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Ecological segregation between sympatrically breeding blue petrels and thin-billed prions

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Running page head: Ecological segregation of two sympatric seabird species

ABSTRACT: Ecological niche theory predicts coexisting species will segregate spatially, temporally or trophically to limit competition. Few studies have investigated niche segregation in multiple dimensions during the breeding season in sympatric, morphologically similar seabird species. Moreover, these studies showed discrepancies between theoretical predictions and observations. We tested the hypothesis of niche segregation during breeding between 2 sympatric small-sized seabirds, the blue petrel *Halobaena caerulea* and the thin-billed prion *Pachyptila belcheri*, by quantifying foraging niche and trophic differences. Combining at-sea GPS and isotopic (stable carbon and nitrogen) data, we assessed spatial, foraging habitat and trophic segregation. We found strong latitudinal and longitudinal segregation between species during incubation. Mean maximum distance from the colony during foraging trips was ~2330 and ~1300 km for blue petrels and thin-billed prions, respectively. Foraging habitat segregation varied during incubation, with blue petrels foraging close to the ice edge and prions foraging in oceanic areas far from ice. Although sample size was low, there was also some evidence for spatial and habitat segregation during chick-rearing, with prions foraging in areas with negative sea surface height anomalies. Trophic segregation was revealed by differences in stable isotopes, with blue petrels feeding on higher trophic level prey than prions (mean plasma $\delta^{15}\text{N}$: 9.6 ± 0.4 and 9.0 ± 0.3 ‰, respectively). Spatial distribution and diet are the primary segregation mechanisms, and patterns of segregation may result from competitive exclusion rather than niche specialization. Spatial and trophic segregation may have evolved to minimize competition, allowing co-existence of these 2 abundant sympatric breeding species.

Keywords: At-sea distribution; Environmental variables; Habitat partitioning; GPS; Stable isotopes; Trophic position

1. INTRODUCTION

The niche concept is fundamental in ecology, originally describing the response of species to a given set of non-interactive variables (Grinnell 1917) or focusing on the biotic interactions and position in trophic webs (Elton 1927). The concept was later formalized as an attribute to the species, not only of the environment, describing the niche as an n-dimensional hyper volume of environmental states within which a species is able to survive (Hutchinson 1957). Armed with these niche concepts and on the concept of resource utilization distribution (MacArthur & Levins 1967), Chase & Leibold (2009) proposed that ecological niche could alternatively be viewed as an irreducible product of the species–environment interactions resulting from both species’ requirements and biotic interactions. This synthetic ecological niche theory, together with density-dependence theory, predicts that when resources are limited, one or more species can coexist locally. This prediction is valid under the following conditions: (1) they trade off the relative ability to compete for different limiting factors, and (2) there is temporal variability in resources (Chase & Leibold 2009). In other words, 2 species that coexist locally are expected to segregate spatially, temporally or trophically to limit competition for resources (Lack 1971, Schoener 1974, Pianka 1981). Investigating this competitive exclusion principle from empirical studies is fundamental to test predictions from ecological niche theory, to understand how and why species coexist and to integrate the ecology of adaptive divergence and radiation (Lack 1971, Schluter 2000). It is also a requisite for assessing a species’ capacity to adapt to ongoing and future environmental changes. Although multi-dimensional segregation mechanisms have been extensively studied with terrestrial species, they have been much less frequently studied in marine species, leading to major taxonomic biases (Melo-Merino et al. 2020, Astarloa et al. 2021, Petalas et al. 2024). Seabirds are interesting model species to study niche segregation because species often breed sympatrically on islands or coastal areas, form large colonies and often have overlapping diets and foraging areas (Bocher et al. 2000, Coulson 2002, Ainley et al. 2009, Chérel & Carrouée 2022). Moreover, as seabird species are central-place foragers during the breeding season, the accessibility to foraging grounds is restricted in space and time (Orlans & Pearson 1979). These characteristics, combined with similarities in life-history traits (Hamer et al. 2001, Gaston 2004) and patchy and ephemeral food resources in the dynamic marine environment (Shealer 2002, Weimerskirch 2007) increase the likelihood of high interspecific competition

during the breeding season, when there are increased demands for food (Ashmole 1963, Cairns 1989). Thus, one would theoretically expect a strong potential for competitive exclusion between seabird species, particularly between those with high similarities in morphology and breeding phenology. Nevertheless, relatively few studies have investigated niche segregation in multiple dimensions during the breeding season in morphologically similar seabird species breeding in sympatry, with some showing evidence for niche segregation (Navarro et al. 2013, Reisinger et al. 2020, Petalas et al. 2021, Fromant et al. 2022) but others not (Weimerskirch et al. 2012, Dehnhard et al. 2020). These discrepancies between theoretical predictions and some observational data may potentially be explained by differences in marine ecosystems, although this is very rarely assessed (Lehodey et al. 2010), but other factors such as ecosystem productivity may be involved (Dehnhard et al. 2020, Reisinger et al. 2020). Therefore, more studies investigating niche segregation in multiple dimensions in sympatric morphologically similar seabird species are needed.

In this study, we tested the hypothesis of niche segregation between 2 closely related and sympatrically breeding seabird species, the blue petrel *Halobaena caerulea* (BP) and the thin-billed prion *Pachyptila belcheri* (TBP), both belonging to the family Procellariidae, by quantifying spatial and foraging habitat as well as trophic differences during the breeding season. Although an earlier study found evidence for latitudinal and trophic segregation between these species during the breeding period, it was based on the isotopic method, which cannot identify longitudinal feeding grounds and has limited capacity for spatial resolution (Cherel et al. 2014). Using an integrative approach combining at-sea movement data obtained from miniaturized GPS loggers and isotopic data, we addressed the following main questions: (1) does spatial, foraging habitat or trophic segregation between BPs and TBPs occur during the incubation and chick-rearing periods; and (2) are the processes leading to niche partitioning similar during the incubation and chick-rearing periods?

BPs and TBPs breed on islands throughout the Southern Ocean and are sympatric at only a handful of subantarctic islands (Harrison et al. 2021). BPs are 30% heavier and 17% larger than TBPs but share similarities in bill characteristics (Table 1). At Kerguelen Islands, where they breed sympatrically in large numbers, BPs lay on average 3 week earlier than TBPs, but the longer duration of incubation and chick-rearing periods (Table 1) results in a strong overlap in breeding phenologies (see Fig. 2). Both species feed mainly by surface seizing or dipping (Croxall & Prince 1980) or by making shallow dives (Chastel & Bried 1996). Diet studies at

Kerguelen showed a strong overlap in the crustacean species consumed by BPs and TBPs during the chick-rearing period (Table 1). Isotopic studies also suggest that these species forage in different areas during incubation and that there is no obvious spatial or trophic segregation during chick-rearing; however, BPs appear to forage further south due to the noticeable occurrence of Antarctic krill *Euphausia superba* in the chicks' diet (Cherel et al. 2002a,b) and feed on higher trophic level prey than TBPs, likely due to the higher proportion of mesopelagic fish in the BP chicks' food (Table 1) (Cherel et al. 2014). Based on this previously collected information, we predicted (1) spatial segregation during incubation, with BPs foraging further south than TBPs; (2) no spatial segregation during chick-rearing; (3) no trophic segregation during incubation; (4) no or partial trophic segregation during chick-rearing; and therefore (5) partial foraging habitat segregation during chick-rearing.

2. MATERIALS AND METHODS

2.1 Study site and species

Fieldwork was carried out at Mayes Island (49°28'S, 69°57'E), situated in the Golfe du Morbihan, Kerguelen Archipelago, Southern Indian Ocean, between 19 November 2021 and 19 January 2022, which corresponds to the incubation (BP: 19 November to 23 December; TBP: 30 November to 27 December) and early chick-rearing (BP: 22 December to 11 January; TBP: 29 December to 19 January) periods. On average, 148 000 pairs of BPs and a large population of TBPs (several tens of thousands) breed in sympatry on Mayes Island in dense colonies or in loosely aggregated nests (Weimerskirch et al. 1989, Barbraud & Delord 2006). Both species breed in burrows in different terrestrial habitats, although there is some overlap (Genevois & Buffard 1994): TBPs mainly breed in burrows excavated in sandy or stony soils in areas with sparse vegetation, while BPs mainly breed in burrows dug in deep peaty soils in densely vegetated areas.

Both species lay a single egg and use a 2-fold foraging strategy during the chick-rearing period, alternating short trips (BP: 1.8 ± 0.6 d; TBP: 1.7 ± 0.8 d) and long foraging trips (BP: 7.2 ± 1.0 d; TBP: 7.5 ± 1.1 d) (Chaurand & Weimerskirch 1994a, Weimerskirch et al. 1994, Cherel et al. 2002b). Both species also spend the non-breeding season distant from their breeding colony, with partial latitudinal segregation: BPs spend the winter south of the Polar Front (PF) in Antarctic waters while the TBP prefers more northerly waters north and south of the PF

(Quillfeldt et al. 2015). Both species moult at the same time in overlapping areas within Antarctic waters during the Austral autumn after breeding is finished (Cherel et al. 2016).

2.2 Fieldwork for GPS deployment

We undertook daily visits to 34 BP burrows and 32 TBP burrows to monitor the breeding status and duration of the foraging trips and incubation shifts of breeding individuals until hatching. Burrows were selected based on accessibility, and for TBPs, according to the presence of individuals identified from previous breeding seasons (Nevoux & Barbraud 2006) in order to maximize recapture. Incubating birds were identified using their metal ring number.

To examine spatial movements, breeding birds were tracked with miniature GPS loggers (nanoFix-Geo; PathTrack) during both incubation and early chick-rearing periods. A total of 24 (15 females, 3 males and 6 undetermined sex; see Section 2.3 for sexing methods) and 5 (2 females, 1 male and 2 undetermined sex) BPs were tracked during incubation and early chick-rearing periods, respectively and 16 (7 females, 6 males and 3 undetermined sex) and 3 (1 female and 2 undetermined sex) TBPs were tracked during incubation and early chick-rearing periods, respectively. We tracked only one foraging trip per bird during incubation to minimize disturbance and to ensure statistical independence between trips. The devices weighed 2.2–2.7 g, which represented between 1.1 and 1.8% of BP mass (152–198 g) and 1.2 and 2.0% of TBP mass (122–196 g), thus below the 3% threshold advised by Phillips et al. (2003) and just above the 1% desirable target (Bodey et al. 2018). Birds were manually captured at the nest and weighed (± 5 g) in a bag with a Pesola spring balance before being equipped with a GPS. Loggers were attached to the 3 central tail feathers using Tesa[®] tape. The GPS recorded locations at a 120-min minimum interval frequency, which allowed the GPS battery to last for a complete foraging trip. Birds were recaptured on the day they returned to the nest following their foraging trips, weighed and measured (wing length ± 1 mm with a ruler; tarsus length, bill length, and bill depth ± 0.1 mm with a calliper), and the loggers were recovered. All BPs were recaptured except 3 birds whose breeding attempts failed (and thus they could not be recaptured), yielding an 83% recapture rate (29 deployments and 24 recoveries). Data from 35 GPS were retrieved successfully (BP: $n = 19$; TBP: $n = 14$). The GPS devices for 3 BP individuals were lost during the foraging trips, and the GPS failed to record locations for one

individual. All TBPs were recaptured except 3 birds whose breeding attempts failed, yielding a recapture rate of 84% (19 deployments and 16 recoveries).

2.3 Tissue sampling, molecular sexing and stable isotope analyses

Blood samples from adults equipped with GPS loggers were taken for molecular sexing (see paragraph below) and stable isotope analyses. A blood sample (0.05–1 ml) was taken from the alar vein using a 1 ml heparinized syringe and a 25 gauge needle immediately upon capture of a bird when it returned from a foraging trip. Whole blood was maintained at 4°C until being processed within 2–3 h of sampling.

Blood was separated into plasma and red blood cells (RBCs) by centrifugation and then stored frozen at –20°C until analysis at the laboratory in France. For molecular sexing, we conducted DNA extraction with 2 µl of RBCs using a Chelex resin (Chelex 100 Molecular Biology Resin, BIO-RAD; 10%) associated with Proteinase K. We then performed a PCR with amplification of the CHD gene following a standard procedure (Fridolfsson & Ellegren 1999). Of the 48 individuals on which we deployed GPS, 15 could not be sexed.

Stable carbon ($\delta^{13}\text{C}$, $^{13}\text{C}/^{12}\text{C}$) and nitrogen ($\delta^{15}\text{N}$, $^{15}\text{N}/^{14}\text{N}$) isotope values were used to depict the isotopic niche as a proxy of the trophic niche of adult BPs and TBPs. Tissue $\delta^{15}\text{N}$ values of consumers change according to their trophic position in the increasing order planktivorous species < piscivorous species < fish and squid eaters (Cherel et al. 2010), while $\delta^{13}\text{C}$ values reflect the latitudinal $\delta^{13}\text{C}$ gradient at the base of the food web and thus indicate their latitudinal foraging habitats within the Southern Ocean (Cherel & Hobson 2007, Jaeger et al. 2010). The isotopic consumer data allows estimation of the $\delta^{13}\text{C}$ position of the main oceanic fronts within the southern Indian Ocean, and thus delineation of robust isoscapes of the main foraging zones for top predators. Based on blood $\delta^{13}\text{C}$ isoscapes, values less than –22.5 ‰, –22.5 to –19.7 ‰ and greater than –19.7 ‰ were considered to correspond to the Antarctic (AZ), Subantarctic (SAZ) and Subtropical (STZ) zones, respectively (Cherel & Hobson 2007, Jaeger et al. 2010). Plasma and RBCs are metabolically active tissues that record trophic information at different and complementary time scales. Plasma and RBCs have half-lives of 3 d and about 1 month, respectively (Hobson & Clark 1993). Since an almost total renewal of tissues requires 4 half-lives, plasma integrates a shorter period than RBCs (12 days and 4

months, respectively) and represents trophic ecology during the GPS-tracked trips before sampling (Cherel et al. 2005a).

Plasma and RBC samples were freeze-dried and powdered. Unlike RBCs, avian plasma contains a high and variable lipid content that affects its $\delta^{13}\text{C}$ values. Consequently, lipids were removed from plasma samples using a 2:1 chloroform:methanol solution (Cherel et al. 2005a,b). Then the tissue sub-samples were weighed (~ 0.3 mg dry mass) with a microbalance, packed in tin containers and nitrogen and carbon isotope ratios were subsequently determined using a continuous flow mass spectrometer (Thermo Scientific Delta V Plus) coupled to an elemental analyser (Thermo Scientific Flash 2000). Results are presented in the usual δ notation relative to Vienna Pee-Dee Belemnite and atmospheric N_2 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. Replicate measurements of the internal laboratory standards USGS-61 and USGS-63 (caffeine) indicate measurement errors <0.10 and <0.15 ‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, respectively.

2.4 Foraging analysis and spatial usage

Spatial and statistical analyses were performed using the 'stats', 'trip', 'adehabitatHR' and 'adehabitatLT' packages (Calenge 2006, Calenge et al. 2009). From the recorded GPS data, foraging trips were reconstructed (interpolated) and data were discretized to represent one location for each 120 min. Some of the trips were largely incomplete due to the return journey not being initiated (incubation period: $n = 1$ for each species; chick-rearing period: $n = 3$ for TBPs) because of battery limitations; these were removed from the analysis. For each complete and incomplete foraging trip (we consider only slightly incomplete tracks; i.e. the return journey was initiated and the end of the inbound track was missing), we computed the following parameters: maximum distance to the colony (km), trip duration (d) and total distance travelled (km).

The spatial distribution of both species was investigated by producing 25, 50, 75 and 95% utilization distributions (UDs; Worton 1989) for each individual using kernel analysis with a cell size of $0.1^\circ \times 0.1^\circ$ and a smoothing parameter that was estimated using the ad hoc 'href' method. Grid cell size was based on the mean accuracy of the devices (~ 10 m), the mean maximum movement speed of both species (see Section 3.1) and the time interval between 2

GPS locations (120 min). To investigate whether space use differed between species for each stage, we calculated observed overlaps in each UD representing the high core (25%), core (50%), middle (75%) and general (95%) use areas using the utilization distribution overlap index (UDOI), which is the most appropriate measure for quantifying similarity among UD estimates (Fieberg & Kochanny 2005). The extent of overlap between BP and TBP home ranges was estimated using Bhattacharyya's affinity (BA), which ranges from 0 (no overlap) to 1 (complete overlap). Using these metrics, we performed a randomization procedure to test the null hypothesis that there was no difference in the spatial distribution of BPs and TBPs at the population level. The species to which each bird belonged was randomly assigned using the observed ratio in our data set, and the overlap metric between BPs and TBPs was calculated for 25, 50, 75 and 95% kernels. We performed 1000 randomizations of our data set from which the probability of accepting the null hypothesis was calculated as the proportion of random overlaps that were smaller than the observed overlap. Since we were testing only if the observed overlap was smaller than random overlap, we considered this as a one-tailed test.

2.5 Move persistence

To examine changes in movement behaviour, we fitted a continuous-time correlated random walk state-space model to the interpolated and regularized GPS location data using the 'fit_ssm' function in the 'foieGras' package (<https://github.com/ianjensen/foieGras>) in R. This 'move persistence' model permits us to estimate a time-varying behavioural index for each bird (Jonsen et al. 2020). Move persistence is a parameter that encompasses both speed and directionality. The move persistence model estimates a behavioural index that is comparable, but not identical, to the discrete behavioural states estimated in state-space switching models (Jonsen et al. 2019). Rather than discrete behavioural switches, time-varying move persistence is an alternative approach to objectively identify changes in movement patterns using the move persistence parameter (g_t), which ranges from low move persistence (where a value of 0 indicates slow speed and little directionality) to high move persistence (where a value of 1 indicates high speed and constant directionality) (Jonsen et al. 2019). Low g_t values are thus typical of resident or area-restricted searching behaviours (hereafter considered as

foraging), whereas high g_t values represent movement behaviours typical of directed travel associated with dispersal, migration or commuting flight.

2.6 Foraging habitat

To characterize the at-sea foraging habitat used by individual BPs and TBPs, we collated 7 environmental variables at each GPS location. These variables were selected because we had an a priori hypothesis linking them (or a biological–oceanographic process for which they are a proxy) to BP or TBP move persistence probability (Table 2). These were marginal ice zone (MIZ), sea-ice concentration (SIC), distance to the ice edge (distIE), bathymetry (bathy), slope (slope), sea-surface temperature anomaly (SSTA) and sea-surface height anomaly (SSHA). Sea-ice variables (MIZ and SIC) were used as covariates in addition to other oceanographic variables, as BPs and TBPs feed at high latitudes close to sea ice in areas in which the ice has recently melted (Woehler et al. 2010, Quillfeldt et al. 2015). Environmental data were extracted for the study area and period, between 40–70° S and 30–140° E for the period between 22 November 2021 and 15 January 2022.

Daily SIC data (Advanced Microwave Scanning Radiometer, AMSR-2, grid cell resolution of 3.125 × 3.125 km) were downloaded from Sea Ice Remote Sensing at the University of Bremen (<https://seaice.uni-bremen.de/>) (Spren et al. 2008). GeoTIFF format data was transformed into a raster map with the ‘raster’ package (Hijmans 2022) in R v.4.1.3 (R Core Team 2022). Since it is reported, at least for BPs (Ainley et al. 1993, Woehler et al. 2010), that birds are typically observed in the sea-ice region (as defined by the region within >15% SIC isocline; Cavalieri et al. 1991), the SIC data were filtered to retain SIC values >15% to indicate the presence of sea ice. The ice edge was defined as the 15% contour of SIC. The area between the maximum sea-ice cover in August 2021 and the minimum sea-ice cover in February 2022 was defined as the MIZ. For each GPS position, we extracted SIC, the minimum distIE and whether it was within or outside of the MIZ.

We extracted the ocean depth from GEBCO bathy data (15 arc-sec grid; GEBCO Compilation Group 2022). GeoTIFF format data was transformed into a raster map and slope was calculated with the ‘terrain’ function of the ‘raster’ package. Daily SSTA data (GHRSSST Level 4 MUR Global Foundation Sea-Surface Temperature Analysis v4.1, resolution of 1 × 1 km) was

downloaded from PODAAC (JPL MUR MEaSURES Project 2015). Daily SSHA and absolute dynamic topography data (Global Ocean Gridded L 4 Sea Surface Heights and Derived Variables Nrt, resolution of 0.25°) were downloaded from Copernicus Marine Service (doi.org/10.48670/moi-00149). Values were extracted from netCDF format data with the 'ncdf4' package (Pierce 2019). Positions of the oceanic fronts were estimated from the absolute dynamic topography following Venables et al. (2012) as follows: Southern Boundary at -1.22 m, Southern Antarctic Circumpolar Current Front (SACCF) at -1.07 m, PF at -0.59 m and Sub-Antarctic Front (SAF) at 0.15 m.

2.7 Statistical analysis

Differences in foraging trip metrics between species were tested using (1) Wilcoxon rank tests during incubation (only one trip per individual) and (2) generalised linear mixed models (GLMMs) using the 'glmmTMB' package (Brooks et al. 2017) during chick-rearing as there were several trips per individual. Bird ID was used as a random effect. The residuals were checked using the 'DHARMA' package (Hartig 2018) for GLMMs. To make inferences about how move persistence (the dependent variable) varied in relation to environmental variables, we tested the effect using generalised additive mixed models (GAMMs), as we expected strong non-linear effects. The sex of individuals could not be considered as an explanatory factor in the analyses due to unbalanced and relatively small samples. We fitted separate models to foraging trips by species and stage based on segregation evidenced in spatial usage (see Section 3.2). Each model was fitted with individual bird ID and spatial auto-correlation as a random factor to account for pseudo-replication issues (Wood 2004, 2017). Prior to GAMM analysis, we used the generalised variance inflation factor (GVIF) to assess collinearity between predictor variables and removed covariates for which GVIF > 2 (Zuur et al. 2009). The MIZ variable was excluded due to collinearity. Residual normality was visually verified. GAMMs were fitted with a beta distribution and a logit link function using the 'gam' function in the 'gam' package (Hastie & Tibshirani 1990). Model outputs were visualized using the package 'mgcViz' (Fasiolo et al. 2020). The starting models included all main effects (i.e. all environmental variables). The best candidate model was selected based on Akaike's

information criterion (AIC). A difference of more than 2 AIC units was taken to indicate strong support for the model with the lower AIC (Burnham & Anderson 2002).

We investigated the variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (in plasma and RBCs) of BPs and TBPs as a function of the at-sea distribution characteristics (i.e. percentage of locations per oceanic zones) of each individual. For this step, we ran principal components analyses (PCA built with the 'PCA' function, FactoMineR package; Lê et al. 2008) for all stages and species and retained the first 2 principal components (Dim1 and Dim2; Table S1 in the Supplement at www.int-res.com/articles/suppl/m749p159_supp.pdf), which explained 62.5% of the total variance. We tested for the effects of species and stage in Dim1 and Dim2 using a generalised linear model (GLM) with a Gaussian family distribution and identity link function. The GLM model was fitted using the package 'lme4' (Bates et al. 2009). The isotopic niche of the 2 species was established using the metric Stable Isotope Bayesian Ellipses (SIBER), which is based on a Bayesian framework that confers a robust comparison to be made among data sets concerning different sample sizes (Jackson et al. 2011). The area of the standard ellipse (an ellipse having a 40% probability of containing a subsequently sampled datum) was used to compare the BP and TBP isotopic values and their overlap in relation to the total niche width (i.e. both species combined), and a Bayesian estimate of the standard ellipse and its area (SEAB) was used to test whether the isotopic niche of TBPs was narrower than that of BPs (Jackson et al. 2011). The 'standard.ellipse' and 'convexhull' functions were used to calculate these metrics from SIBER implemented in the package 'MixSIAR' (Stock et al. 2018). Isotopic niche patterns were computed using the package 'nicheROVER' (Lysy et al. 2021). All data analyses were carried out in R v.4.1.3 (R Core Team 2022).

3. RESULTS

3.1 Patterns of spatial segregation: at-sea distribution and trip parameters

During the incubation and early chick-rearing periods, BPs and TBPs travelled at sea in a wide southern quadrant, with BPs mainly distributed to the east of Kerguelen over a wider longitudinal area (40°–125° E) compared to TBPs, which were mainly distributed to the west of Kerguelen (50°–90° E) (Fig. 1). Upon departure, on average, BPs and TBPs left the colony travelling west-southwest and returned to their colony from an east-southeast direction in an

anti-clockwise trajectory (Fig. S1). During incubation, BPs undertook some of the longest foraging trips recorded for any animal during breeding, covering up to 10 290 km during a single foraging trip and reaching a maximum distance up to 3744 km from the colony (Table 3). TBPs covered less distance, up to 5115 km during a single incubation trip and reached a maximum distance of up to 1914 km from the colony (Table 3 & Table S2). On average, BPs performed longer incubation foraging trips in terms of distance travelled than TBPs (Table 3). BPs tended (not significant) to exhibit longer trips in terms of duration and greater maximum distance from the colony than TBPs (Table 3). During early chick-rearing, foraging trips were shorter in length and duration than during incubation (Table 3). BPs and TBPs performed short and long foraging trips during chick-rearing. Both species performed shorter trips in terms of duration, distance travelled and maximum distance from the colony during short trips (Table 4). Whichever type of trip was considered, TBPs made shorter trips in distance and duration than BPs (Table 4).

Body mass gains could only be calculated for incubation foraging trips, as equipped birds made several foraging trips during chick-rearing and fed their chick before being recaptured. During incubation, BPs left their burrow at an average mass of 157 ± 12 g ($n = 11$) and gained an average of 2.7 ± 1.3 g d^{-1} when foraging at sea. For TBPs, the average mass at departure was 132 ± 13 g ($n = 11$) and average daily body mass gain at sea was 4.3 ± 2.4 g. The average body mass gain represented $22.4 \pm 8.2\%$ of departure body mass for BPs and $28.1 \pm 14.6\%$ for TBPs. Whichever period was considered, BPs and TBPs ranged over similar oceanic zones (Fig. 2), but there was no spatial overlap as inferred from the BA and UDOI indices (Table 5). Space-use sharing was dissimilar between both species, as the UDOI was significantly lower than the null expectation for the 25, 50, 75 and 95% UD's (Table 5). BP and TBP UD's also differed regardless of the UD's considered since BA values were significantly lower than the null expectation for 25, 50, 75 or 95% UD's (Table 5).

3.2 Drivers of spatial segregation

The spatial distributions of BPs and TBPs during incubation and early chick-rearing periods were best explained by models that included habitat covariates (Tables S3–S6). The move persistence of both species was non-linearly related to several environmental variables.

However, the modelled responses of birds to predictors differed between species and stages. During the incubation period, the best-supported model for move persistence of BPs included SIC, distIE, bathy, slope and SSTA (Table S3), with 63% of the deviance explained. Only smoothers for SIC and distIE were significant as uncertainties were high for the other smoothers (Table S3). Move persistence increased with increasing SIC, being lowest when SIC was near zero, increasing sharply with increasing distIE up to 300 km and then increasing at a lower rate (Fig. 3 & Fig. S2). In other words, BPs foraged in the vicinity of the sea-ice edge in open waters or waters with low sea-ice cover. For TBPs, the best-supported model included distIE, bathy, slope and SSTA (Table S4). This model explained 69% of the deviance. Move persistence decreased with increasing distIE, indicating that TBPs foraged far from the ice edge (Fig. 4a & Fig. S2). Move persistence varied non-linearly with bathy, being minimal at depths of 2700–1700 and <500 m (Fig. 4b) and increasing with slope (Fig. 4c). In other words, TBPs mostly foraged on the Kerguelen-Heard plateau and in areas with the lowest slopes, thus avoiding abyssal plains. Move persistence was minimal for SSTA between 0° and +1°C (Fig. 4d), indicating that TBPs avoided below-average anomalies and anomalies warmer than +1°C when foraging.

During the early chick-rearing period, similar environmental variables were retained in the best models for BPs and TBPs (Tables S5 & S6). Nevertheless, most smoothers had high uncertainties and only distIE for BPs and SSHA for TBP had significant effects on move persistence. For BPs, the foraging intensity increased with distIE, with higher intensity at ~1400 km from the ice edge (Fig. 5a). For TBPs, only SSHA had a significant effect (Table S6), suggesting that individuals targeted waters with negative sea level anomalies in which to forage (Fig. 5b).

3.3 Stable isotopes

A comparison of isotopic values between sexes for BPs (17 females and 4 males) and TBPs (8 females and 6 males) showed no significant differences for both plasma and RBCs (Mann-Whitney U-tests, all $p > 0.13$). Therefore, isotopic values for females and males of each species were pooled in subsequent analyses. Isotopic values were related to tissues, with plasma

values being significantly higher than RBC values (0.3–0.7 and 0.7 ‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively) for both BPs and TBPs (Table 6, Fig. 6).

All $\delta^{13}\text{C}$ values indicated that BPs and TBPs did not forage within the STZ, but instead remained within the Southern Ocean, south of the Subtropical Front. The very low $\delta^{13}\text{C}$ values (less than -22.5 ‰) of plasma and RBCs show that both species feed primarily within the AZ, with only 2 BP individuals having plasma $\delta^{13}\text{C}$ values indicative of subantarctic origin (SAZ). BPs and TBPs showed no significant differences in their plasma and RBC $\delta^{13}\text{C}$ values. By contrast, they were segregated by their $\delta^{15}\text{N}$ values, with plasma and RBCs of BPs being significantly ^{15}N enriched (0.5 ‰) compared to the tissues of TBPs (Table 6, Fig. 6a). Plasma and RBC $\delta^{13}\text{C}$ values were positively and linearly correlated in both BPs and TBPs. In contrast, plasma and RBC $\delta^{15}\text{N}$ values were only marginally correlated in BPs and were not statistically correlated in TBPs (Fig. 6b).

Regardless of the sample type considered (plasma or RBCs), BPs and TBPs exhibited different SEAB (Table 6, Fig. 8 & Fig. S3). The overlap between SEAB areas for BPs and TBPs was 0.270 and 0.167 for plasma and RBC, respectively.

BPs and TBPs had variable isotopic niches, considering both RBCs (BP: 2.28 ± 0.53 ; TBP: 0.95 ± 0.27 ; Fig. S4) and plasma (BP: 4.96 ± 1.26 ; TBP: 2.87 ± 0.79). The pairwise comparisons revealed low to moderate probabilities of isotopic niche overlap (mean overlap for RBCs: 15 and 40%; plasma: 38 and 56%; Fig. S5), which shows the likelihood of trophic differentiation among the 2 species. This moderate overall overlap of isotopic niches indicates a propensity for niche differentiation between BPs and TBPs.

3.4 Principal component analysis

Component loadings indicated (Table 7) that Dim1 integrated the percentage of locations in the Antarctic zones AZ1 (loading: -0.79) and AZ2 (loading: 0.72), respectively south and north of the SACCF in the PF Zone (loading: 0.69) and $\delta^{13}\text{C}$ in plasma (loading: 0.70). In other words, high $\delta^{13}\text{C}$ values in plasma were associated with a high percentage of locations in the AZ2 and PFZ. Conversely, low $\delta^{13}\text{C}$ values in plasma were associated with a high percentage of locations in the zone south of the Antarctic Circumpolar Current (Fig. 7 & Fig. S6). Compared to TBPs, BPs exhibited lower Dim1 values, indicating that they spent a higher proportion of time in

southern oceanic zones (Fig. 7). Component loadings of Dim2 indicated that this axis integrated $\delta^{15}\text{N}$ in plasma (loading: 0.77), $\delta^{13}\text{C}$ in RBCs (loading: 0.73), $\delta^{13}\text{C}$ in plasma (loading: 0.61) and $\delta^{15}\text{N}$ in RBCs (loading: 0.61). Thus, all isotopic ratio values covaried positively regardless of the tissue type. BPs displayed higher Dim2 values than TBPs (Fig. 7).

4. DISCUSSION

In this study, the combination of GPS tracking and stable isotopes demonstrated interspecific niche segregation between 2 closely related and morphologically similar seabird species breeding in sympatry. Based on the competition theory and previous knowledge of the species, and in accordance with our predictions, we found (1) latitudinal and longitudinal spatial segregation during incubation, with BPs foraging further south and east than TBPs, and (2) trophic segregation revealed by subtle differences in stable isotopes. There was some evidence for foraging habitat segregation during early chick-rearing, with TBPs foraging in areas with negative SSHA and avoiding areas with strongly positive SSHA, as well as for spatial segregation during early chick-rearing; however, larger sample sizes would be required for stronger inferences. Additionally, we found trophic and foraging habitat segregation during incubation, with BPs foraging close to the ice edge and TBPs foraging in oceanic areas far from the ice edge. Thus, our findings are in line with the predictions of niche theory: without temporal segregation in breeding phenology between sympatric morphologically similar species, we expected spatial segregation in foraging areas. In addition, investigating niche segregation in multiple dimensions also revealed subtle trophic segregation and clear foraging habitat segregation. One limitation is the small sample size in tracking data during the chick-rearing period, and results obtained during this period should be considered descriptive and exploratory. Despite this limitation, the study provides the first information on the foraging ecology of those poorly known species from the Indian Ocean, and we are confident that the results permit us to address the spatial and foraging habitat segregation between these 2 species during incubation and explore the processes leading to niche partitioning.

4.1 Spatial and trophic segregation

Tracking data indicated that BPs and TBPs strongly differed in their at-sea distribution. During incubation, BPs foraged mainly southeast of Kerguelen in Antarctic waters, south of the SACCF and south of the Antarctic Circumpolar Current, whereas TBPs mainly foraged southwest of Kerguelen in Antarctic zones north of the SACCF. This resulted in longer foraging trip durations and distances from the colony for BPs compared to TBPs. Remarkably, breeding BPs fed in high-latitude areas (down to 64.29° S) in accordance with visual observations during the breeding season (Woehler et al. 2010, J. C. Stahl et al. unpubl. data, CEBC unpubl. data) and undertook the longest foraging trips recorded for any animal during breeding relative to its body size (Ventura et al. 2020). These long foraging trips may be facilitated by morphometry, with BPs having a higher aspect ratio (squared wingspan divided by wing area) compared to TBPs (Warham 1977, Navarro et al. 2013) and likely resulting in lower energy consumption as inferred from allometric relationships and kinematic models (Xie et al. 2023). To our knowledge, no other study has investigated the foraging behaviour of breeding BPs using fine-scale GPS data, although Quillfeldt et al. (2022) GPS-tracked breeding TBPs in the Falkland/Malvinas Islands. Compared to the birds in that study, TBPs from Kerguelen stayed longer at sea and covered greater distances during incubation and chick-rearing trips. TBPs breeding at the Falkland/Malvinas Islands foraged primarily over neritic waters of the Patagonian shelf north of the SAF, while Kerguelen birds favoured the Kerguelen-Heard plateau and oceanic waters south of the PFZ. Together, these findings provide an overview of the differences in foraging strategies and habitats between TBP populations, which could result from phenotypic plasticity or local adaptation due to different environmental constraints.

During the early chick-rearing period, BPs and TBPs also strongly differed in their at-sea distribution, although our sample size was small. Spatial segregation was more marked during early chick-rearing than during incubation, as indicated by smaller metrics for UDOI and BA. Despite similar trip lengths and distances travelled by BPs and TBPs during short foraging trips on the Kerguelen-Heard plateau, there was full spatial segregation, with BPs foraging north of Heard Island and TBPs foraging south of Kerguelen. Interestingly, the foraging area used by TBPs during short trips is similar to that used by South Georgian diving petrels *Pelecanoides*

georgicus breeding in the Kerguelen-Morbihan Gulf during the chick-rearing period (Bost et al. 2022). Although there is overlap in the crustacean species caught by these 2 species to feed their chicks (Bocher et al. 2000), diving petrels feed at greater depths than TBPs and their breeding phenology is about 2 wk earlier than TBPs (Fromant et al. 2022).

Results obtained from GPS-tracking data are in agreement with RBC and plasma $\delta^{13}\text{C}$ values for both species and with earlier inferences made from isotopic data (Cherel et al. 2002a,b, 2014). According to the latitudinal $\delta^{13}\text{C}$ gradient in the Southern Ocean (Cherel & Hobson 2007, Quillfeldt et al. 2010a), RBC and plasma $\delta^{13}\text{C}$ values show that BPs foraged primarily within the Antarctic zone and that TBPs foraged primarily over oceanic waters of the SAZ and Antarctic zone, as found in previous studies (Cherel et al. 2002a,b, 2014). However, the isotopic segregation between the 2 species was much less pronounced than the spatial segregation. RBC and plasma $\delta^{13}\text{C}$ values were similar for both species, but the larger variance (BP: 0.64; TBP: 0.37) and range of values for BPs (from -25.5 to -22.1 ‰ for BPs and from -25.1 to -22.7 ‰ for TBPs) indicated that this species fed within a broader latitudinal range than TBPs during incubation, as observed with tracking data. RBC and plasma $\delta^{13}\text{C}$ values were also similar for individuals during the early chick-rearing period (BP: -23.8 ± 0.9 ‰; TBP: -24.0 ± 0.7 ‰). This could be explained by the longitudinal (but not latitudinal) segregation during the early chick-rearing period, as suggested by tracking data despite the small sample size. Isotopic segregation was more pronounced for RBC and plasma $\delta^{15}\text{N}$ values, with statistically different values indicating that BPs fed on higher trophic level prey than did TBPs. This dietary segregation is likely explained by both the higher proportion of mesopelagic fish in the diet of the BP chicks compared to that of the TBP chicks (Cherel et al. 2002a,b, 2014) and the higher trophic positions of mesopelagic fish compared to pelagic swarming crustaceans (Cherel et al. 2010).

The high and positive correlation in $\delta^{13}\text{C}$ between RBCs and plasma in BPs and TBPs indicates that within each species, individuals foraged in isotopically similar habitats in the medium and short term, respectively (Ceia et al. 2012, Cherel et al. 2018). This does not necessarily indicate that individuals showed fine-scale foraging site fidelity, which could not be tested given that the GPSs were recovered following a single foraging trip, but that they consistently used the same water mass. The $\delta^{15}\text{N}$ values were also positively correlated in RBCs and plasma but only in BPs, suggesting trophic consistency in BPs but not in TBPs. This is partially in agreement with patterns previously found by (Cherel et al. 2014), who described similar RBC and plasma

$\delta^{15}\text{N}$ values in adult BPs during incubation and hatching. The RBC and plasma $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values in our study were similar to those found in previous studies of BPs and TBPs at Kerguelen (Cherel et al. 2002a,b, 2014), thus indicating no major change in trophic position and foraging habitats over the past 20 yr.

The multidimensional approach used here, combining GPS and isotopic data, highlights the longitudinal segregation in feeding grounds between BPs and TBPs during incubation and less pronounced latitudinal segregation. Altogether, these results indicate that during incubation (and possibly during early chick-rearing), BP adults foraged further south and east and fed on higher trophic level prey than did adult TBPs, with a potential full spatial segregation for short foraging trips during the early chick-rearing period. Being central-place foragers, seabirds such as BPs and TBPs have to balance the demands of self and offspring-provisioning within the constraints imposed by foraging from a fixed colony site (Orians & Pearson 1979). Accordingly, since the chick-rearing period is more constraining than the incubation period due to the regular provisioning of chicks, trip durations and distances travelled by BPs and TBPs decreased between incubation and the chick-rearing period, as previously observed in other species (Weimerskirch et al. 1993, Sánchez et al. 2018, Fromant et al. 2022, Petalas et al. 2024). This was paralleled by increased spatial segregation as inferred from smaller metrics for UDOI and BA (incubation > chick-rearing long trips > chick-rearing short trips). Such an increase in spatial segregation is likely a consequence of the dual strategy of short and long foraging trips in these species, with short foraging trips being more profitable to offspring (Weimerskirch et al. 1994, 1997). Indeed, during short trips, adults need to find sufficient prey to feed their chick in a reduced time interval, potentially increasing intra- and inter-specific competition. Given the similarities in morphology between BPs and TBPs, these patterns of spatial and trophic segregations may result from competitive exclusion rather than from niche specialization (Phillips et al. 2004). The trophic segregation and strong spatial segregation of BPs and TBPs observed at Kerguelen could also partly be a consequence of the large population sizes of the 2 species. Segregation tends to increase with colony size, suggesting an effect of competition (Petalas et al. 2024), and Mayes Island (where our study was undertaken) hosts ca. 142 000 breeding pairs of BPs (Barbraud & Delord 2006) and several thousand pairs of TBPs (Weimerskirch et al. 1989). BPs and TBPs breed in sympatry in relatively few localities in the Southern Ocean, and Kerguelen is the only locality where BPs and TBPs breed in high numbers (Brooke 2004) and thus are more likely to experience

competition. Therefore, spatial and trophic segregation may have evolved to minimize competition to allow the co-existence of both species in high numbers. Although there is no quantitative data on the abundance of food resources for these 2 species, strong interannual variations in adult body condition (Chastel et al. 1995) and effects of proxies of food resources on demographic parameters (Barbraud & Weimerskirch 2005, Nevoux & Barbraud 2006) suggest food limitation during some years.

4.2 Foraging habitat segregation

The oceanographic habitat used by BPs and TBPs was different during the incubation period and possibly during the early chick-rearing period. Habitat modelling indicated that during incubation, BPs foraged close to the ice edge but not within the pack ice. As the SIC covariate used in our study defined open water as SIC < 15%, we can conclude that BPs targeted the oceanic areas adjacent to the MIZ, the latter being defined as the area of the ice-covered ocean where the SIC is less than 80% and more than 15% (Dumont 2022). This is in agreement with at-sea observations of BPs feeding within brash ice and open water adjacent to the sea-ice front (Ainley et al. 1993, Woehler et al. 2010). By contrast, incubating TBPs remained far from the ice edge and used the Kerguelen- Heard plateau and its surroundings, avoiding abyssal plains and shelf slopes. There, TBPs seemed to forage mostly in areas with slightly positive SSTA but avoided foraging in areas with strongly negative or positive anomalies. This suggests the existence of optimal SSTA for foraging TBPs during incubation (Gjerdrum et al. 2003, Carroll et al. 2016).

During early chick-rearing, none of the oceanographic covariates contributed to explaining foraging behaviour in BPs except distIE, indicating that BPs foraged far from the ice edge during this period as observed with tracking data. Interestingly, TBPs seemed to mainly forage in areas with negative SSHA. In the Southern Ocean, such areas are characteristic of mesoscale (diameter: 30–300 km) cyclonic eddies and are generally associated with negative SSTA (Frenger et al. 2018, Liu et al. 2023). Physical processes in such eddies lead to both enhanced productivity due to the upwelling of deep, nutrient-rich waters and/or the spatial structuring and entrapment of biological particles (Uchida et al. 2020). Thus, TBPs may target mesoscale eddies as documented for several Southern Ocean seabird and seal species (Nel et al. 2001,

Bost et al. 2009). These results align with those found for TBPs breeding at the Falkland/Malvinas Islands (Quillfeldt et al. 2003, 2007, 2010b) and at Kerguelen (Nevoux & Barbraud 2006), where foraging parameters and/or breeding success were negatively affected by positive SSTA (i.e. potentially corresponding to anticyclonic eddies).

Niche segregation implies that there is a limited overlap within ecological niches between coexisting species. Past competition could have played a role in producing differences in the species' abilities to exploit habitats differently, allowing their coexistence. BPs and TBPs breeding at Kerguelen may be partially overcoming such interspecific competition by segregating the spatial and dietary dimensions of their niche hypervolume. Although there was some strong overlap in breeding phenology, we observed clear species-specific foraging differences in localities, oceanographic habitats and isotopic niches. Whereas BPs foraged southeast of Kerguelen up to the sea-ice edge and at higher trophic levels, TBPs foraged southwest of Kerguelen, at more northern latitudes, in specific water mass structures and at lower trophic levels. This suggests that spatial distribution and diet are the primary segregation mechanisms between BPs and TBPs during the breeding period rather than allochrony. This segregation persists during the inter-breeding period, with BPs targeting Antarctic waters south of the PF and TBPs favouring intermediate latitudes and temperatures (Quillfeldt et al. 2015). Given the evidence of widespread trends in duration and intensity in Southern Ocean phytoplankton blooms linked to climate drivers during the last 2 decades (Thomalla et al. 2023), it will be useful to repeat such studies in the future to determine the consequences of such major changes for these micronekton-dependent species.

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Table 1. Main morphological, phenological and trophic traits of blue petrels and thin-billed prions breeding at Kerguelen Islands. Values are means \pm SD with ranges in parentheses. RBC: red blood cells

Trait	Blue petrel	Thin-billed prion	Reference
Body mass at start of incubation (g)	217 \pm 13	151 \pm 13	1
Wing length (mm)	220 \pm 5	181 \pm 4	2
Culmen length (mm)	26.1 \pm 1.1	25.5 \pm 1.3	3
Maximum bill depth (mm)	9.4 \pm 0.4	12.0 \pm 1.0	3
Laying date	30 oct \pm 4 (22 oct – 07 nov)	22 nov \pm 3 (17 nov – 30 nov)	this study
Duration of incubation (days)	49 \pm 2 (47-52)	46 \pm 1 (44-49)	4, this study
Duration of chick rearing (days)	53 \pm 2 (48-60)	51 \pm 2 (48-55)	4, this study
Diet during chick rearing (% by reconstituted mass)	Fish: 56.8% (<i>Paradiplospinus gracilis</i> , myctophids, melamphids) Crustaceans: 37.4% (<i>Themisto gaudichaudii</i> , <i>Euphausia superba</i>)	Fish: 11.6% (myctophids) Crustaceans: 81.9% (<i>Themisto gaudichaudii</i> , <i>Euphausia superba</i>)	5
Diet during chick rearing (number)	Fish: 0.9% Crustaceans: 98.2% (<i>Themisto gaudichaudii</i> , <i>Thysanoessa</i> spp.)	Fish: 0.1% Crustaceans: 99.7% (<i>Themisto gaudichaudii</i> , <i>Thysanoessa</i> spp.)	5
RBC $\delta^{13}\text{C}$ spring arrival	-23.1 \pm 1.6	-21.5 \pm 1.4	6
RBC $\delta^{13}\text{C}$ incubation	-23.9 \pm 1.2	-22.3 \pm 1.1	6
RBC $\delta^{13}\text{C}$ chick rearing	-24.1 \pm 0.8	-23.7 \pm 0.5	6
RBC $\delta^{13}\text{C}$ chicks	-23.2 \pm 0.4	-23.1 \pm 0.8	6
RBC $\delta^{15}\text{N}$ spring arrival	9.5 \pm 1.1	8.6 \pm 0.7	6
RBC $\delta^{15}\text{N}$ incubation	8.6 \pm 0.4	8.5 \pm 0.1	6
RBC $\delta^{15}\text{N}$ chick rearing	8.1 \pm 0.4	7.8 \pm 0.2	6
RBC $\delta^{15}\text{N}$ chicks	9.2 \pm 0.4	8.4 \pm 0.4	6

1 (Chaurand and Weimerskirch 1994b; Duriez et al. 2000), 2 (Weimerskirch et al. 1989a), 3 (Laranjeiro et al. 2022), 4 (Brooke 2004), 5 (Cherel et al. 2002a, b), 6 (Cherel et al. 2014).

Table 2. Environmental covariates and reasons for inclusion in the move persistent model. MIZ: marginal ice zone; SIC: sea-ice concentration; distIE: distance to the ice edge; bathy: bathymetry; SSTA: sea-surface temperature anomaly; SSHA: sea-surface height anomaly; BP: blue petrel; TBP: thin-billed prion

Variable	Reasons motivating inclusion
MIZ	Biotic and abiotic habitat features and processes lead to elevated abundance in biological communities and potential prey in this zone where sea-ice covered waters transition to open ocean (Ainley et al. 2017).
SIC	Sea-ice cover may favour the abundance of resources by providing a habitat for different prey but may also decrease prey accessibility for BP and TBP by providing a refuge (Ainley et al. 2017; Bluhm et al. 2017).
distIE	Near the ice edge, prey availability is high offering more foraging opportunities for BP and TBP (Brierley et al. 2002).
bathy	Different prey species are distributed in neritic and oceanic waters. At Kerguelen, BP and TBP consume pelagic species. Individuals are predicted to forage in the bathymetric domain with higher preferred prey availability (Godet et al. 2020).
slope	Slope areas are regions of water mixing, where nutrient-rich waters are forced towards the surface. We expect individuals' foraging behaviour to concentrate in the more productive waters over the shelf (Bucciarelli et al. 2001).
ssta	Cooler waters forced to the surface are richer in nutrients and support higher concentration of prey. We predict foraging behaviour to be more strongly associated to cooler, more productive waters (Pakhomov and McQuaid 1996).
ssha	Characterizes mesoscale hydrographic features and indicative of eddies. Negative ssha indicate cold-core eddies. We expect individuals' foraging to be more strongly associated to positive ssha (Hyrenbach et al. 2006).

Table 3. Tracking data of blue petrels and thin-billed prions during the incubation and chick-rearing periods at Mayes Island, Kerguelen Islands. For each parameter, values not sharing the same superscript letter (a and b; Wilcoxon test) or (c and d; generalised linear mixed model) are statistically significantly different. Values are means \pm SD with ranges in parentheses. F: female; M: male; UnS: unknown sex; * $p < 0.05$; ** $p < 0.01$

	Incubation		Chick rearing	
	Blue petrel	Thin-billed prion	Blue petrel	Thin-billed prion
GPS data (N: no. of individuals; n: no. of complete trips)	N= 16; n = 16; 13 F; 2 M; 1 UnS	N = 11; n = 11; 6 F; 5 M	N = 3; n = 5; 2 F; 1 M	N = 3; n = 11; 2 F; 1 UnS
Trip duration (d)	13.2 \pm 3.8 ^{a,*} (7.7–19.0)	7.8 \pm 0.9 ^{b,*} (5.9–8.8)	4.7 \pm 3.1 (0.8–8.7)	2.9 \pm 2.6 (0.7–6.9)
Total distance travelled (km)	7523 \pm 1760 ^{a,*} (4643–10290)	4134 \pm 937 ^{b,*} (2292–5524)	3206 \pm 1798 ^{c,**} (1020–5115)	1611 \pm 1579 ^{d,**} (229–4482)
Maximum distance from colony (km)	2328 \pm 533 ^{a,*} (1698–3744)	1297 \pm 230 ^{b,*} (828–1589)	1092 \pm 645 (268–1914)	765 \pm 596 (146–1656)
Movement speed (km h ⁻¹)	24 \pm 4 (14–33)	23 \pm 5 (14–33)	23 \pm 2 (20–26)	23 \pm 7 (10–35)

Table 4. Tracking data of blue petrels and thin-billed prions during short and long trips during the chick-rearing period at Mayes Island, Kerguelen Islands. For each parameter, values not sharing the same lowercase superscript letter (a and b) are significantly different (generalised linear mixed model). Uppercase superscript letters (A, B, C, and D) indicate values calculated for complete trips for: A 2 individuals and 2 trips; B 4 individuals and 4 trips; C 4 individuals and 9 trips; and D 3 individuals and 4 trips. Values are means \pm SD with ranges in parentheses. *** $p < 0.001$

	Blue petrel		Thin-billed prion	
	Short trips	Long trips	Short trips	Long trips
GPS data (N: no. of individuals; n: no. of trips)	N = 3; n = 3	N = 4; n = 4	N = 5; n = 11	N = 5; n = 6
Trip duration (d)	1.6 \pm 0.6 ^{a,***} (0.8–2.0)	7.8 \pm 0.7 ^{b,***} (6.8–8.7)	1.5 \pm 1.5 ^{c,***} (0.7–5.8)	7.0 \pm 2.1 ^{d,***} (4.8–11.3)
Total distance travelled (km)	1030 ^A \pm 10 ^{a,***} (1020–1039)	4122 ^B \pm 125 ^{b,***} (3963–4257)	641 ^C \pm 415 ^{a,***} (229–1595)	4035 ^D \pm 259 ^{b,***} (3854–4482)
Maximum distance from colony (km)	367 \pm 70 ^{a,***} (268–422)	1684 \pm 191 ^{b,***} (1434–1914)	338 \pm 171 ^{a,***} (146–730)	1547 \pm 83 ^{b,***} (1438–1656)
Movement speed (km h ⁻¹)	22 \pm 1 (20–22)	24 \pm 1 (23–26)	22 \pm 6 (12–33)	24 \pm 8 (10–35)

Table 5. Estimated overlap during the incubation and chick-rearing periods in utilization distributions (UD) between blue petrel and thin-billed prion from Mayes Island, Kerguelen archipelago. UDOI: Utilization distribution overlap index, values >1 indicates higher than normal similarity among UD estimates. BA: Bhattacharyya's affinity, which ranges from 0 (no overlap) to 1 (complete overlap). Significant results ($p < 0.05$) are in bold

UD (%)	Observed UDOI	Randomized UDOI	p	Observed BA	Randomized BA	p	Stage
25	0.005	0.054	0.009	0.014	0.099	0.009	Incubation
50	0.044	0.202	<0.001	0.111	0.312	<0.001	Incubation
75	0.169	0.481	<0.001	0.338	0.620	0.001	Incubation
95	0.378	0.927	<0.001	0.560	0.858	<0.001	Incubation
25	0.000	0.072	<0.001	0.000	0.187	<0.001	Chick-rearing long trips
50	0.028	0.282	0.002	0.079	0.409	0.001	Chick-rearing long trips
75	0.123	0.552	0.002	0.270	0.663	0.001	Chick-rearing long trips
95	0.325	1.029	0.002	0.517	0.898	<0.001	Chick-rearing long trips
25	0.000	0.119	<0.001	0.000	0.199	<0.001	Chick-rearing short trips
50	0.001	0.306	<0.001	0.004	0.444	<0.001	Chick-rearing short trips
75	0.034	0.587	<0.001	0.119	0.694	<0.001	Chick-rearing short trips
95	0.131	1.096	<0.001	0.329	0.903	<0.001	Chick-rearing short trips

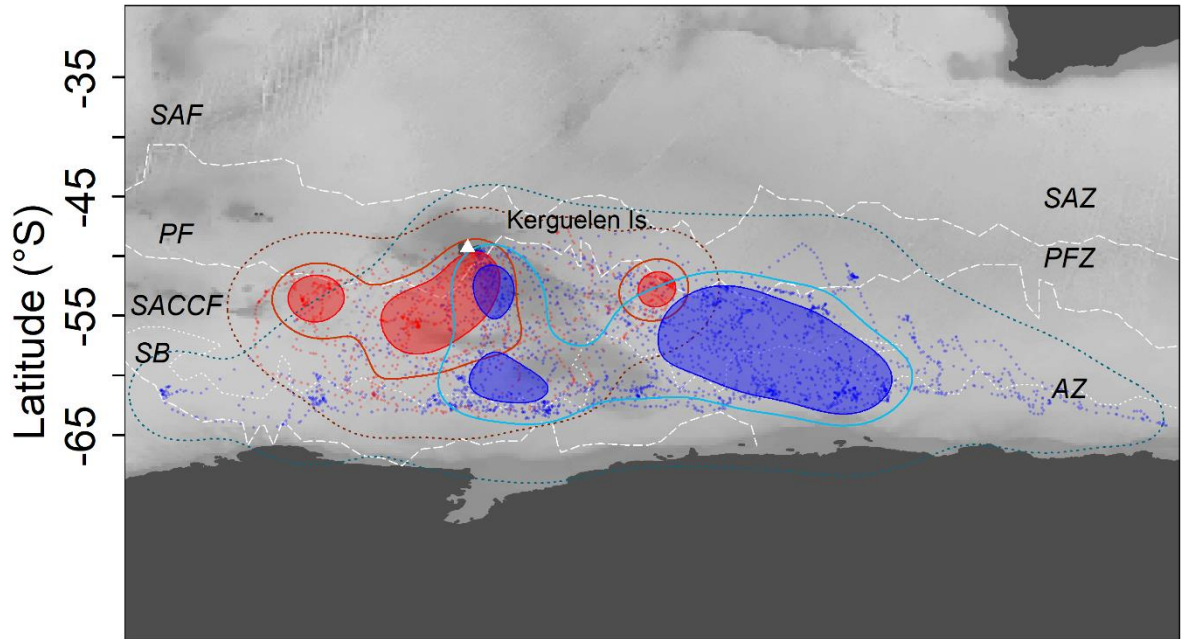
Table 6. Plasma and red blood cell (RBC) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values and associated statistics of GPS-tracked blue petrels and thin-billed prions. Values are means \pm SD with ranges in parentheses. SEAB: Bayesian approximation of the standard ellipse area. Values in brackets indicate 95% credible interval for SEAB. *p* indicates the probability that SEAB of blue petrels and thin-billed prions differ. Significant differences ($p < 0.05$) are in bold

Tissue		Blue petrel	Thin-billed prion	Statistics (2-sample <i>t</i> -tests)
	n	(‰)	(‰)	blue petrel versus thin-billed prion
Plasma	$\delta^{13}\text{C}$	21 −24.2 \pm 0.9 (−25.5 to −22.1)	14 −23.8 \pm 0.6 (−24.7 to −22.7)	$t = -1.14$; $p = 0.263$
	$\delta^{15}\text{N}$	21 9.6 \pm 0.4 (9.1 to 10.8)	14 9.0 \pm 0.3 (8.5 to 9.5)	$t = 4.46$; $p < 0.001$
RBC	$\delta^{13}\text{C}$	21 −24.5 \pm 0.6 (−25.4 to −23.2)	14 −24.6 \pm 0.4 (−25.1 to −23.9)	$t = 0.34$; $p = 0.733$
	$\delta^{15}\text{N}$	21 8.8 \pm 0.2 (8.6 to 9.3)	14 8.3 \pm 0.2 (8.1 to 8.6)	$t = 7.81$; $p < 0.001$
Statistics (paired <i>t</i> -tests) plasma versus RBC	$\delta^{13}\text{C}$	$t = -2.37$; $p = 0.028$	$t = -5.88$; $p < 0.001$	
	$\delta^{15}\text{N}$	$t = -9.84$; $p < 0.001$	$t = -9.16$; $p < 0.001$	
SEAB				<i>p</i>
Plasma		0.83 (0.54–1.31)	0.48 (0.28–0.86)	0.078
RBC		0.36 (0.23–0.58)	0.17 (0.09–0.30)	0.019

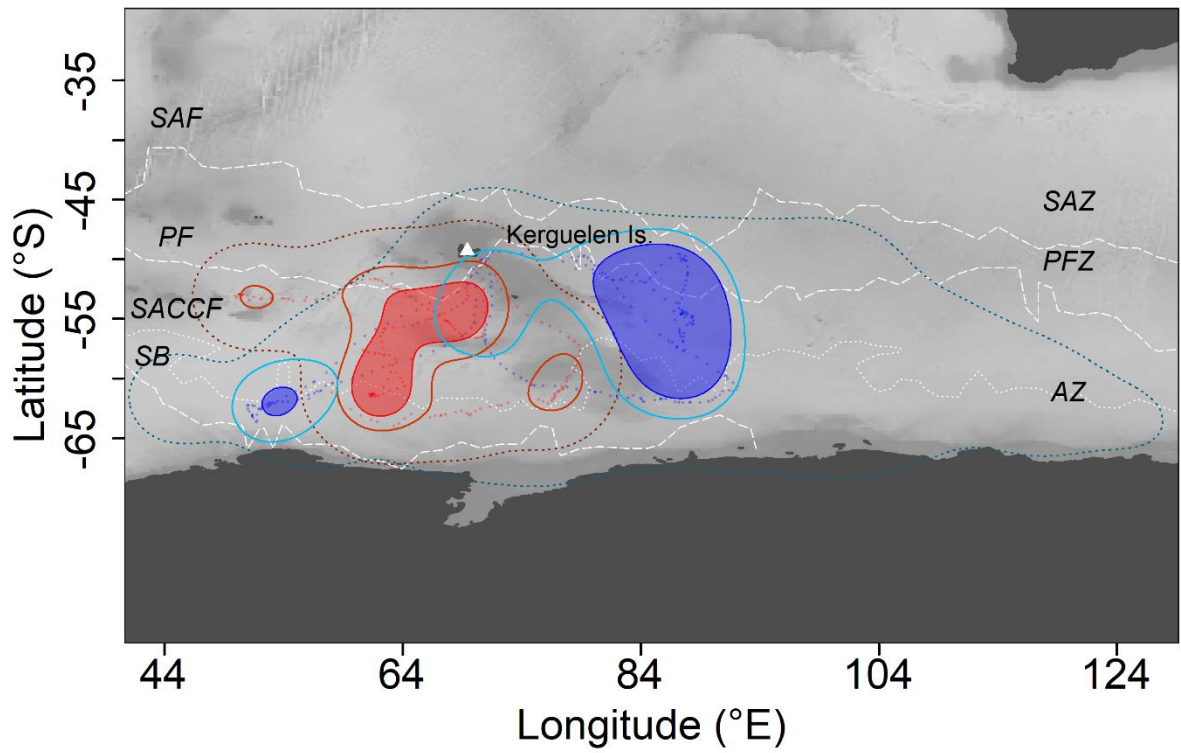
Table 7. Component loadings for the first 2 principal components (Dim) of the principal component analysis performed on variables quantifying the proportion of time spent in different oceanic zones and quantifying $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values in plasma and red blood cells (RBC) of blue petrels and thin-billed prions. The oceanic zones delineated, from north to south, are the polar frontal zone (PFZ), the Antarctic zone south of SACCF (AZ1), north of SACCF (AZ2), and the zone south of the Antarctic Circumpolar Current (SACCZ) following main frontal structures defined by Venables et al. (2012) (see Section 2.6)

Variables	Component loadings	
	Dim1	Dim2
Percentage of locations in SACCZ	0.05	-0.20
Percentage of locations in AZ1	-0.79	0.09
Percentage of locations in AZ2	0.72	-0.46
Percentage of locations in PFZ	0.69	0.44
RBC $\delta^{13}\text{C}$	0.37	0.73
RBC $\delta^{15}\text{N}$	-0.58	0.61
Plasma $\delta^{13}\text{C}$	0.70	0.62
Plasma $\delta^{15}\text{N}$	-0.32	0.77

a



b



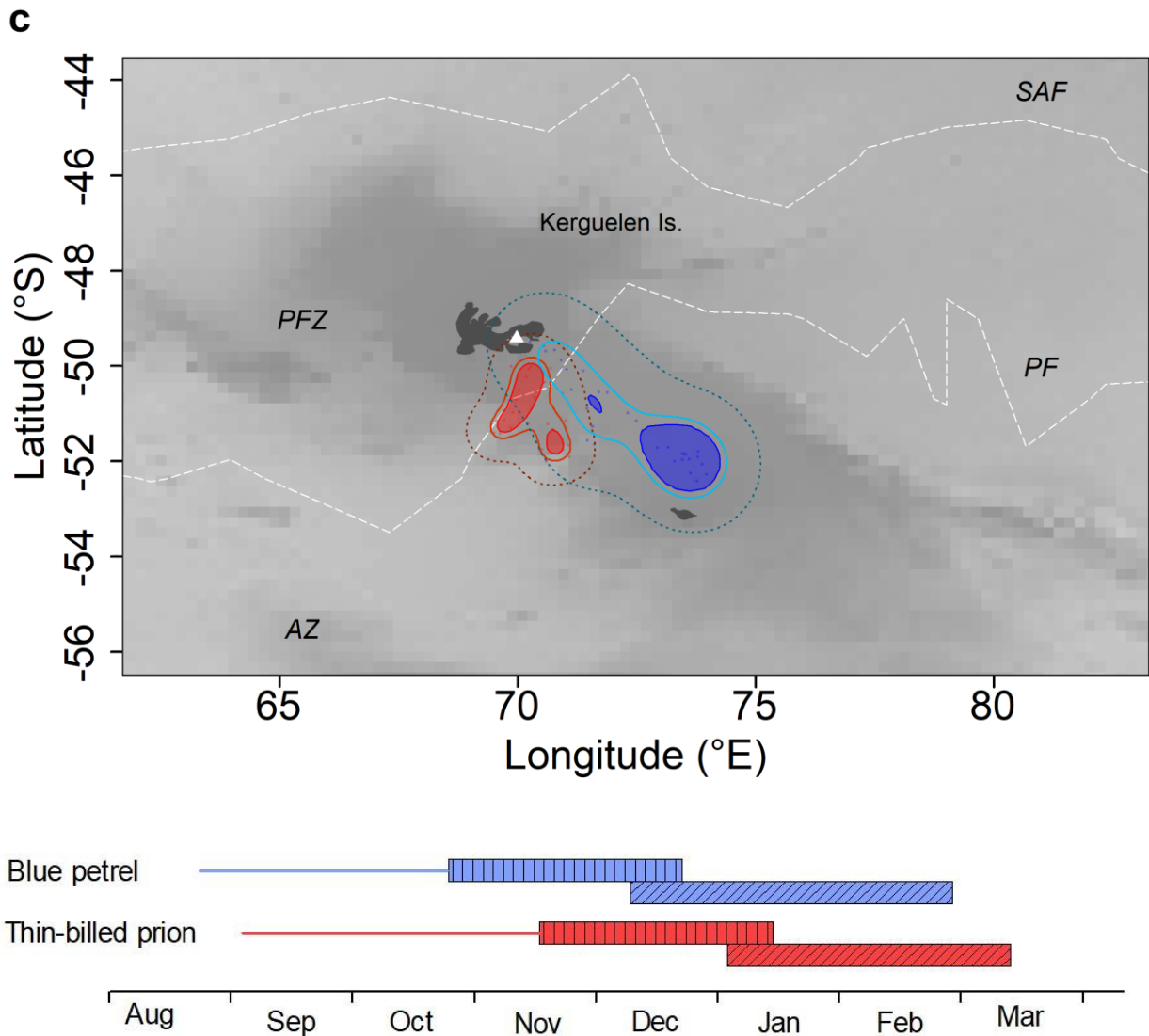


Figure 1. Upper panel: distribution ranges of blue petrel (blue) and thin-billed prion (red) during (a) incubation, (b) chick-rearing (long trips) and (c) chick-rearing (short trips). Dots show raw location data. Kernel density-based utilization distributions at 95% (dotted lines), 50% (solid lines) and 25% (filled areas). Bathymetry is shown in light grey and land in dark grey. Breeding colony (white triangle) is indicated. The main frontal structures, the Subantarctic Front (SAF), Polar Front (PF), Southern Antarctic Circumpolar Current Front (SACCF) and Southern Boundary (SB) are shown by white dashed lines (Venables et al. 2012). They delineate the following oceanic zones, from north to south: the Subantarctic zone (SAZ), polar frontal zone (PFZ) and Antarctic zone (AZ) (which is differentiated north and south of the SACCF, and south of the Antarctic Circumpolar Current). Lower panel: phenology of blue petrels and thin-billed prions breeding in sympatry at Kerguelen Islands. Blocks of vertical lines correspond to incubation, and sloped lines show the chick-rearing period. Horizontal lines indicate the pre-breeding period from when birds return to the colony to the start of the laying period

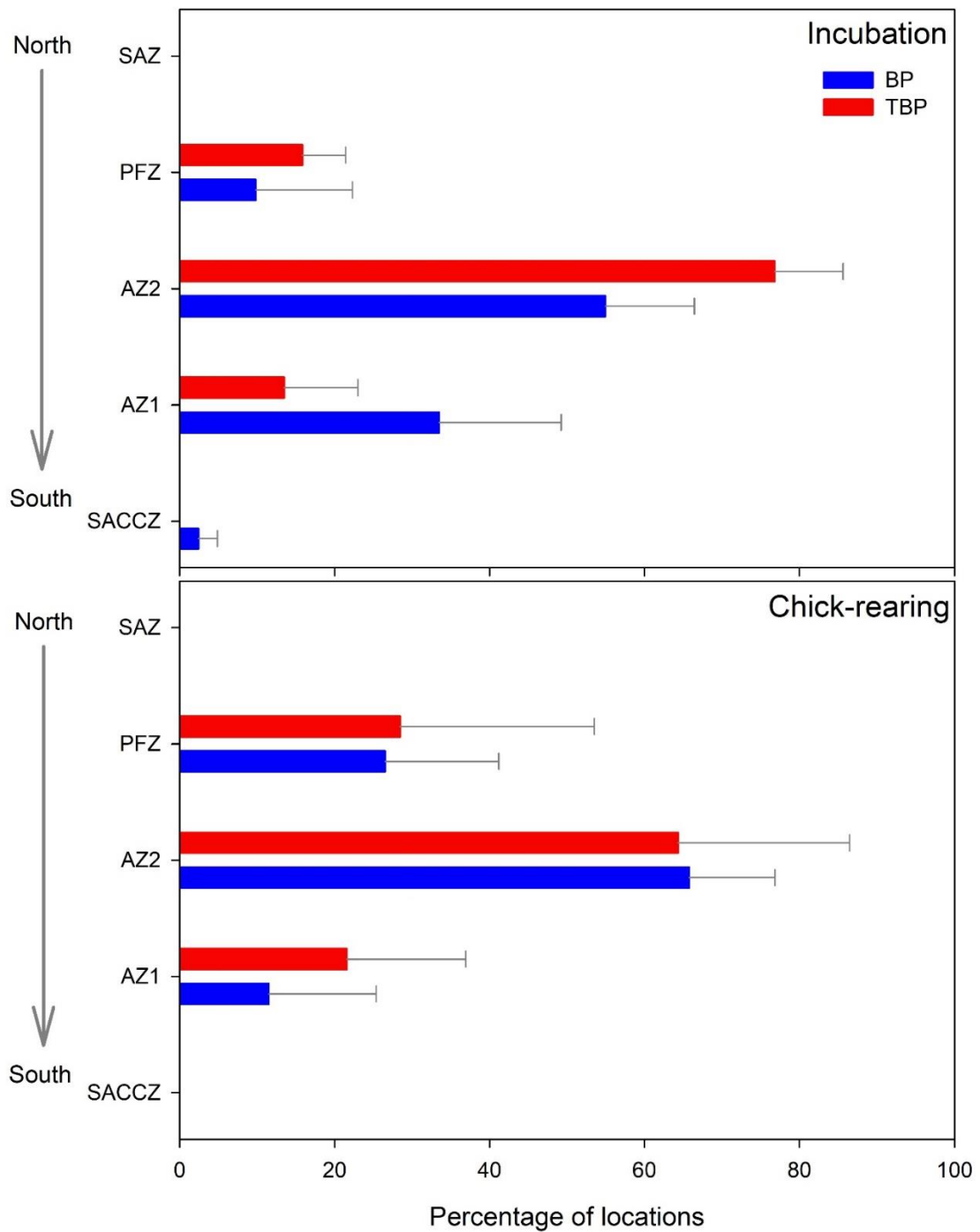


Figure 2. Mean (\pm SD) distribution of locations by oceanic zones of blue petrel (BP) and thin-billed prion (TBP) according to breeding stages. Oceanic zones were delineated using oceanic fronts definition following (Venables et al. 2012), from north to south: SAZ: Subantarctic zone; PFZ: polar frontal zone; AZ1: Antarctic north zone of the Southern Antarctic Circumpolar Current Front (SACCF); AZ2: Antarctic zone south of the SACCF; and SACCZ: south of the Antarctic Circumpolar Current

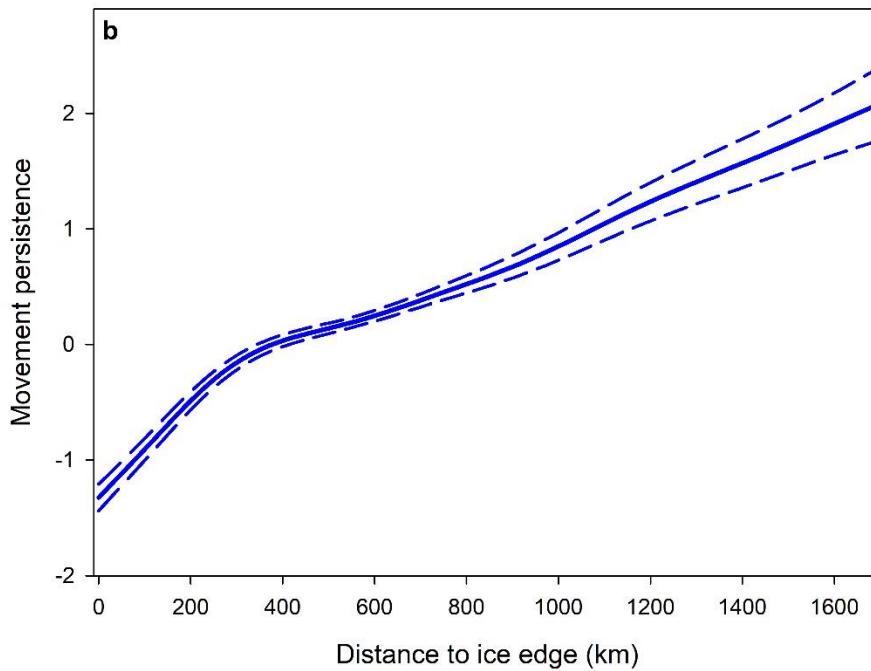
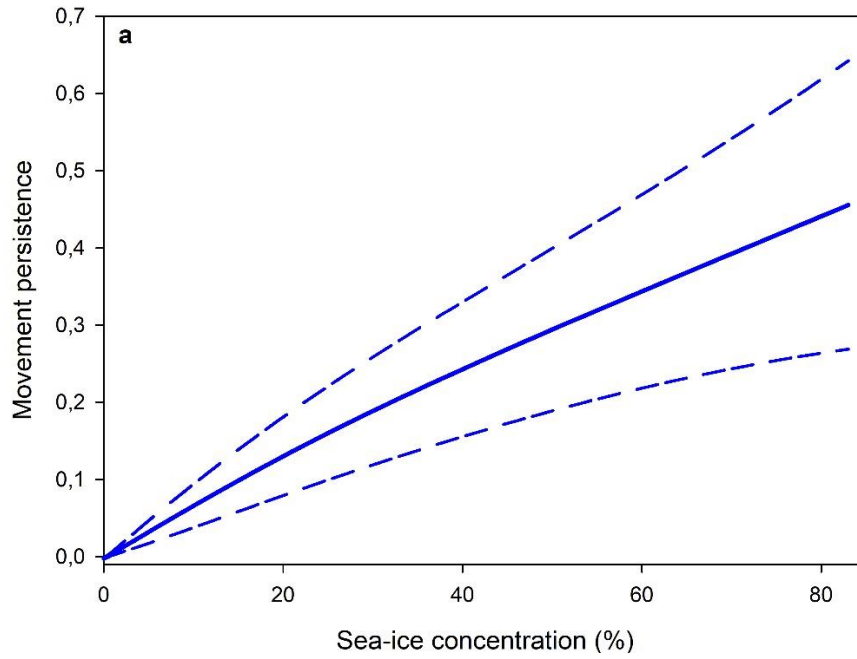
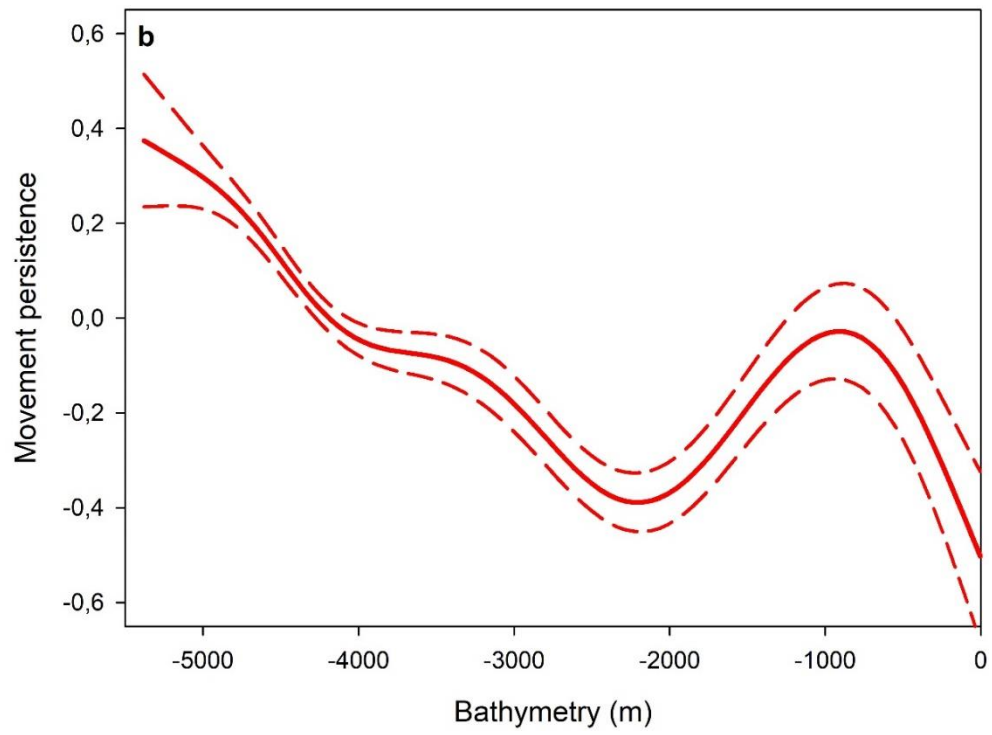
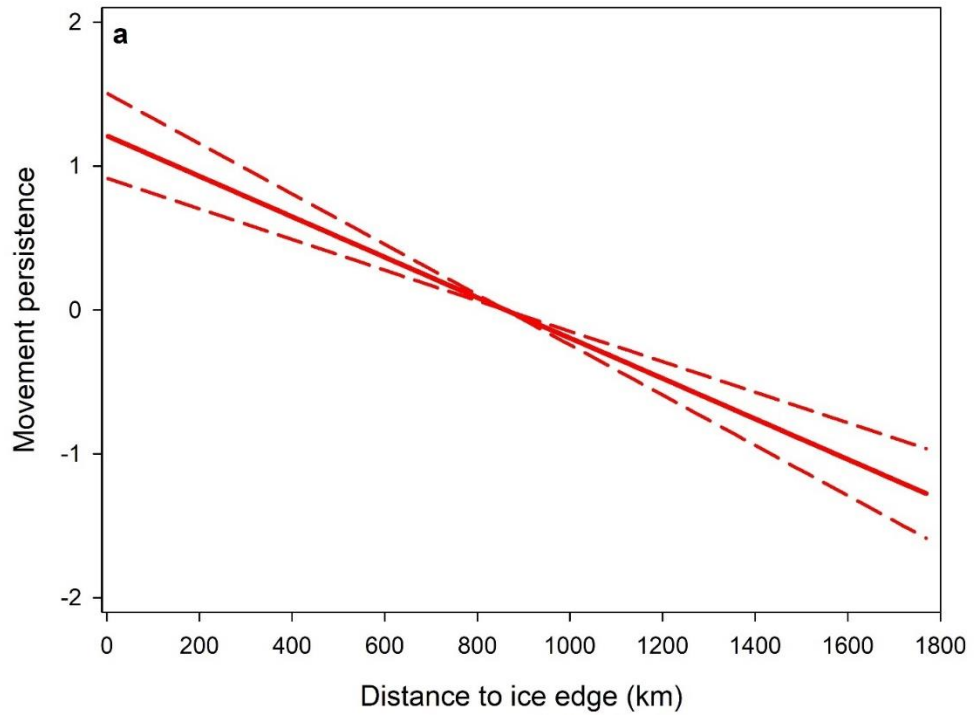


Figure 3. Move persistence during incubation modelled as a function of (a) sea-ice concentration and (b) distance to the sea-ice edge. Plots show the predicted values from the best generalised additive mixed model (solid line) and 95% confidence intervals (dashed lines) for blue petrels from Mayes Island, Kerguelen archipelago. Low move persistence values are typical of foraging; high values represent move behaviour (commuting flight). Data are presented on the x-axis (black vertical dashes)



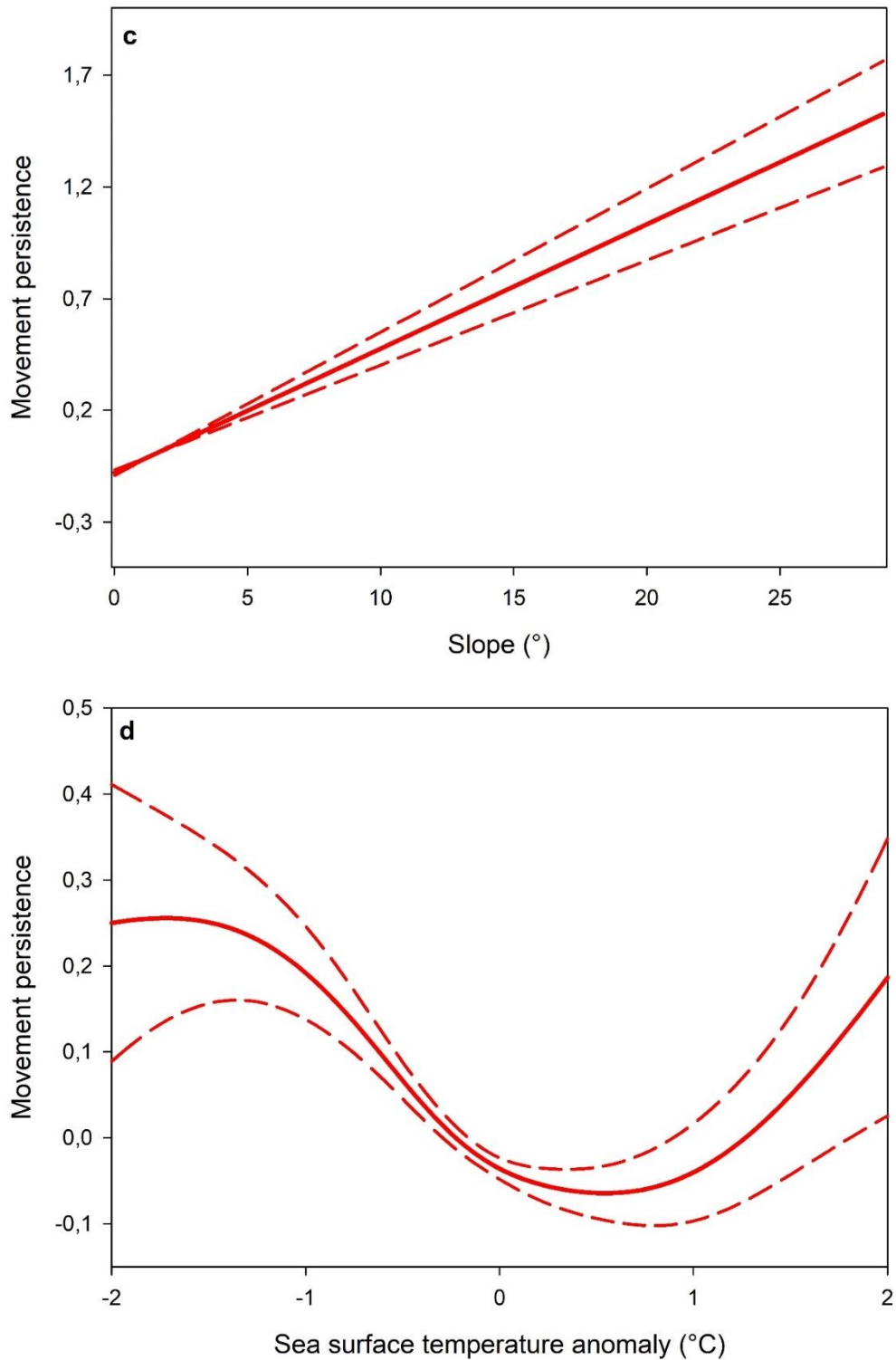


Figure 4. Move persistence during incubation modelled as a function of (a) distance to the sea-ice edge, (b) bathymetry, (c) slope and (d) sea surface temperature anomaly. Plots show the predicted values from the best-generalised additive mixed model (solid line) and 95% confidence intervals (dashed lines) for thin-billed prions from Mayes Island, Kerguelen archipelago. Low move persistence values are typical of foraging; high values represent move behaviour (commuting flight). Data are presented on the x-axis (black vertical dashes)

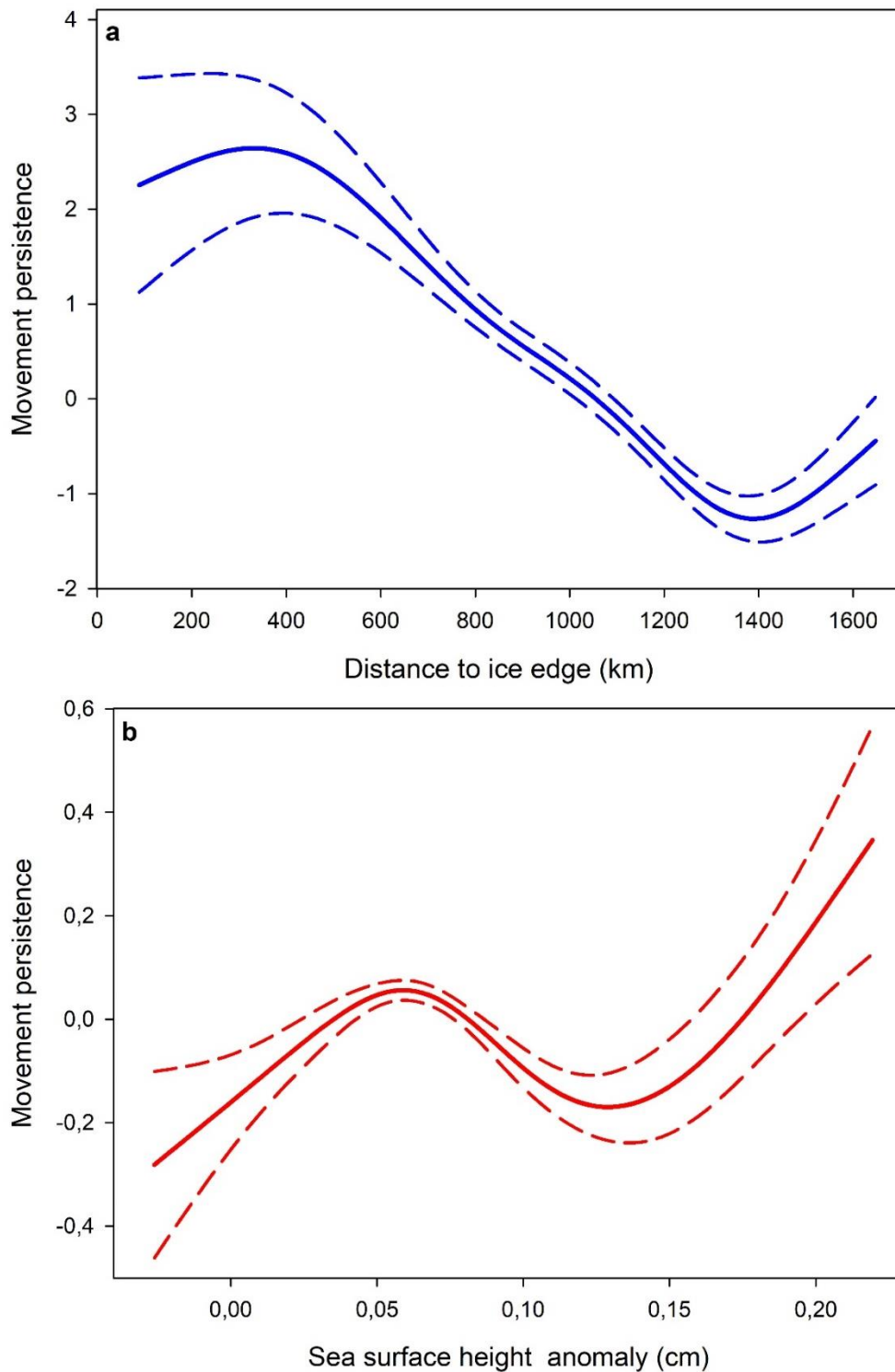


Figure 5. Move persistence during chick-rearing modelled as a function of (a) distance to the sea ice edge for blue petrels and (b) sea surface height anomaly for thin-billed prions sampled at Mayes Island, Kerguelen archipelago during the chick-rearing period. Plots show the predicted values from the best generalised additive mixed model (solid line) and 95% confidence intervals (dashed lines). Low move persistence values are typical of foraging; high values represent move behaviour (commuting flight). Data are presented on the x-axis (black vertical dashes)

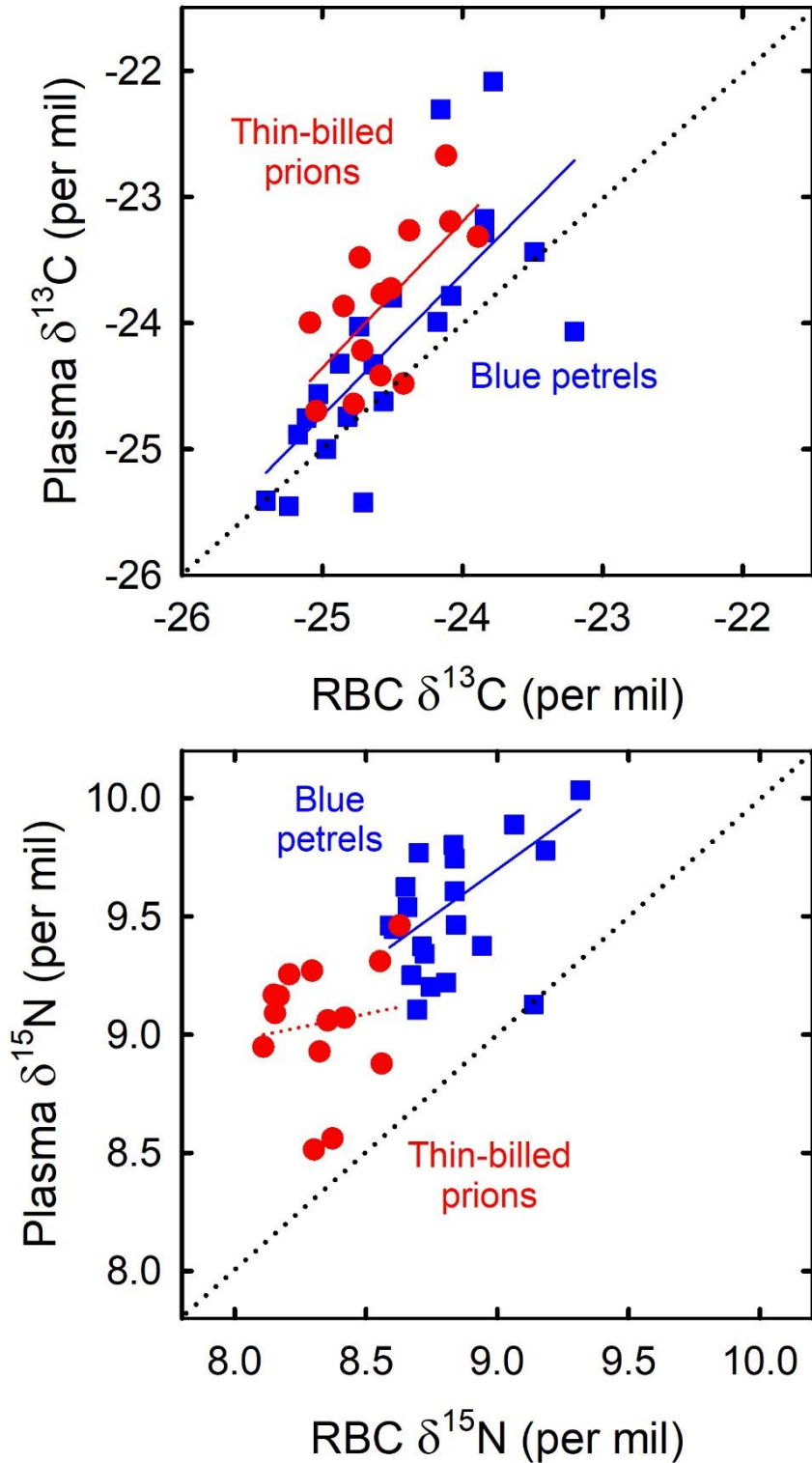


Figure 6. Plasma $\delta^{13}\text{C}$ versus red blood cell (RBC) $\delta^{13}\text{C}$ values (upper panel) and plasma $\delta^{15}\text{N}$ versus RBC $\delta^{15}\text{N}$ values (lower panel) of blue petrels (blue squares) and thin-billed prions (red dots). Regression lines (least squares method and associated ANOVA): blue petrels, $\delta^{13}\text{C}$: $y = 1.12x + 3.30$, $F_{1,19} = 22.60$, $p < 0.0001$, $\delta^{15}\text{N}$: $y = 0.80x + 2.48$, $F_{1,19} = 4.38$, $p = 0.050$; thin-billed prions, $\delta^{13}\text{C}$: $y = 1.17x + 4.76$, $F_{1,12} = 9.91$, $p = 0.008$, $\delta^{15}\text{N}$: $y = 0.23x + 7.10$, $F_{1,12} = 0.26$, $p = 0.622$

PCA

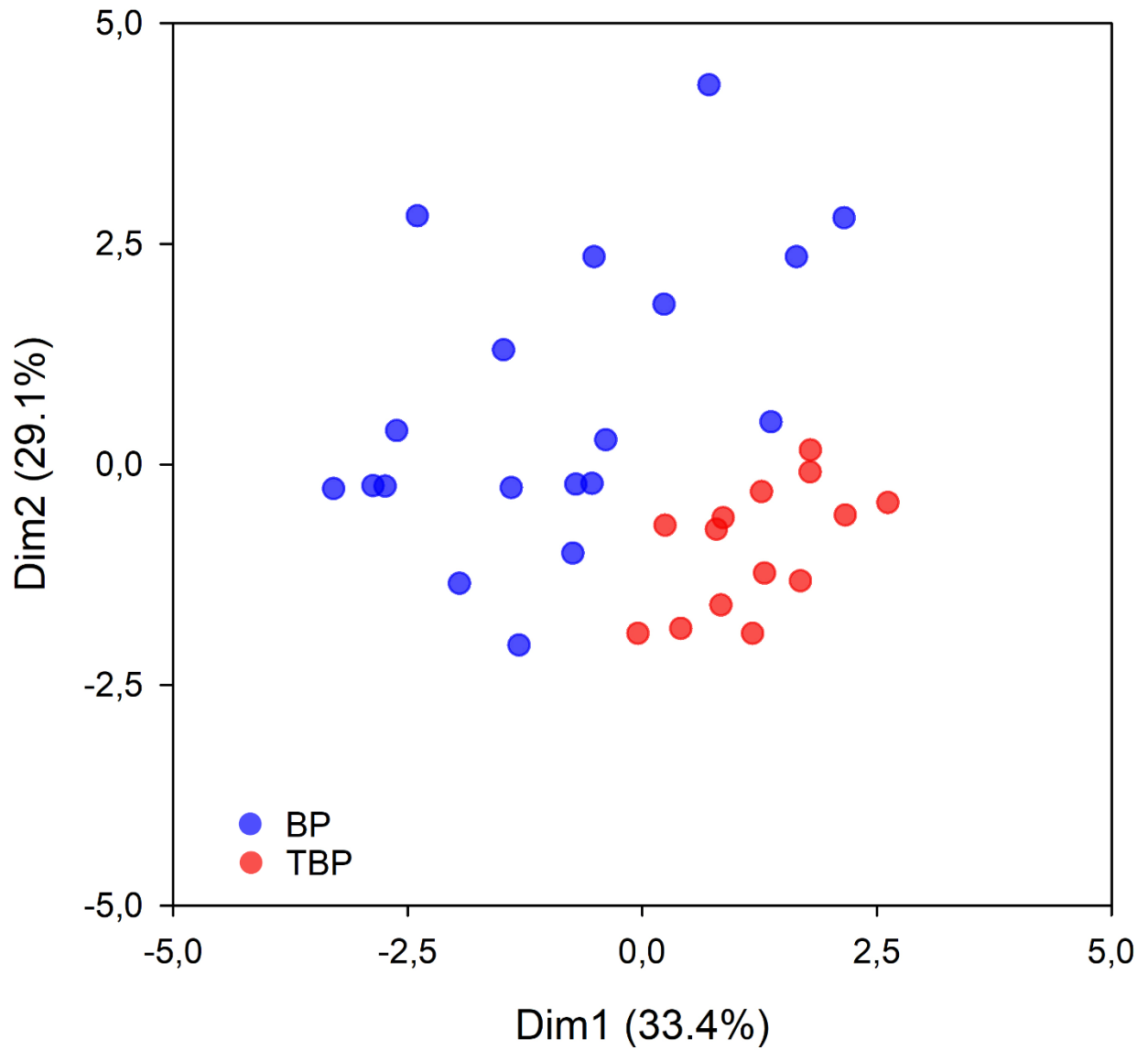


Figure 7. Results from the principal component analysis showing the coordinates of each individual blue petrels (BP) and thin-billed prions (TBP). Dim1 integrates $\delta^{13}\text{C}$ values in plasma and percentage of locations in the Antarctic zones and the Polar Frontal Zone. Dim2 integrates the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in plasma and in red blood cells

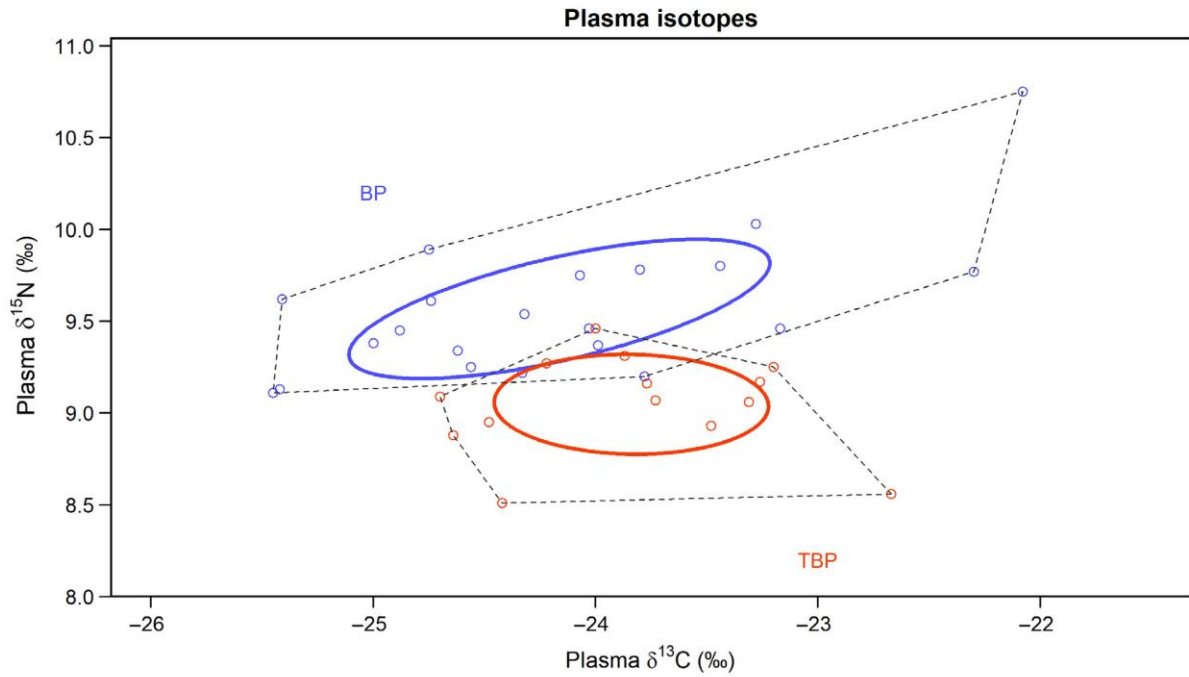


Figure 8. Isotopic niche area based on stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in plasma of blue petrels (BP) and thin-billed prions (TBP) breeding at Kerguelen Islands. Solid lines: areas of the standard ellipses; black dotted lines: the layman metric of convex hull area