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Wintering strategies of two king penguin populations of the Southern Indian Ocean

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ABSTRACT: The king penguin *Aptenodytes patagonicus* is an important model species of the Southern Ocean. While there is extensive knowledge on the foraging movement of this species during the summer in the early chick-provisioning period, little information is available for the winter period. To fill this gap, we tracked 13 individuals during the winter from 2 neighboring populations of the Southern Indian Ocean, namely the Kerguelen and the Crozet Archipelagos, and examined penguin locations with respect to remote sensing data. Tracked penguins from Kerguelen mostly headed east of the archipelago, while those from Crozet islands headed southwest. This resulted in contrasting latitudes used between the 2 wintering locations. The different directions taken possibly result from the distinct oceanic features around the 2 islands: at Kerguelen, extensive spring blooms transported east of the island might sustain prey well until the winter, offering favorable conditions for penguins. At Crozet, blooms are reduced in intensity and penguins might instead head south to benefit from the better foraging conditions near the sea ice. Such distinct foraging distributions relative to the 2 archipelagos are consistent with the at-sea distribution of other penguin species (e.g. *Eudyptes* spp.) breeding in the same localities. We highlight 2 distinct winter foraging strategies in neighboring king penguin populations, shaped by the contrasting oceanographic conditions surrounding their breeding sites.

KEY WORDS: *Aptenodytes patagonicus* · Kerguelen Archipelago · Crozet Archipelago · Migration · Movement

1. INTRODUCTION

Seabirds have long been study models in biology-based movement studies (Weimerskirch et al. 2002, Ryan et al. 2004). Their popularity in avian movement research can in part be attributed to their tendency to nest in colonies, which facilitates the recapture of the tagged individuals. As such, most studies in seabird movement ecology have been conducted in the summer, when breeding birds exhibit colonial central-foraging behaviors (Wakefield et al. 2009). In contrast, the more nomadic movements of

seabirds during the winter are often understudied (Marra et al. 2015), despite being crucial to understanding phenology shifts, mortality, energy budgets, or overlap with fisheries during far less favorable environmental conditions (Croxall et al. 1984, Salton et al. 2015).

The king penguin *Aptenodytes patagonicus* is a diving predator of the Southern Ocean. During the breeding season, it relies on schooling mesopelagic fish (myctophids) at the Polar Front, a circumpolar front of significant ecological importance and the northmost limit of the west-flowing Antarctic Circum-

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polar Current (Bost et al. 2009, Park et al. 2014, Scheffer et al. 2016). As circumpolar marine predators, king penguins can be used to monitor the lower trophic levels of sub-Antarctic waters (Bost et al. 2002, 2015, Proud et al. 2021, Brisson-Curadeau et al. 2023a). While their distribution during the summer has been extensively studied (e.g. Bost et al. 1997, Trathan et al. 2008, Scheffer et al. 2016, Brisson-Curadeau et al. 2024), few studies have looked at their winter movements. The consensus is that king penguins move south in winter, towards the ice limit, likely to feed on prey concentrating just below the shallow thermocline of high latitudes (Charrassin & Bost 2001, Bost et al. 2004). However, these studies have been conducted on a limited number of colonies and may not be representative of the whole population. A deeper understanding of the winter foraging ecology of king penguins is important, as this period of limited food abundance might have an impact on breeding success in the following seasons (e.g. Brisson-Curadeau et al. 2023b).

The populations of the archipelagos of Crozet and Kerguelen provide contrasting environments for studying the foraging behavior of king penguins. While being oceanic neighbors (at 1300 km apart), these 2 large populations are surrounded by drastically different marine dynamics, potentially impacting their foraging strategies in winter. For instance, the Polar Front is located far offshore from the colonies in Crozet, while it circulates much closer to Kerguelen (Pauthenet et al. 2018). Furthermore, the high iron input at Kerguelen sustained by wind-blown dust from the mainland stimulates high productivity around the colonies, while productivity is usually lower around the smaller archipelago of Crozet (Tripathy & Jena 2019). These differences create contrasting foraging conditions in the summer for various marine predators including penguins, influencing the directions, durations, and distances of foraging trips (Bost et al. 1997, Pütz 2002, Scheffer et al. 2016). However, it is unclear if and how these different marine dynamics also affect the wintering distributions.

Here, we investigated the wintering distributions of these 2 king penguin populations; for the Crozet Archipelago, we aimed to confirm the southern wintering waters reported in the few previous studies (Charrassin & Bost 2001, Bost et al. 2004, Orgeret et al. 2019), and for the Kerguelen Archipelago, this is the first report of wintering locations. We then explore potential explanations for the observed distribution patterns by analyzing tracking data in conjunction with available remotely sensed oceanographic data.

2. MATERIALS AND METHODS

2.1. Study site and phenology

The study took place in 2 king penguin colonies located in neighboring archipelagos of the southern Indian Ocean. La Grande Manchotière (46° 25' S, 51° 51' E) is located on Possession Island (Crozet Archipelago) and hosts around 24 000 breeding pairs (Barbraud et al. 2020). The Ratmanoff colony (49° 14' S, 70° 33' E) is located in the Kerguelen Archipelago and hosts around 87 000 breeding pairs (Barbraud et al. 2020). Crozet and Kerguelen have 2 of the largest king penguin populations in the world, collectively containing over 45% of the total population (Bost et al. 2013, Barbraud et al. 2020).

Breeding phenology at both colonies is similar: king penguins provision their chick frequently in the austral summer (end of January to March) but leave their chick in creche at the colony in winter (May to August) and spend most of their time foraging at sea (Saraux et al. 2012, Bost et al. 2013). Chick provisioning resumes in spring (late September) and fledging occurs from November to January.

2.2. Biologging equipment

Biologging studies took place during the winters of 2021 and 2022, at Crozet and Kerguelen, respectively. We equipped breeding adults in April, before their winter departure, and retrieved the loggers in spring, when they returned to the colony.

Penguins were captured using a pole with a large crook, allowing us to trap the chest area. Birds were then equipped by gluing the biologger to the back feathers using Loctite 401 glue, secured by 2 cableties. Two types of loggers were used in the study. The first type was SPLASH10-283 tags (99 g; Wildlife Computers). These tags transmitted 1 data point daily via the ARGOS satellite network. Eight penguins were equipped with these loggers at Crozet and 4 at Kerguelen. The second type of loggers were Intigeo C330 light-recorders (3.2 g, 17 × 19 × 8 mm; Migrate Technology). These solar geolocator (GLS) units collect light intensity data every 60 s and maximum light values every 5 min. These tags need to be retrieved to download the data. Equipped penguins can be undetected when they return to the colony in spring, even when feeding their chick, and can molt their feathers on land before the biologgers are retrieved. To avoid losing

loggers during molting, we glued these tags to V2G 154C VHF tags (42 g, 65 × 28 × 13 mm excluding antenna) from Lotek. These VHF tags can be remotely detected with a radio antenna, increasing the likelihood of detections of adults when returning to the colony, but also greatly facilitating the search for loggers that fell on the ground during molting if birds were undetected. To limit interfering with the birds' hydrodynamics, we glued the VHF tags on the side of the GLS, rather than on top. All loggers were centrally placed on the back of the birds. Fifteen penguins were equipped with these GLS/VHF loggers, all at Kerguelen, as we did not have these loggers available when deploying in Crozet. All equipment types weighed less than 2% of each penguin's body weight.

2.3. Data processing

Only datapoints from June and July (hereafter 'winter') were retained in the analysis of winter distributions, as May and August typically include long inward/outward trips to the colony.

For Splash tags, class B ARGOS localization were discarded due to their poor precision. For GLS data, we used the light sensor data to determine sunrise and sunset and combined the output with the internal clock of the logger to estimate latitude and longitude (Afanasyev 2004). Individual locations were estimated following Lisovski et al. (2020) to obtain 2 positions per day, with an average accuracy of ~180 km (Phillips et al. 2004). The first step of this analysis was to detect the twilight periods using the R package 'BASTag' (Wotherspoon et al. 2013). We chose a light threshold value of 1.5 to automatically demarcate all sunrises and sunsets (Rakhimberdiev et al. 2016). This step was followed by a visual inspection of each individual sunrise and sunset identified by 'BASTag'. The annotated light data were then analyzed with the 'GeoLight' package to estimate location data (Lisovski et al. 2015).

2.4. Oceanographic variables

June and July averages of sea ice and sea surface temperature (SST) over the 2 winters were extracted from Copernicus Marine Environment Monitoring Service (CMEMS) at 0.083° resolution (<https://doi.org/10.48670/moi-00016>). The climatological position of the Polar Front was extracted from Pauthenet et al. (2018).

2.5. Analysis

The kernels for the winter foraging distribution of both colonies were calculated using a 90% quartic kernel function (Silverman 2018). Headings of foraging trips for all individuals were calculated by averaging the angle between foraging coordinates of regular intervals with the coordinates of the colony. The differences in latitude and SST between the zones targeted by the 2 colonies were assessed using linear mixed effect models (LMM), with colony as the fixed effect, individual as the random effect, and the 2 variables of interest (latitude and SST) successively as the response variable.

The position of the kernels relative to the Polar Front and the sea ice limit was overlaid on the kernel maps for visual assessment. All statistical analyses were conducted in R (R Core Team 2021). The Lagrangian model was performed in Python. Maps were created using ArcGIS Pro 3.1 (Environmental Systems Research Institute 2010).

2.6. Post hoc analysis

After examining the results on the winter distribution, it was suspected that king penguins might target zones of post-bloom waters, i.e. prey-rich waters initially originating from the phytoplankton bloom in spring, but that continue to sustain or attract the higher-level consumers long after the phytoplankton has been consumed. Because these waters are advected between the peak season of primary production (spring) and the period of interest (winter), we used a Lagrangian approach (Lehahn et al. 2018) to assess where these post-blooms would be located in winter. This model mimics redistribution effects by the surface currents. We first mapped the location of chlorophyll blooms around both colonies by selecting the 90th chlorophyll *a* (chl *a*) percentile in spring and then advected them as in Cotté et al. (2015) and Sergi et al. (2020). Monthly surface chl *a* concentrations during the spring bloom period (November of the previous calendar year to January) were extracted from CMEMS at 16 km² resolution (<https://doi.org/10.48670/moi-00283>; see Figs. S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m752p187_supp.pdf). The position shift of the water from spring to winter was computed using the Lagrangian Manifolds and Trajectories Analysis (LAMTA; Rousselet et al. unpubl.). Surface geostrophic velocity fields data at 0.25° resolution from

CMEMS (<https://doi.org/10.48670/moi-00145>) were used to model water particle movement in the LAMTA Lagrangian code.

To test whether penguins from each colony could target zones that were associated with post-bloom water masses, we calculated the distance between each penguin's tracking coordinates and the closest post-bloom water. We then averaged the values among individuals and ranked each average with the averages computed similarly using a data set of 100 simulations. These simulations were built by randomly redistributing the penguin's coordinates within the available habitat, defined as the ice-free area within the maximum foraging distance and south of the 45° latitude line, i.e. approximate location of the sub-Antarctic front (Kostianoy et al. 2004) and theoretical northern limit of the king penguin range.

3. RESULTS

Of the 12 ARGOS tags, 3 stopped emitting data before June and could not be used for analysis. Only 1 of the remaining 9 ARGOS tags was not recovered, although the remotely downloaded satellite data could still be used for the analysis.

Of the 15 GLS deployed, 4 were retrieved the next spring. The GLS seemed to have been holding well on the feathers, but the retrieved VHF were often about to fall off, likely explaining our low recapture rate for GLS-equipped birds. As king penguins do not have defined nest locations, recapturing birds after the winter is difficult without a VHF.

The total sample size of recovered devices was 7 birds at Crozet (all with ARGOS tags) and 6 at Kerguelen (2 equipped with ARGOS tags and 4 equipped with GLS). Deployment details for retrieved biologgers can be found in Table S1.

All 7 birds at Crozet headed south or south-west of the Island after departure. At Kerguelen, 5 birds headed east and only 1 headed south (Fig. 1). There was a clear dichotomy in the wintering water of the 2 colonies (Fig. 2).

Crozet birds foraged at a higher latitude (mean ± SD = 55.5 ± 2.6° S, n = 7) than the Kerguelen birds (53.3 ± 3.2° S, n = 6, LMM: p < 0.0001; Table S2). Consequently, the mean SST experienced by the birds was lower for Cro-

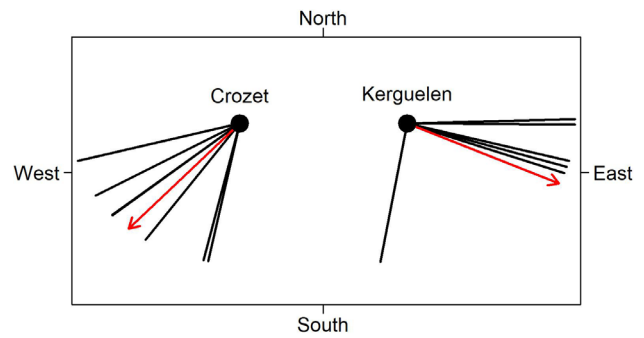


Fig. 1. Average direction of the wintering location for each tracked king penguin, from the perspective of the colonies. The red arrow represents the average direction across all penguins from a given colony

zet ($0.7 \pm 0.9^\circ\text{C}$, n = 7) than Kerguelen ($3.1 \pm 2.5^\circ\text{C}$, n = 6, LMM: p = 0.02; Table S2).

All birds at Crozet foraged well below (>800 km) the Polar Front, close to or at the sea ice limit and towards the post-bloom waters as defined by the Lagrangian model (Figs. 2 & 3). The average distance to the post-bloom waters was lower than 95% of random simulations, although visual assessment shows that penguins did not always forage in the post-bloom water itself (Fig. 3).

At Kerguelen, most birds foraged at or above the Polar Front (Fig. 2), closer to the post-bloom water than what was predicted by chance (>95% of simulations; Fig. 4). In fact, most of the foraging locations overlapped with the post-bloom waters, except for the single individual who went south, far from post-bloom waters.

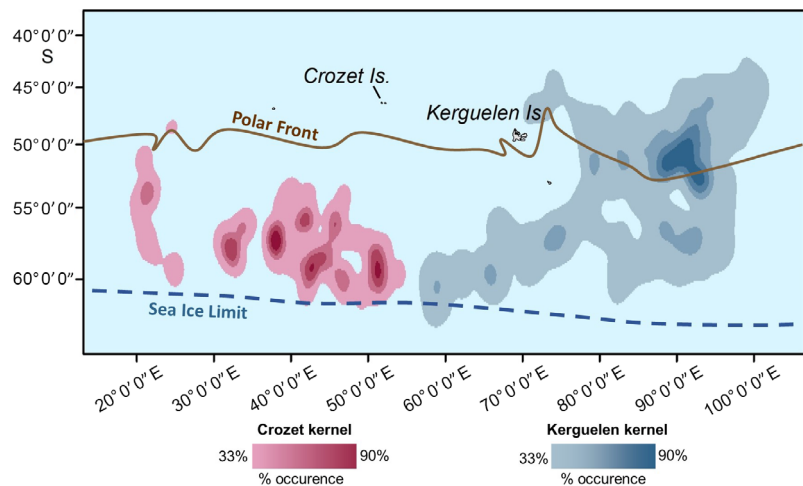


Fig. 2. Kernel densities of the wintering location of Crozet (red) and Kerguelen (blue) king penguins. Locations from all equipped penguins in a colony are pooled. The average Polar Front position and sea ice limit are displayed with a solid and a dashed line, respectively

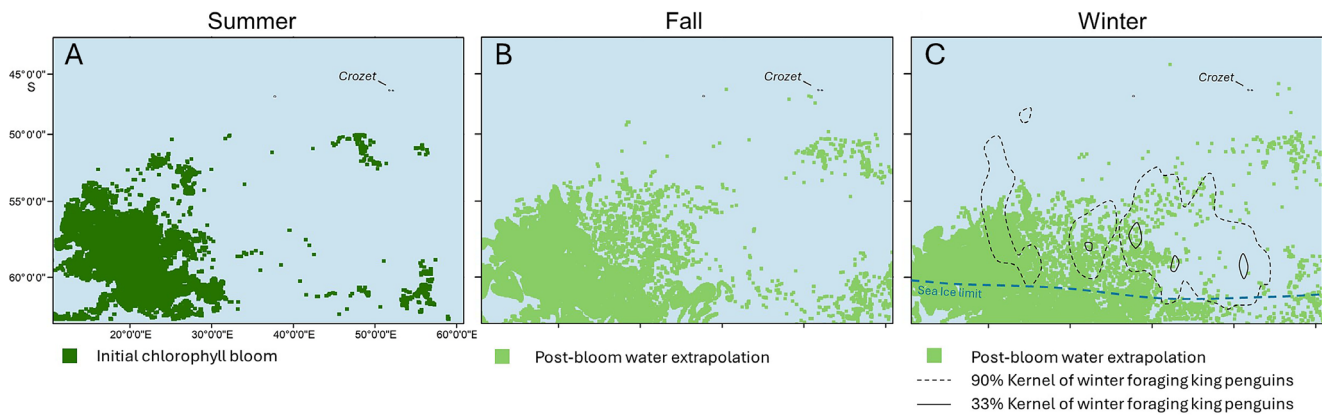


Fig. 3. (A) Position of the initial bloom waters around Crozet during late spring, i.e. the 90th percentile of chlorophyll concentration. (B) Extrapolation of the bloom water position 90 d later (i.e. fall), as determined using the Lagrangian approach. (C) Extrapolation of the bloom water position 180 d later (i.e. winter), as determined using the Lagrangian approach. This last period corresponds to the winter foraging of king penguins, as shown with the overlaid kernel densities

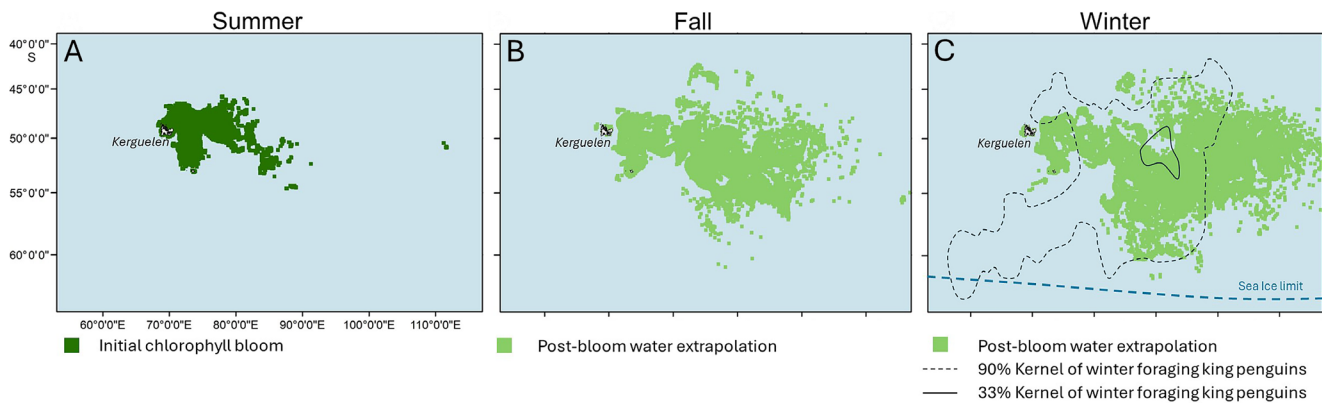


Fig. 4. As in Fig. 3, but for Kerguelen

4. DISCUSSION

Wintering locations of breeding king penguins in the Southern Indian Ocean were only known from a handful of studies at Crozet (Charrassin & Bost 2001, Bost et al. 2004). We provide additional support that king penguins at Crozet head south in winter. In addition, we show for the first time — albeit with a small sample size — that a portion of Kerguelen's population heads east in the winter, foraging at similar latitudes as their breeding site. Similar patterns of wintering movements (southerly in Crozet, easterly in Kerguelen) have been recorded in other sympatric diving predators, namely macaroni penguins *Eudyptes chrysolophus* and southern rockhopper penguins *E. chrysocome*, breeding on those 2 islands (Thiebot et al. 2011, 2012). These 2 distinct waters used might indicate different wintering strategies driven by the oceanographic features surrounding the 2 archipelagos. While a larger sample size across multiple years

is essential to definitively assess the strategies of the 2 colonies, we offer an initial explanation for the observed patterns.

At Kerguelen, the Polar Front interacts with the extensive archipelago's plateau and enhances circulation of minerals such as iron (Blain et al. 2001, Mongin et al. 2008). These nutrients enhance primary production and favor phytoplankton blooms around the archipelago in spring, when light and temperature are optimal. Such blooms typically also sustain a higher biomass of zooplankton, the main consumer of phytoplankton (Razouls et al. 1998). The aftermath of these blooms, composed of zooplankton as well as the remaining phytoplankton, is then moved east by the southeastward flow of the Antarctic Circumpolar Current and; by the next winter, it is located further east and southeast of the archipelago (see Fig. 4 and Lehahn et al. 2018). Such post-bloom waters might attract a high abundance of mesopelagic fish such as myctophids, which feed on macrozooplankton (Pak-

homov et al. 1996). This potential enhancement of marine resources southeast of Kerguelen might explain why the local population of penguins targeted this region. Similar processes of advection of post-bloom waters have been shown to explain the spatial mismatch between predators and areas of high primary production in the Southern Ocean (Cotté et al. 2015, Sergi et al. 2020).

At the meso- or submeso-scale, features like eddies and current filaments are omnipresent east of Kerguelen (Rosso et al. 2014) and might further benefit king penguins. These processes interact with the post-bloom water and can enhance prey availability through mechanisms including upwelling or eddy trapping (Schmid et al. 2020, Receveur et al. 2024). Examples of species that have been shown to use these features include seals, whales, and various penguin species (Bailleul et al. 2010, Cotté et al. 2011, Bon et al. 2015, Scheffer et al. 2016).

At Crozet, the smaller size of the shelf limits the iron input in the nearby waters. Furthermore, the Polar Front is located hundreds of kilometers south, in deep waters, with limited interactions with nutrients of terrestrial origin (Ardyna et al. 2017, Sergi et al. 2020). The result is a much more homogeneous, generally low-chlorophyll landscape (Fig. 3; Figs. S1 & S2). This could explain why penguins at Crozet headed south up to the limit of the sea ice, where blooms supported by the Antarctic continent might offer better conditions in the winter. As shown in Fig. 3, these blooms (and post-bloom waters) are found year-round at southern latitudes, likely because strong currents passing through the Southwest Indian Ridge (located just north of these blooms) prevent the plankton from any significant northward movement (Orsi et al. 1995). Southern latitudes might thus create a good alternative when prey around the colony is scarce, i.e. during the winter. However, any preference of the Crozet population for post-bloom waters in winter would likely be less strong than at Kerguelen, as the movement of penguins did not exactly coincide with post-bloom waters (Fig. 3). As such, other marine processes might also influence prey availability at these latitudes.

Prey depth might be another factor driving the distribution of penguins in winter. King penguins forage near the thermocline, where prey aggregates. At Kerguelen, the area targeted by the wintering penguins was very close to the Polar Front, where the particularly shallow thermocline brings prey closer to the surface (Charrassin & Bost 2001). Penguins at Crozet might also partly benefit from shallower prey, as the thermocline near the sea ice is

also particularly shallow (Charrassin & Bost 2001, Bost et al. 2004). Diving data are needed to confirm the importance of prey depth in winter habitat choice.

Naturally, there is potentially much variability within king penguin populations, and the observed tendencies might not reflect strategies for all individuals. At Crozet, non-breeding individuals target other areas in the winter than breeders, with tracks heading west rather than south (Orgeret et al. 2019). Non-breeders are less time constrained compared to breeders, as the latter must return early in spring to resume chick provisioning. This release of breeding constraints may allow non-breeding individuals to target prolific areas outside the reach of breeding individuals. At Kerguelen, no tracking data on non-breeders are available. However, we did observe some variability among breeders, with 1 individual heading south and feeding near the ice limit, similarly to the Crozet population. It is also possible that factors other than prey availability could influence king penguin movements in the winter, such as current-induced impacts on swimming direction or water visibility (e.g. Ballard et al. 2010, Jongsomjit et al. 2024). More research is needed to understand wintering variability in these 2 populations.

5. CONCLUSION

We explored the winter distribution of king penguins from 2 neighboring colonies in the South Indian Ocean and found contrasting habitat use and foraging strategies. More research is needed to further validate winter habitat selection by king penguins, as it might have implications regarding the resilience of these populations to climate change. For instance, a decrease of sea ice might affect populations, like that in Crozet, which seem to use the ice-edge for foraging. Similarly, changes in bloom occurrence could affect populations like the one in Kerguelen that use post-bloom water in the winter. These results indicate that the ability of penguin colonies to adapt to a changing environment is likely shaped by the specific oceanographic features of their foraging grounds. Further research is essential to better understand these dynamics and their long-term implications.

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LITERATURE CITED

- Afanasyev V (2004) A miniature daylight level and activity data recorder for tracking animals over long periods. *Mem Natl Inst Polar Res (Jpn)* 58:227–233
- ✦ Ardyna M, Claustre H, Sallée JB, d'Ovidio F and others (2017) Delineating environmental control of phytoplankton biomass and phenology in the Southern Ocean. *Geophys Res Lett* 44:5016–5024
- ✦ Bailleul F, Cotté C, Guinet C (2010) Mesoscale eddies as foraging area of a deep-diving predator, the southern elephant seal. *Mar Ecol Prog Ser* 408:251–264
- ✦ Ballard G, Toniolo V, Ainley DG, Parkinson CL, Arrigo KR, Trathan PN (2010) Responding to climate change: Adélie penguins confront astronomical and ocean boundaries. *Ecology* 91:2056–2069
- ✦ Barbraud C, Delord K, Bost CA, Chaigne A, Marteau C, Weimerskirch H (2020) Population trends of penguins in the French Southern Territories. *Polar Biol* 43:835–850
- ✦ Blain S, Tréguer P, Belviso S, Bucciarelli E and others (2001) A biogeochemical study of the island mass effect in the context of the iron hypothesis: Kerguelen Islands, Southern Ocean. *Deep Sea Res I* 48:163–187
- ✦ Bon C, Della Penna A, d'Ovidio F, Arnould JYP, Poupart T, Bost CA (2015) Influence of oceanographic structures on foraging strategies: Macaroni penguins at Crozet Islands. *Mov Ecol* 3:32
- ✦ Bost CA, Georges JY, Guinet C, Chérel Y and others (1997) Foraging habitat and food intake of satellite-tracked king penguins during the austral summer at Crozet Archipelago. *Mar Ecol Prog Ser* 150:21–33
- ✦ Bost CA, Zorn T, Le Maho Y, Duhamel G (2002) Feeding of diving predators and diel vertical migration of prey: King penguins' diet versus trawl sampling at Kerguelen Islands. *Mar Ecol Prog Ser* 227:51–61
- ✦ Bost CA, Charrassin JB, Clerquin Y, Ropert-Coudert Y, Le Maho Y (2004) Exploitation of distant marginal ice zones by king penguins during winter. *Mar Ecol Prog Ser* 283:293–297
- ✦ Bost CA, Cotté C, Bailleul F, Chérel Y and others (2009) The importance of oceanographic fronts to marine birds and mammals of the southern oceans. *J Mar Syst* 78:363–376
- Bost CA, Delord K, Barbraud C, Chérel Y and others (2013) King penguin. In: Borboroglu PG, Boersma PD (eds) *Penguins: natural history and conservation*. University of Washington Press, Seattle, WA, p 7–19
- ✦ Bost CA, Cotté C, Terray P, Barbraud C and others (2015) Large-scale climatic anomalies affect marine predator foraging behaviour and demography. *Nat Commun* 6:8220
- ✦ Brisson-Curadeau É, Elliott K, Bost CA (2023a) Contrasting bottom-up effects of warming ocean on two king penguin populations. *Glob Change Biol* 29:998–1008
- ✦ Brisson-Curadeau É, Scheffer A, Trathan P, Roquet F and others (2023b) Investigating two consecutive catastrophic breeding seasons in a large king penguin colony. *Sci Rep* 13:12967
- ✦ Brisson-Curadeau É, Bost CA, Chérel Y, Elliott K (2024) King Penguins adjust foraging effort rather than diet when faced with poor foraging conditions. *Ibis* 166:723–731
- ✦ Charrassin JB, Bost CA (2001) Utilisation of the oceanic habitat by king penguins over the annual cycle. *Mar Ecol Prog Ser* 221:285–298
- ✦ Cotté C, d'Ovidio F, Chaigneau A, Lévy M, Taupier-Letage I, Mate B, Guinet C (2011) Scale-dependent interactions of Mediterranean whales with marine dynamics. *Limnol Oceanogr* 56:219–232
- ✦ Cotté C, d'Ovidio F, Dragon AC, Guinet C, Lévy M (2015) Flexible preference of southern elephant seals for distinct mesoscale features within the Antarctic Circumpolar Current. *Prog Oceanogr* 131:46–58
- ✦ Croxall JP, Ricketts C, Prince PA (1984) Impact of seabirds on marine resources, especially krill, of South Georgia waters. In: Whittow GC, Rahn H (eds) *Seabird energetics*. Springer, Boston, MA, p 285–317
- Environmental Systems Research Institute (2010) ArcGIS Pro [GIS software] version 3.2. ESRI, Redlands, CA
- ✦ Jongsomjit D, Lescroël A, Schmidt AE, Lisovski S and others (2024) Going with the floe: Sea-ice movement affects distance and destination during Adélie penguin winter movements. *Ecology* 105:e4196
- ✦ Kostianoy AG, Ginzburg AI, Frankignoulle M, Delille B (2004) Fronts in the Southern Indian Ocean as inferred from satellite sea surface temperature data. *J Mar Syst* 45:55–73
- ✦ Lehahn Y, d'Ovidio F, Koren I (2018) A satellite-based Lagrangian view on phytoplankton dynamics. *Annu Rev Mar Sci* 10:99–119
- ✦ Lisovski S, Wotherspoon S, Sumner M, Bauer S, Emmenegger T, Lisovski MS (2015) Package 'GeoLight'. <https://github.com/slisovski/GeoLight>
- ✦ Lisovski S, Bauer S, Briedis M, Davidson SC and others (2020) Light-level geolocator analyses: a user's guide. *J Anim Ecol* 89:221–236
- ✦ Marra PP, Cohen EB, Loss SR, Rutter JE, Tonra CM (2015) A call for full annual cycle research in animal ecology. *Biol Lett* 11:20150552
- ✦ Mongin M, Molina E, Trull TW (2008) Seasonality and scale of the Kerguelen plateau phytoplankton bloom: a remote sensing and modeling analysis of the influence of natural iron fertilization in the Southern Ocean. *Deep Sea Res II* 55:880–892
- ✦ Orgeret F, Péron C, Enstipp MR, Delord K, Weimerskirch H, Bost CA (2019) Exploration during early life: distribution, habitat and orientation preferences in juvenile king penguins. *Mov Ecol* 7:29
- ✦ Orsi AH, Whitworth T III, Nowlin WD Jr (1995) On the meridional extent and fronts of the Antarctic Circumpolar Current. *Deep Sea Res I* 42:641–673
- ✦ Pakhomov EA, Perissinotto R, McQuaid CD (1996) Prey composition and daily rations of myctophid fishes in the Southern Ocean. *Mar Ecol Prog Ser* 134:1–14
- ✦ Park YH, Durand I, Kestenare E, Rougier G and others (2014) Polar Front around the Kerguelen Islands: an up-to-date determination and associated circulation of surface/subsurface waters. *J Geophys Res Oceans* 119:6575–6592
- ✦ Pauthenet E, Roquet F, Madec G, Guinet C and others (2018) Seasonal meandering of the Polar Front upstream of the Kerguelen Plateau. *Geophys Res Lett* 45:9774–9781

- Phillips RA, Silk JRD, Croxall JP, Afanasyev V, Briggs DR (2004) Accuracy of geolocation estimates for flying seabirds. *Mar Ecol Prog Ser* 266:265–272
- Proud R, Le Guen C, Sherley RB, Kato A and others (2021) Using predicted patterns of 3D prey distribution to map king penguin foraging habitat. *Front Mar Sci* 8:745200
- Pütz K (2002) Spatial and temporal variability in the foraging areas of breeding king penguins. *Condor* 104:528–538
- R Core Team (2021) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <https://www.R-project.org/>
- Rakhimberdiev E, Senner NR, Verhoeven MA, Winkler DW, Bouten W, Piersma T (2016) Comparing inferences of solar geolocation data against high-precision GPS data: annual movements of a double-tagged black-tailed godwit. *J Avian Biol* 47:589–596
- Razouls S, Du Reau G, Guillot P, Maison J, Jeandel C (1998) Seasonal abundance of copepod assemblages and grazing pressure in the Kerguelen Island area (Southern Ocean). *J Plankton Res* 20:1599–1614
- Receveur A, Menkes C, Lengaigne M, Ariza A and others (2024) A rare oasis effect for forage fauna in oceanic eddies at the global scale. *Nat Commun* 15:4834
- Rosso I, Hogg AM, Strutton PG, Kiss AE, Matear R, Klocker A, van Sebille E (2014) Vertical transport in the ocean due to sub-mesoscale structures: impacts in the Kerguelen region. *Ocean Model* 80:10–23
- Ryan PG, Petersen SL, Peters G, Grémillet D (2004) GPS tracking a marine predator: the effects of precision, resolution and sampling rate on foraging tracks of African penguins. *Mar Biol* 145:215–223
- Salton M, Saraux C, Dann P, Chiaradia A (2015) Carry-over body mass effect from winter to breeding in a resident seabird, the little penguin. *R Soc Open Sci* 2:140390
- Saraux C, Friess B, Le Maho Y, Le Bohec C (2012) Chick-provisioning strategies used by king penguins to adapt to a multiseasonal breeding cycle. *Anim Behav* 84: 675–683
- Scheffer A, Trathan PN, Edmonston JG, Bost CA (2016) Combined influence of meso-scale circulation and bathymetry on the foraging behaviour of a diving predator, the king penguin (*Aptenodytes patagonicus*). *Prog Oceanogr* 141:1–16
- Schmid MS, Cowen RK, Robinson K, Luo JY, Briseño-Avena C, Sponaugle S (2020) Prey and predator overlap at the edge of a mesoscale eddy: fine-scale, in-situ distributions to inform our understanding of oceanographic processes. *Sci Rep* 10:921
- Sergi S, Baudena A, Cotté C, Ardyna M, Blain S, d'Ovidio F (2020) Interaction of the Antarctic Circumpolar Current with seamounts fuels moderate blooms but vast foraging grounds for multiple marine predators. *Front Mar Sci* 7: 416
- Silverman BW (2018) Density estimation for statistics and data analysis. Routledge, New York, NY
- Thiebot JB, Cherel Y, Trathan PN, Bost CA (2011) Inter-population segregation in the wintering areas of macaroni penguins. *Mar Ecol Prog Ser* 421:279–290
- Thiebot JB, Cherel Y, Trathan PN, Bost CA (2012) Coexistence of oceanic predators on wintering areas explained by population-scale foraging segregation in space or time. *Ecology* 93:122–130
- Trathan PN, Bishop C, Maclean G, Brown P, Fleming A, Collins MA (2008) Linear tracks and restricted temperature ranges characterise penguin foraging pathways. *Mar Ecol Prog Ser* 370:285–294
- Tripathy SC, Jena B (2019) Iron-stimulated phytoplankton blooms in the Southern Ocean: a brief review. *Remote Sens Earth Syst Sci* 2:64–77
- Wakefield ED, Phillips RA, Matthiopoulos J (2009) Quantifying habitat use and preferences of pelagic seabirds using individual movement data: a review. *Mar Ecol Prog Ser* 391:165–182
- Weimerskirch H, Bonadonna F, Bailleul F, Mabile G, Del'Orno G, Lipp HP (2002) GPS tracking of foraging albatrosses. *Science* 295:1259
- Wotherspoon S, Sumner M, Lisovski S (2013) BASTag: basic data processing for light based geolocation archival tags. R package version 0.1-3. <https://github.com/SWotherspoon/BASTag>

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