reached the same environmental conditions despite differences in habitat availability between the two sites.

4. Discussion

This study assesses the sea-ice habitat of a sentinel species of Antarctic ecosystems combining historical and modern state-of-the-art sea-ice products with historic tracking data of movements at-sea over different months, years and sites. The selection/use of habitat was very consistent among months, years, sexes and sites. This indicates that emperor penguins consistently use areas with specific environmental properties, even in a dynamic sea-ice habitat. To our knowledge, very few studies of Antarctic marine predators compared and quantified such ecological niches using tracking data of different breeding sites, years and sexes simultaneously (but see e.g Ainley et al., 2004; Hindell et al., 2016).

Emperor penguins foraged in ephemeral polynya openings between the fast ice and the pack ice areas near to or over the continental slope, instead of using the well-studied persistent polynyas, such as the Mertz Glacier or Cape Darnley polynyas. These ephemeral openings are only detectable with fine temporal and spatial scale sea-ice products. Persistent polynyas are driven by prevailing wind speed and direction while ephemeral openings occur due to temporary shifts in the wind direction. Different studies hypothesized the use of polynyas between the fast ice edge and the pack ice over or near the continental slope as a prime foraging habitat during the breeding season (Ancel et al., 1992; Kirkwood and Robertson, 1997a, 1997b; Wienecke and Robertson, 1997; Rodary et al., 2000; Zimmer et al., 2007). However, the distinction in terms of the temporal characteristics and location of the polynya use by penguins has never been assessed in previous studies.

Using coarse temporal products at an annual scale (i.e. March-October) one could have concluded that penguins do not use polynyas, but with fine scale, daily sea-ice products we were able to show that ephemeral polynya openings comprised a large component of penguins' foraging habitat. We speculate that penguins did not visit large/yearly persistent polynyas for two possible reasons. First, persistent/yearly polynyas have higher sea-ice production than small/ephemeral polynyas. This has implications on the mixing of the water column and in turn on the prey availability; the deepening of the winter mixed layer is function of wind and sea-ice formation. Polynyas with minor sea-ice production will have a relatively shallow winter mixed layer while in polynyas with strong sea-ice production, the winter mixed layer extends all the way to the bottom seafloor. Penguins may be advantaged by hunting prey aggregated at the boundary of the Winter Mixed layer in ephemeral polynyas rather than foraging in a homogeneous water column in yearly/persistent polynyas likely associated with strong sea ice production (Williams et al., 2011; Labrousse et al., 2018). In addition, ephemeral polynyas are more likely to sustain food resources for emperor penguin than persistent large polynyas. Several studies in the Ross sea polynya identified the south-central waters, the most deeply mixed due to extremely high sea-ice production, as a virtual "desert" in terms of birds and mammals, while most top predators were observed in the marginal ice zone ringing the polynya (Ainley et al., 1984). Short-term polynya openings, ringing the yearly/persistent large polynyas or small areas created by change in the wind direction, may be preferred by emperor penguins as they may harbor higher quantities of fish and krill than persistent polynyas' central waters. Indeed, in the Ross Sea/Terra Nova Bay polynyas, well-lit waters often harbor more diatoms compared to central mixed waters, due to their higher nonlimited growth rate and resistance to photo-inhibition (Karnovsky et al., 2007). Diatoms were found to dominate the phytoplankton community in the marginal ice zone of the Ross sea polynya and represented a major food source for krill (Quetin and Ross, 1985; Quetin and Ross, 1991). In contrast, the genus *Phaeocystis* was found to dominate the more deeply mixed open waters of the Ross sea polynya due to an ability to grow faster at variable irradiance levels. From acoustic surveys, krill, the staple of the food chain, is presumably mostly confined to the edge of the marginal ice zone in the Ross sea polynya (Azzali and Kalinowski, 1999), where it preferentially feed on diatoms over the genus *Phaeocystis* (Haberman et al., 2003). These processes may explain why emperor penguins spent more time in the ephemeral polynya openings instead of the large/persistent polynyas associated with deeply mixed waters; the former being probably associated with a diatom-based trophic chain based fuelling a higher secondary production. Finally, these persistent polynya openings were slightly further away from the two colonies we considered than the ephemeral polynyas were.

Penguin locations also occurred outside the polynya areas, near the fast ice edge, likely in small open water areas such as cracks or flaw leads. Fast ice extent is thus influencing emperor penguin's ability to acquire resources during the breeding season. Indeed, a fast ice breakout event over a large section of the Mawson Coast coincided with a change in the diet of emperor penguins (Kirkwood and Robertson, 1997b) from continental pelagic slope species to benthic shelf species. Formation of fast ice throughout the season is complex and may be non-symmetrical. This was particularly clear for the Pointe Géologie colony, where in 1996 the fast ice broke out over the deep-water trough to the north-northwest of Pointe Géologie; this is likely to happen when storms cross the region (Massom et al., 2009). The fast ice extent should then be assessed locally (i.e., for each colony) and its variability should be taken into account to understand and predict emperor penguin responses to climate change.

The formation, position and extent of the fast ice may influence the type of foraging strategy used by emperor penguins (benthic versus pelagic, including very shallow dives of 0-30m). This has important implications for their foraging performance through the type of prey they may be able to catch, whether krill, squid or fish. The Antarctic krill species *Euphausia superba* lives on the continental slope and offshore waters while on the shelf this species is replaced by crystal krill *E. crystallorophias* (smaller than *E. superba* and not abundant in the emperor penguin diet) and the Antarctic silverfish *Pleuragramma antarctica* (Kirkwood and Robertson, 1997b). Regions with particular bathymetric features, such as the one northeast of the Pointe Géologie colony with continental slopes from 200 m to 500 m depths (used by adults in 1996 and 1997 and previously observed by Ancel et al. (1992) and Zimmer et al. (2007) in 1990 and 2005, respectively), or the continental slope for the Auster colony, may aggregate prey where local upwelling stimulates primary production (Nicol et al., 2000).

Resource acquisition during the breeding season is critically important for raising offspring successfully. A strong correlation between fast ice extent and the breeding success of emperor penguins was found at the Pointe Géologie colony (Massom et al., 2009). However, there was no relationship between fast ice and breeding success at another colony at Taylor Glacier ~ 150 km west of Auster (Robertson et al., 2014) highlighting the complex interactions between environment and penguin foraging behavior, and their consequences for breeding performances. We hypothesise that the fast ice extent may be much more constant across years at Taylor glacier than it is at Pointe Géologie, leading to higher and less variable breeding success. This may explain why there is no relationship with breeding success and fast ice extent while emperor penguins still likely use a similar sea-ice habitat.

Some differences in the sea-icescape were observed between the sites on the satellite images. Particularly, fast ice formation creating an inlet or fast ice breakout over the deep-water bathymetric trough in Terre Adélie and the close proximity between the fast ice edge and the continental slope at the Mawson Coast led to slight differences in the habitat availability between the two sites. The sea-ice habitat also differs across different sectors of Antarctica where emperor penguin colonies are located. For example, in the Ross Sea sector, the fast ice edge (e.g. Cape Crozier, Franklin and Coulman Islands, Cape Roget and Washington) is much closer to emperor penguin colonies than in East Antarctica, and shows different configurations relative to the continent and the ice shelves (Ancel et al., 1992; Kooyman et al., 1993; M. Larue, pers. comm). However, at our two study sites the ecological niche remained consistent, and this indicates that in a dynamic habitat the relationship between this species and its foraging environment remains stable, defining its ecological niche.

Finally, fields of small icebergs which define the limits of stable fast ice extent are generally quite static (Fig. 6 in Fraser et al., 2010); however, on short (daily to monthly) time-scales, changes in fast ice distribution may occur in response to changes in wind properties (e.g., Fraser, 2011), precipitating commensurate changes in adjacent polynya size and production (e.g., as shown in the Cape Darnley polynya by Fraser et al., 2019). Moreover, larger changes in the coastal configuration (including fast ice and polynya distribution) are precipitated by the passage/grounding/ungrounding of large tabular icebergs (e.g., the grounding of B15 and C16 west of McMurdo Sound in the early 2000s; Kim et al., 2018). These events are currently impossible to predict, due to the stochastic nature of iceberg calving and grounding processes (Kim et al., 2018). The response of predators to changes in the sea-icescape is governed by their physiological plasticity to tolerate change, adapt to new environmental conditions or disperse/migrate to alternative foraging grounds that enable survival (Jenouvrier et al., 2017). Our study calls for more research on the role of Antarctic polynyas (ephemeral or persistent water openings under wind action) and fast ice on the at-sea movements of emperor penguins in different sectors of Antarctica during the breeding season.

5. Conclusion

Using fine scale sea ice products we found that emperor penguins spent time foraging in ephemeral (i.e. daily to monthly scale) polynya openings instead of large/yearly-persistent coastal polynyas (question (i)). Our study calls for more research on the geophysics of Antarctic polynyas (ephemeral or persistent water openings under wind action) to better understand the impact on the ecosystems. In addition, we found that emperor penguins spent time diving and foraging at short distance from the fast ice edge (ii) and the continental slope (iii), regardless of colony location. To understand better the consequences on breeding performance, hence population persistence, it is thus important to characterize how fast ice mean and variability, as well as the presence of topographic features vary across different region. Finally, there is no clear influence of the presence of icebergs (iv) and patches with thin ice (v), although a previous study has shown that giant iceberg can strongly impact the reproduction and survival of upper level predator (seals and penguins).

This study highlights (i) the important role of geophysics in ecological studies; (ii) the need for more multidisciplinary approach, combining historical satellite sea ice images, state-of-the-art sea-ice products with revisited, historical data on the movements of predators at-sea; (iii) the unprecedented opportunity to use geoscience (e.g. sea ice and ocean-atmosphere interactions) to better understand polar species responses to the sea-icescape and its variability. Quantifying such sea-ice niches is important for understanding the extinction risk predicted for polar species under climate change (Thomas et al., 2004). Moreover, this is essential from regional to circumpolar scales, if we are to provide conservation bodies with relevant information on the habitats that must be preserved for the sake of wildlife in the Southern Ocean.

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Figures

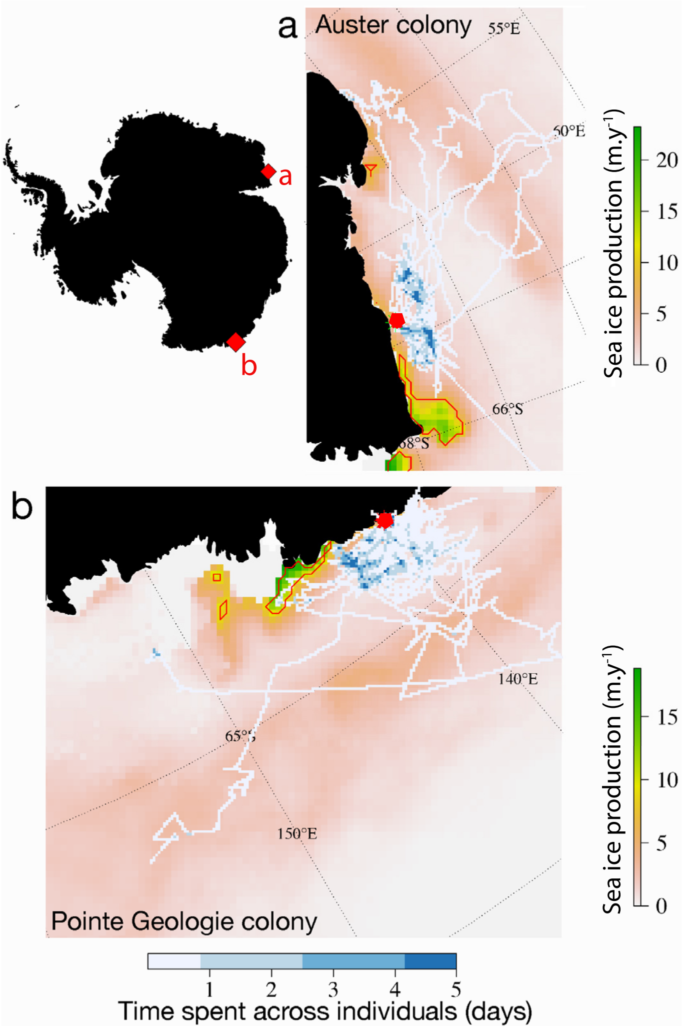

Figure 1. Habitat usage (hours spent by all individuals per 5 km^2 grid cell) of 47 breeding emperor penguins equipped at (a) Auster (1993, 1994) and (b) Pointe Géologie (1996, 1997) colonies relative to the presence of recurrent yearly coastal polynyas (green indicates greatest open water). For each colony, annual sea-ice production (determined from March through October) was averaged between the two years and the polynya definition (delineated in red) was determined using a threshold of 8 m.y^{-1} of sea-ice production. The colony locations are represented by red polygons.

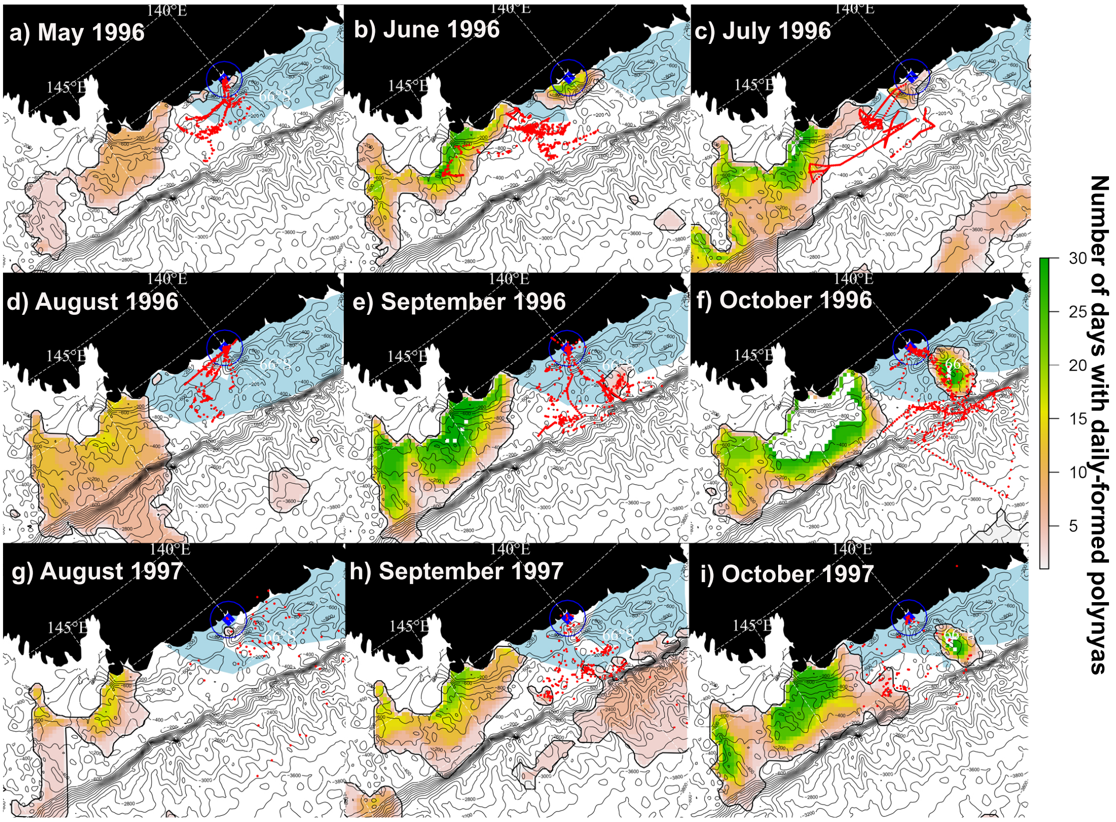

Figure 2. Polynya usage of 29 breeding emperor penguins equipped at Pointe Géologie in 1996 and 1997 (locations = 4373). Each map represents the number of days of presence within each month of daily-formed polynya based on a sea-ice production threshold of 0.002 m.d^{-1} (grid cell of 6.25 km × 6.25 km). Penguin locations are represented by red dots. The monthly fast ice extent is represented by a blue polygon and was obtained from the fast ice images from the AVHRR Coastal Atlas of East Antarctica with a 1.1 km resolution. Sometimes the polynya delineation overlapped the fast ice extent as one is at a daily-scale while the other is at the monthly scale. The colony location is represented by a blue polygon and a radius of 30 km around the colony is represented by a blue circle. The bathymetry contours are from ETOPO1 (1 arc-minute). For illustration purposes, November 1996 and 1997 were not represented due to insufficient data.

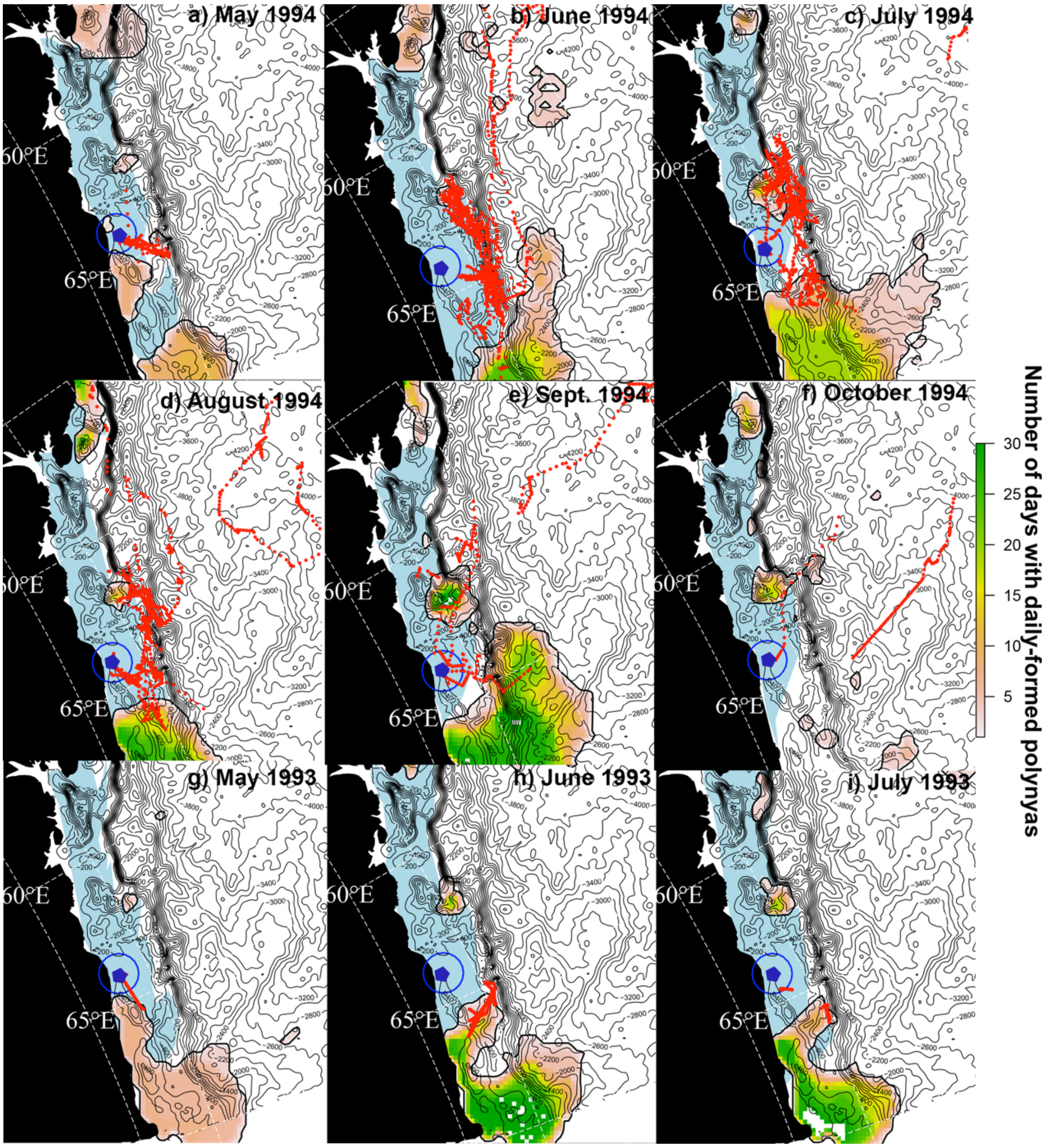

Figure 3. Polynya usage of 18 breeding emperor penguins equipped at Auster in 1993 and 1994 (locations = 5289). Refer to Figure 2 for the legend description. For illustration purposes, August 1993 and November 1994 were not represented due to insufficient data.

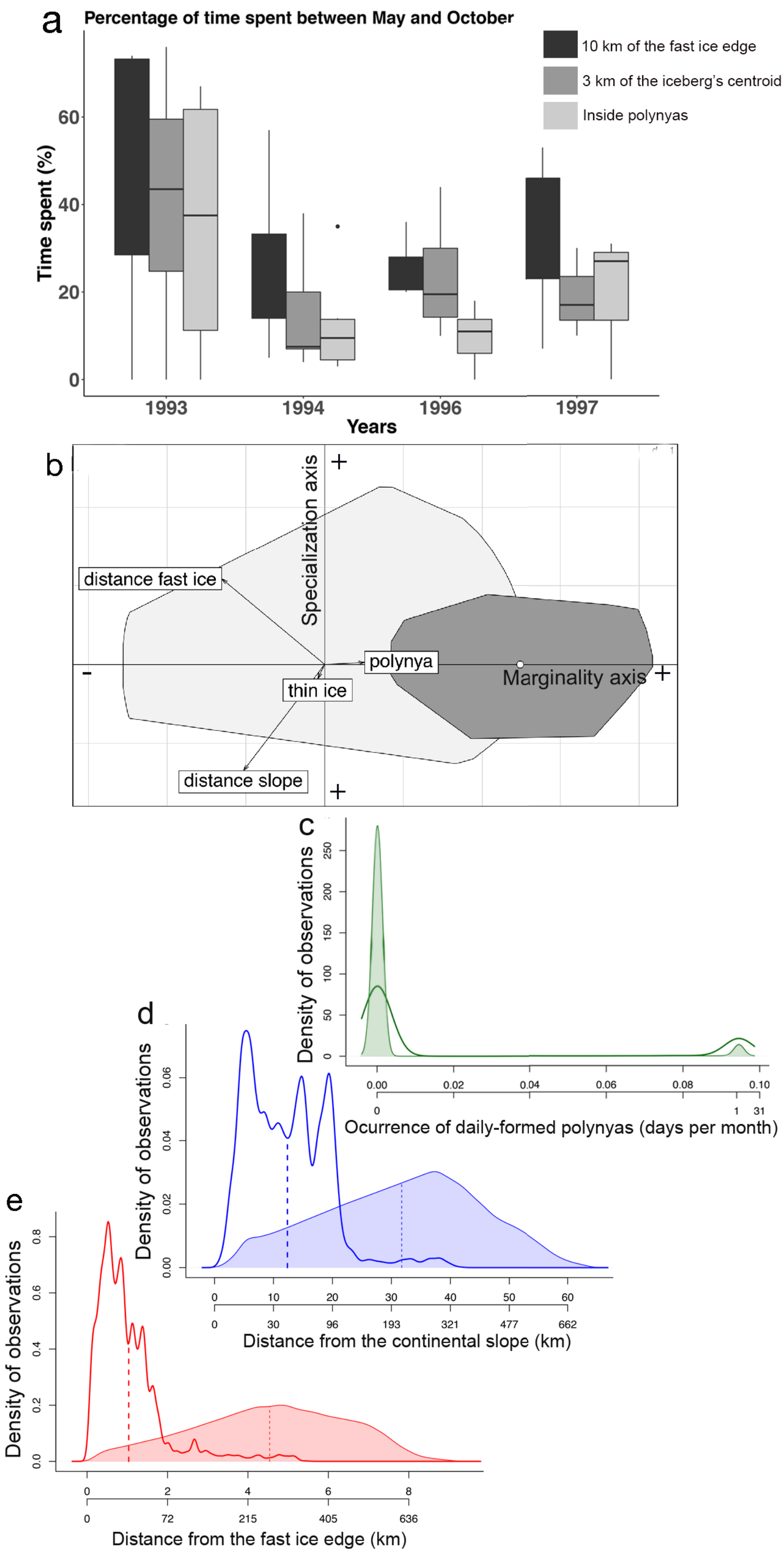

Figure 4. Time spent between sea-ice habitats and ecological niche modelling for the 47 breeding emperor penguins tracked in 1993, 1994, 1996, 1997 at the Auster and Pointe Géologie colonies. Panel (a) shows the time spent among years by adult emperor penguins within 10 km of the fast ice edge on top of ice or in the water,

within 3 km of the icebergs' centroid and daily-identified polynyas. The time spent (expressed in %) represented by a boxplot was computed per month between May and October for each year. Panel (b) shows the main result of the Ecological Niche Factor Analysis with the four variables considered: distance from the fast ice and continental slope edges, the occurrence of daily formed-polynyas and thin ice patches. The abscissa axis represents the marginality axis (the direction and the magnitude, positive or negative, from which the distribution of habitat use - displayed by a dot - differs from the distribution of the habitat available – the origin of the axes). The ordinate axis is the specialization axis (represented by absolute values, it shows which proportion of the habitat available is used; large values represent a narrow and specialized used, while small value represent a larger used of the habitat available and less specialized). The dark grey polygon shows the position of the distribution of the habitat used, whereas the light grey polygon displays the position of the distribution of the habitat available. Panels (c), (d) and (e) represent the probability density distribution of the habitat available (thinner colour-filled curves) versus the habitat used (thicker non-filled curves) for the transformed variables used in the Ecological Niche Factor Analysis: the occurrence of daily formed-polynyas (expressed in days per month), the distance from the fast-ice edge and the continental slope (expressed in km) respectively. The x-axis displays both the transformed and observed values.