Foraging niche partitioning by Antarctic petrels and snow petrels breeding in sympatry

Gildwin Philippot[1], Ewan D. Wakefield[2], Marie-Anne Blanchet[1,3] Nigel G. Yoccoz[3], Richard A. Phillips[4], Erin L. McClymont[2], W. James Grecian[2], Lea Lipphardt[1] & Sébastien Descamps[1]

[1]: Norwegian Polar Institute, The Fram Centre, Tromsø, 9296, Norway

[2]: Department of Geography, Durham University, Lower Mountjoy, South Road, Durham, DH1 3LE, UK

[3]: UiT The Arctic University of Norway, Tromsø, 9509, Norway

[4]: British Antarctic Survey, Natural Environment Research Council, High Cross, Madingley Road, Cambridge, CB3 0ET UK

Corresponding author:
Sebastien Descamps
descamps@npolar.no

Abstract: Breeding in sympatry may increase competition among closely related species, especially when these species are colonial central-place foragers. Niche partitioning, for example through segregation in space, time, habitat or diet, can help mitigate such competition. Here, we test for differences in the movement, space use and habitat selection of two closely-related pelagic seabirds, the Antarctic petrel *Thalassoica antarctica* and snow petrel *Pagodroma nivea,* breeding sympatrically in Antarctica. To do so, we tracked the foraging movements of breeders from a large colony at Svarthamaren, Dronning Maud Land using GPS loggers. We found that during incubation, Antarctic petrels traveled faster, and trips were longer in duration and travel distance than those of snow petrels. Antarctic petrels foraged predominantly northeast of the colony whereas snow petrels foraged further west, closer to the coastline. This led to spatial segregation, with < 15% mean overlap between foraging areas of the two species. Snow petrels foraged more frequently among sea ice, and closer to the sea-ice edge than Antarctic petrels. These results support the hypothesis that the foraging niches of the two species are differentiated in geographical space and habitat, possibly mediated by differences in size and therefore flight performance. These results imply that foraging snow petrels are more directly dependent on sea ice than Antarctic petrels and consequently more immediately affected by loss of sea ice due to climate change.

Keywords: Climate change, Procellariiformes; interspecific competition; niche partitioning; central-place foraging; GPS tracking; sea ice.

1. INTRODUCTION

Understanding how different species use space and resources is an important question in ecology (Roswag *et al.* 2015), because interspecific interactions strongly influence where species occur and which habitats they select. This use of the environment can be framed by the concept of the ecological niche, which Hutchinson (1957) defined as a multi-dimensional space determined by both abiotic and biotic factors. If the use of environmental space by several species overlaps in one or more niche dimensions, they can reduce competition by segregating in geographical space or other dimensions of niche space (Schoener 1974). This adjustment results in what is called the realized niche, as opposed to the fundamental niche, which corresponds to the conditions that an animal would use in the absence of competition (Hutchinson 1957). Such niche segregation can allow the co-existence of species in the same geographical space (Volterra 1928, Gause 1934, Hutchinson 1957, Schoener 1974). As ecological niches have multiple dimensions, there are numerous ways in which animals can achieve niche segregation, for example, through differences in diet (e.g., Chillo *et al.* 2010, Steenweg *et al.* 2011, Florencio *et al.* 2013), use of geographical space (e.g., Pita *et al.* 2010, Kappes *et al.* 2015, Picket *et al.* 2018, Rodríguez *et al.* 2020), allochrony (e.g., Bentley *et al.* 2022, Granroth-Wilding & Philips 2019, Ramos *et al.* 2016) or habitat (e.g., Astarloa *et al.* 2021, Barger *et al.* 2016, Granroth-Wilding & Philips 2019), where habitats are defined by combinations of environmental conditions (Aarts et al. 2008).

Although Hutchinson's multidimensional niche concept remains foundational in ecology, it has been refined to include dynamic and evolutionary processes that influence how species interact with and modify their environments (Ferrante 2025, Holt 2009, Leibold 1995, McInermy & Etienne 2012). We acknowledge these developments but rely here on the Hutchinsonian "requirement niche" framework (Leibold 1995), which remains particularly suitable for describing patterns of space and habitat use in central-place foraging seabirds.

Seabirds are central-place foragers during the breeding season, i.e., they must return regularly to the colony to incubate their egg(s) or feed their chick(s) (Petalas et al. 2024). When two seabird species breed sympatrically, their potential home ranges overlap, and competition is often mitigated via niche segregation (Philips *et al.* 2005, Connan *et al.* 2014, Pickett *et al.* 2018, Granroth-Wilding & Philips 2019), either by specializing on different prey (Croxall & Prince 1980, Steenweg *et al.* 2011, Connan *et al.* 2014), segregating in space (Philips *et al.* 2005, Pickett *et al.* 2018, Granroth-Wilding & Philips 2019) or partitioning habitat (Barger *et al.* 2016, Granroth-Wilding & Philips 2019). One mechanism behind these segregation patterns is the influence of morphology on foraging behaviour. Variations in body size affect wing loading, energy reserves, and the ability to exploit wind, leading larger species to travel faster or over greater distances (Pennycuick *et al.* 1984, Spear & Ainley 1997, Dehnhard *et al.* 2021). These flight and energetic differences can promote spatial segregation even when species rely on similar diet.

In this study, we aim to use tracking to confirm whether differences in space use and habitat use by Antarctic petrels *Thalassoica antarctica* and snow petrels *Pagodroma nivea* previously previously inferred from ship-based observations (Ainley et al. 1992, 1993, 1994, 1998) also occur among sympatric breeders and whether these may be mediated by differences in flight performance during central-place foraging. These two closely-related fulmarine petrels are endemic to Antarctica and have similar life histories and foraging ecology (Marchant *et al.* 1990). Both breed from late November to early March, during the Austral summer and feed mainly on krill, fish and squid (Griffiths 1983, Marchant *et al.* 1990, Lorentsen *et al.* 1998, Ferretti *et al.* 2001). Both are associated with sea-ice habitats (Griffiths 1983, Ainley *et al.*

1984, Fauchald *et al*. 2017, Tarroux *et al.* 2020, Delord *et al.* 2016). However, in these studies, the breeding status and provenance of observed birds was unknown so it is unclear how central-place constraint and flight performance during breeding affect niche partitioning". Hence, we tracked Antarctic petrels and snow petrels breeding sympatrically at Svarthamaren, in Dronning Maud Land, Antarctica with the aim of testing the following predictions: (1) breeding Antarctic petrels fly faster and make foraging trips that are longer in duration and distance (maximal and total) than those of breeding snow petrels due to their difference in wing loading (Spear & Ainley 1997); (2), the foraging areas of the two breeding species are segregated in geographical space due to habitat partitioning (Ainley *et al.* 1993, Ainley *et al.* 1994), and (3) breeding Antarctic petrels are less associated with sea-ice habitats than breeding snow petrels (Ainley *et al.* 1984, Ainley *et al.* 1993, Ainley *et al.* 1994).

Antarctic marine ecosystems are undergoing major transformations due to climate change, with effects on sea-ice dynamics and prey availability (e.g. Stokes *et al.* 2022, Kawaguchi *et al.* 2013, 2024). Understanding niche partitioning among Antarctic seabird species is a priority in this context, as it can reveal how climate-driven changes may affect species differently. This knowledge is critical for predicting the impacts of climate change on these species and the wider ecosystem.

2. METHODS

2.1. Study species and data collection

Antarctic petrels and snow petrels (order Procellariiformes, family Procellariidae) have a similar breeding phenology, laying eggs in late November to early December and early to mid

December, with hatching in early to mid January and mid to late January, and fledging in late February and late February to early march, respectively (Marchant *et al.* 1990, del Hoyo *et al.* 1992; Descamps *et al.* 2016). In Dronning Maud Land, Antarctic petrels and snow petrels weigh approximately 675 g and 250g, respectively, with a wingspan of 100-110 cm (Antarctic petrel) and 75-95 cm (snow petrel). They occur at sea all around Antarctica up to 48°S, and breed in snow-free areas (Marchant *et al.* 1990). Antarctic petrels nest in shallow depressions in gravel and snow petrels in cavities under exposed rocks. Both species produce one egg that is incubated for approximately 45 days. The chick-rearing period lasts approximately 45 days and 48 days for Antarctic petrels and snow petrels, respectively (Marchant *et al.* 1990).

The colony at Svarthamaren (71°53'S, 5°10'E) is located 200 km from the coast and is one of the largest inland seabird colonies in Antarctica (Mehlum *et al.* 1988), a Specially Protected Area (Antarctic Treaty Secretariat 2009*)*. In the 2022/23 season (our study period), there was an estimated 80,500 breeding pairs of Antarctic petrels, and 3,500 breeding pairs of snow petrels (Descamps unpubl. data) at Svarthamaren. During this season, we captured breeding Antarctic petrels and snow petrels at the nest and attached GPS loggers (nanoFix GEO+RF with a solar panel for snow petrels, Pathtrack Ltd., Otley, UK) to the base of the middle two rectrices using Tesa® tape (Table 1). Some data were excluded due to (1) tag loss or failure (22%), (2) breeding failure which led to nest desertion (5%) and (3) trip coverage was incomplete due to battery failure (11%). The GPS loggers were programmed to record locations every 30 min, although this interval could increase if the battery became depleted. Loggers weighed approximately 4 g for snow petrels and 5 g for Antarctic petrels, which is less than 2% of mean body mass (Philips *et al.* 2003). Both during incubation and chick-rearing, most loggers were deployed on birds that were about to be replaced by their partner on the nest and therefore about to start a foraging trip (Table 1). Data from the loggers were downloaded automatically to base stations installed in the colony. If possible, GPS loggers deployed during incubation were recovered that season. Tags deployed during chick-rearing were not recovered but continued to transmit data to base stations until the tags failed, were lost, or the bird stopped visiting the colony. These tags would have been shed during feather moult which occurs in March and April (Marchant *et al.* 1990). Tracking durations ranged from 1.5 to 13 days for Antarctic petrels, and from 2.5 to 11 days for snow petrels. We obtained data on 60 foraging trips during the breeding period for snow petrels (2.0 trips on average per individual) and 51 for Antarctic petrels (2.3 trips on average per individual).

2.2. Data preparation

All data processing and analyses were performed using R software version 4.3.1 (R Core Team 2023). The GPS locations were separated into individual trips with the tripSplit function from the "Track2KBA" package (Beal *et al.* 2021). To do so, a minimum buffer of 35 km was defined around the colony and all birds which travelled outside this buffer were considered as starting a foraging trip. Trips were deemed to have been recorded completely if they returned to a buffer of 1 km around the colony. Following Tarroux et al. (2016), excursions from the colony of < 3 h were discarded because they were too brief for the bird to have foraged at sea. Trips were also discarded if they did not end at the colony or had gaps between locations of >12 h. The breeding status assigned to each trip corresponds to the last observed status at the start of the trip (incubation or chick-rearing; nests were monitored 2-3 times a weekby direct observation of the nest concent). A few foraging trips could not be associated with a specific breeding status due to birds not being observed on the nest prior to the trip (Table 1).

To regularize location data to constant time interval of 30 minutes, we fitted correlated random walk models for each trip and each bird using the aniMotum package (Jonsen *et al.* 2023). We used as starting parameters a maximum speed of 40 m/s, turning angles of 5-10 degrees and step lengths of 5-10 km.

2.3. Trip characteristics

We calculated five foraging trip metrics (i) cumulative distance, (ii) maximum great circle distance (maximum range) from the colony, (iii) duration, (iv) mean speed, and (v) bearing between the colony and the distal location using the function tripSummary from the package track2KBA (Beal *et al.* 2021).

To test for a difference in foraging trip metrics between the two species, we used linear mixed-effects models fitted using the nlme package (Pinheiro *et al.* 2002). Fixed effects included species and breeding stage (incubation vs. chick rearing) and their interaction. We included the trip number nested within bird ID as random factors, to account for the hierarchical dependency of the tracking data. We used Akaike Information Criterion for model selection (Burnham & Anderson 2002), considering five different models (Table 2). If the difference in AIC values between two models was <2, we assumed that the one with fewer parameters was more parsimonious (Burnham & Anderson 2002). We used maximum likelihood (ML) to fit the models and calculate AIC values, as all models considered here had the same random effect structure but different fixed effects. However, to obtain unbiased estimates of the random effects, the selected models were refitted using restricted maximum likelihood (REML, Zuur *et al.* 2009).

2.4. Identification of foraging areas

Our study species do not forage on land and in our study system make long (≥200 km) overland commutes prior to reaching the sea. We therefore restricted this part of our analysis to the at-sea segments of foraging trips. Positions on land were identified and removed using a medium-resolution shapefile from Quantarctica defining the Antarctic coastline (Matsuoka *et al.* 2018). As these points only occurred at the start and end of trips, their removal did not affect the continuity of tracks required for the HMM analyses. To identify locations where birds engaged in putative foraging behavior, we used Hidden Markov Models (HMM) fitted with the momentuHMM package (McClintock et al. 2018), following Wakefield et al. (In review) and Honan et al. (In Press). In brief, we assumed that three behavioral states could be discriminated based on step length and turning angle: Travelling (step length high, turning angle concentrated), foraging (step length intermediate, turning angle dispersed); and resting at sea (step length low, turning angle very dispersed) (Hooten et al. 2017, Bennison et al. 2018). Initially, we fitted 25 models, randomly drawing starting parameters from within realistic ranges defined based on previous studies (Tarroux et al. 2020, Wakefield et al. 2024, Wakefield et al. In review). Using the model with the highest likelihood (Michelot and Langrock 2022, Table 3), we predicted the most likely sequence of states using the Viterbi decoding algorithm (Zucchini et al. 2016).

Using only locations classified as foraging, we created surfaces containing the 95% of the utilization distribution (UD) of each species (the UD describes the probability density of an animal's use of space (Worton 1989)). We estimated UDs using a kernel density estimate with a smoothing parameter of 1 km on a 3.125 x 3.125 km regular grid (matching the spatial resolution of the sea-ice concentration data used in our analyses - see below). We calculated the overlap between the 95% foraging UDs of the two species, using the kerneloverlap function (Calenge 2006), and the Home Range (HR) method (Fieberg & Kochanny 2005). This method gives the proportion of each UD that overlaps with that of the other, ranging from 0 (no overlap) to 1 (complete overlap). To quantify the uncertainty in the overlap, a bootstrap was used, with

500 iterations. At each iteration, the foraging locations from 22 Antarctic petrels and 30 snow petrels were randomly selected with replacement and the overlap was calculated. The 95% confidence interval of these 500 overlap scores was then used to estimate the uncertainty around the overlap.

2.5. Use of sea ice

To quantify sea-ice conditions at locations used by the two species, we considered sea-ice concentration (SIC) and distance to sea-ice edge. The SIC is the percentage of a given grid cell's surface covered by sea ice. Daily sea ice concentration at a 3.125 km resolution was downloaded from Bremen University sea-ice dataset (https://data.seaice.uni-bremen.de/databrowser/). The SIC data results from applying the ARTIST Sea Ice algorithm to the brightness temperature obtained by the AMSR2 sensors flown aboard the JAXA satellite (Spreen *et al.* 2008).

We used these sea-ice data to answer three questions. (i) How frequently do the two species forage in areas covered by sea ice? (ii) What is the mean SIC in those areas? (iii) When the two species forage in open water, how far are they from the ice edge? For the first two questions, we used zero-inflated mixed-effect beta-regression models fitted using the glmmTMB package (Brooks *et al.* 2017) to account for the large number of zeros in our dataset. This type of model has two components: The first, the zero-inflation component, is a logistic regression that models the probability of a SIC value being exactly zero (completely open water), which is used to answer our first question. The second component, a beta regression, then models the SIC values that are strictly between 0 and 1 (i.e., >0 - 1), after converting the percentages to proportion, using a logit link function. This allows us to evaluate how SIC usage varies between species and breeding stages, conditional on the bird foraging in areas with some sea-ice cover, answering our second question. To address the third question, we defined the sea-ice edge as the 15% SIC contour, marking the boundary between open water and ice-covered areas and for each foraging GPS location in open water (i.e., SIC < 15%), calculated the absolute distance to the nearest point on the 15% SIC contour. We modelled these distances using linear mixed models fitted with the lme function from the "nlme" package (Pinheiro *et al.* 2002). We included random intercepts for bird ID and trip number nested within bird ID. The distance to the ice edge was square root transformed to further meet the assumptions of homoscedasticity and normality of residuals (model residuals were checked visually). For both the zero-inflated, beta regression and linear models, we used AIC to assess whether model performance was improved by including species, breeding status or their interactions as fixed effects.

3. RESULTS

3.1. Foraging trip metrics

Maximum range, cumulative distance and trip duration were highly correlated (Pearson's r > 0.85; Table A1) so we only report the former. AIC provided evidence that maximum range varied between species and breeding stages, whereas mean speed and bearing to distal location varied only between species (Tables 2 and 4; Fig. 1). During incubation and chick-rearing, maximum range was on average 608 and 145 km further, respectively, from the colony for Antarctic petrels than snow petrels but the difference was significant only during incubation (Table A2). During both incubation and chick-rearing, distal locations of trips of Antarctic petrels were 62° further east and travel speeds were 4 km h^{-1} faster than for snow petrels (Figs. 1; Tables 4 and A2).

3.2. Spatial segregation

HMMs classified 37% of locations of Antarctic petrels and 35% of locations of snow petrels as foraging (Table A3). Antarctic petrels foraged in areas further east and north than snow petrels (Fig. 2). The latter's UD was centred closer to the coast, predominantly to the west of the colony. There was very little overlap between core UDs of the two species (overlap index: snow petrels over Antarctic petrels, 12% [95% confidence interval: 1% - 21%]; Antarctic petrels over snow petrels, 14% [95% CI: 0% - 28%]).

3.3. Use of sea-ice habitats

Among the models of SIC at foraging locations, the best models for the zero-inflated section included species, breeding status, and their interaction. In contrast, for the beta-regression section, the null model was most parsimonious, suggesting that neither species nor breeding status had a significant effect (Fig. 3, Table 5). The zero-inflated section, testing the use of completely open water (i.e., the logistic regression predicting whether a proportion is 0 or not) indicated that Antarctic petrels and snow petrels foraged for a similar proportion of time in completely open water (0% SIC) during incubation (56% vs. 44%). However, during chick-rearing, Antarctic petrels foraged more frequently in open water than snow petrels (90% vs. 50%; Fig. 3, Table 6).

Distances to the sea-ice edge of foraging locations in open water (>15% SIC), beyond the ice edge, differed according to species, breeding status, and their interaction (Table 5). On average, Antarctic petrels foraged 357 km farther from the ice edge than snow petrels during incubation, and 9 km farther during chick-rearing (Fig. 3, Table 6).

4. DISCUSSION

Sympatric central-place foragers, especially those that are closely related, are expected to develop strategies that mitigate the effects of competition, leading to spatial, temporal, behavioral or some other form of segregation (González-Solís *et al.* 2000, Navarro *et al.* 2013, Fromant *et al.* 2022). Our study revealed that, despite many similarities in their foraging behavior, Antarctic petrels generally travelled faster and covered greater distances than snow petrels during incubation. The small overlap in their foraging areas (12% and 14% during incubation and chick-rearing, respectively) supports the hypothesis that these species segregate spatially, presumably to reduce competitive pressures, even though they share a similar fundamental niche. Moreover, our results reveal habitat segregation: although both species forage in sea-ice habitats, snow petrels were more closely associated with sea-ice than Antarctic petrels. However, it is important to stress that our study is limited to a single breeding season. Segregation among Antarctic and snow petrels may vary across years depending on environmental conditions.

4.1. Difference in foraging trip metrics

During the incubation period, Antarctic petrels made longer foraging trips, both in terms of distance and duration, and traveled further from the colony than snow petrels. This is potentially attributable to differences in wing loading (Spear & Ainley 1997). Antarctic petrels have a higher wing loading than snow petrels and consequently have higher optimal airspeeds, enabling them to cover greater distances in a given time (Griffiths 1983; Marchant *et al.* 1990, Spear & Ainley 1997). Moreover, during incubation, foraging duration might be influenced by the fasting capacity of the partner. The larger body size of Antarctic petrels likely allows the incubating partner to withstand longer fasting periods, allowing the foraging bird to undertake longer trips than snow petrels (Shoji *et al.* 2015).

Both species traveled shorter distances during chick-rearing than incubation. Foraging trips in chick-rearing need to meet the energetic requirements of both parents and the chick(s) (Varpe *et al.* 2004), which represent an intrinsic constraint, especially during early chick rearing – the period observed in our study – when the energy demands of chicks is important, requiring the parent to do shorter trip. In addition, the progressive melting of sea ice throughout the breeding season likely allows Antarctic and snow petrels to forage closer to the colony during chick-rearing, reducing trip distances and potentially enabling more frequent chick provisioning. This habitat shift represents a key extrinsic factor that shapes foraging decisions. The observed convergence in foraging trip distances between the two species could be the result of Antarctic petrels' and snow petrels' chicks having similar mass-specific energy requirements. However, our results also suggest that snow petrels tended to forage slightly farther from the colony during chick-rearing than Antarctic petrels, although this difference was not statistically significant. The reason for this pattern could be that by the chick-rearing period, the ice edge has reached the coast, forcing snow petrels to travel farther west along the coast and into the Weddell Sea embayment to find suitable ice-edge or MIZ habitat. In contrast, Antarctic petrels can access open water close to the colony.

4.2. Spatial Segregation

We found clear spatial segregation between the two species. We presume that this is a way of reducing competition, which otherwise might be intense given the ecological similarities between these two species, including overlapping diets (Marchant *et al.* 1990, del Hoyo *et al.* 1992). However, previous studies on sympatrically breeding petrels have yielded mixed results regarding spatial segregation. Some reported evidence of segregation (e.g., González-Solís *et al.* 2000 and Granroth-Wilding & Phillips 2019 for giant petrel spp.; Navarro *et al.* 2013 for blue petrels, Antarctic prions, common diving petrels, and South Georgian diving petrels; Fromant *et al.* 2022 for common and South Georgian diving petrels), while others did not (e.g., Dehnhard *et al.* 2020 for Antarctic petrels, southern fulmars and cape petrels; Delord *et al.* 2016 for southern fulmars, cape petrels, and snow petrels). These contrasting findings may reflect differences in local ecological conditions, as the studies were conducted at different colonies, varying in distance to the sea and across distinct Antarctic regions. It is also possible that in those locations, competition was reduced through other mechanisms, such as dietary or temporal segregation. Indeed, a lack of spatial segregation can arise when sympatric species target different prey taxa (Delord *et al.* 2016), prey of different sizes, or prey caught at different depths or times of day. These strategies can reduce the need for spatial segregation to avoid competition. At Svarthamaren, the clear spatial segregation between Antarctic petrels and snow petrels suggests that alternative strategies, such as dietary or temporal segregation, may not be needed. This is supported by previous findings indicating similarities in their diets (Marchant *et al.* 1990; del Hoyo et al., 1992), similarities inforaging tactics, such as surface-seizing and surface-diving and difference in preferred foraging habitat (Marchant *et al.* 1990, Ainley *et al.* 1993, Ainley *et al.* 1994). However, environmental conditions such as sea-ice concentration, ocean temperature, and productivity strongly affect prey availability and distribution in Antarctic waters (Ainley *et al.* 1998, Ainley *et al.* 1993, Ainley *et al.* 1994, Ribic & Ainley 1997, Ribic *et al.* 2011). Consequently, spatial segregation observed in one season may not necessarily persist under different environmental regimes.

One potential explanation for the pronounced segregation at Svarthamaren lies in the considerable distance that birds must travel to reach the sea, which increases the energetic cost of commuting. Although prey in Antarctic waters during summer is often considered superabundant and not typically limiting for seabirds, this additional travel cost may reduce the net energetic return from prey, thereby amplifying the effects of competition. Moreover, even under conditions of high overall prey abundance, prey can be patchily distributed, and energetic constraints linked to the long commuting distance from Svarthamaren may favor segregation as a way to reduce overlap and competition in profitable foraging zones.As such, spatial segregation may become more advantageous in distant colonies like Svarthamaren, compared to sites located closer to the coast, such as those studied by Dehnhard et al. (2020) and Delord et al. (2016).

However, our study is based on a single breeding season, and the observed segregation patterns should therefore be interpreted with caution. Inter-annual variations in sea-ice extent, prey availability, and environmental conditions could influence the degree, or even the direction, of spatial segregation between these two species (Ainley *et al.* 1993, Ainley *et al.* 1994, Ainley *et al*. 1998). Consequently, spatial segregation observed in one season may not necessarily persist under different environmental regimes. However, very few studies (e.g. Picket et al 2018) have investigated such inter-annual variation and it remains unclear how changes in the environment may affect spatial segregation in seabird. Further studies would be valuable to assess whether the pattern observed at Svarthamaren is consistent across years or specific to the environmental context of our study period.

4.3. Difference in sea-ice use

Previous studies on snow petrels and Antarctic petrels suggest that the former forage in close association with sea-ice, whereas the latter often forages in open water near or beyond the ice edge (Ainley *et al.* 1984; Ainley *et al.* 1993, Ainley *et al.* 1994, Ribic *et al.* 2008; Woehler *et* *al.* 2003, 2010; Zink 1981). Notably, all of these previous studies relied on at-sea observations and cannot determine whether birds observed are breeders and therefore subject to central-place foraging constraints; our study is the first to use tracking data to compare habitat use by breeding birds from the two species, providing a more nuanced picture of their foraging ecology. Our results support these previous findings and indicate that snow petrel had, as predicted, a higher probability than Antarctic petrel of foraging in areas with some (> 0%) sea-ice cover. However, there were no significant differences between species or breeding stages in the SIC. This suggests that once within the ice, both species utilize similar sea-ice conditions. As expected, snow petrels foraged on average closer to the sea-ice edge than Antarctic petrels, particularly during incubation, consistent with the studies cited above. Despite this general pattern, snow petrels showed substantial variability in the distance to the ice edge during incubation, with some individuals foraging far into open water (Fig. 2). This variation may be due to the use of small sea-ice patches or icebergs in open water that fall below the detection threshold of the satellite data used in this study (3.125 km cell size), suggesting that finer-scale sea-ice data would be needed to verify this hypothesis. A similar pattern was observed in Antarctic petrels, which also foraged significantly farther from the ice edge during incubation than during chick-rearing.

Foraging ranges of both species reduced during chick-rearing, likely due to the need to return regularly to the nest to feed chicks. This shift toward more localized foraging may explain the closer proximity to the sea-ice edge observed during this stage. Alternatively, both species may simply track the ice edge and associated habitats (e.g., post-melt blooms) as they recede towards the coastline over the breeding season, as shown for Antarctic petrels by Fauchald et al. (2017). This could also help explain the unexpectedly high association with open water from snow petrels, as both species may target recently melted areas that support ephemeral, highly productive habitats.

Despite the stronger overall association of snow petrels than Antarctic petrels with sea ice, our results indicate that their probability of occurrence in sea-ice habitats was only slightly above 50%. This could indicate that, even if snow petrels have a preference for sea-ice habitats, they show a larger flexibility in their foraging habitats than previously inferred by at-sea studies (Ainley *et al.* 1984; Ainley *et al.* 1993, Ainley *et al.* 1994, Ribic *et al.* 2008; Woehler *et al.* 2003; Woehler *et al.* 2010; Zink 1981).

Overall, these patterns suggest a difference in how the two species interact with sea-ice habitats: snow petrels could be more reliant on the physical presence of sea ice, while Antarctic petrels might be more influenced by its broader ecological effects, targeting areas recently modified by ice retreat (Fauchald *et al.* 2017).

However, we caution that our study analyzed habitat *use*. Formal analysis of habitat *selection* (i.e., use relative to availability) would be required to test whether sea-ice habitats are preferred over open-water habitats and whether this depends on availability (Wakefield et al. 2009). This approach could also test whether habitat selection differs between the two species.

CONCLUSION

Our findings enhance the knowledge of the at-sea foraging behavior and habitats of Antarctic petrels and snow petrels. Such insights are valuable for informing conservation efforts and guiding the design of future marine protected areas in the Southern Ocean (Teschke et al., 2020). The contrasting population trends at Svarthamaren (i.e. Antarctic petrels decline (Descamps et al. 2016, 2023) versus relatively stable snow petrels' numbers (Descamps unpubl.

data)) raise the question of whether differences in spatial segregation and habitat dependence might contribute to species-specific responses to environmental change, a possibility that warrants further investigation. Given the projected reductions in Antarctic sea-ice extent (Turner *et al.* 2019, 2022), snow petrels may also become increasingly vulnerable, due to their stronger dependence on habitats directly associated with sea ice. As such, continued monitoring and targeted research will be essential to anticipate species-specific responses to climate change and to inform adaptive conservation strategies in the Southern Ocean.

ACKNOWLEDGEMENT

We thank the personnel at the Troll Research Station for support in the field and Sophie Bourgeon and Caitlin Frankish for very useful comments on a first draft. We also thank W.J. Miloch who helped in deploying loggers in 2022. Funding was provided by the Leverhulme Trust (Research Leadership Award RL-2019-023), the European Research Council H2020 (grant no. 864637) and the Antarctic programme of the Norwegian Polar Institute.

Author contribution

SD, EW, RP and ELM designed the study. GP, MAB and EW analyzed the data with support from NGY and SD. SD, EW and WJG collected the data. GP wrote the first draft with contributions from SD, EW and MAB. All co-authors contributed to revisions of subsequent versions of the manuscript.

LITERATURE CITED

Aarts G, MacKenzie M, McConnell B, Fedak M, Matthiopoulos J (2008) Estimating space-use and habitat preference from wildlife telemetry data. *Ecography* 31:140–160. https://doi.org/10.1111/j.2007.0906-7590.05236.x

Ainley DG, O'Connor EF, Boekelheide RJ (1984) The marine ecology of birds in the Ross Sea, Antarctica. *Ornithol Monogr* 32:iii–97. https://doi.org/10.2307/40166773

Ainley DG, Ribic CA, Fraser WR (1994) Ecological structure among migrant and resident seabirds of the Scotia–Weddell Confluence region. *J Anim Ecol* 63:347–364. https://doi.org/10.2307/5553

Ainley DG, Ribic CA, Fraser WR (1992) Does prey preference affect habitat choice in Antarctic seabirds? *Mar Ecol Prog Ser* 90:207–221. https://doi.org/10.3354/meps090207

Antarctic Treaty Secretariat (2009) Management plan for Antarctic Specially Protected Area No. 142: Measure 8, Annex. https://documents.ats.aq/recatt/Att426_e.pdf (accessed 25 Jan 2013)

Astarloa A, Glennie R, Chust G, García-Baron I, Boyra G, Martínez U, Rubio A, Louzao M (2021) Niche segregation mechanisms in marine apex predators inhabiting dynamic environments. *Divers Distrib* 27:799–815. https://doi.org/10.1111/ddi.13229

Ballard G, Jongsomjit D, Veloz SD, Ainley DG (2012) Coexistence of mesopredators in an intact polar ocean ecosystem: the basis for defining a Ross Sea marine protected area. *Biol Conserv* 156:72–82. https://doi.org/10.1016/j.biocon.2011.11.017

Barger CP, Young RC, Will A, Ito M, Kitaysky AS (2016) Resource partitioning between sympatric seabird species increases during chick-rearing. *Ecosphere* 7:e01447. https://doi.org/10.1002/ecs2.1447

Beal M, Oppel S, Handley J, Pearmain EJ, Morera-Pujol V, Carneiro APB, Davies TE, Phillips RA, Taylor PR, Miller MGR, Franco AMA, Catry I, Patrício AR, Regalla A, Staniland I, Boyd C, Catry P, Dias MP (2021) track2KBA: an R package for identifying important sites for biodiversity from tracking data. *Methods Ecol Evol* 12:2372–2378. https://doi.org/10.1111/2041-210X.13713

Bennison A, Bearhop S, Bodey TW, Votier SC, Grecian WJ, Wakefield ED, Hamer KC (2018) Search and foraging behaviors from movement data: a comparison of methods. *Ecol Evol* 8:13–24. https://doi.org/10.1002/ece3.3593

Bentley LK, Manica A, Dilley BJ, Ryan PG, Phillips RA (2023) Divergent foraging habitat preferences between summer-breeding and winter-breeding *Procellaria* petrels. *Ibis* 165:618–628. https://doi.org/10.1111/ibi.13152

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Mächler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J* 9:378–400. https://doi.org/10.32614/RJ-2017-066

Burnham KP, Anderson DR (2002) *Model selection and multimodel inference: a practical information-theoretic approach.* Springer-Verlag, New York

Calenge C (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecol Model* 197:516–519. https://doi.org/10.1016/j.ecolmodel.2006.03.017

Chillo V, Rodríguez D, Ojeda RA (2010) Niche partitioning and coexistence between two mammalian herbivores in the Dry Chaco of Argentina. *Acta Oecol* 36:611–616. https://doi.org/10.1016/j.actao.2010.09.002

Connan M, McQuaid CD, Bonnevie BT, Smale MJ, Cherel Y (2014) Combined stomach content, lipid and stable isotope analyses reveal spatial and trophic partitioning among three sympatric albatrosses. *Mar Ecol Prog Ser* 497:259–272. https://doi.org/10.3354/meps10606

Croxall JP, Prince PA (1980) Food, feeding ecology and ecological segregation of seabirds at South Georgia. *Biol J Linn Soc* 14:103–131. https://doi.org/10.1111/j.1095-8312.1980.tb00101.x

Delord K, Barbraud C, Pinaud D, Letournel B, Jaugeon B, Cherel Y, Weimerskirch H (2016) Species-specific foraging strategies and segregation mechanisms of sympatric Antarctic fulmarine petrels throughout the annual cycle. *Ibis* 158:569–586. https://doi.org/10.1111/ibi.12365

del Hoyo J, Elliott A, Sargatal J, Cabot J (1992) *Handbook of the birds of the world, vol. 1: ostrich to ducks.* Lynx Edicions, Barcelona

Dehnhard N, Masello JF, Quillfeldt P, Chastel O, Cherel Y, Eens M, Poisbleau M (2020) High inter- and intraspecific niche overlap among three sympatrically breeding seabird species. *J Anim Ecol* 89:104–119. https://doi.org/10.1111/1365-2656.13078

Dehnhard N, Klekociuk AR, Emmerson L (2021) Interactive effects of body mass changes and species-specific morphology on flight behaviour of fulmarine petrels. *Ecol Evol* 11:4972–4991. https://doi.org/10.1002/ece3.7501

Descamps S, Aars J, Fuglei E, Kovacs KM, Lydersen C, Pavlova O, Pedersen ÅØ, Ravolainen V, Strøm H (2016) Large-scale oceanographic fluctuations drive Antarctic petrel survival and reproduction. *Ecography* 39:496–505. https://doi.org/10.1111/ecog.01388

Descamps S (2021) Antarctic petrel population size, Svarthamaren, 1984–2019. Npolar Data Centre. https://doi.org/10.21334/NPOLAR.2021.424D11BA

Descamps S, Tarroux A, Lorentsen SH, Moe B, Falk K, Anker-Nilssen T (2023) Extreme snowstorms lead to large-scale seabird breeding failures in Antarctica. *Curr Biol* 33:R176–R177. https://doi.org/10.1016/j.cub.2022.12.055

Fauchald P, Tarroux A, Lorentsen SH, Anker-Nilssen T, Descamps S, Strom H, Moe B (2017) Spring phenology shapes the spatial foraging behavior of Antarctic petrels. *Mar Ecol Prog Ser* 568:203–215. https://doi.org/10.3354/meps12082

Ferrante M (2025) The niche concept in a changing world. *Nat Rev Biodivers* 1:419. https://doi.org/10.1038/s44358-025-00060-x

Ferretti V, Soave G, Casaux R, Coria NR (2001) Diet of the snow petrel *Pagodroma nivea* at Laurie Island, Antarctica, during the 1997/98 breeding season. *Mar Ornithol* 29:71–73

Fieberg J, Kochanny CO (2005) Quantifying home-range overlap: the importance of the utilization distribution. *J Wildl Manag* 69:1346–1359. https://doi.org/10.2193/0022-541X(2005)69[1346:QHOTIO]2.0.CO;2

Florencio DF, Marins A, Rosa CS, Cristaldo PF, Araújo APA, Silva IR, DeSouza O (2013) Diet segregation between cohabiting builder and inquiline termite species. *PLoS One* 8:e66535. https://doi.org/10.1371/journal.pone.0066535

Fromant A, Cherel Y, Barbraud C, Delord K, Weimerskirch H (2022) Stage-dependent niche segregation: insights from a multi-dimensional approach of two sympatric sibling seabirds. *Oecologia* 199:537–548. https://doi.org/10.1007/s00442-022-05181-0

Gause GF (1934) Experimental analysis of Vito Volterra's mathematical theory of the struggle for existence. *Science* 79:16–17. https://doi.org/10.1126/science.79.2036.16-a

González-Solís J, Croxall J, Wood A (2000) Foraging partitioning between giant petrels *Macronectes* spp. and its relationship with breeding population changes at Bird Island, South Georgia. *Mar Ecol Prog Ser* 204:279–288. https://doi.org/10.3354/meps204279

Granroth-Wilding HMV, Phillips RA (2019) Segregation in space and time explains the coexistence of two sympatric sub-Antarctic petrels. *Ibis* 161:101–116. https://doi.org/10.1111/ibi.12584

Griffiths AM (1983) Factors affecting the distribution of the snow petrel *Pagodroma nivea* and the Antarctic petrel *Thalassoica antarctica*. *Ardea* 71:145–150

Gulka J, Ronconi RA, Davoren GK (2019) Spatial segregation contrasting dietary overlap: niche partitioning of two sympatric alcids during shifting resource availability. *Mar Biol* 166:1–17. https://doi.org/10.1007/s00227-019-3553-x

Harper PC (1987) Feeding behaviour and other notes on 20 species of Procellariiformes at sea. *Notornis* 34:169–192

Hedd A, Montevecchi WA, Phillips RA, Fifield DA (2014) Seasonal sexual segregation by monomorphic sooty shearwaters *Puffinus griseus*. *PLoS One* 9:e85572. https://doi.org/10.1371/journal.pone.0085572

Honan EM, Wakefield ED, Phillips RA, Grecian WJ, Prince S, Robert H, Descamps S, Rix A, Hoelzel AR, McClymont EL (in press) The foraging distribution and habitat use of chick-rearing snow petrels from two colonies in Dronning Maud Land, Antarctica. *Mar Biol*

Hooten MB, Johnson DS, McClintock BT, Morales JM (2017) *Animal movement: statistical models for telemetry data.* CRC Press, New York

Holt RD (2009) Bringing the Hutchinsonian niche into the 21st century: ecological and evolutionary perspectives. *Proc Natl Acad Sci USA* 106:19659–19665. https://doi.org/10.1073/pnas.0905137106

Hutchinson GE (1957) Concluding remarks. *Cold Spring Harb Symp Quant Biol* 22:415–427. https://doi.org/10.1101/SQB.1957.022.01.039

Hyrenbach KD, Fernández P, Anderson DJ (2002) Oceanographic habitats of two sympatric North Pacific albatrosses during the breeding season. *Mar Ecol Prog Ser* 233:283–301. https://doi.org/10.3354/meps233283

Ito M, Takahashi A, Kokubun N, Kitaysky A, Watanuki Y (2010) Foraging behavior of incubating and chick-rearing thick-billed murres *Uria lomvia*. *Aquat Biol* 8:279–287. https://doi.org/10.3354/ab00229

Jonsen ID, McMahon CR, Patterson TA, Auger-Méthé M, Harcourt R, Hindell MA, Bestley S, Thums M (2023) aniMotum: an R package for animal movement data. *Methods Ecol Evol* 14:806–816. https://doi.org/10.1111/2041-210X.14060

Kappes MA, Weimerskirch H, Pinaud D, Barbraud C, Delord K, Cherel Y (2015) Reproductive constraints influence habitat accessibility, segregation, and preference of sympatric albatross species. *Move Ecol* 3:34. https://doi.org/10.1186/s40462-015-0063-4

Karney CFF (2013) Algorithms for geodesics. *J Geod* 87:43–55. https://doi.org/10.1007/s00190-012-0578-z

Kawaguchi S, Ishida A, King R, Raymond B, Waller N, Constable A, Nicol S (2013) Risk maps for Antarctic krill under projected Southern Ocean acidification. *Nat Clim Change* 3:843–847. https://doi.org/10.1038/NCLIMATE1937

Kawaguchi S, Atkinson A, Bahlburg D, Bernard KS, Cavan EL, Cox MJ, Hill SL, Meyer B, Veytia D (2024) Climate change impacts on Antarctic krill behaviour and population dynamics. *Nat Rev Earth Environ* 5:43–58

Klug H (2018) Why monogamy? A review of potential ultimate drivers. *Front Ecol Evol* 6:12. https://doi.org/10.3389/fevo.2018.00030

Lawler JJ, Shafer SL, White D, Kareiva P, Maurer EP, Blaustein AR, Bartlein PJ (2009) Projected climate-induced faunal change in the Western Hemisphere. *Ecology* 90:588–597. https://doi.org/10.1890/08-0823.1

Leibold MA (1995) Niche concept revisited: mechanistic models and community context. *Ecology* 76:1371–1382. https://doi.org/10.2307/1938141

Lorentsen SH, Klages N, Røv N (1998) Diet and prey consumption of Antarctic petrels *Thalassoica antarctica* at Svarthamaren. *Polar Biol* 19:414–420. https://doi.org/10.1007/s003000050267

Marchant S, Higgins PJ, Ambrose SJ (1990) *Handbook of Australian, New Zealand and Antarctic birds, vol. 1A: ratites to ducks.* Oxford Univ Press, Melbourne

Marko PB (2008) Sympatry. In: Jørgensen SE, Fath BD (eds) *Encyclopedia of ecology*, vol. 4. Elsevier, Amsterdam, p 3450–3458. https://doi.org/10.1016/B978-008045405-4.00549-8

Matsuoka K, Skoglund A, Roth G (2018) Quantarctica. Norwegian Polar Institute. https://doi.org/10.21334/npolar.2018.8516e961

McClintock BT, Michelot T, Goslee S (2018) momentuHMM: R package for generalized hidden Markov models of animal movement. *Methods Ecol Evol* 9:1518–1530. https://doi.org/10.1111/2041-210X.12995

McInerny GJ, Etienne RS (2012) Ditch the niche: is the niche a useful concept in ecology or species distribution modelling? *J Biogeogr* 39:2096–2102. https://doi.org/10.1111/jbi.12033

Mehlum F, Gjessing Y, Haftorn S, Bech C (1988) Census of breeding Antarctic petrels and physical features of the colony at Svarthamaren. *Polar Res* 6:1–9. https://doi.org/10.3402/polar.v6i1.6841

Michelot T, Langrock R (2022) A short guide to choosing initial parameter values for moveHMM. https://cran.r-project.org/web/packages/moveHMM/vignettes/moveHMM-starting-values.pdf

Miller AK, Kappes MA, Trivelpiece SG, Trivelpiece WZ (2010) Foraging-niche separation of gentoo and chinstrap penguins. *Condor* 112:683–695. https://doi.org/10.1525/cond.2010.090221

Navarro J, González-Solís J, Viscor G, Phillips RA (2013) Ecological segregation in space, time and trophic niche of sympatric planktivorous petrels. *PLoS One* 8:e62897. https://doi.org/10.1371/journal.pone.0062897

Pebesma E, Bivand R (2023) *Spatial data science: with applications in R.* Chapman & Hall/CRC, Boca Raton. https://doi.org/10.1201/9780429459016

Pennycuick CJ, Croxall JP, Prince PA (1984) Scaling of foraging radius and growth rate in petrels and albatrosses (Procellariiformes). *Ornis Scand* 15:145–154. https://doi.org/10.2307/3675955

Péron C, Delord K, Phillips RA, Charbonnier Y, Marteau C, Louzao M, Weimerskirch H (2010) Seasonal variation in oceanographic habitat and behaviour of white-chinned petrels *Procellaria aequinoctialis* from Kerguelen Island. *Mar Ecol Prog Ser* 416:267–284. https://doi.org/10.3354/meps08785

Petalas C, van Oordt F, Lavoie RA, Elliott KH (2024) A review of niche segregation across sympatric breeding seabird assemblages. *Ibis 166(4):1123–1145.* https://doi.org/10.1111/ibi.13310

Peterson AT, Ortega-Huerta MA, Bartley J, Sánchez-Cordero V, Soberón J, Buddemeier RH, Stockwell DRB (2002) Future projections for Mexican faunas under global climate change scenarios. *Nature* 416:626–629. https://doi.org/10.1038/416626a

Phalan B, Phillips RA, Silk JRD, Afanasyev V, Fukuda A, Fox J, Catry P, Higuchi H, Croxall JP (2007) Foraging behaviour of four albatross species by night and day. *Mar Ecol Prog Ser* 340:271–286. https://doi.org/10.3354/meps340271

Phillips RA, Xavier JC, Croxall JP (2003) Effects of satellite transmitters on albatrosses and petrels. *Auk* 120:1082–1090. https://doi.org/10.1642/0004-8038(2003)120[1082:EOSTOA]2.0.CO;2

Phillips RA, Silk JRD, Croxall JP (2005) Foraging and provisioning strategies of the light-mantled sooty albatross at South Georgia. *Mar Ecol Prog Ser* 285:259–270. https://doi.org/10.3354/meps285259

Phillips RA, Lewis S, González-Solís J, Daunt F (2017) Causes and consequences of individual specialization in foraging and migration strategies of seabirds. *Mar Ecol Prog Ser* 578:117–150. https://doi.org/10.3354/meps12217

Pickett EP, Fraser WR, Patterson-Fraser DL, Cimino MA, Torres LG, Friedlaender AS (2018) Spatial niche partitioning may promote coexistence of *Pygoscelis* penguins as climate-induced sympatry occurs. *Ecol Evol* 8:9764–9778. https://doi.org/10.1002/ece3.4445

Pinheiro JC, Bates DM, Raudenbush SW (2002) Mixed-effects models in S and S-Plus. *Sociol Methods Res* 31:110–118

Pita R, Mira A, Beja P (2010) Spatial segregation of two vole species within habitat patches in fragmented farmland. *Eur J Wildl Res* 56:651–662. https://doi.org/10.1007/s10344-009-0360-6

R Core Team (2023) *R: a language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna. https://www.R-project.org/

Ramos R, Ramírez I, Paiva VH, Militão T, Biscoito M, Menezes D, Phillips RA, Zino F, González-Solís J (2016) Global spatial ecology of three closely related gadfly petrels. *Sci Rep* 6:23447. https://doi.org/10.1038/srep23447

Rey AR, Pütz K, Simeone A, Hiriart-Bertrand L, Reyes-Arriagada R, Riquelme V, Lüthi B (2013) Comparative foraging behaviour of sympatric Humboldt and Magellanic penguins. *Emu* 113:145–153. https://doi.org/10.1071/MU12040

Ribic CA, Ainley DG, Reid J (1997) Relationships of seabird assemblages to physical habitat in Pacific equatorial waters. *ICES J Mar Sci* 54:593–599. https://doi.org/10.1006/jmsc.1997.0244

Ribic CA, Chapman E, Fraser WR, Lawson GL, Wiebe PH (2008) Top predators in relation to bathymetry, ice and krill during austral winter in Marguerite Bay. *Deep-Sea Res II* 55:485–499. https://doi.org/10.1016/j.dsr2.2007.11.006

Ribic CA, Ainley DG, Glenn Ford R, Fraser WR, Tynan CT, Woehler EJ (2011) Water masses, ocean fronts, and the structure of Antarctic seabird communities. *Deep-Sea Res II* 58:1695–1709. https://doi.org/10.1016/j.dsr2.2009.09.017

Ricklefs RE (1983) Some considerations on the reproductive energetics of pelagic seabirds. *Stud Avian Biol* 8:84–94

Ridoux V, Offredo C (1989) The diets of five summer-breeding seabirds in Adélie Land, Antarctica. *Polar Biol* 9:137–145. https://doi.org/10.1007/BF00297168

Rodríguez A, Urra F, Jubete F, Román J, Revilla E, Palomares F (2020) Spatial segregation between red foxes, European wildcats and domestic cats. *Diversity* 12:268. https://doi.org/10.3390/d12070268

Roswag A, Becker NI, Encarnação JA (2015) Importance of multidimensional analyses of resource partitioning in highly mobile species. *Popul Ecol* 57:601–611. https://doi.org/10.1007/s10144-015-0508-z

Sakamoto Y, Ishiguro M, Kitagawa G (1986) *Akaike information criterion statistics.* Tokyo: KTK Scientific Publishers.

Schielzeth H, Nakagawa S, Freckleton R (2013) Nested by design: model fitting and interpretation in the mixed-model era. *Methods Ecol Evol* 4:14–24. https://doi.org/10.1111/j.2041-210X.2012.00251.x

Schoener TW (1974) Resource partitioning in ecological communities. *Science* 185:27–39. https://doi.org/10.1126/science.185.4145.27

Shoji A, Elliott KH, Aris-Brosou S, Wilson RP, Gaston AJ, Pichegru L (2015) Predictors of incubation costs in seabirds. *Ibis* 157:44–53. https://doi.org/10.1111/ibi.12219

Spear LB, Ainley DG (1997) Flight behaviour of seabirds in relation to wind and wing morphology. *Ibis* 139:221–233. https://doi.org/10.1111/j.1474-919X.1997.tb04620.x

Spreen G, Kaleschke L, Heygster G (2008) Sea-ice remote sensing using AMSR-E 89 GHz channels. *J Geophys Res Oceans* 113:C02S03. https://doi.org/10.1029/2005JC003384

Steele WK (2005) Stable isotope ratios of Antarctic petrel and snow petrel bone collagen. *Polar Biol* 28:672–679. https://doi.org/10.1007/s00300-005-0736-3

Steenweg RJ, Ronconi RA, Leonard ML (2011) Seasonal and age-dependent dietary partitioning between great black-backed and herring gulls. *Condor* 113:795–805. https://doi.org/10.1525/cond.2011.110004

Stokes CR, Abram NJ, Bentley MJ, Edwards TL, England MH, Foppert A, Jamieson SS, Jones RS, King MA, Lenaerts JT (2022) Response of the East Antarctic Ice Sheet to past and future climate change. *Nature* 608:275–286. https://doi.org/10.1038/s41586-022-04946-0

Tarroux A, Weimerskirch H, Wang S-H, Bromwich DH, Cherel Y, Kato A, Ropert-Coudert Y, Varpe Ø, Yoccoz NG, Descamps S (2016) Flexible flight response to challenging wind conditions in a commuting Antarctic seabird. *Anim Behav* 113:99–112. https://doi.org/10.1016/j.anbehav.2015.12.021

Tarroux A, Cherel Y, Fauchald P, Kato A, Love OP, Ropert-Coudert Y, Spreen G, Varpe Ø, Weimerskirch H, Yoccoz NG, Zahn S, Descamps S, Grémillet D (2020) Foraging tactics in dynamic sea-ice habitats affect individual state in a long-ranging seabird. *Funct Ecol* 34:1839–1856. https://doi.org/10.1111/1365-2435.13632

Teschke K, Pehlke H, Siegel V, Bornemann H, Knust R, Brey T (2020) An integrated compilation of data sources for the development of a marine protected area in the Weddell Sea. *Earth Syst Sci Data* 12:1003–1023

Turner J, Phillips T, Thamban M, Rahaman W, Marshall GJ, Wille JD, Favier V, Winton VHL, Thomas E, Wang Z, Broeke M, Hosking JS, Lachlan-Cope T (2019) The dominant role of extreme precipitation in Antarctic snowfall variability. *Geophys Res Lett* 46:3502–3511. https://doi.org/10.1029/2018GL081517

Turner J, Holmes C, Caton Harrison T, Phillips T, Jena B, Reeves-Francois T, Fogt R, Thomas ER, Bajish CC (2022) Record low Antarctic sea ice cover in February 2022. *Geophys Res Lett* 49:e2022GL098904. https://doi.org/10.1029/2022GL098904

Varpe O, Tveraa T, Folstad I (2004) State-dependent parental care in the Antarctic petrel. *Oikos* 106:479–488

Vasdekis VGS, Vlachonikolis IG (2005) On the difference between ML and REML estimators in the modelling of multivariate longitudinal data. *J Stat Plann Inference* 134:194–205. https://doi.org/10.1016/j.jspi.2004.01.020

Volterra V (1928) Variations and fluctuations of the number of individuals in animal species living together. *ICES J Mar Sci* 3:3–51. https://doi.org/10.1093/icesjms/3.1.3

Wakefield ED, Phillips RA, Matthiopoulos J (2009) Quantifying habitat use and preferences of pelagic seabirds using movement data: a review. *Mar Ecol Prog Ser* 391:165–182. https://doi.org/10.3354/meps08203

Wakefield ED, McClymont EL, Carneiro APB, Croxall JP, González-Solís J, Granroth-Wilding HMV, Thorne L, Warwick-Evans V, Wood AG, Xavier JC, Phillips RA (2024) Seasonal resource tracking and use of sea-ice foraging habitats by albatrosses and large petrels. *Prog Oceanogr*. https://doi.org/10.1016/j.pocean.2024.103334

Woehler EJ, Raymond B, Watts DJ (2003) Decadal-scale seabird assemblages in Prydz Bay. *Mar Ecol Prog Ser* 251:299–310. https://doi.org/10.3354/meps251299

Woehler EJ, Raymond B, Boyle A, Stafford A (2010) Seabird assemblages during the BROKE-West survey of the Antarctic coastline. *Deep-Sea Res II* 57:982–991. https://doi.org/10.1016/j.dsr2.2008.12.041

Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164–168. https://doi.org/10.2307/1938423

Zink RM (1981) Observations of seabirds during a cruise from Ross Island to Anvers Island, Antarctica. *Wilson Bull* 93:1–20

Zucchini W, MacDonald IL, Langrock R (2016) *Hidden Markov models for time series: an introduction using R*, 2nd edn. Chapman & Hall/CRC, Boca Raton

Zuur A, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) *Mixed effects models and extensions in ecology with R.* Springer, New York

Tables

Table 1. Number of Antarctic petrels and snow petrels equipped with GPS loggers, and availability of tracking data during each breeding stage at Svarthamaren, Dronning Maud Land. ‘Unknown’ breeding stage refers to cases where nest monitoring prior to deployment did not allow us to reliably determine whether the bird was incubating, chick-rearing, or had failed, due to limited visibility of the nest chamber. Breeding stage was subsequently updated during data analysis by comparing the trip start date with the closest nest monitoring session (conducted biweekly).

Species		**Snow petrel**	**Antarctic petrel**
Deployed		45	38
Tracks available for analysis		30	22
Breeding stage	Incubating	19	13
	Chick-rearing	11	9
	Unknown	5	0
	Time period	2 Dec. 2022 – 12 Jan. 2023	6 Dec. 2022 – 17 Jan. 2023

Table 2: Relative performance of generalized linear mixed-effects models of foraging trip metrics of breeding Antarctic petrels and snow petrels tracked from Svarthamaren, Dronning Maud Land.

Response	**Fixed effects**	**Deviance**	**ΔAIC**
Cumulative distance	$\beta_0 + \beta_1 \cdot \text{species} + \beta_2 \cdot \text{status} + \beta_3 \cdot (\text{species} \times \text{status})$	**1704.67**	**0.00**

	$\beta_0 + \beta_1\cdot\text{species} + \beta_2\cdot\text{status}$	1764.82	58.15
	$\beta_0 + \beta_1\cdot\text{status}$	1784.11	74.44
	$\beta_0 + \beta_1\cdot\text{species}$	1788.80	80.13
	β_0	1798.53	87.86
Maximal range	**$\beta_0 + \beta_1\cdot\text{species} + \beta_2\cdot\text{status} + \beta_3\cdot(\text{species} \times \text{status})$**	**1476.33**	**0.00**
	$\beta_0 + \beta_1\cdot\text{species} + \beta_2\cdot\text{status}$	1506.46	28.13
	$\beta_0 + \beta_1\cdot\text{status}$	1515.93	35.60
	$\beta_0 + \beta_1\cdot\text{species}$	1533.84	53.51
	β_0	1538.28	55.95
Trip duration	**$\beta_0 + \beta_1\cdot\text{species} + \beta_2\cdot\text{status} + \beta_3\cdot(\text{species} \times \text{status})$**	**1067.54**	**0.00**
	$\beta_0 + \beta_1\cdot\text{species} + \beta_2\cdot\text{status}$	1114.46	44.93
	$\beta_0 + \beta_1\cdot\text{status}$	1121.93	50.39
	$\beta_0 + \beta_1\cdot\text{species}$	1144.12	72.58
	β_0	1147.10	73.56
Bearing	**$\beta_0 + \beta_1\cdot\text{species}$**	**996.28**	**0.00**
	$\beta_0 + \beta_1\cdot\text{species} + \beta_2\cdot\text{status}$	995.19	0.91
	$\beta_0 + \beta_1\cdot\text{species} + \beta_2\cdot\text{status} + \beta_3\cdot(\text{species} \times \text{status})$	993.68	2.40
	β_0	1036.84	39.56
	$\beta_0 + \beta_1\cdot\text{status}$	1036.61	41.33
Mean speed	**$\beta_0 + \beta_1\cdot\text{species}$**	**581.43**	**0.00**
	$\beta_0 + \beta_1\cdot\text{species} + \beta_2\cdot\text{status}$	581.32	1.89
	$\beta_0 + \beta_1\cdot\text{species} + \beta_2\cdot\text{status} + \beta_3\cdot(\text{species} \times \text{status})$	581.31	3.88
	β_0	595.63	12.20
	$\beta_0 + \beta_1\cdot\text{status}$	595.50	14.07

[1] Bird ID is the identity of each individual bird and trip ID the identity given to each trip, used as random intercepts

---

Table 3: Movement parameters estimated by Hidden Markov Models fitted to locations of Antarctic petrels and snow petrels tracked from Svarthamaren, Dronning Maud Land at 30-minute intervals.

Species	**State**	**Step length (m)**		**Turning angle (radians)**	
		Mean	sd	Mean	concentration
Antarctic petrel	Resting	1642	1460	0.04	0.74
	Foraging	9077	5016	-0.01	2.07
	Travelling	18770	6271	-0.01	40.23
Snow petrel	Resting	1131	1094	0.04	0.69
	Foraging	7471	4075	0.03	1.39
	Travelling	15316	5675	0.00	10.47

Table 4: Mean ± SD (range) of trip metrics of breeding Antarctic petrels and snow petrels tracked from Svarthamaren, Dronning Maud Land, Antarctica, during the 2022/23 breeding season.

Metric	**Antarctic petrel**		**Snow petrel**	
	Incubation	Chick-rearing	Incubation	Chick-rearing
Trip duration (h)	267 ±35 (207 – 312)	63 ±15 (37 – 96)	153 ±61 (67 – 264)	103 ±30 (61 – 186)
Cumulative distance (km)	5893 ±968 (4256 – 8457)	1445 ±433 (732 – 2232)	2622 ±1086 (1203 – 4595)	1936 ±566 (1080 – 3431)
Maximum range (km)	1437 ±276 (935 – 1810)	462 ±163 (270 – 853)	819 ±381 (405 – 1513)	603 ±199 (295 – 1109)
Bearing (°)	9 ±39 (-75 – 74)	-5 ±23 (-40 – 42)	-60 ±21 (-96 – -3)	-67 ±30 (-117 – 49)
Mean speed (km/h)	22 ±2 (18 – 27)	22 ±5 (15 – 30)	18 ±4 (13 – 26)	19 ±4 (10 – 31)

Table 5: Relative performance of generalized linear mixed-effects models of sea-ice use as a function of species and breeding status (incubating vs. chick-rearing) for Antarctic petrels and snow petrels tracked from Svarthamaren, Dronning Maud Land.

Response		**Fixed effects**	**Deviance**	**ΔAIC**
Ice Concentration[1]	Conditional section	**β_0**	**12431.31**	**0.00**
		$\beta_0 + \beta_1 \cdot \text{status}$	12430.25	0.94
		$\beta_0 + \beta_1 \cdot \text{species}$	12431.21	1.91
		$\beta_0 + \beta_1 \cdot \text{species} + \beta_2 \cdot \text{status}$	12430.05	2.75
		$\beta_0 + \beta_1 \cdot \text{species} + \beta_2 \cdot \text{status} + \beta_3 \cdot (\text{species} \times \text{status})$	12430.04	4.74
	Zero inflated section	**$\beta_0 + \beta_1 \cdot \text{species} + \beta_2 \cdot \text{status} + \beta_3 \cdot (\text{species} \times \text{status})$**	**11437.10**	**0.00**
		$\beta_0 + \beta_1 \cdot \text{species} + \beta_2 \cdot \text{status}$	11716.88	277.77
		$\beta_0 + \beta_1 \cdot \text{species}$	12055.08	613.97
		$\beta_0 + \beta_1 \cdot \text{status}$	12206.16	765.06
		β_0	12431.31	988.20
$\sqrt{\textbf{Distance to ice edge}}$		**$\beta_0 + \beta_1 \cdot \text{species} + \beta_2 \cdot \text{status} + \beta_3 \cdot (\text{species} \times \text{status})$**	**35309.49**	**0.00**
		$\beta_0 + \beta_1 \cdot \text{species} + \beta_2 \cdot \text{status}$	35299.42	16.58
		$\beta_0 + \beta_1 \cdot \text{status}$	35281.08	31.25
		$\beta_0 + \beta_1 \cdot \text{species}$	35264.41	49.59
		β_0	35245.83	57.66

[1] Modelled via zero inflated beta regression.

The most parsimonious models are indicated in bold. Bird ID is the identity of each individual bird and trip ID the identity given to each trip, used as random intercepts

Table 6: Sea-ice habitat use estimated via zero-inflated mixed-effects beta-regression for Antarctic petrels (AP) and snow petrels (SP) tracked from Svarthamaren, Dronning Maud Land, during incubation (INC) and chick-rearing (CR). The model estimates (1) the probability of foraging locations being ice-free and (2), among ice-free locations, the mean distance to the ice edge.

Ice Concentration *(zero inflated section)*	
Group	*Estimated values*
AP INC	55.70%
AP CR	86.95%
SP INC	43.78%
SP CR	49.24%

Distance to Ice Edge (km)	
Group	*Estimated values*
AP INC	534
AP CR	65
SP INC	177
SP CR	56

Figures

Figure 1: Metrics of foraging trips made by Antarctic petrels and snow petrels breeding Svarthamaren, Dronning Maud Land, Antarctica, during the 2022/23 breeding season. The Total distance and Speed plots show mean (± Standard Error). Bearings are from Svarthamaren to the distal foraging location of each trip. INC = incubation and CR = chick-rearing.

Figure 2: Foraging areas (95% and 50% utilization distribution contours) used by Antarctic petrels and snow petrels tracked from Svarthamaren, Dronning Maud Land, Antarctica (red dot), during the 2022/23 breeding season.

Figure 3: Mean (± Standard Error) sea-ice conditions at foraging locations used by Antarctic petrels and snow petrels tracked from Svarthamaren, Dronning Maud Land, Antarctica, during the 2022/23 breeding season. INC = incubation and CR = chick-rearing. Distance to ice edge only includes locations found beyond the ice edge.

Fig. 1

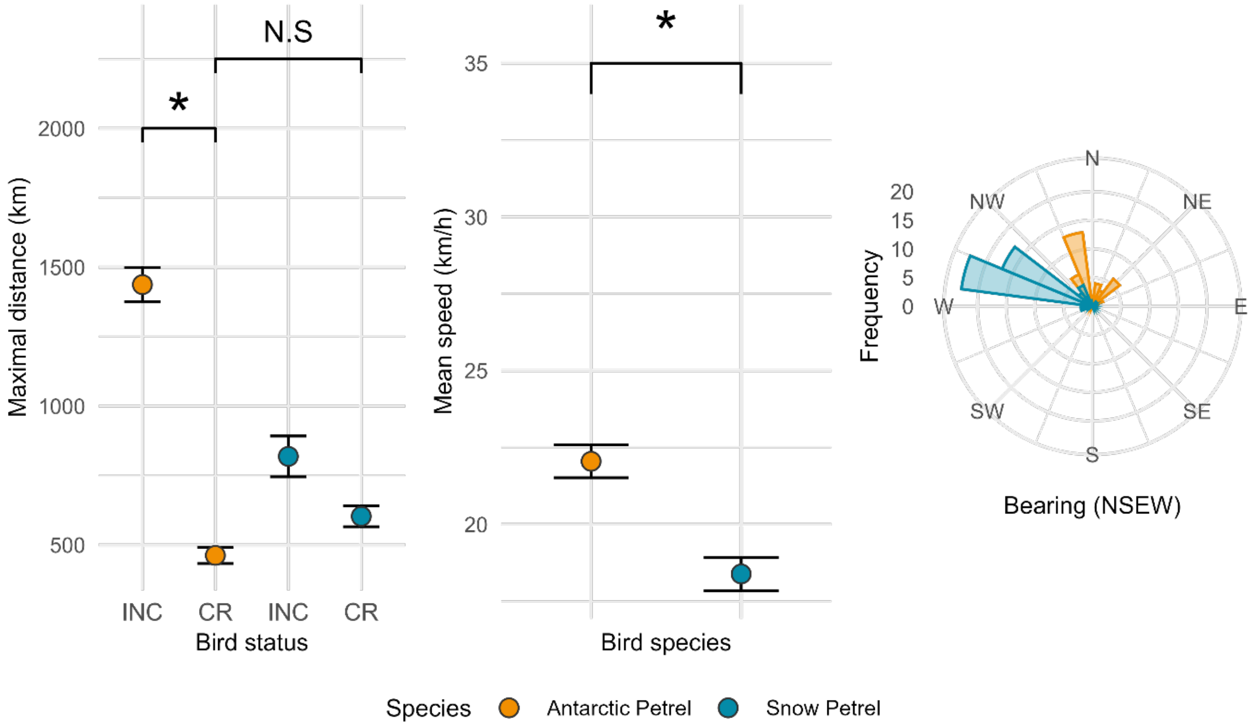
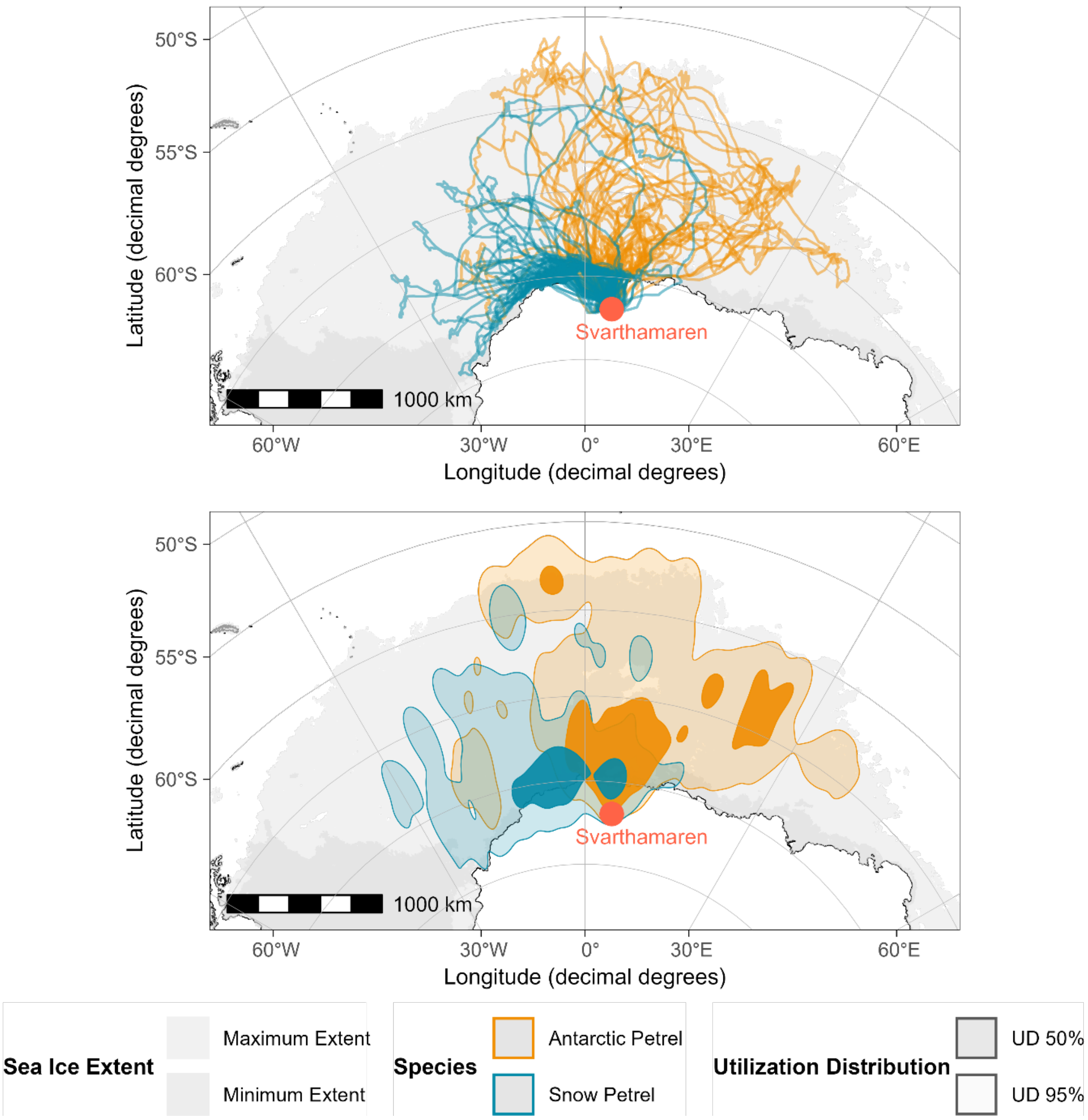
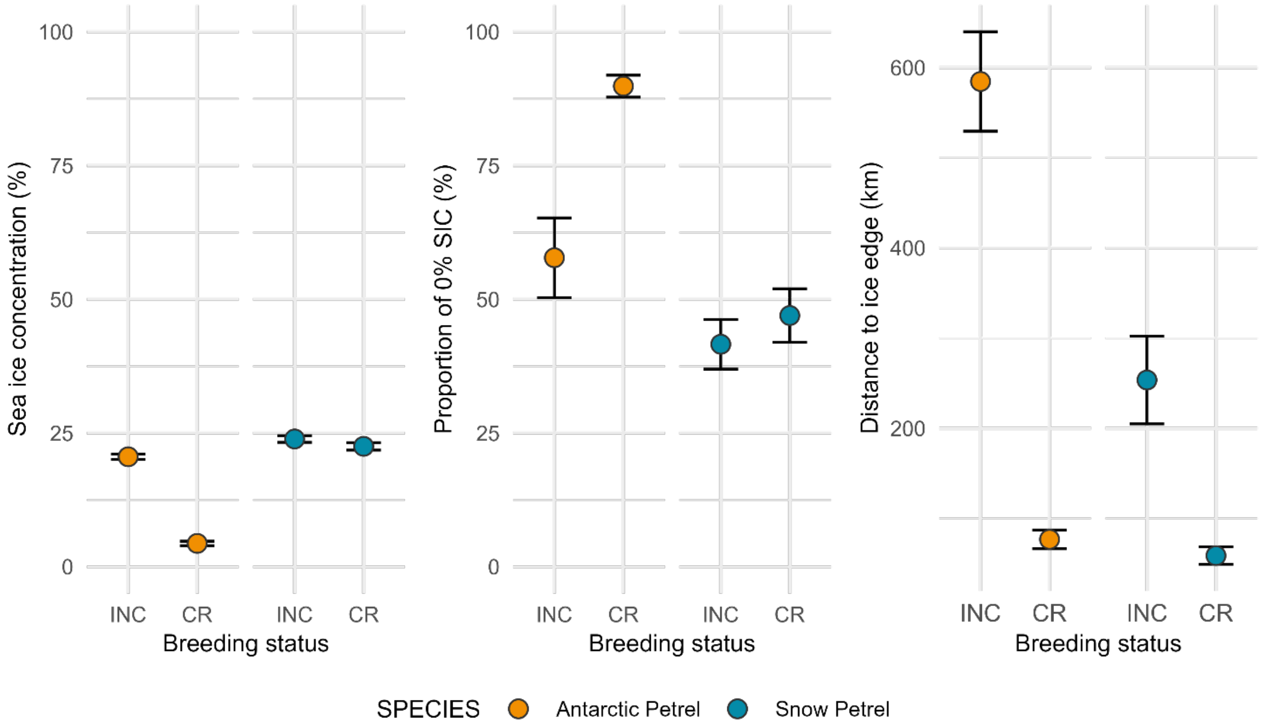

N.S
*
2000
1500
1000
500
Maximal distance (km)
INC
CR
INC
CR
Bird status
*
35
30
25
20
Mean speed (km/h)
Bird species
20
15
10
5
0
Frequency
N
NW
NE
W
E
SW
SE
S
Bearing (NSEW)
Species
Antarctic Petrel
Snow Petrel

Fig. 2


50°S
55°S
60°S
Latitude (decimal degrees)
Svarthamaren
1000 km
60°W
30°W
0°
30°E
60°E
Longitude (decimal degrees)
50°S
55°S
60°S
Latitude (decimal degrees)
Svarthamaren
1000 km
60°W
30°W
0°
30°E
60°E
Longitude (decimal degrees)
Sea Ice Extent
Maximum Extent
Minimum Extent
Species
Antarctic Petrel
Snow Petrel
Utilization Distribution
UD 50%
UD 95%

784 Fig. 3


Sea ice concentration (%)
100
75
50
25
0
INC
CR
INC
CR
Breeding status
Proportion of 0% SIC (%)
100
75
50
25
0
INC
CR
INC
CR
Breeding status
Distance to ice edge (km)
600
400
200
INC
CR
INC
CR
Breeding status
SPECIES
Antarctic Petrel
Snow Petrel

785