Adélie penguins' extensive seasonal migration supports dynamic Marine Protected Area planning in Antarctica

Jean-Baptiste Thiebot[a,*], Yan Ropert-Coudert[b], Thierry Raclot[c], Timothée Poupart[b,d], Akiko Kato[b], Akinori Takahashi[a]

[a] *National Institute of Polar Research, 10-3 Midori-cho, Tachikawa, Tokyo, Japan*
[b] *UMR 7372 CEBC, CNRS – La Rochelle Université, Villiers-en-Bois, France*
[c] *UMR7178 IPHC DEPE, CNRS – Université de Strasbourg, Strasbourg, France*
[d] *School of Life and Environmental Sciences, Deakin University, Burwood, Victoria, Australia*

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ABSTRACT

Spatiotemporal dynamics of ecosystems can challenge the pertinence of Marine Protected Area (MPA) planning. Seasonal environmental changes are extreme in polar regions, however MPA planning in East Antarctica relies mostly on species' summer distribution only. Thirteen Adélie penguins were tracked from Ile des Pétrels (Terre Adélie), and their seasonal distribution and behaviour were compared to the proposed "D'Urville Sea-Mertz" MPA. During the phase of high food-demand preceding moult, penguins used mostly (68.4%) this proposed area. However, following autumnal sea ice extension, penguins migrated north-westwards: overall, 73% of their locations were outside the MPA proposal, and this was up to > 99% during winter (in July), the season when penguins maximized their dive depth and time (August and September, respectively). This study thus supports the proposal of implementing a "krill no-take zone" policy in this MPA, in line with the pre-moult foraging of these krill predators in this area. Further protection of the year-round habitats of migratory Adélie penguins could be achieved by inter-connecting the East Antarctic MPA proposals along the ice edge during winter, thereby mirroring the ecosystem's seasonal dynamics.

1. Introduction

In 2010, the 192 State Parties to the United Nations' Convention on Biological Diversity (CBD) adopted a Strategic Plan to halt biodiversity loss and ensure the sustainable and equitable use of natural resources (www.cbd.int/sp/targets/). Among these measures, the CBD established a target of 10% of the marine and coastal regions to be protected by 2020 ('Aichi Target 11'). In this context, proposals for new Marine Protected Areas (MPAs) are implemented at an accelerating pace [1,2]. However spatiotemporal dynamics of ecosystems can challenge the pertinence of the designated areas.

The polar regions are Earth's extreme seasonally contrasted habitats, with dramatic changes in daylight duration and sea ice coverage [3]. Accordingly, organisms from high-latitude regions may undertake extensive migrations to track seasonally suitable habitats. This is especially prevalent in the long-lived megafauna, including seabirds, for which this redistribution at sea across the non-breeding season is critical for survival [4].

In the Indian sector of the Southern Ocean, Australia, France and the European Union jointly proposed to establish a network of MPAs: the East Antarctic Representative System of MPAs ('EARSMPA'; [5]). The current proposal aims to adequately protect representative areas of coastal, open ocean and seabed biodiversity in East Antarctica, over three zones [6]. These include habitats that are vulnerable to disturbance and play an important ecological role, notably trophic, such as fish nursery grounds and foraging areas for marine mammals and penguins [7,8].

Among the three proposed areas, the D'Urville Sea-Mertz region (136–148°E) is considered as an oasis of biodiversity at the scale of Antarctica, especially regarding endotherms. Among the 14 species of seabirds breeding in Antarctica, eight nest on Pointe Géologie archipelago (Terre Adélie), making it one of the key Antarctic sites for bird diversity [9]. Adélie penguins (*Pygoscelis adeliae*), consuming mostly krill [10], are the most abundant seabird locally with about 40×10^3 breeding pairs, half of which breed on Ile des Pétrels alone. Although Adélie penguin populations have grown during recent decades in East

Antarctica [11], two episodes of total breeding failure at Ile des Pétrels were recently reported [12,13]. Such cases illustrate the vulnerability of this ecosystem to chaotic environmental events [14], thus calling for the regional implementation of MPAs to prevent additional disturbance. In this context, the proposed EARSMPA is expected to be instrumental, with scientists suggesting a prohibition on fishing for krill in the D'Urville Sea-Mertz area to monitor long-term ecosystem changes [6]. If implemented before any fisheries begin in the region, the EARSMPA would be a unique system to disentangle the effect of climate change and human direct impact through fisheries. Fisheries can indeed severely impact predator populations: directly through prey stock depletion [15] and indirectly through incidental capture of non-target species [16]. Industrial krill fisheries in Antarctica may bring the risk of a limiting resource for krill-eating predators, which may already undergo perturbed population dynamics under reduced prey availability caused by natural variability [17].

Antarctic land-based predators have long been used as bio-indicators in ecosystem monitoring programmes, as they are accessible components of the Antarctic marine ecosystem [18]. Situated at the upper trophic levels, these consumers may indeed reflect variations in prey availability or perturbations in the ecosystem functioning, through their foraging behaviour, distribution and/or demography [17,19]. Adélie penguins are notably considered as prime bio-indicators of Antarctic marine ecosystems because of their tight association with sea ice, and their distribution at sea can be used to infer the areas of high biological productivity [20]. However, tracking data used in the EARSMPA proposal to infer Adélie penguins' at-sea distribution relates to the summer breeding season only. Adélie penguins may yet expand their distribution range during winter (e.g., [21]), although this is not always the case (e.g., [22]). In addition, penguins start the non-breeding season with a phase of intensive feeding during which the daily energy expenditure peaks [23]. This period prepares for penguins' moult, an energy-intensive process during which they must remain out of the water, surviving exclusively off their body reserves for up to three weeks [24]. Prey abundance during the pre-moult phase is therefore crucial for the penguins' annual survival. Furthermore, species distribution models, which may be useful in predicting animal movements from one population to another, show poor prediction power outside the breeding period [25]. Hence, tracking penguins' seasonal movements is needed to examine the genuine relevance of the MPA proposal to the year-round requirements of local penguin populations.

In this study, non-breeding movement and activity data were collected in Adélie penguins from Ile des Pétrels, using geolocation and depth loggers, to compare with the "D'Urville Sea-Mertz" MPA proposal. It was anticipated that post-breeding penguins would widely disperse at sea following the autumnal sea ice extension, and would exhibit seasonally-contrasted foraging effort [26]. It was also specifically examined where penguins foraged before moulting. Food demand peaks during this period, so that the preservation of trophic food webs in no-take zones is likely beneficial to the conservation of the species as well as other keystone predators. The goal of this study was hence to provide new scientific basis to assess potential strengths and weaknesses of the EARSMPA proposal, based on the seasonal habitat use of a major bio-indicator species of Antarctic marine ecosystems.

2. Methods

To examine the penguins' seasonal distribution and activity, LAT2500 data loggers (8 × 36 mm, 3.6 g; Lotek Wireless, Canada) were used. These loggers recorded daily locations by on-board processing of ambient light level data. Loggers were attached to 15 breeding male Adélie penguins from Ile des Pétrels, near the Dumont d'Urville station (66°40′S; 140°01′E), using flexible leg bands ([27]; details in Supporting Methods S1). Surveyed penguins were captured on 16 and 17 January 2015 (end of the chick-guard period) when walking away from their nests, after their partners returned from the sea to feed their

chick(s). They were weighed (average body mass: 4217 ± 329 g), PIT-tagged and the geolocator was attached to the left leg. Handling took < 10 min and the penguins were immediately released. As soon as they were found at the colonies on the next breeding seasons, instrumented individuals were recaptured, and the logger retrieved.

Geolocation data were downloaded onto a computer and analysed using R 3.4.2 [28]. Due to large uncertainties on the geolocation estimates [29], penguins' daily locations were re-estimated from the logged sunrise and sunset times, using the R package "probGLS" [30]. In this probabilistic framework, accuracy can be increased by incorporating year-round information on travel speed and behaviour, and environmental data. Assumed penguins' speed distribution was $2\,m\,s^{-1}$ for the likely fastest movement over 24 h when the logger was immerged (i.e., travel by swimming; with a standard deviation = $1.5\,m\,s^{-1}$ and a maximum allowed value of $3\,m\,s^{-1}$). Assumed highest speed was $1\,m\,s^{-1}$ when the logger was emerged (i.e., travel by walking; with a standard deviation = $1\,m\,s^{-1}$ and a maximum = $2\,m\,s^{-1}$). Satellite-derived daily mean data on the physical environment (sea ice cover and sea-surface temperature) were downloaded from http://www.esrl.noaa.gov/psd/data/gridded/data.noaa.oisst.v2.highres.html at a 0.25° spatial resolution. A tolerance value of 3 °C around the observed temperature was set for the matching procedure with satellite-derived data, and positions where sea ice concentration were above 99% were deemed unrealistic in the model. A land mask was also downloaded from this database at 0.25° spatial resolution and was used to prevent any location estimate to occur on land. First and last point of the trips were defined as the last date the individual was seen on the colony (from field observations), and the first date of continuous > 24 h "dry" state of the logger at the onset of the following breeding season, respectively. These first and last points were set to occur at the colony, except in the case of the three incomplete tracks for which the last location estimate had no such added constraint. Final locations were subsequently re-interpolated at constant 1-d interval with the R packages "sp" and "trip".

The tracking sample's representativeness was examined by measuring how the population's utilization core area changed with increased inclusion of data [31]. This iterative approach randomly selected individual trips (50 iterations) and computed for each sample size a 50% kernel utilization distribution contour from the sampled data. The function then measured what proportion of the un-sampled data was included within this 50% contour. This asymptotic 'inclusion value' was thus used to indicate how well the sampled data can predict the space use of individuals in the un-sampled data, and thus to estimate whether a sample of tracked individuals was representative of the population. This indicated an appropriate representativeness (92%; Supporting Methods S2) of the studied sample for the population's space use.

Loggers also recorded depth and wet/dry state every 120 s throughout the year-long recording period. Although not sufficient to identify individual dives, this sampling interval enabled to infer daily diving effort and seasonal patterns of depth use [26]. Igor Pro 6.3.7.2 (WaveMetrics, Inc., USA) was used to summarize the 2-min immersion and depth readings by the tags into daily values. Following the manufacturer's instructions, pressure readings in decibar were converted into meters with 1 dbar = 1.02 m. Only values > 1 m were used in the analyses, to avoid erroneous measures of pressure close to the sea surface.

The proposed MPA boundaries were downloaded from www.mpatlas.org/map/future-marine-protection/. Proportions of locations falling inside versus outside designated areas were calculated; the statistical effect of individual and month on these proportions were examined using Kruskal-Wallis rank sum tests, after the nil hypothesis on normal distribution was rejected (using Shapiro-Wilk normality test). When a significant difference was measured among months, the Tukey's 'Honest Significant Difference' multiple comparison of means test was used to identify which month(s) differed from others. For all tests the

Table 1
At-sea distribution metrics for the Adélie penguins tracked with geolocators from Ile des Pétrels, in 2015. The last line shows median dates and mean values ± S.D. Individuals marked with an asterisk had incomplete records; the marked values were not included for the mean or median calculations.

Tag ID	Departure date	Return or last record date	Maximum range (km)	Date of maximum range	% pre-moult in MPA	% moult in MPA	% trip in MPA
3016*	3 Feb.	9 Sep.*	1754	24 Jun.	62.5	6.3	11.9*
3017	4 Feb.	26 Oct.	531	23 Sep.	100.0	100.0	66.0
3018	27 Jan.	3 Nov.	764	1 Oct.	100.0	100.0	72.6
3019	31 Jan.	30 Oct.	1612	26 Jul.	33.3	0.0	5.5
3022	29 Jan.	2 Nov.	979	29 Jun.	73.2	0.0	13.3
3023*	3 Feb.	28 Jun.*	1933*	27 Jun.	22.6	0.0	25.3*
3024	21 Jan.	29 Oct.	1287	28 Jul.	100.0	64.7	27.3
3025*	3 Feb.	20 Oct.*	1258	1 Jul.	37.9	0.0	25.4*
3026	3 Feb.	28 Oct.	999	2 Sep.	100.0	100.0	26.9
3027	21 Jan.	5 Nov.	1576	1 Jul.	28.1	0.0	4.8
3028	19 Jan.	8 Nov.	806	22 Aug.	100.0	58.8	16.7
3029	27 Jan.	1 Nov.	1422	11 Jul.	75.0	38.9	9.3
3031	4 Feb.	6 Nov.	1072	3 Jul.	56.4	41.2	23.9
Median/Mean	31 Jan.	1 Nov.	1172	18 Jul.	68.4	39.2	26.6
S.D.	5.9	4.2	377	35	30.4	41.7	24.0

significance threshold was set at $p = 0.05$. All statistical tests were performed using R 3.4.2. Values given are mean ± standard deviation unless specified otherwise.

3. Results

In total 13 loggers were recovered (*c.* 87%) over the two following breeding seasons: 12 in 2015–2016 and one in 2016–2017. The surveyed penguins were found at the same nesting location, or in an adjacent nest; the two un-recaptured birds had their initial breeding location buried under heavy snow from 2015 to 2016 onward. Loggers recorded for one year, but three stopped prematurely (in June, September and October 2015).

The tracked Adélie penguins were last seen at their colony on 31 January (median date, range: 19 January–4 February; Table 1). They then moved towards the northwest (Fig. 1), pursuing the pack-ice edge northward extension (Fig. 2; Fig. S1) and were thus located further away from the colony during winter than during pre-moult. On average, penguins moved 32 km daily and reached their greatest distance to the colony (1172 km) on 18 July (median date, range: 24 June–1 October). Individuals started their return migration while sea ice was further

extending after July; estimated return at the colonies was on 1 November (median date, range: 26 October–8 November, n = 10). Overall, the penguins' distribution ranged 60.0–66.7°S and 101.4–154.3°E, an area spanning 1,906,620 km².

Daily time spent diving peaked in February and further in September (7.9 ± 2.4 h, up to 13.3 h for one individual; Fig. 3a). In contrast, continuous emersion was observed during 17.5 ± 2 d in all individuals, presumably reflecting moult (from 3 to 21 March, on average). The birds were not synchronous in their moult (Table S1); consequently, the average diving activity was never nil during this period but remained low (2.4 ± 3.3 h). Daily time spent diving also decreased markedly during the winter solstice in June, and when the birds returned in November. Daily dive depths followed a similar pattern. Mean depth mostly remained shallower than 25 m from February through June, but peaked in August (35.6 ± 15.8 m, up to 72.5 m), and declined during the birds' return (Fig. 3b). Accordingly, daily maximum dive depth sharply decreased in March and June, peaked in August (100.6 ± 25.6 m) and dropped during spring, suggesting a higher foraging effort from late July to early October (Fig. S2). The absolute maximum dive depth recorded was 165.0 m, in July.

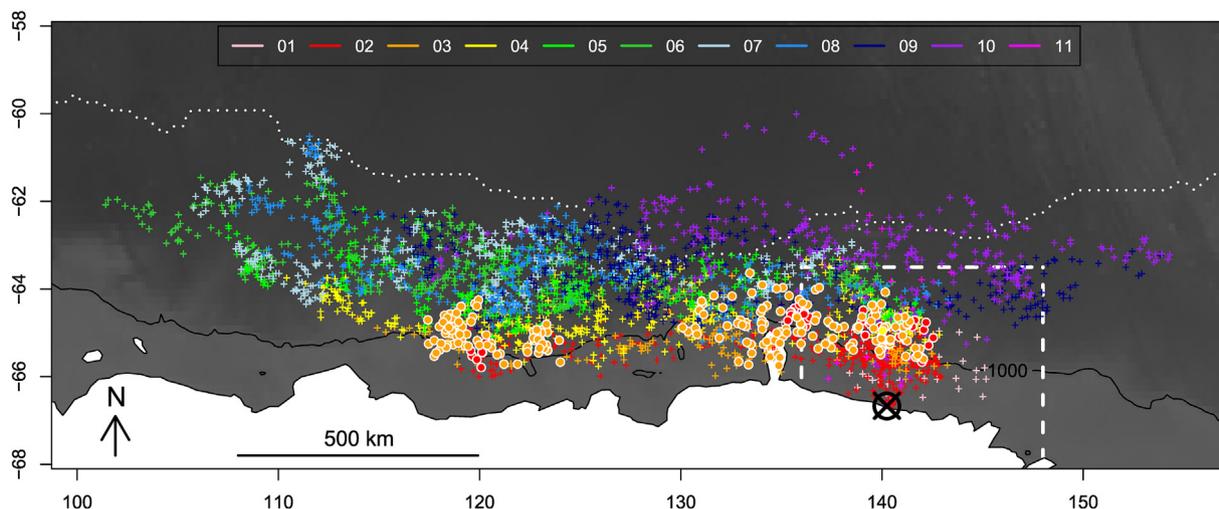All 13 surveyed individuals reached beyond the proposed MPA

Fig. 1. Map of daily locations of the 13 Adélie penguins tracked during their 2015 non-breeding period. Colours symbolize months (January–November); filled circles represent the birds' location during their inferred timing of moulting. The colony of origin of the birds (Ile des Pétrels, Terre Adélie, Antarctica) is shown with the black circle and cross. Boundaries of the proposed "D'Urville Sea-Mertz" Marine Protected Area are shown with thick white dashed lines. The northernmost extent of the pack-ice edge in 2015 is indicated with the thin dotted white line. Bathymetry is displayed in the background (grey scale; black thin line highlights the −1000 m depth). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)
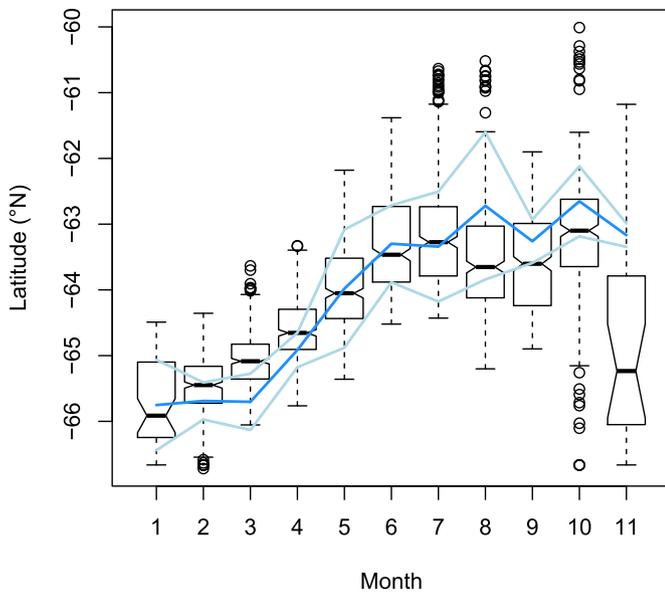
Fig. 2. Latitudinal distribution of: the pack-ice edge (15% line of sea ice concentration; blue lines: mean ± standard deviation) in the study area (101.4–154.3°E), and the Adélie penguins tracked from Ile des Pétrels (boxes), for each month of the 2015 non-breeding period. Boxes' midline show the median of each monthly dataset, with the lower and upper limits of the box being the first and third quartile (25th and 75th percentile), respectively. Dashed lines extend up to 1.5 times the interquartile range from the box edge to the furthest point within that distance: data beyond that distance ('outliers') are represented individually as circles. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

boundaries. Only an average 26.6% of complete tracks were located inside this area (Table 1), and this fraction was less when months are considered individually (down to 0.5% in July, Fig. 4) except for the penguins' departure and return phases (January, February and November). Looking at monthly subsets of each individual track, there was not a single daily location within these boundaries in the majority of cases (55.2%, Table S2; 52.4% for the 10 complete trips). However, 68.4% of locations during the pre-moult phase, between departure and moult, occurred inside the MPA proposal (100% for five individuals); and 39.2% of moulting locations were also in this area (100% for three individuals; but 0% for five others). Finally, 77% of all penguin daily locations occurred within ± 1° of latitude from the monthly sea ice edge, and this was up to 100% of locations in 43 monthly subsets of individual tracks (Table S3). Even during the winter months, this proportion was generally close to 80% on average, with the notable exception of August when it decreased to 49% (Fig. 4).

Statistical tests supported that there were significant differences among individuals in the proportion of time spent within the MPA boundaries (Kruskal-Wallis $X_{12}^2 = 28.8$, $p = 0.004$), but not within the region of 1° latitude around the sea ice edge ($X_{12}^2 = 3.8$, $p = 0.9$). Moreover, the proportion of locations within the MPA boundaries was significantly affected by the month (Kruskal-Wallis $X_{10}^2 = 60.0$, $p < 0.001$): values in January, February and November differed significantly from values in all other months (except February versus March, nearly significant, Table S4); all other pairs of values did not differ significantly. The proportion of locations within 1° of latitude around the sea ice edge was also significantly affected by the month (Kruskal-Wallis $X_{10}^2 = 42.8$, $p < 0.001$): values in November differed significantly from values in all other months, and values in August differed significantly from values in January through June; all other pairs of values did not differ significantly (Table S5).
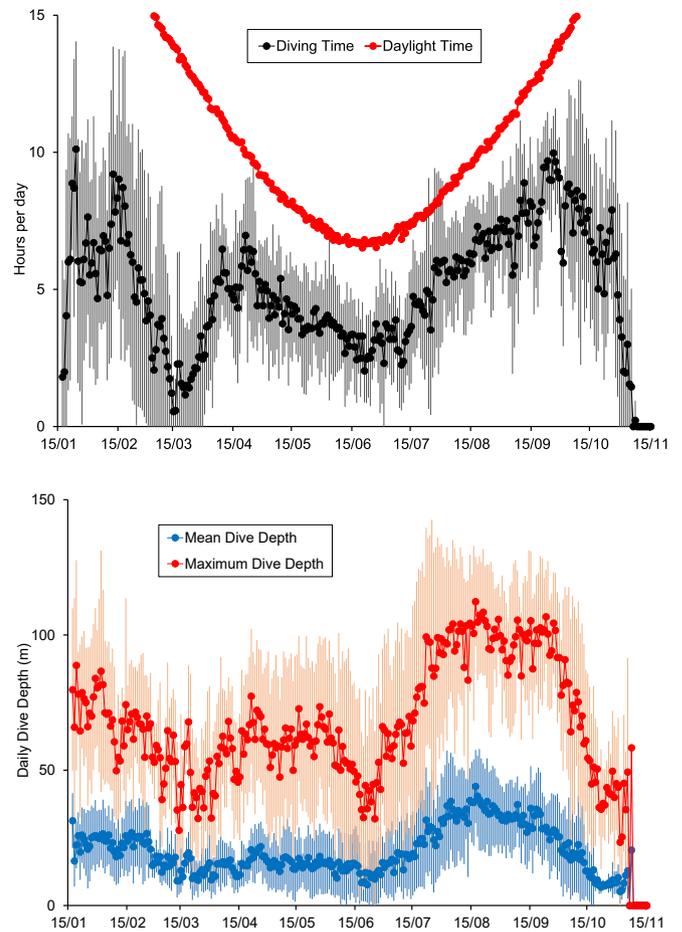

Fig. 3. (a) Daily time spent diving by the birds during their non-breeding period (January–November); the red line depicts the mean daylight time at the birds' location. (b) Daily mean and maximum dive depths recorded (blue and red circles, respectively). Values shown are mean ± standard deviation. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)
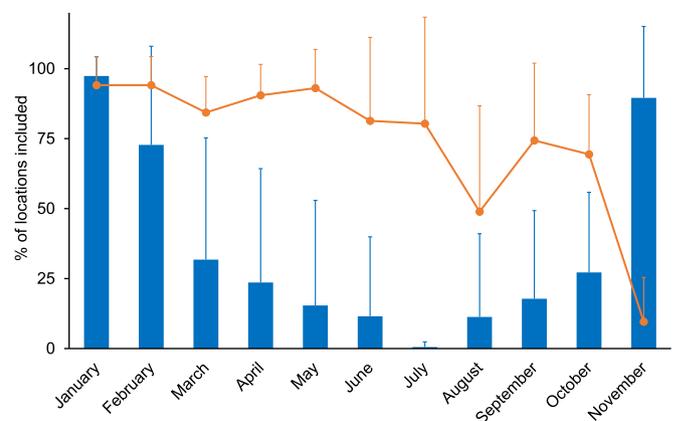

Fig. 4. Proportion of bird daily locations falling within the spatial boundaries of the proposed "D'Urville Sea-Mertz" Marine Protected Area (blue bars), and within the area of ± 1 latitude degree around the pack-ice edge (orange line), for each month of the non-breeding period (January–November). Values are inter-individual mean; error bars show standard deviation. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

4. Discussion

Continuity in space is the key issue in delineating protected areas for migratory wildlife [32,33]. During the non-breeding period, seabirds typically distribute over larger areas than during breeding: this behaviour may drive them far beyond the limits of protected areas (e.g., [34]), potentially exposing them to a larger range of threats in their habitat (e.g., [35]). In line with this paradigm, the foraging range of post-breeding Adélie penguins from Ile des Pétrels approached 1200 km, which is nine-fold and more than three-fold compared to the chick-guard and incubation stages, respectively [36]. These results obtained during a year of normal local sea ice conditions (Fig. S3) are comparable with studies from other sites (continental Antarctica: [21,26]; Peninsula region: [29,37]). Notably, the general westward distribution from the colony is remarkably consistent among non-breeding Adélie penguins from East Antarctica [26,38]. Most importantly, the present study shows that across this extensive migration, all the surveyed individuals seasonally distributed outside the proposed D'Urville Sea-Mertz MPA and were predominantly outside this area from March through October. Adélie penguins from Ile des Pétrels thus seem to spend a substantial proportion of their adult life outside these boundaries, and this may apply to their sub-adult phase too, as suggested from other tracking studies [38].

It is unlikely that these striking results originate from the spatial error associated with light-based geolocation approach. Indeed, the inherent imprecision of geolocation estimates typically relates to the latitudinal axis (16–727 km; [29]), while it is much reduced in longitude (< 60 km). Here, penguin distribution mostly spread outside the MPA boundaries longitudinally (Fig. 1). However, tracking post-breeding penguins on a multi-year basis would understandably further increase confidence in these results.

Adélie penguins also increased their foraging effort during the non-breeding period, compared with summer [39], confirming the patterns observed in another population [26] and species [40]. Typically, Adélie penguins increased their daily diving time and dive depth before moulting (January–February), and more so in the late winter (late July to early October).

Taken together, the results have two important implications. First, when penguins increased their foraging effort in pre-moult, they were distributed predominantly within the proposed MPA. As Adélie penguins need to build up considerable energy reserves before moulting, primarily from consuming krill [41], this finding strongly supports the krill no-take policy in this area, for the sake of effective conservation [42]. Second, and opposite, while penguins are maximizing their foraging effort in late winter, possibly reflecting the paucity of resources at that time, they are then distributed only marginally within the proposed area (< 1% of locations included in July, to < 18% in September; Table S2). This survey across the non-breeding period thus shows that the D'Urville Sea-Mertz MPA proposal is not wide enough to fully encompass the year-round at-sea distribution of the local Adélie penguin population, but that it includes most of their foraging grounds at the time of peaking food demand.

In the Southern Ocean, the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) is the international decision-making body for the conservation and rational use of marine living resources. Considering the conservation value of the Antarctic marine ecosystems, CCAMLR developed a model of precautionary approach from 1986, to ensure that industrial catches of marine resources would not impede the predators meeting their feeding requirements; and this approach further encompasses a pioneering feedback-type of stocks management adjusted in response to information available from the different ecosystem components [43]. In this context, the objective of the CCAMLR's Scientific Committee to develop a network of MPAs was endorsed by the Commission as a matter of priority. In keeping with this founding precautionary approach, the EARSMPA is anticipated to contain scientific reference zones to assist with understanding the effects of fishing outside the MPAs as well as the consequences of climate change on Antarctic and Southern Ocean ecosystems. A prohibition on fishing for krill in the D'Urville Sea-Mertz area has notably been discussed to monitor important environmental changes in this area since 2010. Besides, the delineation of the EARSMPA boundaries was developed using the scientific principles of comprehensiveness, adequacy and representativeness, and has been endorsed by CCAMLR's Scientific Committee as containing the best scientific evidence available at that time to conserve examples of biodiversity in the high latitudes of the Indian sector of the Southern Ocean [6]. These boundaries thus likely reflect a consensus on the habitats to protect and the concentration of biodiversity in this area [7,8]. However the seasonal at-sea distribution of Adélie penguins, a keystone predator species in this ecosystem, suggests that important foraging habitats are exploited mostly outside this proposed area during winter, and thus that ecologically-significant processes supporting the local biota are currently and mostly not included in the EARSPMA. Hence, the present study does not intend to criticize the implementation of this MPA, but after testing the seasonal relevance of its boundaries to this migratory population of a bio-indicating species, the conclusions would advocate for a wider area to protect this ecosystem more comprehensively.

The concept of mobile protected areas, based on naturally-varying habitat boundaries rather than on static limits, has been proposed to better protecting highly dynamic marine species or systems [44]. Although it may be difficult to implement and might complicate commercial activities' planning due to spatiotemporal dynamics of the marine environment, this concept seems particularly valid in the polar regions, where the ecosystems are largely structured according to sea ice seasonality [3]. In the present study, the penguins' distribution did not only follow the latitudinal ice extension, but mostly spread out in longitude. Thus, adjusting the MPAs' northern boundary to the seasonal ice edge would be insufficient to capture the Adélie penguins' year-round distribution. However, at their maximal westward extent (101.4°E), the tracked penguins approached the next planned MPA to the West in the EARSMPA proposal (the Drygalski MPA, 82–95°E). Hence, since non-breeding Adélie penguins in this region disperse mostly to the west [26,38] and several large populations of Adélie penguins are found in this area [45], it seems highly valuable to connect the three MPAs composing the EARSMPA from autumn to spring (March through October). For example, a winter buffer zone spanning 1° latitude on each side of the sea ice edge (Fig. 2) would considerably increase the conservation scope of the EARSMPA (Fig. 4), encompassing the overwintering habitat of migratory wildlife more consistently among individuals than the current proposal. Such an extension during winter would benefit not only to post-breeding Adélie penguins, but also to wider predator-prey communities and habitats, with Adélie penguins' distribution taken as an indicator of these ecologically-significant areas. The suite of consumers potentially benefiting from extending the EARSPMA to the ice edge foraging habitat during winter includes the dispersing juvenile Adélie penguins [38], as well as other predators utilizing sea ice edge during winter, notably emperor penguins (*Aptenodytes forsteri*; e.g., [46]), a community of pagophilic flying seabird species (e.g., [47]) but also southern elephant seals *Mirounga leonina* [48] and Antarctic fur seals *Arctocephalus gazella* [49]. Such an aggregation of predators to specifically this ice edge habitat during winter again indicates that developed trophic chains thrive at that time in this habitat, which can thus be seen as a seasonal hotspot of biodiversity. As such, this habitat would deserve further consideration for protection. The seasonal connection proposed here between the distinct planned MPAs would be in line with the CCAMLR's objective of developing a network of MPAs in the Southern Ocean; moreover, with its seasonally larger extent, the EARSMPA would potentially achieve greater conservation outcomes. Indeed, large-scale MPAs show disproportionate ecological value and contribution to global marine conservation targets [50].

In conclusion, this study has clear implications in terms of marine

policy, as it is the first evaluation of the relevance of a marine spatial planning in the Southern Ocean on a seasonal, yearly basis. These direct implications are relevant to (1) the designated area itself, which the data support to be ecologically significant; (2) its size and boundaries, which are likely too restrictive to fully protect this marine ecosystem on a seasonal basis; and (3) its management planning, with the krill no-take policy being strongly supported by the bio-indicating approach followed here. Therefore, this study confirms that in order to monitor ecological changes and facilitate the understanding of potential effect of industrial krill fisheries outside this area, policy makers should follow the precautionary approach and implement the "D'Urville Sea-Mertz" MPA proposal as a scientific reference zone. Further, and more broadly, it is recommended to scientific committees in charge of delineating such protected areas, to examine (1) a variety of data sources for wildlife distribution, beyond the breeding season alone, in order to fully grasp the habitat requirements of species, and (2) options such as seasonal corridors between MPAs. A recent evaluation [2] showed that although there has been remarkable progress in the last decade, currently only 3.6% of the global ocean is in implemented MPAs, of which only 2% are strongly or fully protected areas. It is therefore questionable whether the U.N.'s 'Aichi Target 11' for global ocean protection can be met: conclusions drawn from our study provide options to help meeting this goal.

Declarations of interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpol.2019.103692.

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