RESEARCH ARTICLE

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Foraging tactics in dynamic sea-ice habitats affect individual state in a long-ranging seabird

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Abstract

1. Individual heterogeneity in diet and foraging behaviour is common in wild animal populations, and can be a strong determinant of how populations respond to environmental changes. Within populations, variation in foraging behaviour and the occurrence of individual tactics in relation to resources distribution can help explain differences in individual fitness, and ultimately identify important factors affecting population dynamics. We examined how foraging behaviour and habitat during the breeding period related to the physiological state of a long-ranging seabird adapted to sea ice, the Antarctic petrel *Thalassoica antarctica*.

2. Firstly, using GPS tracking and state-switching movement modelling (hidden Markov models) on 124 individual birds, we tested for the occurrence of distinct foraging tactics within our study population. Our results highlight a large variation in the movement and foraging behaviour of a very mobile seabird, and delineate distinct foraging tactics along a gradient from foraging in dense pack ice to foraging in open water.

3. Secondly, we investigated the effects of these foraging tactics on individual state at return from a foraging trip. We combined movement data with morphometric and physiological measurements of a suite of plasma metabolites that provided a general picture of a bird's individual state. Foraging in denser sea ice was associated with lower gain in body mass during brooding, as well as lower level of energy acquisition (plasma triacylglycerol) during both brooding and incubation. We found no clear relationship between the foraging tactic in relation to sea ice and the energetic stress (changes in plasma corticosterone), energetic balance (β-hydroxybutyrate) or trophic level ($\delta^{15}N$). However, a shorter foraging range was related to both the energetic balance (positively) and the trophic level (negatively).

4. Our results highlight a diverse range of foraging tactics in relation to sea ice in Antarctic petrels. While the various foraging tactics do not seem to strongly alter energetic balance, they may affect other aspects of Antarctic petrels' physiology. Future changes in sea-ice habitats can thus be expected to have an impact on the individual state of seabirds such as Antarctic petrels, which could ultimately affect their population dynamics. Nonetheless, strong individual heterogeneity in the use of sea-ice habitats by a typical pagophilic species might strengthen its resilience to environmental changes and in particular to forecasted sea-ice loss.

1 | INTRODUCTION

Differences in behaviour among individuals are ubiquitous within free-living populations and can be expressed, for example, in terms of individual variation in diet, movements (e.g. Vardanis, Klaassen, Strandberg, & Alerstam, 2011) and/or habitat use (e.g. Phillips, Bearhop, Mcgill, & Dawson, 2009). Such heterogeneity in the way individuals use, and adjust to changes in, their environment (e.g. Jenouvrier, Péron, & Weimerskirch, 2015; Jonsen et al., 2019) may affect an overall population's response to environmental variation (Vindenes & Langangen, 2015) and is thus important to understand. Movement and foraging behaviours represent a link between resources in the environment and individual fitness (Matthiopoulos et al., 2015; Weimerskirch, 2018). Optimal Foraging Theory predicts that individuals will forage in a way that maximizes their net gain in energy while minimizing the inherent risks, so as to allocate sufficient energy to their survival and reproduction, and consequently their fitness (Perry & Pianka, 1997; Pyke, 1984). Different foraging behaviours yielding a similar average net gain can therefore lead to the coexistence of several foraging tactics within the same population (Dall, Bell, Bolnick, & Ratnieks, 2012, but see: Elliott, Gaston, & Crump, 2010), which is also supported theoretically (Real, 1980). Populations composed of very mobile individuals and experiencing large variation in habitat or resource distribution naturally offer strong potential for the emergence of distinct foraging tactics. Such tactics can involve different patterns of movement, habitat use or diet (Hückstädt et al., 2012; Jaeger et al., 2014; Weise, Harvey, & Costa, 2010). Considering the tight link between foraging behaviour, individual fitness, and population dynamics (Matthiopoulos et al., 2015; Morales et al., 2010), it is necessary to assess the occurrence of different foraging tactics within a given population to correctly evaluate how this population may respond to environmental changes that affect resource availability (Sydeman, Poloczanska, Reed, & Thompson, 2015).

Habitat and the spatiotemporal heterogeneity in the distribution of resources are critical aspects shaping the foraging behaviour of seabirds (Fauchald, 2009; Weimerskirch, 2007). In Polar Regions, sea ice is an important feature of marine ecosystems (Post et al., 2013). It is highly dynamic and has a strong seasonal component relating directly to spatiotemporal variation in the abundance and distribution of resources. Sea ice can indeed provide a productive foraging habitat to many predators, with high availability of prey such as fish and invertebrates (David et al., 2016; Flores et al., 2012), but can also hinder access to prey by predators (Langbehn & Varpe, 2017; Sauser, Delord, & Barbraud, 2018). Furthermore, sea ice can occasionally constitute an important resting or hunting platform (Descamps et al., 2017; Moore & Huntington, 2008). Spatiotemporal variation in sea ice is therefore an essential feature of the foraging habitat of many polar predators (Ainley, Woehler, & Lescroël, 2016; Amélineau et al., 2019). Many studies have investigated the relationship between sea ice and foraging in pagophilic (ice-adapted) species and suggested that the variability in sea-ice concentration is a prominent driver of foraging activity in polar seabirds (Dehnhard et al., 2020; Stirling, 1997; van Franeker, 1992; Woehler, Raymond, Boyle, & Stafford, 2010). Some species, like the snow petrel *Pagodroma nivea* (Forster, 1777) are defined as ice-obligate, being tightly associated to sea ice all year round and having their fitness directly dependent on the sea-ice habitat (Sauser et al., 2018). Others, like the Antarctic petrel *Thalassoica antarctica* (Gmelin, 1789) are defined as ice-tolerant, being found both in dense pack ice and in open waters, sometimes hundreds of kilometres north of the pack ice (Ainley, Ribic, & Fraser, 1992; Fraser & Ainley, 1986; Ribic et al., 2011). This degree of behavioural flexibility makes Antarctic petrels well suited to the study of individual variation in foraging behaviour and habitat use in relation to variability in sea ice.

We used fine-scale tracking data to assess the relationship between foraging flexibility and sea-ice use in a pagophilic species. Firstly, we tested for the occurrence of distinct foraging tactics in relation to sea ice during the breeding season, when birds are central-place foragers (Obj. 1). Here 'tactics' refer to specific patterns of habitat use that could potentially vary among and within individuals, although we could not test for intra-individual variation or specialization in foraging owing to a lack of repeated measurements at

the individual level. Secondly, by combining geospatial tracking data with information on dietary and energetic physiology, we looked into the potential consequences of individual variation in the use of sea ice as foraging habitat (Obj. 2). To do so, we modelled the extent of the use of sea ice during foraging on an integrated suite of indicators (body condition, trophic level, stress/energetic physiology) that collectively provide a comprehensive assessment of the state of an individual following its return to the colony from a foraging trip. Assessing these relationships will help identify state-based mechanisms linking environmental variation with individual variation in fitness (Liedvogel, Chapman Ben, Muheim, & Åkesson, 2013).

2 | MATERIALS AND METHODS

2.1 | Study species and site

The Antarctic petrel is a 600-g seabird that breeds in mountain scree slopes on the Antarctic continent and on some of the islands in the Southern Ocean (Mehlum, Gjessing, Haftorn, & Bech, 1988; van Franeker, Gavrilo, Mehlum, Veit, & Woehler, 1999). Our study took place at the Svarthamaren breeding colony (71°53′S, 5°10′E) in Queen Maud Land, Antarctica, from December to February for three consecutive years (2011/2012 to 2013/2014). This colony is among the largest known to date (Mehlum et al., 1988; Schwaller, Lynch, Tarroux, & Prehn, 2018; van Franeker et al., 1999), with an estimated 100,000–200,000 breeding pairs (Descamps, Tarroux, Lorentsen, et al., 2016). It is located 184 km from the edge of the Antarctic ice shelf, that is, the nearest point of potentially open water (Figure 1). At the end of November/early December females lay one egg, which both parents incubate until hatching (around mid-January). Parents alternate between incubation shifts and foraging trips. Females initiate the first foraging trip shortly after egg laying. Chicks are fed mainly with crustaceans, primarily Antarctic krill *Euphausia superba* (Dana, 1852), and to a lesser extent fish until fledging occurs in early March (Descamps, Tarroux, Cherel, et al., 2016; Lorentsen, Klages, & Røv, 1998; Lorentsen & Røv, 1995).

2.2 | Morphological and sexing data

Bird captures (*n* = 124 individuals) and handling procedures were conducted in accordance with the permit delivered by the Norwegian Animal Research Authority (NARA/FDU permits #3714 & 5746). Upon capture for GPS-logger deployment or recovery (see below), breeding birds were weighed to the nearest 5 g using 1000-g Pesola® scales and structural size (right wing's chord) was measured to the nearest millimetre with a 50-cm ruler. At deployment, some birds remained on their nests for up to several days before eventually leaving for a foraging trip. Their mass measurements were corrected following Lorentsen and Røv (1995) to account for the number of days separating the initial capture and the bird's actual departure date determined from the GPS record (Appendix S1). At recovery,

birds were generally captured up to several hours, but less than a day, after having returned to their nest, and we assumed that they had already delivered their food load to their chick. The ratio body mass/wing chord (mm) was used as an index of body condition in order to account for the difference in structural size between males and females in Antarctic petrel (Lorentsen & Røv, 1994). Sex could be determined for *n* = 118 individuals, using genetic analyses or morphometric measurements (details in Appendix S2).

2.3 | Stable isotope data

We collected *c.* 1.5 ml blood from all individuals at both deployment (pre-departure to a foraging trip) and recovery (return from a foraging trip) of the GPS units, using heparinized syringes with a 26G needle and heparinized collection tubes. All blood samples were collected within 3 min after a bird's capture to ensure that capture stress did not affect physiological parameters (Romero & Reed, 2005). We prevented samples from freezing and centrifuged them within 10 hr of collection to extract the plasma fraction. A small part of the extracted plasma was stored separately for later measurement of metabolites linked to the physiological state (see below, Section 2.4), while the remainder was used for analyses of $\delta^{15}N$ values. Only plasma was used for stable isotope analyses, which owing to a relatively quick tissue turnover rate (Hong et al., 2019) assumedly integrates dietary information over the past few days or week before collection, that is, while the birds were foraging at sea. Technical details on the stable isotope analyses are in the Supporting Information (Appendix S3). The resulting nitrogen stable isotope ratios are expressed as ‰ of the deviation from isotopic ratios of atmospheric N_2, which is the international standard (Table S1).

2.4 | Physiological indicators

Physiological markers of energetic demand, energy acquisition and energy used (i.e. baseline corticosterone, triacylglycerols and β-hydroxybutyrate, respectively) were measured in the plasma using previously validated laboratory procedures (Hennin, Bêty, et al., 2016; Lamarre, Franke, Love, Legagneux, & Bêty, 2017). Details on the laboratory analyses performed are in Appendix S4. Baseline corticosterone (the primary glucocorticoid in birds) is responsible for managing and inducing feeding behaviour (Hennin, Wells-Berlin, & Love, 2016), and can be used as proxies of an individual seabird's need for energetic refuelling (Angelier & Wingfield, 2013) and food availability (Benowitz-Fredericks, Shultz, & Kitaysky, 2008; Kitaysky, Piatt, & Wingfield, 2007). In addition, variation in baseline corticosterone has been linked to fitness metrics in seabirds, with high corticosterone concentration being generally associated with low breeding success for example (Sorenson, Dey, Madliger, & Love, 2017). Plasma triacylglycerols are the storage form of fatty acids and thus can be used as an indicator of fat deposition or energy intake, where high circulating levels are indicative of energy gain (Williams, Warnock, Takekawa, & Bishop, 2007). Elevated plasma levels
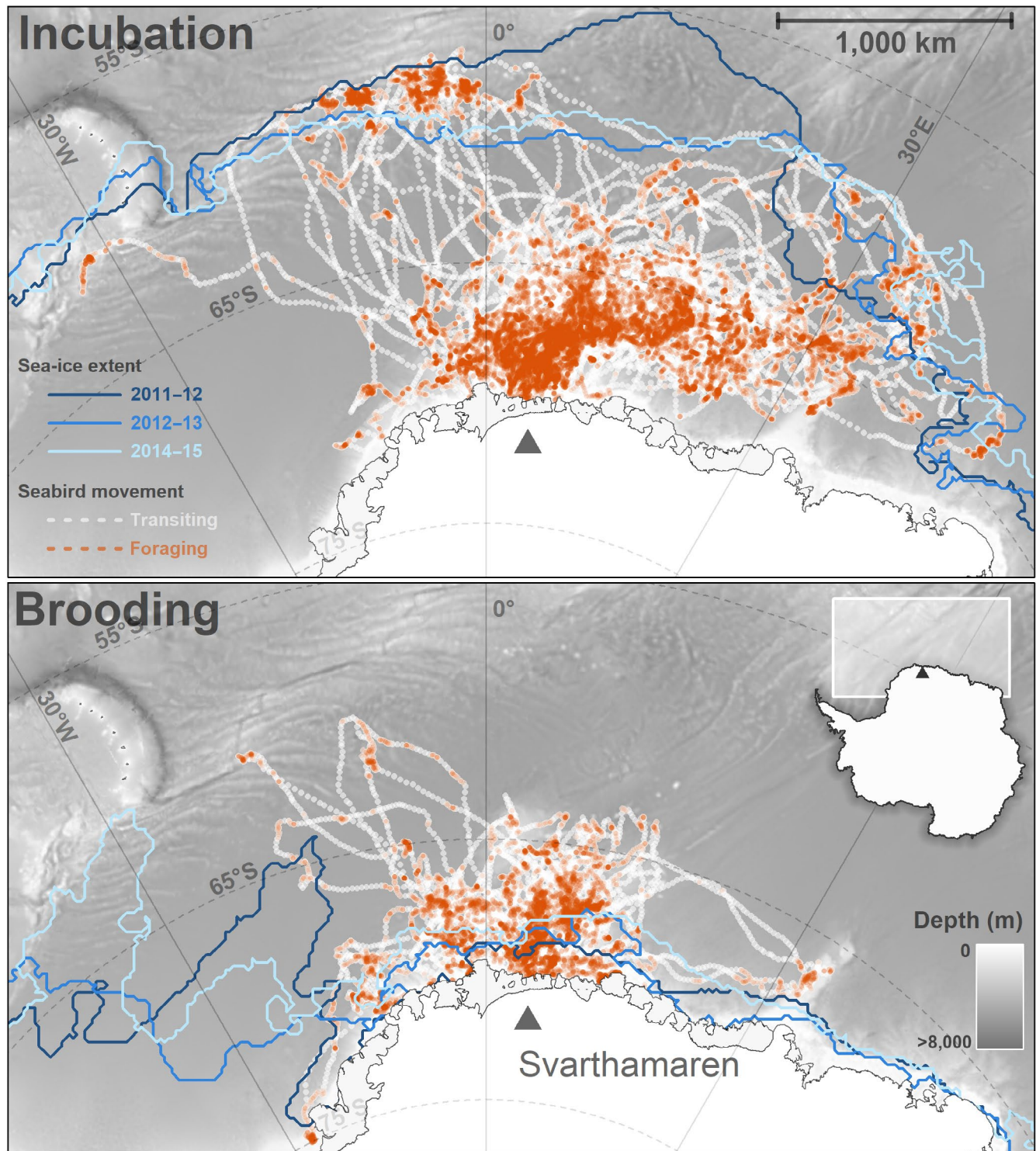
FIGURE 1 Foraging movements of Antarctic petrels from the Svarthamaren breeding colony, Dronning Maud Land, Antarctica (black triangle) during the incubation (*N* = 73 GPS tracks) and brooding (*N* = 60) period. Only locations above the ocean/sea ice are shown. Blue lines show the maximum extent of sea ice on 1 December (incubation) and 1 February (brooding) and for each breeding year. Projection is polar stereographic. Base map (Scambos, Haran, Fahnestock, Painter, & Bohlander, 2007) and bathymetry (Amante & Eakins, 2009) data are shown for descriptive purposes

of β-hydroxybutyrate are indicative of lower energetic condition, fasting or mass loss (Cherel et al., 1988) since during fasting or body mass loss this metabolite is synthesized from free fatty acids to be used as fuel for tissues (Williams, Guglielmo, Egeler, & Martyniuk, 1999).

2.5 | GPS-logger deployment and tracking data

We deployed miniaturized Global Positioning System (GPS) units (CatTrack 1, Catnip Technologies Ltd.) on adult birds during both the

incubation and chick-rearing (brooding hereafter) stages (Table S2). Deployment procedures follow Tarroux et al. (2016). The nests of all GPS-tracked birds were individually marked with numbered tags and monitored at least once every 2 days throughout the field season. During each field season, nest monitoring was conducted during at least two consecutive months, never started later than 5 December and never ended earlier than 31 January, enabling us to attribute a failure or hatching date (±1 day) to each nest. Each GPS track was consequently assigned a breeding stage (incubation or brooding) based on the status of the corresponding nest of each individual at the time of its departure from the colony. We obtained 133 foraging tracks from 124 individuals (six birds were tracked over multiple trips; Table S2). We used the R statistical software v.3.6.2 for all data processing, mapping and statistical analyses (details in Appendix S5). Due to early GPS failure, some foraging trips were incomplete. A track was considered to be complete whenever the GPS recorded 80% or more of the duration of the foraging trip (based on date of departure and date of recovery). Using this criteria, $N = 16$ tracks (corresponding to 16 individuals) in total were found to be incomplete (Table S2).

2.6 | Sea-ice concentration data

We calculated daily sea-ice concentration data from observations of the SSMIS satellite microwave radiometer. Brightness temperature measurements at 91 GHz from SSMIS were used to obtain sea-ice concentrations at the highest possible grid resolution of 12.5 km. The method from Spreen, Kaleschke, and Heygster (2008) is used for the sea-ice concentration calculation. 'Weather filters' based on lower frequency channels and a sea-ice climatology plus a 200-km safety margin are applied to remove spurious ice in the open ocean. To allow ice concentration close to the foraging locations no land mask was applied. Similar data but with land mask can be obtained from the University of Bremen (www.seaice.uni-bremen.de). Sea-ice edge was defined as the boundary delimiting areas with at least 15% concentration, which is a commonly used definition for the sea-ice extent (e.g. Parkinson & Cavalieri, 2008). For each foraging location (see below Section 2.7.1), sea-ice concentration and distance to the nearest sea-ice edge were extracted from the gridded sea-ice concentration data. The distance to the nearest sea-ice edge was negative for locations within the ice (i.e. within an area covered with more than 15% sea ice), and positive for locations over open water (sea-ice concentration ≤ 15%). The proportion of the study area covered by sea ice (Figure 2) was calculated as the proportion of non-land pixels with ice concentration >15% within a 2,100-km radius around the breeding colony, that is, a zone just large enough to encompass the longest foraging trips.

2.7 | Statistical analyses

2.7.1 | Step 1—Identify foraging locations with hidden Markov models

The first step aimed at identifying the locations where each individual was in a foraging state, that is, either feeding or actively searching for food. We used hidden Markov models (HMMs; Boyd, Punt, Weimerskirch, & Bertrand, 2014; Zucchini, MacDonald, & Langrock, 2016) to identify the most likely sequence of behavioural states of an individual along its foraging track. In the context
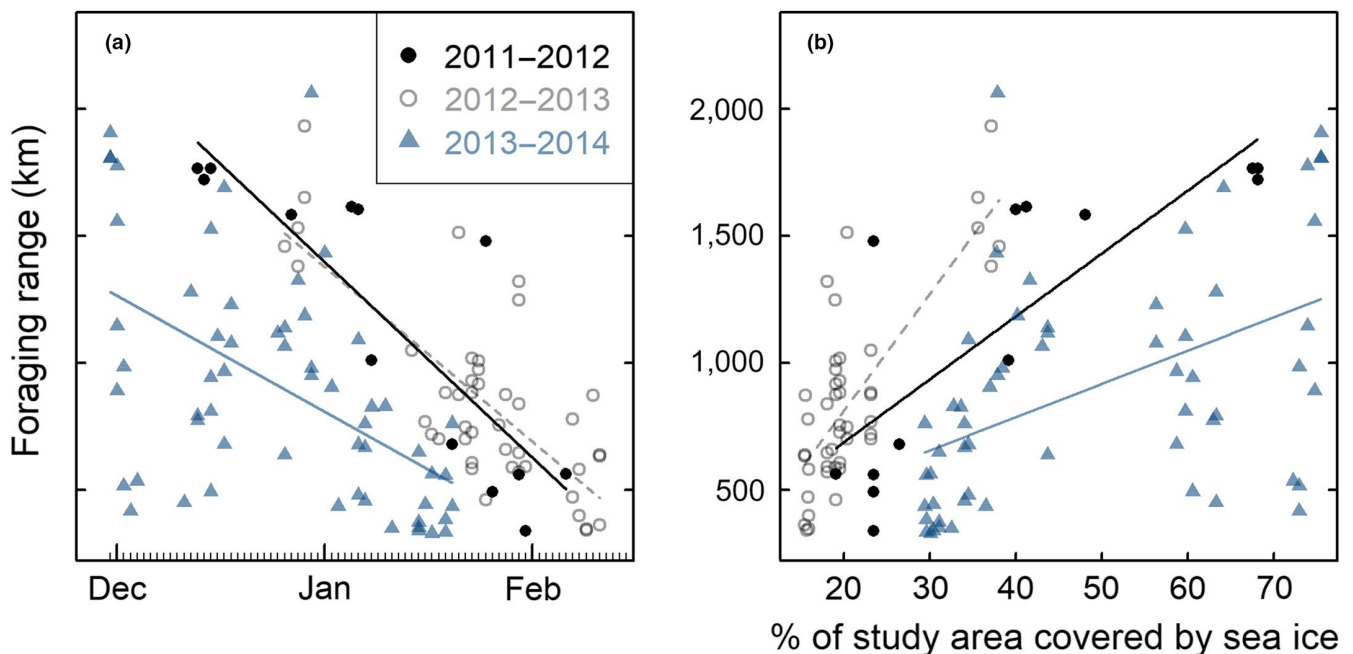
FIGURE 2 Foraging range of breeding Antarctic petrels plotted against time (a) and proportion of the study area covered by sea ice (b). Regression lines from linear models are shown for each breeding year

of animal movement analysis, HMMs relate the distributions that generate observations of one or several parameters (typically step length and turning angle) to underlying and a priori unknown discrete states (Langrock et al., 2012; Patterson, Basson, Bravington, & Gunn, 2009). We used the R package moveHMM (Michelot, Langrock, & Patterson, 2016) to fit the HMMs, using the Weibull and wrapped Cauchy distributions to model the frequency distributions of step lengths and turning angles, respectively (details in Appendix S6). Only locations which modelled behavioural state corresponded to foraging behaviour (Appendix S6 and Figure S1) were extracted and used in subsequent analyses (*n* = 29,056).

2.7.2 | Step 2—Identifying foraging tactics in relation to sea ice (Obj. 1)

Environmental variables related to sea-ice (concentration and distance to the nearest sea-ice edge) were extracted at each foraging location. We used the 5th and 95th percentiles in order to account for the extreme variation in sea-ice habitat used, regarding both the sea-ice concentration and the distance to the nearest sea-ice edge, and as complementary statistics to the median. Additionally, using quantiles allowed a better characterization of the habitat used than alternative metrics such as the mean and standard deviation (Real, 1980), for example, when individuals are using both open ocean (<15% sea-ice concentration) and densely ice-covered areas (>80% sea-ice concentration) but not areas of intermediate sea-ice concentrations (Figure 3). A final set of six covariates was thus created by computing the 5th, 50th (median) and 95th percentiles from the frequency distributions of these two covariates for each individual foraging trip, to account for different track lengths. All six covariates related to sea ice were detrended to account for temporal trends throughout the breeding period (Appendix S7 and Figure S2). Covariates were then standardized before applying a K-means partitioning to group the foraging trips that were more similar with regard to the use of sea-ice habitat (Borcard, Gillet, & Legendre, 2011), thereby defining distinct foraging tactics (Appendix S7; Figure S3). The procedure indicated that an optimal partition was achieved by grouping the tracks into four clusters (Figure S3). We then ran a principal component analysis (PCA) based on the same sea-ice covariates. We used the package vegan v.2.4-3 (Oksanen et al., 2019), in combination with scripts provided by Borcard et al. (2011). The coordinates of the tracks on the first principal component (Figure S4) were then used as a continuous proxy for the intensity of use of the sea-ice habitat (thereafter referred to as intensity of sea-ice use, or ISU) while foraging.

### 2.7.3 | Step 3—Effect of foraging tactics on individual state (Obj. 2)

To test whether the use of sea ice as foraging habitat affected the individual state of Antarctic petrels, we used five indicators of individual state (summarized in Table 1). For each physiological-state indicator, we fitted a total of 16 biologically plausible a priori candidate models, without conducting any model simplification (Table 2). Each physiological-state indicator was modelled as a function of the ISU, sex and breeding stage (incubation/brooding), using linear models (with a Gaussian error distribution). Additionally, to account for potential inter-annual variation all models included an additive effect of year as a three-level factor. Finally, due to the highly seasonal dynamics of sea-ice melt, there was a potential confounding effect of the foraging distance to the colony on the response variables. Therefore, our set of candidate models also included models that comprised an additive effect of the foraging range (Table 2). Here we defined foraging range as the maximum distance to the colony reached within a foraging trip. The Variance Inflation Factor (VIF) was <5 for all models, indicating the absence of any severe problem of multicollinearity (Dormann et al., 2013).

A few individuals (*n* = 6) were tracked more than once, but this was generally over two consecutive trips; in such cases the birds were not recaptured between the consecutive trips. Consequently, all our models are based on only one foraging trip per individual. Because we are using physiological/morphological measurements made upon return, only the second, most recent trip could be used. In addition, only birds whose nest was still alive at their time of departure were included in our models.

To identify the model with most support from the data (Table 2) we used the Akaike Information Criterion corrected for small sample size (AICc; Burnham & Anderson, 2002). The AICc is calculated as follows: AICc = AIC + (2*k*(*k* + 1))/(*n* − *k* − 1), where *k* is the number of parameters in a given model and *n* is the number of observations used in that model. It is advised to use the AICc whenever *n*/*k* < 40 (Burnham & Anderson, 2002). The model with the lowest AICc was selected (Table 2). The fit of each model was assessed by verifying that the residuals were normally distributed and homoscedastic. Modelling was done using function lm from package stats v.3.6.2.

Some foraging trips were incompletely recorded, and we tested whether this could affect our model estimates by fitting all the selected models again with a dataset excluding incomplete trips (*N* = 16). The results indicated that including incomplete trips did not alter the parameter estimates in our models (Figure S5), and therefore all foraging trips were used in the final models. Finally, we tested for a potential confounding effect of the duration of a foraging trip on the improvement of the body condition (Δ_{bc}) and fat gain (plasma TAG). We fitted a new set of candidate models using the residuals of each of these two physiological indicators regressed against the foraging trip duration. Both the results of the model selection and the parameter estimates remained very similar and did not change any of the results or conclusions. Moreover, this is in line with the conclusions from two distinct studies at the same site, showing that longer foraging trips do not lead to higher mass gain at return (Tveraa, Sæther, Aanes, & Erikstad, 1998; Varpe, Tveraa, & Folstad, 2004). Therefore, we did not include those additional checks to the current manuscript.
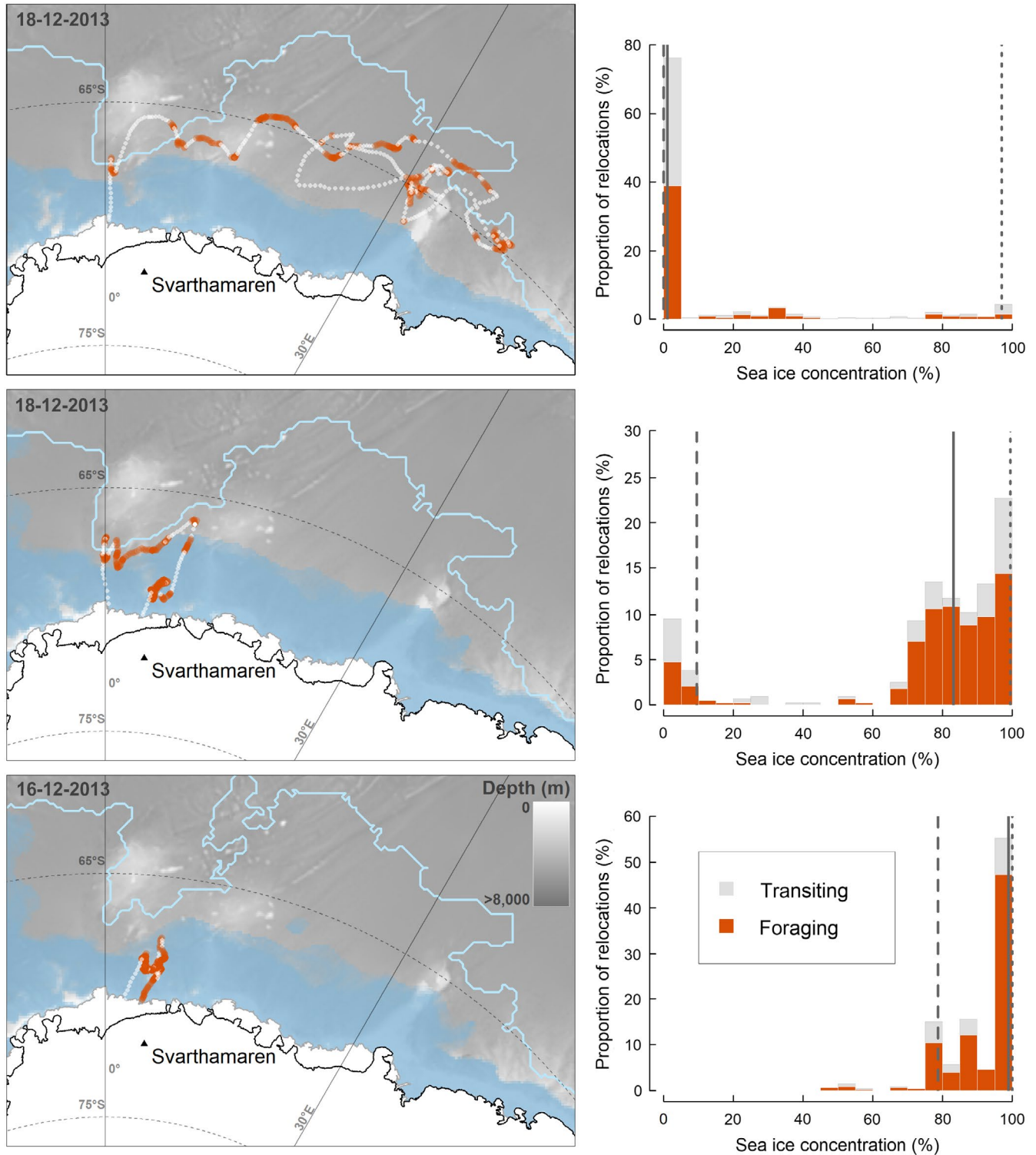
FIGURE 3 Examples of the foraging tactics of three male Antarctic petrels during a similar period of their breeding season during the incubation (i.e. with similar sea-ice conditions), showing a gradient of tactics, from foraging almost exclusively in open waters (top) to foraging exclusively within sea ice (bottom). All three nests were active at the time of departure. Hidden Markov models (HMM)-predicted foraging locations (see Section 2.7.1) are in orange. Projection is polar stereographic. Base map (Scambos et al., 2007) and bathymetry (Amante & Eakins, 2009) data are shown for descriptive purposes. Left panels: GPS tracks, with sea-ice concentration and sea-ice edge information. Light blue continuous lines: sea-ice edges at the beginning of each foraging trip (date in upper left corner). Blue shaded area: ice conditions (concentration) at the end of the foraging trip. Right panels: corresponding frequency distributions of the sea-ice concentration values at all locations. The vertical lines show the 5th (dashed), 50th (i.e. median; continuous) and 95th (dotted) percentiles, as calculated for each individual foraging trip for use in further analyses

Physiological indicator	Name	Unit	Biological interpretation
Net difference in body condition at return versus departure ($bc_{ret} - bc_{dep}$)	Δ_{bc}	g/mm	Change in body condition
Logarithm of the ratio of baseline corticosterone at return versus departure ($\log[CORT_{ret}/CORT_{dep}]$)	Δ_{CORT}	Unitless	Higher Δ_{CORT} values indicate an increase in energetic stress during foraging (Sorenson et al., 2017)
Triacylglycerol concentration in plasma (log-transformed) at return from a foraging trip	TAG	Unitless	Higher TAG values indicate more successful foraging
β-Hydroxybutyrate concentration in plasma (log-transformed) at return from a foraging trip	β-OHB	Unitless	Higher β-OHB values indicate more negative energetic balance (Cherel et al., 1988; Lamarre et al., 2017)
Stable nitrogen isotopic ratios in plasma	$\delta^{15}N$	‰	Higher $\delta^{15}N$ values indicate recent feeding on prey of higher trophic level

TABLE 1 Summary of the physiological indicators used in our study and their biological interpretation

3 | RESULTS

Antarctic petrels are highly mobile and this was reflected in their foraging movement patterns. The longest trip, which occurred during incubation, was 8,422 km long (cumulative distance covered) and lasted 19 days (considering only birds whose nest was still active when they left the colony; Table S2). The largest foraging ranges reached 2,061 and 1,513 km, during the incubation and brooding periods, respectively (Figures 1 and 2; Table S2). Foraging range was largest during incubation and decreased linearly throughout the breeding season; every passing week, Antarctic petrels foraged on average 117 km (95% CI = [86; 141]; all years pooled) further south, thus closer to their breeding colony (Figure 2a). This contraction of the foraging range occurred in parallel to the retreat of the sea ice (Figures 1 and 2b). However, superimposed on these temporal trends, we also found high individual variation in foraging range throughout the breeding period (Figure 2). This was particularly noticeable when comparing the tracks and sea-ice concentration in the foraging habitat of birds that left the colony at a similar date (Figure 3).

3.1 | Sea-ice habitat and foraging tactics of Antarctic petrels

Based on the foraging habitat characteristics related to sea ice, we found clear evidence for the occurrence of distinct foraging tactics in Antarctic petrels. These tactics could be optimally clustered into four separate groups and ordinated along a gradient from dense pack ice to open water (Figures S3 and S4). The first two axes of the PCA together explained 76.3% of the total variance in the dataset and the four foraging tactics previously identified were well discriminated along the first PCA axis (Figure S4), which was thus considered to provide a satisfactory proxy for the ISU.

Sea-ice cover varied greatly within each breeding season, although the temporal pattern was similar among years (Figure S6). Sea-ice concentration varied greatly among foraging trips. However, the probability density distribution of foraging trips was clearly bi-modal: 45% (52/115) of all foraging trips occurring in ice-free waters (median sea-ice concentration ≤15%, Figure 4a) while 31% (36/115) occurred in very densely covered areas (i.e. with median sea-ice concentration >80%; Figure 4a). Foraging trips were particularly concentrated around sea-ice edges, either in ice-covered areas or in open waters, with 41% (47/115) occurring within 50 km of a sea-ice edge (Figure 4b). However, variation in the median distance to sea-ice edges was high (range = [−313; 883 km]) and a higher proportion (59%) of foraging trips occurred 50 km away or more from a sea-ice edge, either in ice-covered areas or in open waters. Finally, 32% (37/115) were situated farther than 50 km from a sea-ice edge and in the open ocean (Figure 4b).

3.2 | Consequences of foraging tactics on the individual state

The ISU was associated with change in body condition and plasma TAG (foraging success). We did not, however, detect any effect of the ISU on changes in plasma CORT (energetic stress), β-OHB (energetic balance), or $\delta^{15}N$ values (trophic level). However, plasma levels in β-OHB and $\delta^{15}N$ values were best explained by models including the foraging range (Table 2).

3.2.1 | Difference in body condition (Δ_{bc})

The Δ_{bc} at return from a foraging trip was generally positive (mean Δ_{bc} = +0.30 g/mm ± 0.16 *SD*), except for six individuals (Figure 5), although the details revealed a more complex pattern. The most supported model explained 15% of the deviance (Table 2) and included an effect of the ISU in interaction with sex and breeding stage (Table 3; Figure 6a,b). During incubation the ISU had no effect on the males' Δ_{bc} (Figure 6a) and only a slight positive effect on the females'

TABLE 2 Linear model selection on five individual state parameters as a function of intensity of sea-ice use (ISU), sex and breeding stage (Breeding). Additive effects of sampling year (Year) and foraging range (Range) were included to account for potential confounding factors. The selected models are shaded. The Null model, indicated in italics, included only an effect of sampling year. Sample size (N) varied owing to missing individual state data for some of the foraging trips. k indicates the number of model parameters

Response variable	N	Fixed effects	k	Log-Likelihood	AICc	ΔAICc	R^2
Difference in body condition (Δ_{bc})	98	ISU × (Sex + Breeding) + Year	8	49.4	−78.7	0	0.15
		ISU × (Sex + Breeding) + Year + Range	9	50.5	−78.5	0.2	0.17
		ISU + Sex + Year + Range	6	46.2	−77.1	1.6	0.1
		ISU × Sex + Year	6	46.1	−76.9	1.8	0.09
		ISU × Sex + Year + Range	7	47.2	−76.8	1.9	0.12
		ISU + Sex + Breeding + Year	6	46	−76.7	2	0.09
		ISU + Sex + Year	5	44.7	−76.5	2.2	0.07
		ISU + Sex + Breeding + Year + Range	7	46.8	−75.9	2.8	0.11
		Year	*3*	*41.9*	*−75.4*	*3.3*	*0.01*
		ISU × Breeding + Year	6	45.2	−75.2	3.5	0.08
		Year + Range	4	42.5	−74.3	4.4	0.03
		ISU × Breeding + Year + Range	7	45.8	−73.9	4.8	0.09
		ISU + Year	4	42	−73.3	5.4	0.02
		ISU + Breeding + Year	5	43	−73	5.7	0.04
		ISU + Year + Range	5	42.7	−72.4	6.3	0.03
		ISU + Breeding + Year + Range	6	43.3	−71.3	7.4	0.04
Change in baseline Corticosterone, log-transformed (Δ_{CORT})	89	*Year*	*3*	*−136.4*	*281.2*	*0*	*0.08*
		Year + Range	4	−135.4	281.6	0.4	0.1
		ISU + Year + Range	5	−134.9	282.9	1.7	0.11
		ISU + Year	4	−136.3	283.4	2.2	0.08
		ISU + Breeding + Year	5	−135.8	284.6	3.4	0.09
		ISU + Breeding + Year + Range	6	−134.8	285.1	3.9	0.11
		ISU + Sex + Year + Range	6	−134.9	285.2	4	0.11
		ISU + Sex + Year	5	−136.3	285.6	4.4	0.08
		ISU × Breeding + Year	6	−135.8	287	5.8	0.09
		ISU + Sex + Breeding + Year	6	−135.8	287	5.8	0.09
		ISU × Breeding + Year + Range	7	−134.8	287.4	6.2	0.11
		ISU × Sex + Year + Range	7	−134.8	287.5	6.3	0.11
		ISU + Sex + Breeding + Year + Range	7	−134.8	287.5	6.3	0.11
		ISU × Sex + Year	6	−136.3	288	6.8	0.08
		ISU × (Sex + Breeding) + Year	8	−135.7	291.7	10.5	0.09
		ISU × (Sex + Breeding) + Year + Range	9	−134.6	292	10.8	0.11
Plasma β-hydroxybutyrate, log-transformed (β-OHB)	93	Year + Range	4	−61.4	133.5	0	0.05
		ISU × Sex + Year	6	−59.8	134.9	1.4	0.08
		Year	*3*	*−63.4*	*135.3*	*1.8*	*0*
		ISU × Sex + Year + Range	7	−59	135.7	2.2	0.09
		ISU + Year	4	−62.6	135.8	2.3	0.02
		ISU + Year + Range	5	−61.4	135.8	2.3	0.05
		ISU + Breeding + Year	5	−62	136.9	3.4	0.03
		ISU + Breeding + Year + Range	6	−61.3	137.9	4.4	0.05
		ISU + Sex + Year + Range	6	−61.3	138	4.5	0.05
		ISU + Sex + Year	5	−62.5	138.1	4.6	0.02
		ISU × Breeding + Year	6	−61.5	138.2	4.7	0.05

(Continues)

TABLE 2 (Continued)

| Response variable	N	Fixed effects	k	Log-Likelihood	AICc	ΔAICc	R^2
		ISU × Breeding + Year + Range	7	−60.5	138.7	5.2	0.06
		ISU × (Sex + Breeding) + Year	8	−59.4	138.9	5.4	0.09
		ISU + Sex + Breeding + Year	6	−62	139.2	5.7	0.03
		ISU × (Sex + Breeding) + Year + Range	9	−58.7	140	6.5	0.1
		ISU + Sex + Breeding + Year + Range	7	−61.2	140.2	6.7	0.05
Plasma triacylglycerol, log-transformed (TAG)	93	ISU + Year	4	−28.7	68.2	0	0.2
		ISU + Breeding + Year	5	−28	69	0.8	0.21
		ISU + Year + Range	5	−28.2	69.4	1.2	0.21
		ISU + Sex + Year	5	−28.3	69.6	1.4	0.21
		ISU + Sex + Breeding + Year	6	−27.6	70.6	2.4	0.22
		ISU + Breeding + Year + Range	6	−27.8	71	2.8	0.21
		ISU + Sex + Year + Range	6	−27.9	71.1	2.9	0.21
		Year + Range	4	−30.3	71.2	3	0.17
		ISU × Breeding + Year	6	−28	71.3	3.1	0.21
		ISU × Sex + Year	6	−28.1	71.6	3.4	0.21
		ISU + Sex + Breeding + Year + Range	7	−27.5	72.7	4.5	0.22
		ISU × Sex + Year + Range	7	−27.6	72.9	4.7	0.22
		ISU × Breeding + Year + Range	7	−27.7	73.2	5	0.22
		ISU × (Sex + Breeding) + Year	8	−27.2	74.6	6.4	0.23
		ISU × (Sex + Breeding) + Year + Range	9	−27	76.6	8.4	0.23
		Year	*3*	*−35.4*	*79.3*	*11.1*	*0.08*
Plasma δ¹⁵N value	91	Year + Range	4	−49.1	108.9	0	0.21
		ISU + Year + Range	5	−48.9	110.8	1.9	0.21
		ISU + Sex + Year + Range	6	−48.8	113	4.1	0.21
		ISU + Breeding + Year + Range	6	−48.9	113.1	4.2	0.21
		ISU × Sex + Year + Range	7	−48.6	115	6.1	0.22
		ISU × Breeding + Year + Range	7	−48.8	115.4	6.5	0.22
		ISU + Sex + Breeding + Year + Range	7	−48.8	115.4	6.5	0.21
		ISU × (Sex + Breeding) + Year + Range	9	−48.6	119.9	11	0.22
		ISU + Year	4	−55.2	121.1	12.2	0.1
		ISU + Breeding + Year	5	−54.4	121.8	12.9	0.11
		ISU + Sex + Year	5	−55	123.1	14.2	0.1
		ISU × Breeding + Year	6	−54.1	123.5	14.6	0.12
		ISU + Sex + Breeding + Year	6	−54.3	123.9	15	0.12
		Year	*3*	*−58.3*	*125.1*	*16.2*	*0.03*
		ISU × Sex + Year	6	−55	125.4	16.5	0.1
		ISU × (Sex + Breeding) + Year	8	−53.9	128	19.1	0.12

Δ_{bc} (Figure 6b), with the 95% Confidence Interval overlapping zero (+0.06 g/mm; 95% CI = [−0.05; 017]; Table 3). During brooding however, the ISU had a negative effect on the Δ_{bc} of both males and females (Figure 6a,b). This negative trend occurred concurrently to a negative trend in the foraging range, which decreased with increasing ISU for both sexes (Figure 6c,d). In other words, foraging in denser sea ice was associated with shorter trips and to lower increase in body condition during brooding. This was, however, not the case during incubation.

3.2.2 | Change in plasma corticosterone (Δ_{CORT})

On average, plasma CORT levels tended to decrease between the departure to and return from a foraging trip (mean Δ_{CORT} = −0.40 ± 0.12 SE). However, this trend was blurred by large individual variation Δ_{CORT} (SD = 1.17) and we found no clear relationship between the ISU and Δ_{CORT} at return from a foraging trip (Figure S7).
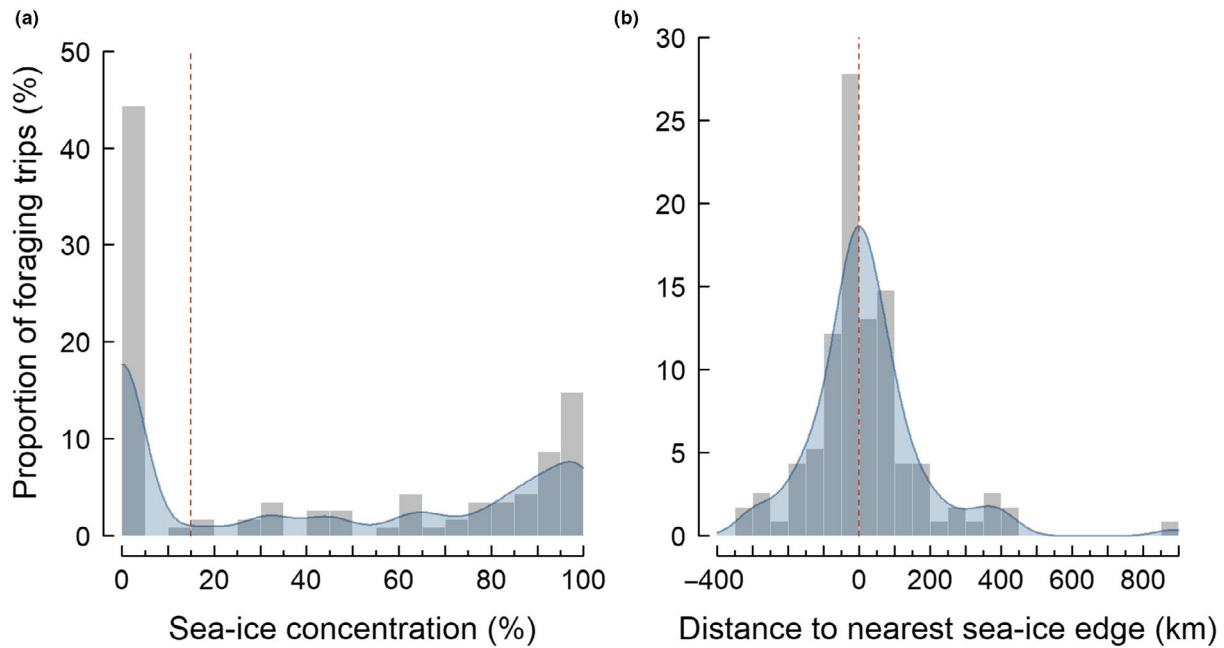
FIGURE 4 Frequency distributions and corresponding density curves summarizing two of the covariates used to characterize the habitat used during foraging in Antarctic petrels ($N = 115$): the median concentration in sea ice (a) and the median distance to the nearest sea-ice edge (b). The vertical dashed lines indicate the boundary between ice-covered and open ocean areas
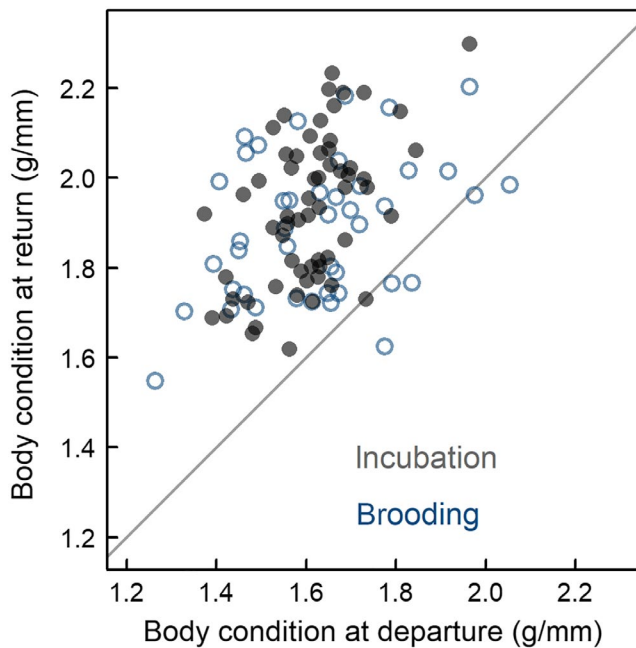
FIGURE 5 Body condition index of Antarctic petrels at return from versus departure to a foraging trip ($n = 115$)

3.2.3 | Plasma β-hydroxybutyrate (β-OHB)

There was large individual variation in plasma β-OHB level (mean β-OHB = 0.25 ± 0.48 SD; untransformed values: 1.42 mm/L ± 0.61 SD), although none of the candidate models including ISU as a covariate could performed better than a model including the foraging range. However, the latter only explained 5% of the variance (Table 2), and β-OHB

increased only slightly with increasing foraging range ($B_{Foraging\ range}$ = 0.2; 95% CI = [0.11; 0.29]; Table 3; Figure 7).

3.2.4 | Plasma triacylglycerols (TAG)

The plasma TAG was also highly variable among individuals (mean TAG = −0.55 ± 0.37 SD; untransformed values: 0.61 mm/L ± 0.22 SD; Figure 8). The selected model included only an effect of the ISU (beside an effect of the sampling year). This model predicted a clear negative effect of the ISU on TAG (B_{TAG} = −0.34; 95% CI = [−0.53; −0.16]) and explained 20% of the variance (Table 3; Figure 8).

3.2.5 | Plasma δ15N values

Plasma $\delta^{15}N$ values were high (mean = 9.1 ‰ ± 0.47 SD) and varied among individuals (range = [8.0; 10.6‰]; Figure 9). Although including ISU in models did lead to lower AICc values, none of the candidate models including ISU as a covariate performed better than a model including foraging range (Table 2). This latter model suggested a positive effect of the foraging range on plasma $\delta^{15}N$ (B_{ISU} = +0.20‰; 95% CI = 0.11; 0.29]; Table 3; Figure 9), and explained 21% of the variance.

4 | DISCUSSION

Seabirds become central-place foragers during their breeding season, being both spatially (by the location of their colony) and energetically (by the additional costs associated with breeding) constrained (Elliott

TABLE 3 Estimates and associated confidence intervals from three selected linear models (Table 1) predicting four individual state parameters at return from a foraging trip. Estimates which 95% CI does not overlap zero are shaded. The sampling year (Year) was added to all models only to account for potential confounding effects

Response variable	Effects	β	SE	t	2.5% CI	97.5% CI
Difference in body condition (Δbc)	*Intercept*	0.20	0.07	2.84	0.06	0.34
	ISU	0.06	0.06	1.14	−0.05	0.17
	Sex (males)	0.10	0.03	2.80	0.03	0.16
	Breeding (brooding)	−0.06	0.05	−1.16	−0.15	0.04
	Year (2012–2013)	0.09	0.08	1.08	−0.07	0.24
	Year (2013–2014)	0.09	0.07	1.18	−0.06	0.23
	ISU:Sex (males)	−0.07	0.08	−0.96	−0.23	0.08
	ISU:Breeding (brooding)	−0.14	0.07	−2.05	−0.28	−0.01
Plasma β-hydroxybutyrate, log-transformed (β-OHB)	*Intercept*	9.40	0.19	49.50	9.03	9.78
	Year (2012–2013)	−0.28	0.20	−1.40	−0.68	0.13
	Year (2013–2014)	−0.38	0.20	−1.90	−0.78	0.01
	Range	0.20	0.05	4.42	0.11	0.29
Plasma triacylglycerol, log-transformed (TAG)	*Intercept*	−0.33	0.14	−2.40	−0.60	−0.06
	ISU	−0.34	0.09	−3.70	−0.53	−0.16
	Year (2012–2013)	−0.46	0.15	−3.00	−0.76	−0.16
	Year (2013–2014)	−0.08	0.15	−0.50	−0.37	0.22
Plasma δ^{15}N value	*Intercept*	9.40	0.19	49.50	9.03	9.78
	Year (2012–2013)	−0.28	0.20	−1.40	−0.68	0.13
	Year (2013–2014)	−0.38	0.20	−1.90	−0.78	0.01
	Range	0.20	0.05	4.42	0.11	0.29

et al., 2009). In such context, the ability of seabirds to adjust their foraging behaviour and optimize their energy acquisition and allocation is thus critical to their survival and reproductive success (Bolton, Conolly, Carroll, Wakefield, & Caldow, 2018; Chastel, Weimerskirch, & Jouventin, 1995). The high mobility of Antarctic petrels, clearly illustrated in this study, enables them to cover wide areas in search of food during breeding, hence relaxing the spatial constraints compared to less mobile seabirds. This allows Antarctic petrels to explore and forage in various habitats, from the dense pack ice to the open, ice-free waters of the Southern Ocean. Our results highlight the ubiquitous nature of foraging Antarctic petrels (Ainley, O'Connor, & Boekelheide, 1984) and reveal the occurrence, within a single breeding population, of distinct foraging tactics in relation to the sea-ice habitat (Obj. 1). Furthermore, differences in the use of the sea-ice habitat while foraging seem to affect their own individual state, notably their body condition and foraging success (in terms of energy digested), as well as the trophic level at which they feed (Obj. 2). The foraging range also seemed to affect the individual state, and birds that foraged farther from the breeding colony had a higher trophic level upon return.

4.1 | Sea-ice habitat and foraging tactics of Antarctic petrels

Foraging Antarctic petrels are undoubtedly associated with the sea-ice habitat while breeding (Dehnhard et al., 2020), a

characteristic that is also well documented outside the breeding period (Ainley et al., 2016; Stirling, 1997; van Franeker, 1996). While our study confirms the important role of sea-ice edges as foraging habitat for Antarctic petrels, it also shows that foraging activity occurs extensively farther from, and on both sides of, sea-ice edges (Fraser & Ainley, 1986). We found indeed clear evidence for the occurrence of distinct foraging tactics constituting a discretized representation of a continuous gradient between two extremes—from foraging in open ocean with low sea-ice concentration and far beyond an ice edge, to foraging in areas with high sea-ice concentration and deeper within the sea-ice zone. Interestingly, the two extreme tactics along this gradient (i.e. foraging in dense ice versus open ocean) sometime occurred in different individuals and within the same period (Figure 3), hence with similar overall sea-ice conditions, suggesting that the choice of a given tactic does not solely depend on the environmental conditions.

There seemed to be a preference for foraging within sea ice when being close to an ice edge, in the marginal ice zone (MIZ), a very dynamic transition zone between the open ocean and the dense pack ice (Wadhams, Squire, Goodman, Cowan, & Moore, 1988). The MIZ has some of the highest levels of primary production in the Southern Ocean (Taylor, Losch, & Bracher, 2013), and is therefore considered highly attractive to many top-predators (Stroeve, Jenouvrier, Campbell, Barbraud, & Delord, 2016).
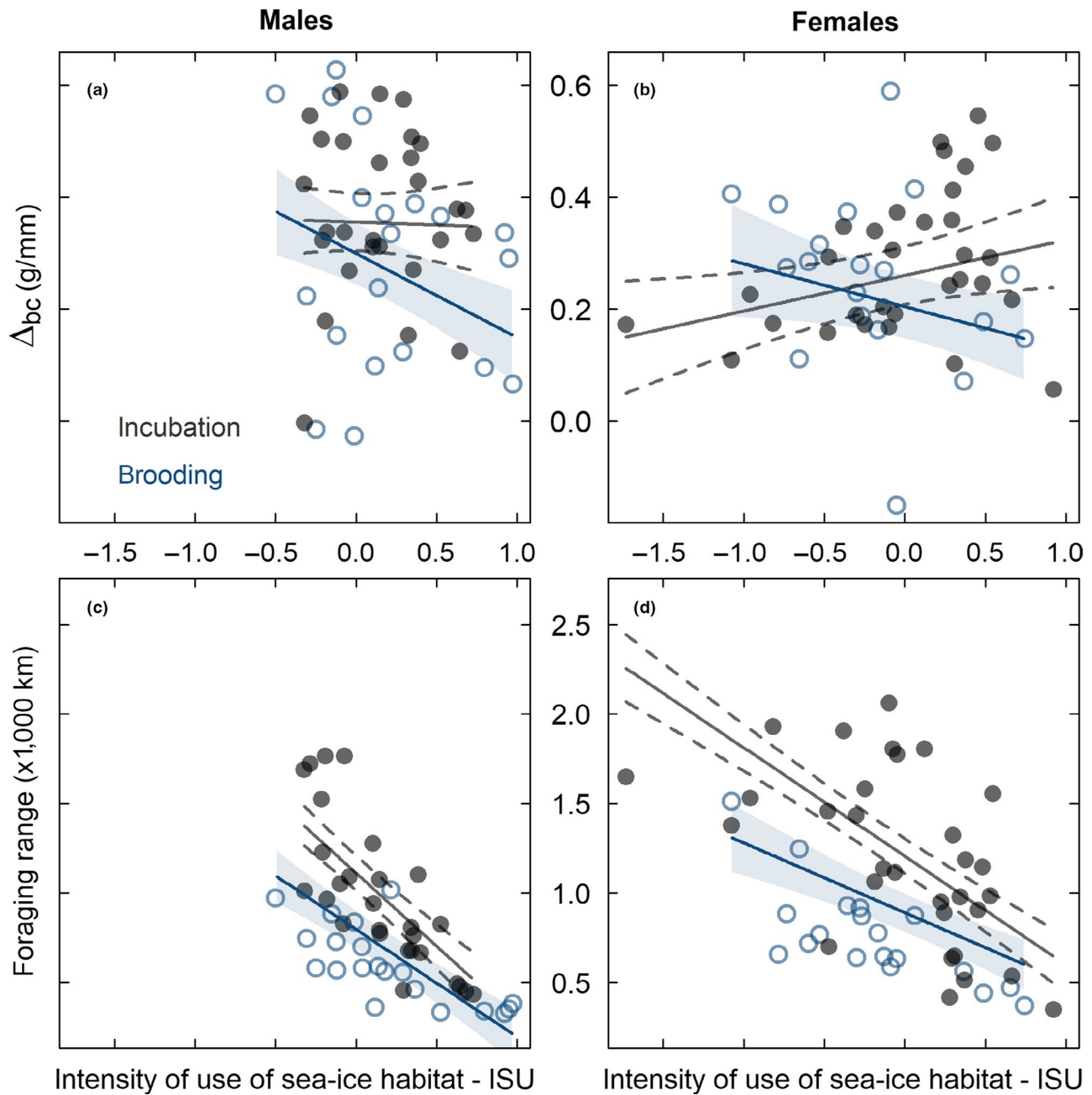
FIGURE 6 Upper panels: Effect of the intensity of sea-ice use (ISU) on the change in body condition index during incubation and brooding for male (a) and female (b) Antarctic petrels. The lines show the predictions (±*SE*, dashed lines/shaded area) from the linear model that had most support from our data (Tables 1 and 2). Lower panels: Relationship between the ISU and the foraging range during incubation and brooding for males (c) and females (d). The continuous lines show the predicted response (±*SE*, dashed lines/shaded area) from linear models, for comparative purposes

However, our results clearly indicate that foraging Antarctic petrels are not solely targeting the MIZ, but also the dense pack ice. This is in line with previous studies suggesting that the productivity and resource abundance in dense sea ice are high enough to sustain a predator community (van Franeker, 1992). Ainley et al. (1992) also showed that the stomach contents of non-breeding Antarctic petrels were heavier when foraging in denser sea ice (but see Dehnhard et al., 2020).

Antarctic petrels are known to reduce the duration of their foraging trips throughout the breeding season (Lorentsen & Røv, 1995), and in our study the reduction of their foraging range was clearly associated with the seasonal retreat of the sea ice. However, despite a large decrease in sea-ice extent (thus despite the sea-ice edge being closer to the colony) as the season progresses, the whole range of possible sea-ice concentrations was used by petrels throughout the summer, both during the incubation and brooding stages. There was
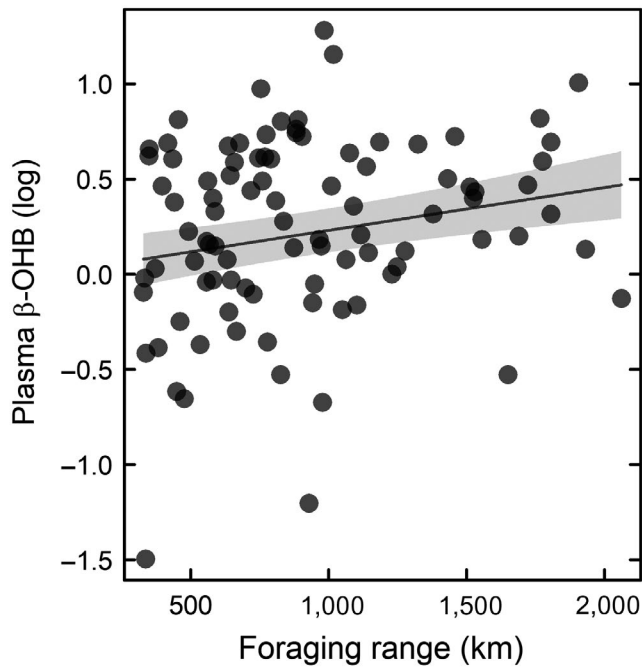
FIGURE 7 Relationship between the foraging range and the plasma β-OHB level in Antarctic petrels. The lines show the predictions (±*SE*, dashed lines/shaded area) from the linear model that had most support from our data (Tables 1 and 2)
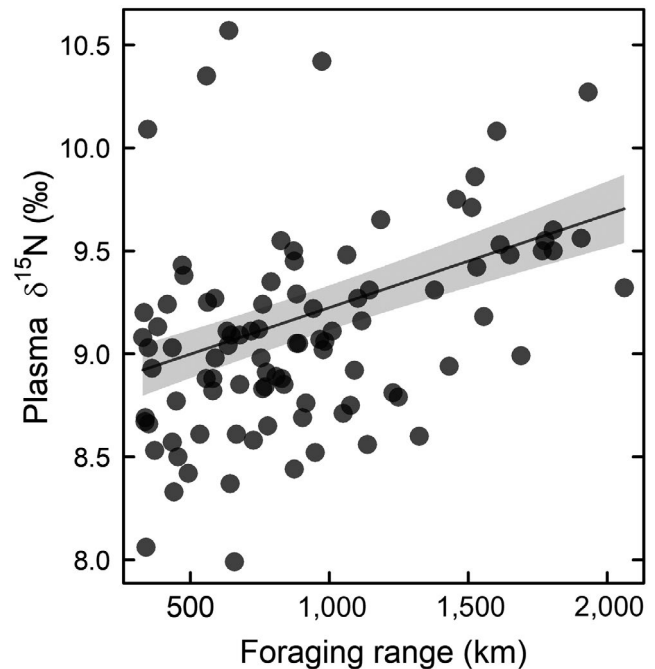
FIGURE 9 Relationship between the foraging range and the plasma $\delta^{15}N$ (‰) in Antarctic petrels. The line shows the predictions (±*SE*, shaded area) from the linear model that had most support from our data (Tables 1 and 2)
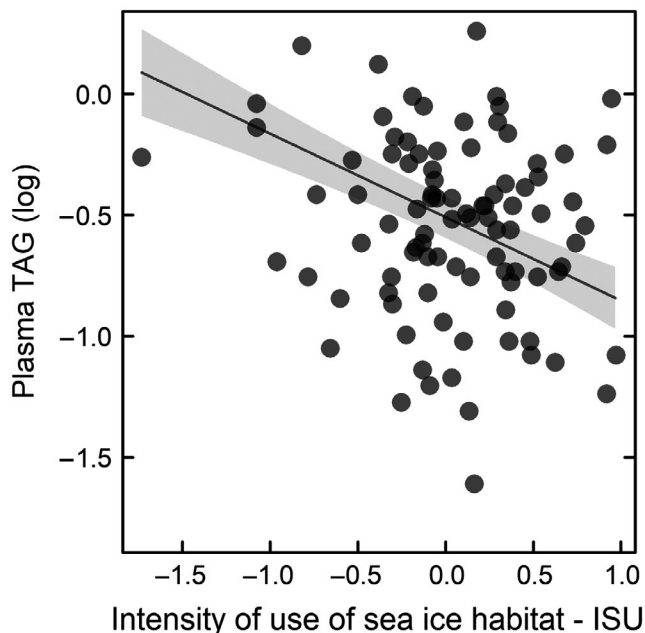
FIGURE 8 Relationship between the intensity of sea-ice use (ISU) and the plasma triacylglycerols (TAG) level during incubation and brooding in Antarctic petrels. The lines show the predictions (±*SE*, dashed lines/shaded area) from the linear model that had most support from our data (Tables 1 and 2)

also inter-annual variation in the way Antarctic petrels used sea ice as foraging habitat. However, sea-ice cover was similar among years (Figure S6), suggesting that this year-to-year variation could have other causes.

4.2 | Consequences of foraging tactics on individual state

Our results suggest that the different foraging tactics in relation to sea ice may affect several aspects of the physiology of Antarctic petrels. In particular, foraging in areas with higher concentration of sea ice was associated with a lower gain in body mass for both males and females during brooding, while it had no statistically significant effect during incubation. The lower improvement in body condition during brooding cannot be explained by higher energy expenditure to reach the foraging grounds as the length of foraging trips is lower by almost one order of magnitude when foraging in denser sea-ice habitat. It could nevertheless be caused by lower energetic gains, which fits with the lower plasma triacylglycerol levels measured upon colony return in birds foraging in denser sea-ice habitat.

Overall, two complementary explanations could be proposed: firstly, denser sea ice was associated with shorter foraging ranges that were associated to a lower trophic level (shown by lower plasma $\delta^{15}N$ values), which could indicate the inclusion of more crustaceans (likely Antarctic Krill) into the diet. Krill are less energy-rich than myctophid fish (Schaafsma et al., 2018), both of which being important prey to Antarctic seabirds (Ainley et al., 1992), and this could explain a lower energy intake in birds feeding more on krill. However, the difference in $\delta^{15}N$ was weak and did certainly not indicate a complete dietary shift. Secondly, during brooding, Antarctic petrels are mainly undertaking short foraging trips and return quickly to their breeding colony to provide their chicks with non- or only partially digested food,

thereby prioritizing the energy intake of their offspring (Lorentsen & Røv, 1995). The choice among the various tactics would thus ultimately result from a trade-off between adult versus chick survival, implying that Antarctic petrels would take into account additional information and parameters not used in the current study, such as their partner's condition and that of their chick (Tveraa, Lorensten, & Sæther, 1997; Varpe et al., 2004). Both explanations are complementary, and fit with previous observations that krill dominate the food regurgitated to chicks by Antarctic petrels at Svarthamaren (Lorentsen et al., 1998; but see: Creuwels et al., 2010). Nevertheless, the lower apparent foraging success indicated by lower plasma tri-acylglycerols levels was not reflected in the energetic stress, as the level in plasma baseline corticosterone did not vary according to the foraging tactic used. In addition, shorter foraging trips were also associated to a less negative energetic balance (lower levels of plasma β-hydroxybutyrate), which could therefore compensate for a lower foraging success. However, even if a given foraging tactic is energetically less favourable, it is not necessarily detrimental in terms of fitness. This could also explain why such large individual variation in foraging can occur within a population.

4.3 | Individual variation in foraging tactics

Given the numerous constraints imposed on Antarctic petrels during the breeding season (e.g. their internal state and that of their mate) and the highly dynamic nature of their foraging habitat (Fauchald et al., 2017), a flexible behaviour might be necessary to cope with a constantly changing, unpredictable environment (Dall, Houston, & McNamara, 2004; Dehnhard et al., 2020; Trevail et al., 2019). There is evidence that Antarctic petrels do not exhibit individual specialization with regard to habitat or environmental conditions while foraging (Dehnhard et al., 2020). Fauchald et al. (2017) suggested that, in response to an elusive and unpredictable environment, Antarctic petrels adopt a highly flexible foraging behaviour in which their decisions are based on real-time cues (i.e. their experiences during the foraging bout) rather than geographically or environmentally fixed foraging areas. Still, further studies are needed to assess whether the Antarctic petrel population at Svarthamaren is made of generalists using the whole range of habitats that they can access (Type A generalist population, composed of generalist individuals), or of specialists that adopt specific tactics (Type B generalist population, sensu Bearhop, Adams, Waldron, Fuller, & Macleod, 2004). Our study highlights a strong individual heterogeneity in the use of sea-ice habitat in what is considered a typical pagophilic species. Such heterogeneity could potentially increase the resilience of the Antarctic petrel population to environmental changes and in particular the forecasted sea-ice loss. More generally, assessing the heterogeneity in the relationship between animal foraging behaviour and habitats is needed to understand, and ultimately forecast accurately the distribution of animal populations. This could additionally shed light on the factors underlying current demographic trends and help predicting future trends.

AUTHORS' CONTRIBUTIONS

A.T., S.D. conceived the ideas and designed methodology; A.T., S.D., Y.C. and H.W. collected the data; A.T. processed the samples for isotopic analyses and O.P.L. processed the samples for plasma physiology analyses; A.T. analysed the data with help from N.G.Y. and led the writing of the manuscript. All co-authors discussed the interpretation of the results, commented on the successive drafts and gave final approval for publication. The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The seabird positional data used for this study are available from the Norwegian Polar Data Centre (NPDC, https://data.npolar.no), with https://doi.org/10.21334/npolar.2020.8a2f44d4. Data on morphometric and physiological measurements (Table S1) and on the foraging trip characteristics (Table S2) are also available from this archive.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.