



High inter- and intraspecific niche overlap among three sympatrically breeding, closely related seabird species: Generalist foraging as an adaptation to a highly variable environment?

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Abstract

1. Ecological niche theory predicts sympatric species to show segregation in their spatio-temporal habitat utilization or diet as a strategy to avoid competition. Similarly, within species individuals may specialize on specific dietary resources or foraging habitats. Such individual specialization seems to occur particularly in environments with predictable resource distribution and limited environmental variability. Still, little is known about how seasonal environmental variability affects segregation of resources within species and between closely related sympatric species.
2. The aim of the study was to investigate the foraging behaviour of three closely related and sympatrically breeding fulmarine petrels (Antarctic petrels *Thalassoica antarctica*, cape petrels *Daption capense* and southern fulmars *Fulmarus glacialis*) in a seasonally highly variable environment (Prydz Bay, Antarctica) with the aim of assessing inter- and intraspecific overlap in utilized habitat, timing of foraging and diet and to identify foraging habitat preferences.
3. We used GPS loggers with wet/dry sensors to assess spatial habitat utilization over the entire breeding season. Trophic overlap was investigated using stable isotope analysis based on blood, feathers and egg membranes. Foraging locations were identified using wet/dry data recorded by the GPS loggers and expectation-maximization binary clustering. Foraging habitat preferences were modelled using generalized additive models and model cross-validation.
4. During incubation and chick-rearing, the utilization distribution of all three species overlapped significantly and species also overlapped in the timing of foraging during the day—partly during incubation and completely during chick-rearing. Isotopic centroids showed no significant segregation between at least two species for feathers and egg membranes, and among all species during incubation (reflected by blood). Within species, there was no individual specialization in foraging sites

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or environmental space. Furthermore, no single environmental covariate predicted foraging activity along trip trajectories. Instead, best-explanatory environmental covariates varied within and between individuals even across short temporal scales, reflecting a highly generalist behaviour of birds.

5. Our results may be explained by optimal foraging theory. In the highly productive but spatio-temporally variable Antarctic environment, being a generalist may be key to finding mobile prey—even though this increases the potential for competition within and among sympatric species.

KEYWORDS

Antarctica, biologging, expectation-maximization binary clustering, fulmarine petrel, generalized additive model, kernel distribution, model cross-validation, stable isotope analysis

1 | INTRODUCTION

Coexisting species, especially when they are closely related and share similar morphological traits, may compete for resources (Hutchinson, 1957; MacArthur, 1958). When resources are limited, the principle of competitive exclusion predicts that coexisting species will exhibit resource partitioning (spatial, temporal or dietary segregation) and thus occupy different ecological niches (Pianka, 1981; Schoener, 1974). The most common formalization of the ecological niche is an n-dimensional hypervolume, where each dimension represents a habitat and/or resource-related requirement of the studied organism (Hutchinson, 1957). While conceptually powerful, its practical use has long been impaired by the challenges of producing quantitative estimates of niche parameters. Technical improvements towards smaller biologging devices have assisted this by increasing our capacity to investigate the spatial distribution of animals (Cagnacci, Boitani, Powell, & Boyce, 2010) and, when combined with satellite-derived environmental data, the identification of key environmental features or habitat for foraging (Morrison, Marcot, & Mannan, 2006). Hence, we are getting closer to assessing actual environmental conditions of the realized ecological niche of species. The isotopic niche concept, which provides a proxy of a species' realized ecological niche in a minimally invasive way (Bearhop, Adams, Waldron, Fuller, & MacLeod, 2004; Newsome, Martinez del Rio, Bearhop, & Phillips, 2007), extends this further since the isotopic niche reflects effective habitat use and dietary habits of a consumer (Newsome et al., 2007). The combination of spatial tracking and isotopic niche has allowed the investigation of resource use and trophic overlap and therefore potential competition among species and populations (e.g., Navarro et al., 2013; Thiebot, Cherel, Trathan, & Bost, 2012).

In recent years, there has been growing awareness that, in addition to interspecific segregation in resource use, many generalist species across the animal kingdom also show segregation of resource use on an individual level (also called individual specialization; Araújo, Bolnick, & Layman, 2011; Bolnick et al., 2003). Similar to interspecific resource use segregation, individual specialization

is mostly seen as a strategy to avoid competition within populations (Araújo et al., 2011). For example, in Eurasian oystercatchers (*Haematopus ostralegus*), individuals may specialize on either worm or shellfish species as prey or maintain an intermediate, generalist diet (van de Pol, Brouwer, Ens, Oosterbeek, & Tinbergen, 2010). Notably, in oystercatchers specialists and generalists have distinctly different survival probabilities under different winter climate conditions, indicating that stochasticity in environmental conditions is contributing to the maintenance of specialists and generalists in populations (van de Pol et al., 2010). However, individual specialization is not limited to diet, but may also be expressed by individuals repeatedly visiting the same foraging locations and thus creating a spatial segregation within their population (e.g., in northern gannets, *Morus bassanus*; Patrick et al., 2014; Wakefield et al., 2015). Such individual foraging site fidelity is thought to be at least partly driven by a predictable and desirable feature of the environment, for example specific oceanic features like upwelling zones, shelf breaks, sea surface temperature (SST) or chlorophyll concentration, which may influence the presence of prey (Patrick et al., 2014; Phillips, Lewis, González-Solís, & Daunt, 2017; Wakefield et al., 2015). In fact, in addition to specialization on a specific foraging site (i.e., defined by latitude and longitude), individuals may also specialize in environmental space and thus show environmental preferences on the individual level (Bonnet-Lebrun, Phillips, Manica, & Rodrigues, 2018). From a theoretical perspective, individuals in a predictable environment may revisit foraging sites if they had high foraging success on a previous foraging trip but switch if foraging success was low ('win-stay; lose-switch strategy'; Switzer, 1993). On the other hand, this rule does not seem to apply in unpredictable environments (Phillips et al., 2017; Switzer, 1993; Weimerskirch, Corre, Jaquemet, & Marsac, 2005) such as tropical oceans where prey availability is low and food is patchily distributed (Weimerskirch, 2007). Stable environmental conditions thus seem to favour specialization of foraging behaviour on the population level, and the same is thought to be true on the species level: Generalist strategies are selected for in heterogeneous and perturbed environments, while specialization is favoured in spatio-temporally stable environments (Futuyama &

Moreno, 2008; Kassen, 2002). As a consequence, specialist species are more vulnerable to impacts of habitat and climate disturbances, and show higher extinction rates (Clavel, Julliard, & Devictor, 2011). The Antarctic marine habitat shows extreme seasonality with extensive sea ice during winter which reduces by more than 80% in summer (Cavalieri & Parkinson, 2008). The regional extent of sea ice during summer and the timing of breaking up (triggered by wind and temperature) is highly variable among years, and this contributes to the patchy spatio-temporal distribution of Antarctic krill (*Euphausia superba*) swarms (Nicol, 2006). While productivity of the marine ecosystem, which is triggered by 24 hr of daylight and high levels of nutrients, is high during the summer months (Massom & Stammerjohn, 2010; Smetacek & Nicol, 2005), physical access to these plentiful resources is not guaranteed in each year as extensive or consolidated sea ice may also form a physical barrier, limiting access to feeding grounds (Barbraud, Delord, & Weimerskirch, 2015; Emmerson & Southwell, 2008).

The short polar summer means that birds breeding in Antarctica have high levels of overlap in the timing of foraging activities radiating from their colonies, which potentially results in overlap in resource use unless specific foraging behaviours create niche segregation. Central-place foraging combined with seasonal overlap in the timing of the breeding season enhances the potential for prey depletion near the colony (*sensu* Ashmole's halo; Birt, Birt, Goulet, Cairns, & Montevecchi, 1987; Gaston, Ydenberg, & Smith, 2007). Given the almost 24-hr daylight during summer, temporal segregation in timing of foraging activities during the course of a day may however be a mechanism of temporal segregation.

In this paper, we investigate inter- and intraspecific resource use of predators under the seasonally varying Antarctic environment, focusing on three closely related, sympatrically breeding Antarctic fulmarine petrels, namely Antarctic petrel (*Thalassoica antarctica*), cape petrel (*Daption capense*) and southern fulmar (*Fulmarus glacialis*), which all belong to the family Procellariidae. Compared to other groups of seabirds, few tracking studies have been conducted on Antarctic fulmarine petrels (Delord et al., 2016; Descamps et al., 2016; Jenouvrier, Péron, & Weimerskirch, 2015), and no single study has investigated all three of these species simultaneously. These species have been observed foraging in the sea ice zone during summer (Woehler, Raymond, & Watts, 2003), but it is not clear where those birds came from or whether they were breeders or not. We used lightweight state-of-the-art GPS trackers to assess the birds' habitat utilization and habitat preferences throughout the entire breeding season based on satellite-derived environmental covariates matched in time and space to the birds' locations. These spatio-temporal analyses were complemented by stable isotope analyses to assess the species' isotopic niches during the pre-laying period (reflected by egg membranes), incubation (reflected by blood) and the late chick-rearing period (when chicks remain alone on their nests; reflected by feathers).

Our specific aims were to (1) determine foraging areas throughout the breeding season and quantify interspecific overlap in utilized habitat; (2) identify foraging habitat preferences; and (3) determine

any interspecific overlap in (a) timing of foraging during the daytime hours and (b) isotopic niche, using stable isotope analyses. Based on competition theory, we hypothesized that we would find interspecific segregation of resource use, either spatially, temporally or by occupying different isotopic niches (particularly exhibiting different trophic levels). We had no specific expectations about either the spatial distribution, timing of foraging or level of dietary segregation, since literature data were scarce and variable. Consequently, we predicted the species to utilize different habitats and thus show different habitat preferences if they had similar isotopic niches or timing of foraging but share habitats and habitat preferences if they segregated in their isotopic niches (especially trophic level) or timing of foraging. Finally, within species, we hypothesized that the high level of environmental variability within the breeding season would counteract individual specialization in foraging sites and environmental preferences in all three fulmarine petrel species and that they would behave as generalist individuals with little or no individual specialization.

2 | MATERIALS AND METHODS

2.1 | Fieldwork

Fieldwork was conducted in the Rauer Island group near Davis Research Station in the Prydz Bay region, East Antarctica, during the austral summer 2015/16 between December and March. We tracked Antarctic petrels, cape petrels and southern fulmars from two mixed colonies located in the north-west of Hop Island, located within 2 km of each other (68.819°S, 77.689°E and 68.821°S, 77.678°E, respectively). Although egg laying and hatching dates can vary by up to 3 weeks for these species at this site (Table S1.1 in Appendix S1), because the incubation and chick-rearing periods are long in procellariiform seabirds, there is overlap in timing among all three species for each stage (Hodum, 2002), and our GPS-tracking activities occurred during periods of overlap during both incubation and chick-rearing (*cf.* Table S1.1). We used Sterna and Pica GPS loggers from Ecotone Telemetry (Gdynia, Poland). Both types of loggers have a solar panel to recharge their batteries (slightly smaller in Picas) and a remote download function through a UHF link to a receiver unit (hereafter: base station). Whenever in range (approximately 500 m) of the base station, data are automatically remotely downloaded from the loggers to the base station. Two base stations were set up on the island, located approximately 250 m away from and in direct line of sight of the two study colonies. Loggers were programmed to record GPS positions (every 15 min) and wet/dry data (dive in/dive out; every second) when out of range of the base stations (to save energy while birds were on their nests).

We selected birds for GPS deployments which were within range of communication to a base station while at their nests and which were safely accessible. Only birds with eggs or chicks were chosen. Birds were slowly approached at their nest and caught by hand. The bird's head was covered with a cloth bag to reduce stress during handling. Eggs or chicks were removed from the nest and kept warm

and safe from predators, while the tracker was attached to the parent. GPS loggers were attached to the feathers on the middle of the back using waterproof adhesive white Tesa® tape (Beiersdorf) and warmed mastic (3M). Loctite 401 (Henkel) was used to seal off tape ends but was not applied directly to the feathers. Including the weight of the tape, mastic and glue, devices weighed 6–8 g, which is <2% of the birds' body mass (lightest cape petrel weighed in this study: 410 g). Handling time was on average 14 min and did not exceed 21 min. Birds were released approximately 50 cm away from their nests after the eggs or chicks had been returned.

We deployed 65 GPS devices, and in total, 297 foraging trips from 43 active breeders were recorded. Fourteen trips of cape petrels were excluded due to large data gaps (multiple hours to days) caused by battery problems with two GPS loggers. Three cape petrels, one Antarctic petrel and two southern fulmars abandoned their nests temporarily after release leading to breeding failure in three cases. Data from these birds were also excluded from this study, resulting in 253 trips of 39 birds in our final dataset (see Table 1).

Blood and eggshell samples (from hatched, abandoned or predated eggs) were collected from birds at nearby nests or colonies from individuals that were not part of the GPS study (for sample sizes, see Table 2). This minimized disturbance to the birds with trackers attached. Blood samples were collected between the 8 and 13 January 2016. At this stage, cape petrels and southern fulmars were still incubating eggs, while Antarctic petrels had either very young chicks (<5 days old) or pipping eggs. Blood (<200 µl) was taken from the foot web vein, using a 26 gauge needle and a CB-300 Microvette capillary. Blood samples were stored on ice for up to 6 days in the field and frozen back at Davis Research Station. Feathers (back and moulted secondary wing feathers; sample sizes in Table 2) were

collected opportunistically when deploying/retrieving GPS trackers (i.e., handling birds). In addition, we collected secondary wing feathers from the ground next to active nests with breeding birds and we made sure not to include multiple feathers from the same bird/nest.

2.2 | Stable isotope analyses and integrated times

Three tissues with different turnover times were analysed for stable isotope composition: blood, egg membrane and feathers. Isotopic values of blood reflect approximately the last 52 days before sampling (corresponding to four isotopic half-lives; Vander Zanden, Clayton, Moody, Solomon, & Weidel, 2015) and thus the incubation period of all three species, also in Antarctic petrels which had already small chicks (<5 days) at the time of blood sampling. Egg membranes and feathers remain metabolically inert after formation (Hobson & Clark, 1992; Quillfeldt et al., 2009) and hence reflect the trophic niche during the pre-laying and moult period, respectively. Adult fulmarine petrels moult annually and start moulting their wing and body feathers from the end of the incubation period and finish after the breeding season ends (Beck, 1969; Marchant & Higgins, 1990). We collected moult feathers during the chick-rearing period and therefore assumed that these were formed 1 year prior to the collection date and thus represent the trophic niche of the chick-rearing period 1 year earlier (austral summer 2014–2015).

Blood samples were oven-dried at 50°C for 24 hr and subsequently ground. Egg membranes were removed from the shell using stainless steel forceps, and any remaining yolk or albumen was rinsed off with de-ionized water. Egg membranes and feather samples were dried in an oven for 24 hr and cut with stainless steel scissors. For feather samples, we used a part of the barb that had no/least coloration and

TABLE 1 Number of deployments and recorded trips per species and breeding stage. Numbers in brackets refer to the number of tracked individuals. Only trips from actively breeding birds were analysed (incubating eggs or feeding chicks). Numbers of trips and individuals differed among species because some southern fulmars and Antarctic petrels actively removed their loggers and hence produced fewer trips

	Number of GPS deployments		Number of recorded foraging trips	
	Incubation	Chick-rearing	Incubation	Chick-rearing
Antarctic petrel	15	10	7 (5)	21 (8)
Cape petrel	15	0	36 (12)	85 (10)
Southern fulmar	16	9	11 (5)	93 (10)

TABLE 2 Stable isotopic signatures and C/N mass ratios of the three study species and tissues. Values are means ± standard deviations

Species	Tissue	N	δ ¹³ C	δ ¹⁵ N	C/N mass ratio
Antarctic petrel	Egg membrane	15	-22.6 ± 0.8	9.2 ± 0.6	3.3 ± 0.3
	Whole blood	8	-25.1 ± 0.4	10.0 ± 0.6	3.4 ± 0.1
	Feathers	17	-23.5 ± 1.7	9.6 ± 1.5	3.2 ± 0.1
Cape petrel	Egg membrane	15	-22.7 ± 0.6	8.4 ± 0.8	3.2 ± 0.1
	Whole blood	10	-24.7 ± 0.3	10.1 ± 0.8	3.4 ± 0.1
	Feathers	17	-22.9 ± 1.5	10.2 ± 1.6	3.2 ± 0.1
Southern fulmar	Egg membrane	15	-22.3 ± 0.9	9.6 ± 1.4	3.3 ± 0.2
	Whole blood	13	-24.6 ± 0.4	10.2 ± 0.4	3.4 ± 0.1
	Feathers	12	-22.7 ± 1.5	11.4 ± 2.3	3.2 ± 0.1

that showed no obvious contamination. Feather samples were not washed, and none of the samples were delipidized. Stable isotope ratios of carbon ($^{13}\text{C}/^{12}\text{C}$) and nitrogen ($^{15}\text{N}/^{14}\text{N}$) were determined by analysing 1 mg aliquots through continuous-flow elemental analysis–isotope ratio mass spectrometry (CF-EA-IRMS) at the University of Liège using a vario MICRO cube elemental analyser (Elementar Analysensysteme GmbH) coupled to an IsoPrime100 mass spectrometer (Isoprime). Isotopic ratios were expressed using the widespread δ relative notation (Coplen, 2011), in ‰ and relative to the international isotopic references Vienna Pee Dee Belemnite (for carbon) and Atmospheric Air (for nitrogen). IAEA-certified reference materials sucrose (IAEA-C6, $\delta^{13}\text{C} = -10.8 \pm 0.5\text{‰}$) and ammonium sulphate (IAEA-N1, $\delta^{15}\text{N} = 0.4 \pm 0.2\text{‰}$) were used as primary analytical standards. Glycine (Merck, $\delta^{13}\text{C} = -47.3 \pm 0.3\text{‰}$, $\delta^{15}\text{N} = 2.2 \pm 0.3\text{‰}$) was used as secondary analytical standard. Standard deviations on multi-batch replicate measurements of secondary analytical and laboratory standards analysed interspersed among the samples (two laboratory standards for 15 samples) were 0.2‰ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

2.3 | Definition of breeding stages, foraging trips and foraging activity

Breeding stage (incubation and chick-rearing) was based on observations when teams were present and chick-hatching dates from the literature (see Table S1.1). Trip distance, duration and maximum distance from the colony were calculated based on the first/last position at the nest. We defined foraging trips to be those that exceeded a distance of 10 km from the nest and contained dive data. Shorter trips/those without dive data were excluded based on the binomial distribution on maximum distance in comparison with other trips (cf. Table S1.1) and observational data which indicated that these trips were ‘stretching the wings and preening trips’ and therefore not related to foraging.

We interpolated positions when minor data gaps were present using great circle distances of each bird to regular 15-min intervals. The occurrence of dive events (originally recorded every second as dive in or dive out event) was aggregated over each 15-min interval, taking any dives in the previous and following 7.5-min intervals into account. This resulted in a binary variable which we used as our response variable (0 = no foraging activity [no dive event]; 1 = foraging activity [one or more dives within 15 min interval]). To distinguish between foraging activities and surface resting, we examined dive data in conjunction with speed and turning angle data. To do this, we used Expectation-Maximization binary Clustering (EMbC; Garriga, Palmer, Oltra, & Bartumeus, 2016) to indicate likely foraging activity and to identify and remove spurious observations of zero values in our data which may be a result of resting on the surface of the water after a bout of foraging (see Appendix S2). Since all three species are typical surface feeders (Carboneras, 1992), the use of dive data detected by a back-mounted GPS logger may have resulted in underestimating foraging events if birds did not submerge when picking prey from the surface although this is unlikely to have been achieved without the device being wet at all.

2.4 | Environmental covariates

Environmental covariates were extracted from satellite imagery and matched in time and space to the GPS position data using *raadtools* (Sumner, 2017). The set of environmental covariates included sea ice concentration, sea surface height (SSH), SST, wind speed, bathymetry and chlorophyll a concentration (Appendix S3). Using great circle distance, we furthermore included distance to sea ice edge and distance to shelf break and determined time since sea ice melt. We chose these environmental covariates based on previous literature, which identified their importance in affecting seabird foraging (e.g., Raymond et al., 2015; Scheffer, Trathan, Edmonston, & Bost, 2016). Even in a highly dynamic environment, certain environmental features such as ocean currents or upwelling zones may be spatially stable and we therefore also included the seasonal average of sea ice concentration and SST in our candidate dataset. Finally, following Louzao et al. (2009), we used the seasonal averages to quantify the spatial gradients along the flight trajectories of the birds for sea ice concentration, SST and bathymetry. Within a 3×3 grid around the focal point (dimensions of the grid depending on the resolution of the environmental covariates in Appendix S3), we determined the highest and lowest value for each of the environmental covariates and quantified the spatial gradient = $[(\text{maximum value} - \text{minimum value}) * 100 / (\text{maximum value})]$. In this context, a high spatial gradient would correspond to a bird moving across a shelf break or ocean front (indicated by crossing water masses of different temperatures), which can be associated with foraging opportunities (Freeman et al., 2010; Scheffer, Bost, & Trathan, 2012).

Using the R package *maptools* (Bivand & Lewin-Koh, 2016), we extracted the times for sunrise, sunset, nautical dusk and nautical dawn (when the sun is 12° below the horizon) for each of the birds' GPS positions to determine light levels as daytime (between sunrise and sunset), nautical twilight (between nautical dusk and sunrise as well as sunset and nautical dawn) or darkness (between nautical dawn and dusk) experienced by the birds during their foraging trips.

2.5 | Statistics

2.5.1 | Interspecific overlap in spatial foraging distribution

All statistical procedures were run in R (version 3.4.0; R Core Team, 2018). We used the R package *adehabitatHR* (version 0.4.14; Calenge, 2006) to calculate kernel density estimations of the utilization distribution (UD) and Bhattacharyya's affinity (BA) for all locations at which foraging activity occurred (see definition above). We calculated the 20%, 40%, 60% and 80% UD kernels and determined kernel overlap using BA following Fieberg and Kochanny (2005) which ranges from 0 (*no overlap*) to 1 (*identical UDs*). The grid factor was set to 200, and h was estimated with the href smoothing parameters, resulting in h -values between 0.24 and 1.22, respectively. We tested for significant species overlap in UD by carrying out an analysis of similarity (ANOSIM) based on the BA-estimated kernel overlap among individuals of all species (tested separately per

breeding stage) using the R package *vegan* (Oksanen et al., 2018). As previously performed by Carneiro et al. (2016), we included the dissimilarities between the UDAs as a dissimilarity matrix on which the bootstrap randomization procedure of ANOSIM was based. ANOSIM yields significant differences between groups (here: species), when dissimilarities between groups are larger than dissimilarities within groups. The resulting *R* value from an ANOSIM ranges from -1 to 1 , with 0 indicating random grouping (Oksanen et al., 2018).

2.5.2 | Interspecific overlap in marine habitat preferences

To investigate marine habitat preferences of each species, we ran generalized additive models (GAMs) with foraging activity as a binary response variable (see definition above) and environmental covariates (see list above) as predictor variables. GAMs allow the fitting of nonlinear responses to predictor variables, which is a major advantage, as animals rarely respond linearly to their environment (Aarts, MacKenzie, McConnell, Fedak, & Matthiopoulos, 2008; Barbraud et al., 2011). GAMs were run using the R package *mgcv* (Wood, 2016) with a logit link function. All records with incomplete information (i.e., missing values for environmental data or dive data) were removed before analyses.

Generalized additive models were run separately for each species with only one environmental covariate as a smooth term initially at a time and breeding stage (incubation and chick-rearing) as an additional factor. Smooth terms were produced using penalized cubic regression splines. We initially set the maximum number of knots to 5 in order to avoid overfitting, and used the functions `gam.check` and `compareML` (R package *itsadug*; van Rij, Wieland, Baayen, & Rijn, 2017) to check whether models with more knots had a better fit. We followed a forward-stepwise approach, which included stepwise addition of environmental covariates. To avoid collinearity among environmental covariates in the same model, we did not include environmental covariates in the same model, which had a Spearman's rank correlation of ≥ 0.5 .

To compare GAMs and assess the most useful environmental covariates to explain foraging probability, we used model cross-validation. Model cross-validation forms a relatively robust and conservative method of model comparison for tracking data, which are typically spatially and temporally auto-correlated (Aarts et al., 2008; Carneiro et al., 2016). We used this approach to identify the most supported models and therefore the most supported environmental predictors for foraging activity. To perform model cross-validation, we used trip as a data-fold to train each model on all but one foraging trip (training dataset), and subsequently tested the model on the remaining foraging trip (testing dataset). This procedure was repeated multiple times so that every trip formed the testing dataset once. We then used the area under the receiver curve (AUC; PresenceAbsence package in R; Freeman & Moisen, 2008) to assess performance of environmental covariates in models, separately for each species. AUC values < 0.7 were considered poor, 0.7 – 0.9 reasonable and > 0.9 very good model performance (Carneiro et al., 2016; Clay, Phillips, Manica, Jackson, & Brooke Mde, 2017). After

identifying the best-performing environmental covariate for each species, we assessed the inclusion of a second and subsequently third environmental covariate following the approach of Carneiro et al. (2016) and Clay et al. (2017) to test whether additional environmental covariates improved model fit using paired *t* tests.

2.5.3 | Individual specialization of foraging location and habitat

To assess whether individuals specialized in foraging locations or in environmental niche space, we used the multidimensional individual specialization index (MISI) developed by Bonnet-Lebrun et al. (2018). The MISI is based on the definition of individual specialization within a population as $1 - ((\text{within-individual component})/(\text{total population niche width}))$ (Bolnick et al., 2003). The within-individual component for each individual (WIC_i) is calculated as its hypervolume enclosing all locations visited by the individual—or alternatively all the environmental covariates at these locations. Instead of total niche width, the MISI uses the total niche hypervolume (TNV), encloses all locations (or all environmental variables, respectively) visited by all individuals in the study. MISI_{*i*} is thus defined as $1 - WIC_i/TNV$ and provides a value of specialization for each individual of a population. Using a randomization procedure, one can subsequently compare the median of MISIs over the sampled population with the median for the same number of randomized individuals, and thus determine whether a population is composed of specialist individuals (if the median MISI is higher than that expected by chance) or generalist individuals.

We used the example code provided by Bonnet-Lebrun et al. (2018) to assess—separately for each breeding stage—individual specialization in spatial foraging locations and in environmental niche space at foraging locations. We visually inspected grid cell sizes in comparison with polyhedra and adjusted grid cell sizes based on species and breeding stage (ranging between 13 and 50 km for geographical and 0.02 and 0.03 (unitless) for environmental space, respectively).

We encountered computation issues when trying to include more than three environmental covariates and therefore selected for each species those three environmental covariates that on a species level gained the highest support in the GAMs, that is showed the highest AUC values (cf. Table 3). For Antarctic petrels, we thus included SST, time since/to melt of sea ice and seasonal average of sea ice concentration; for cape petrels, SST, SSH and seasonal average of SST; and for southern fulmars, SST, distance to sea ice and seasonal average of SST. All environmental covariates were standardized, and a negligible random jitter was added to each value to avoid computing problems due to a flat polyhedra (Bonnet-Lebrun et al., 2018).

2.5.4 | Interspecific overlap in daily foraging activities

We visually assessed species segregation in foraging time throughout the day following a similar procedure as Wilson (2010). Specifically, we calculated for each hour of the day, separately for each species

TABLE 3 Area under the receiver curve (AUC) as indicator of model fit for GAMs testing the effect of different environmental covariates on the probability of foraging. GAMs were run separately for species and included breeding stage as factor and one single environmental covariate (as a smooth term) as variables. We conducted model cross-validation (see Materials and Methods for details) based on trip as a data-fold and thus obtained one AUC value for each trip and each environmental covariate. Shown are the average \pm SD, minimum and maximum AUC values across all models with the same environmental variable. # best model indicates the number of times that each environmental variable had the highest AUC among all models for a given trip, numbers in brackets indicate how many of these 'best' models had an AUC of ≥ 0.7 (indicating reasonable model fit). $N = 28$ models (=trips) for Antarctic petrels, 121 for cape petrels and 102 for southern fulmars

	Sea ice concentration	Sea surface height	Distance to ice	Distance to shelf	Time since/ to melt	Sea surface temperature (SST)		Bathymetry		SST		Sea ice		Chlorophyll a–summer average		Wind speed
						Bathymetry gradient	SST seasonal average	SST gradient	Sea ice seasonal average	Sea ice gradient	Chlorophyll a–summer average					
Antarctic petrel																
Average \pm SD	0.63 \pm 0.13	0.61 \pm 0.09	0.59 \pm 0.08	0.53 \pm 0.11	0.66 \pm 0.11	0.66 \pm 0.11	0.66 \pm 0.11	0.58 \pm 0.06	0.57 \pm 0.07	0.63 \pm 0.11	0.62 \pm 0.11	0.64 \pm 0.11	0.60 \pm 0.10	0.61 \pm 0.09	0.61 \pm 0.09	0.58 \pm 0.09
Range	0.38–0.90	0.45–0.82	0.46–0.82	0.34–0.77	0.49–0.93	0.47–0.87	0.51–0.79	0.43–0.72	0.48–0.89	0.48–0.89	0.44–0.87	0.48–0.79	0.43–0.76	0.43–0.76	0.45–0.83	0.45–0.83
# best model	1 (0)	2 (1)	2 (1)	1 (1)	7 (6)	2 (2)	1 (0)	2 (0)	4 (4)	1 (1)	1 (1)	1 (1)	2 (0)	2 (0)	2 (0)	0 (0)
Cape petrel																
Average \pm SD	0.61 \pm 0.13	0.65 \pm 0.10	0.64 \pm 0.10	0.62 \pm 0.09	0.64 \pm 0.11	0.66 \pm 0.10	0.59 \pm 0.09	0.58 \pm 0.08	0.67 \pm 0.12	0.62 \pm 0.10	0.63 \pm 0.10	0.63 \pm 0.10	0.61 \pm 0.09	0.61 \pm 0.09	0.61 \pm 0.09	0.58 \pm 0.09
Range	0.30–0.88	0.38–0.90	0.44–0.84	0.43–0.82	0.35–0.85	0.40–0.95	0.44–0.84	0.40–0.82	0.42–0.91	0.37–0.84	0.38–0.85	0.44–0.86	0.37–0.87	0.37–0.87	0.42–0.89	0.42–0.89
# best model	6 (5)	14 (12)	11 (6)	7 (5)	3 (3)	14 (13)	3 (3)	2 (1)	20 (19)	7 (5)	7 (4)	11 (9)	8 (6)	8 (6)	8 (5)	8 (5)
Southern fulmar																
Average \pm SD	0.55 \pm 0.12	0.66 \pm 0.13	0.66 \pm 0.14	0.63 \pm 0.14	0.65 \pm 0.14	0.67 \pm 0.14	0.64 \pm 0.13	0.63 \pm 0.11	0.66 \pm 0.14	0.62 \pm 0.11	0.64 \pm 0.12	0.62 \pm 0.11	0.62 \pm 0.11	0.61 \pm 0.10	0.61 \pm 0.10	0.65 \pm 0.13
Range	0.33–0.88	0.35–0.94	0.37–1.00	0.33–1.00	0.31–1.00	0.44–1.00	0.41–1.00	0.38–0.97	0.37–0.97	0.40–0.89	0.42–0.92	0.33–0.91	0.37–0.98	0.37–0.98	0.44–0.95	0.44–0.95
# best model	2 (2)	10 (9)	17 (15)	7 (1)	4 (4)	15 (14)	6 (6)	2 (2)	12 (12)	6 (6)	2 (2)	7 (3)	3 (3)	3 (3)	11 (9)	11 (9)

and breeding stage, the proportion of 15 min GPS intervals during which foraging activity occurred as [(number of 15 min GPS intervals during which foraging activity was registered)/(number of 15 min GPS intervals in total)]. For visualization, we added smoothing lines based on cyclic GAMs (since time of day is periodic).

We further tested for statistical differences in the timing of foraging activities among species by running Generalized Linear Mixed Models in the R package lme4 (Bates, Maechler, & Bolker, 2011). Models were run separately for the incubation period and the chick-rearing period. Foraging activity was set as dependent variable and bird ID as random variable. Time and species were included as explanatory variables. Since time is cyclical, we included both the sinus and cosinus of daytime into models (Guyot, Arlettaz, Korner, & Jacot, 2017; Sládeček, Vozabulová, Šálek, & Bulla, 2019), and further the two-way interactions between species and both cosinus(daytime) and sinus(daytime). In this model, a significant effect of species would indicate differences in the underlying foraging activity among species: a significant effect of the cosinus(daytime), a difference in foraging activity between night and midday, and a significant effect of the sinus(daytime), a difference in foraging activity between morning and evening. A significant interaction term between species and sinus(daytime) would indicate differences in the foraging activity between morning and evening among the species, and finally, a significant interaction term between species and cosinus(daytime) would indicate differences in the foraging activity between night and midday among the species. As model outputs, we present *F*-values and *p*-values, obtained from comparing the model with and without the variable (interaction term) of interest. In the case of significant interaction terms, we split the dataset and continued to test for which species pairs interactions were significant.

2.5.5 | Interspecific isotopic niche overlap

We used isotopic niches as proxies for realized ecological niches. Isotopic niches for each species and tissue were compared using SIBER (Stable Isotope Bayesian Ellipses in R) version 2.1.3 package (Jackson, Inger, Parnell, & Bearhop, 2011) under R 3.4.3 (R Core Team, 2018). Individual $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were used as model inputs. SIBER was used to generate bivariate standard and 95% ellipses that represent the isotopic niche of consumers. The standard ellipse area (SEA) is a bivariate equivalent of standard deviation. The standard ellipse contains only the 'typical' members of a population, that is 40% of the individuals. The 95% ellipse area is a bivariate equivalent of the 95% confidence interval. The 95% ellipse contains nearly all members (95%) of the population and therefore reflects the total isotopic niche. It can be used as a proxy of all trophic and habitat resources used by the population. The joint use of standard and 95% ellipses allows a complete view of the isotopic niches, by focusing not only on the full extent of resources used by the animals (95% ellipses) but also on those that are most commonly used (standard ellipses). SEA was estimated using a correction for small sample size (SEAc; Jackson et al., 2011). Overlap among standard ellipses and 95% ellipse areas for

different species for a given tissue was used to reflect the amount of trophic and habitat resources commonly shared by these two species (Layman & Allgeier, 2012). In addition, we determined centroid locations (with the centroid being the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for all individuals of a species/tissue) as defined in Layman, Arrington, Montaña, and Post (2007) and used the approach by Turner, Collyer, and Krabbenhoft (2010) based on a residual permutation procedure to test for statistical differences between the Euclidian distances among centroids of the three species.

3 | RESULTS

3.1 | Interspecific overlap in spatial foraging distribution

Antarctic petrels, cape petrels and southern fulmars showed significant overlap in their foraging distribution both during incubation and chick-rearing (Figure 1). Although foraging trip duration and trip distance were longer in Antarctic petrels compared to both cape petrels and southern fulmars (Table S1.2), there was no significant segregation in the utilized areas among all three species (BA range: 0.56–0.79; ANOSIM $R = 0.044$, $p = .305$; Figure 1). During incubation, all three species foraged partly in pelagic waters beyond the Antarctic shelf, along the edges of the sea ice, and partly closer to their colonies over the shelf and at the shelf break and thus within the coastal polynya (Figure 1). Spatial overlap among species was particularly pronounced over the shelf and within the coastal polynya area (Figure 1).

During chick-rearing, all species foraged exclusively over the shelf, the shelf break and at the edge of the sea ice. The spatial overlap among the three species was higher during chick-rearing than during incubation (BA: 0.66–0.82) again without a significant spatial segregation among species (ANOSIM $R = .081$, $p = .068$).

3.2 | Interspecific overlap in marine habitat preferences

Of the 14 environmental covariates included in GAMs, no single environmental covariate qualified as consistently good or even reasonable predictor for foraging. Mean AUC values across all models with the respective covariate were on average below 0.7 for all three species (see Table 3). Also, adding a second environmental predictor variable to the 'best' performing environmental covariate (the one with the highest mean AUC) did not improve the average model fit above 0.7 for any species. In Antarctic petrels and southern fulmars, the AUC of the additive models with two or more environmental covariates was not significantly higher than that of the more parsimonious model with only one environmental covariate (paired *t* tests, $p \geq .226$, $|t| \leq 1.237$). For cape petrels, the additive model containing the seasonal average of SST (SST_season) and SSH performed significantly better than the model with SST_season only (paired *t* test, $p = .005$, $t_{120} = -2.828$). However, the AUC of this additive model was 0.68 and a third environmental covariate was not supported in the models either (paired *t* test, $p = .409$, $t_{120} = 0.828$).

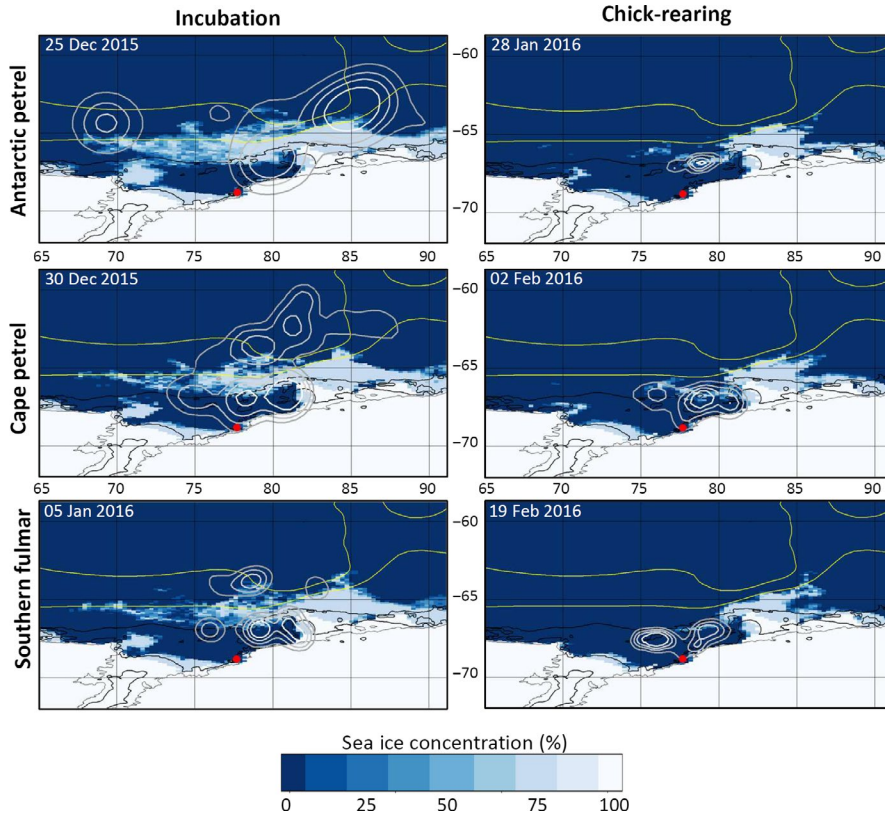


FIGURE 1 Kernel utilization distribution of Antarctic petrels, cape petrels and southern fulmars throughout the breeding season. Kernels represent the 20%, 40%, 60% and 80% utilization distribution of foraging locations (see definition in Materials and Methods) in different shades of grey (from 20% in white to 80% in dark grey). Yellow lines represent the Southern Antarctic Circumpolar Front and the southern boundary of the Antarctic Circumpolar Front. Black lines show the 0, 200 and 1,000 m depth lines. The location of the breeding site (Hop Island) is marked with a red dot. Sea ice concentration (maps obtained from the data archive of the University of Bremen; Spreen, Kaleschke, & Heygster, 2008) is presented in shades of blue as shown in the legend, and maps represent a date (shown in the top left corner of each panel) from the middle of the respective breeding stage of each species

Instead of one or two universally good environmental predictors, we found that the best environmental covariate was highly variable among trips (Table 3; Appendix S4). For the majority of trips, there was at least one environmental covariate, which resulted in an AUC reflecting a reasonable (>0.7) or even good (>0.9) model fit, yet no single environmental covariate consistently predicted foraging probability across trips with a good fit (Table 3; Appendix S4). For example, in seven consecutive trips of a single chick-rearing cape petrel, we identified six different 'best' environmental predictor variables (sea ice concentration, distance to sea ice edge, timing of sea ice melt, SST, seasonal SST-average and seasonal sea ice average), each of them indicating a reasonable model fit ($AUC > 0.7$). Similar results were found for all three species, reflecting the high temporal variability in habitat preferences in all three species.

Notably, habitat preferences, expressed as GAM response curves for the tested environmental covariates, were almost identical for the three sympatric species (Appendix S5). For example, foraging activity was highest in all three species at ~30%–40% sea ice concentration (Figure 2) and increased in all three species with increasing wind speed (Figure 2).

3.3 | Individual foraging site and environmental specialization

In all three species and during incubation and chick-rearing, there was no indication of individual specialization in foraging sites: empirical MISI values were not higher than expected by chance (all $p > .06$; Appendices S6 and S7). Similarly, there was no evidence

of individuals specializing on habitat or environmental conditions (here tested independently of geographical foraging locations) (all $p > .06$; Appendix S6).

3.4 | Interspecific overlap in daily foraging activities

Time of day had a clearly visible effect on foraging activity in all three species except for cape petrels during incubation (Figure 3). While foraging took place throughout all hours of the day in all three species and breeding stages, birds were more likely to forage during the early morning and the afternoon/evening hours.

We found a significant interaction for species with $\cos(\text{daytime})$ during incubation ($F_2 = 8.88$, $p < .001$), while the interaction between species and $\sin(\text{daytime})$ was not significant ($F_2 = 0.58$, $p = .452$). Specifically, Antarctic petrels differed in their timing of foraging activities (night vs. midday, i.e., significant interactions between species and $\cos(\text{daytime})$) from both cape petrels and southern fulmars ($F_2 \geq 10.35$, $p \leq .001$), while southern fulmars and cape petrels showed no significant differences in their timing of foraging activities ($F_2 \leq 0.05$, $p \geq .822$). During chick-rearing, none of the interaction terms was significant, and therefore, there were no significant differences in the timing of foraging activity among species ($F_2 \leq 1.78$, $p \geq .157$).

3.5 | Interspecific isotopic niche overlap

Isotopic niches based on both standard ellipses (i.e., encompassing around 40% of the individuals) and 95% ellipses (i.e., encompassing

FIGURE 2 Generalized additive model (GAM) smoother response curves for the environmental covariates, sea ice concentration (left panel) and wind speed (right panel). Response curves were generated from GAMs run separately for each species and with a single environmental covariate (as smooth term) and breeding stage (as factor) included in the model. Dashed sections of response curves indicate lower model performance due to less data (cf. confidence intervals and rugs in Appendix S5)

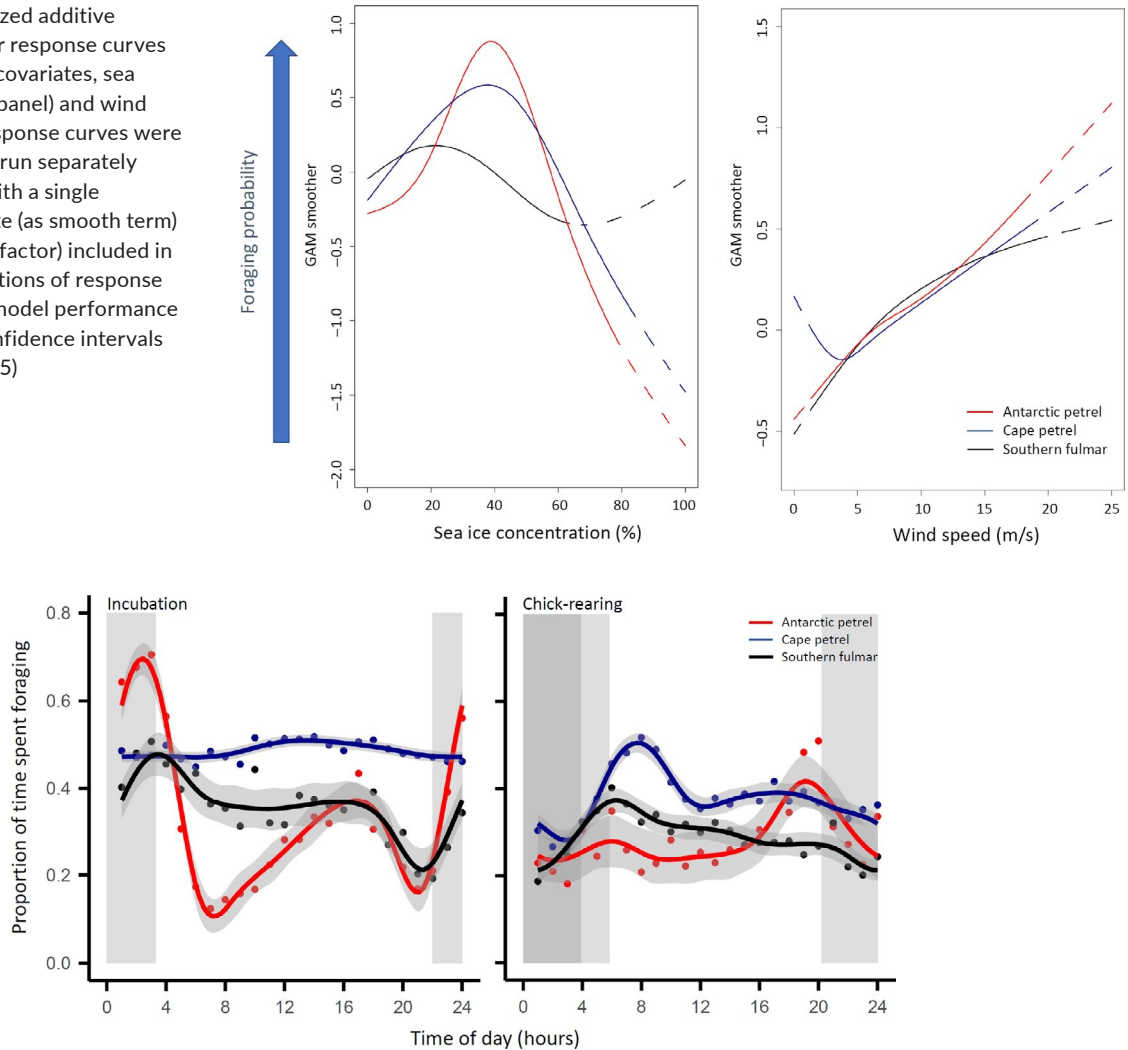


FIGURE 3 Proportion of time spent foraging as a function of time of day throughout the breeding season. The proportion of time spent foraging was assessed for each hour of the day as the number of 15-min intervals during which foraging activity was determined by the wet/dry sensors (see definition in Materials and Methods) divided by the total number of 15-min intervals for which GPS data were recorded. Smoothing lines were based on a cyclic GAM with the standard error margins presented in grey. Light grey rectangles reflect twilight times, and dark grey rectangles reflect periods of darkness (only experienced by southern fulmars at the end of the chick-rearing period)

95% of the individuals) for egg membranes, blood and feathers showed at least partial niche space overlap among all three species, although interspecific differences in centroid location could be seen in some instances (Figure 4, Appendix S8). During the pre-laying period, reflected by egg membranes, Antarctic petrels shared 71% of their standard ellipse with southern fulmars, and there was no significant difference in their centroid locations (Appendix S8). In contrast, standard ellipse overlaps among Antarctic petrels and cape petrels as well as cape petrels and fulmars were lower and centroid locations differed significantly (Appendix S8), while 95% ellipse areas overlapped largely. During the incubation period, reflected by blood, standard ellipse overlap between southern fulmars and cape petrels represented 82% of the southern fulmars' niche area and 41% of both species' niche area. Niche overlap was lower between Antarctic petrels and both cape petrels and southern fulmars for standard but not 95% ellipses, and centroid locations did not differ significantly among any species pair (Appendix

S8). Isotopic niches of feathers, reflecting the previous year's chick-rearing period, were substantially larger than those of the other two tissues. Niche overlap based on feathers was also more pronounced than for the two other tissues. Antarctic petrels and southern fulmars were the only species showing significant differences in centroid locations (Figure 4; Appendix S8). Accordingly, the isotopic niche overlap was the lowest for this species pair (Figure 4; Appendix S8).

4 | DISCUSSION

Our results indicate that three sympatrically breeding fulmarine Antarctic species occupy similar ecological niches, despite the potential increase in competitive interactions that this creates. Against our expectations, we found significant overlap in spatio-temporal habitat use, limited segregation in daily foraging patterns and no complete

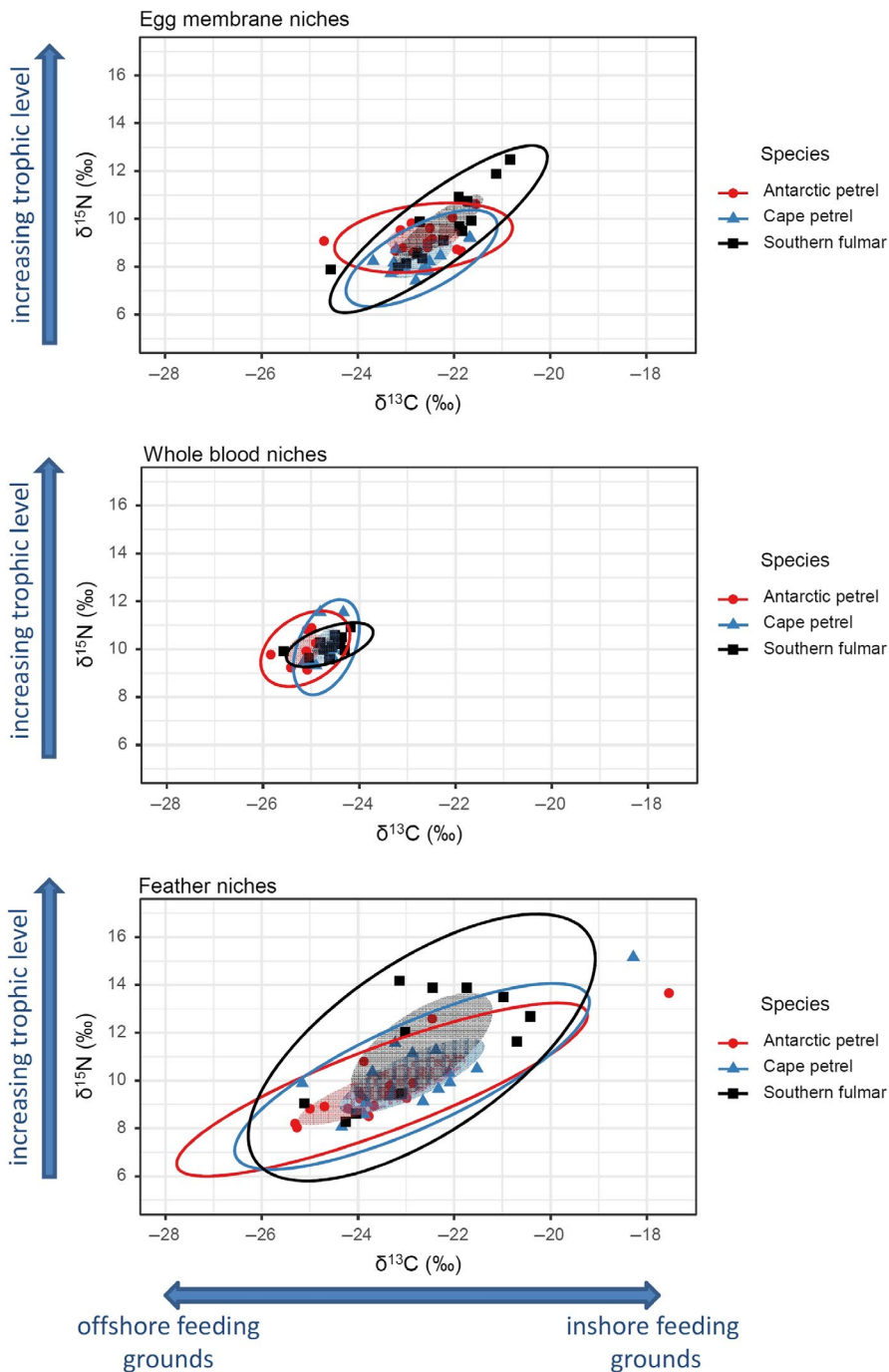


FIGURE 4 Isotopic niches expressed as standard and 95% ellipses for small sample sizes of Antarctic petrels, cape petrels and southern fulmars for the three analysed tissues: egg membrane (reflecting the pre-incubation period), whole blood (reflecting the incubation period) and feathers (reflecting the chick-rearing period (albeit of previous year(s))). Standard ellipses encompass around 40% of individuals and are shown as shades, and 95% ellipses include 95% of individuals and are shown as lines. Dots represent the individual measurements

segregation in isotopic niches among the three species under study. Centroid locations of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values did not differ significantly between one species pair during pre-laying, two species pairs during chick-rearing and all three species pair combinations during incubation, suggesting similar diet or at least a diet with a similar isotopic signature between species during the breeding season. Given the spatial overlap in foraging distribution, it was not surprising that the birds' response to environmental covariates was also similar. In agreement with our final hypothesis that high environmental variability would counteract individual specialization, we found no evidence that individuals of any of the three species specialized in particular foraging sites (i.e., geographical space) or environmental niche

space—individuals thus showed generalist behaviour. These results highlight that the three petrel species coexist despite overlap in their resource use, a finding that conflicts with ecological niche theory.

Before discussing the results in detail, we think it is important to draw attention to potential limitations of this study. For animal ethics reasons, we collected tissue samples for stable isotope analyses from different individuals than those that were carrying GPS trackers. Hence, our results on trophic niche reflect the broader population rather than those individuals that we GPS-tracked. However, viewed objectively, because blood isotopic values (reflecting the incubation period) showed a very narrow niche width and thus low variation within species, the chance that the broader population

did not reflect the GPS-tracked birds seems low. However, the limitations in our sampling strategy for blood, feathers and egg membranes meant that we were unable to test whether individuals may have specialized in diet (or dietary items with similar isotopic values) or foraging at a specific trophic level (Ceia et al., 2012; Dehnhard et al., 2016). Finally, in the case of feather samples, which showed a high isotopic variance within species, there is the possibility that not all feathers reflect the chick-rearing period. Feathers remain metabolically inert and therefore reflected the trophic niche during the moult of the previous year (Hobson & Clark, 1992; Quillfeldt et al., 2009). The feathers we included in our study (back and wing feathers) normally get moulted annually at the end of the summer (Beck, 1969; Marchant & Higgins, 1990), which coincides with the chick-rearing period. However, we do not know whether the birds that we collected the feathers from were actively breeding in the year prior to our study or not. In the case of non-breeding or failed breeding, birds may have started moulting earlier and possibly utilized different foraging areas and different prey. This could in fact explain the higher variance in feather isotopic values (e.g., if some feathers were from breeders and reflected chick-rearing, but others not) and might thus require caution when interpreting the results of feather isotopic values.

4.1 | Interspecific overlap in spatial foraging distribution and isotopic niches

Based on competition theory, we expected that Antarctic petrels, cape petrels and southern fulmars would display segregation in either their spatio-temporal habitat utilization and/or their isotopic niches, enabling them to coexist. We found significant overlap in spatial habitat utilization at each stage throughout the breeding season (Figure 1), no temporal segregation in foraging activities throughout the day during chick-rearing and only partial segregation in timing of foraging during incubation (Figure 3). We can rule out segregation in dive depth since Antarctic fulmarine petrels are typical surface feeders (Carboneras, 1992). Indeed, <25% of dives of all three studied species exceeded 5 s, which translates to a maximum dive depth of around 5 m (Navarro et al., 2013). We also found significant isotopic niche overlap between at least two species and partial overlap among all three species across the entire breeding season. Therefore, our results either contradict hitherto ecological theory, since niche segregation among species is considered necessary for coexisting species under limited resources or they indicate that resources in this region are not limited.

When resources are abundant, species may show high resource overlap (Pianka, 1981). For example, Forero et al. (2004) found high isotopic niche overlap among 14 seabird species breeding at the Argentinian Patagonian coast and explained this by super-abundant food, namely anchovy (*Engraulis anchoita*). Upwelling systems are another marine environment with high food abundance, and indeed, Weimerskirch, Bertrand, Silva, Bost, and Peraltilla (2012) found that sympatrically breeding Guanay cormorants (*Phalacrocorax bougainvillii*) and Peruvian boobies (*Sula variegata*) in the Humboldt Current

system did not segregate in their foraging habitats, dive depth or timing of foraging while feeding on super-abundant Peruvian anchovy (*Engraulis ringens*). In agreement with this, dietary niche overlap among mid-trophic-level predators in the Northern California Current varied among years depending on oceanographic conditions and niche specialization was higher during El Niño years with poorer foraging conditions compared to La Niña years (Gladics, Suryan, Brodeur, Segui, & Filliger, 2014). These results raise the question whether resources for our three study species during the 2015/2016 Antarctic summer in the Prydz Bay region could also have been abundant.

This is possible given that summer productivity in Prydz Bay is considered high (Arrigo & Dijken, 2003) with dense krill swarms over the shelf and especially around the shelf break (Bestley et al., 2018; Jarvis, Kelly, Kawaguchi, Wijk, & Nicol, 2010), where the birds foraged particularly during chick-rearing. Prydz Bay also supports the largest breeding populations of Adélie penguins (*Pygoscelis adeliae*) in East Antarctica (Southwell et al., 2017) and considerable numbers of fulmarine petrels (Harris & Woehler, 2004). A previous stable isotope study on Antarctic petrels, cape petrels and southern fulmars at Hop Island also found interspecific isotopic overlap among adult birds during two consecutive years (Hodum & Hobson, 2000). Our findings of isotopic niche overlap may therefore support a consistent pattern among the fulmarine petrels of Prydz Bay. In contrast, a recent study on southern fulmars, cape petrels and the closely related snow petrel (*Pagodroma nivea*), some 2,500 km east of Prydz Bay, indicated prey partitioning during the summer months when there was spatial foraging overlap in a less productive coastal polynya area (Arrigo & Dijken, 2003; Delord et al., 2016).

Unfortunately, there are few studies on Antarctic breeding seabirds examining multi-species resource use overlap to understand how general our results are. One study shows similar resource overlap for sympatric breeding Pygoscelid penguins (Adélie, gentoo [*P. papua*] and chinstrap penguins [*P. antarctica*]) on King George Island (Wilson, 2010). All three species fed predominantly on krill and overlapped in foraging areas, dive depth and time of foraging during the course of the day (Wilson, 2010). A more recent study from the South Orkney Islands confirmed high dietary overlap between Antarctic and chinstrap penguins, and with gentoo penguins to a lower degree (Bertolin & Casaux, 2019). Wilson (2010) extended the analysis to consider the total (hypervolume) niche overlap among the three species (prey, location, dive depth and time of foraging) and found that although this reduced the level of overlap may have permitted coexistence, interspecific competition would have been inevitable given that krill are able to move among hypervolumes (Nicol, 2006). This raises the question of whether the apparent ecological niche overlap in our study and that of Wilson (2009) could be explained by the high variability in the distribution of the prey field. Optimal foraging theory may offer an explanation here, since quality of prey patch and travel time between patches will determine how long individual birds should stay in each patch (Cowie, 1977; Krebs, 1977). At the same time, with increasing competition, optimal foraging theory predicts

that animals will add prey to their diet, widening their isotopic niche and becoming more generalist (Araújo et al., 2008; Fontaine, Collin, & Dajoz, 2008; Stephens & Krebs, 1986). Hence, optimal foraging theory in a highly variable environment may explain why our three study species showed interspecific overlap.

4.2 | Individual foraging site and environmental specialization

In accordance with our hypothesis based on the high degree of environmental variability, we found no indication of individual specialization in foraging sites—nor did individuals show environmental specialization—neither during incubation nor during chick-rearing. However, during the incubation period, our conclusions about individual specialization could have been limited by small sample sizes for Antarctic petrels and southern fulmars ($N = 5$ individuals for both species, which performed 7 and 11 trips, respectively). More compelling though, if individual specialization was to occur as a measure of competition avoidance and to increase individual efficiency in foraging success (Phillips et al., 2017), it should be most pronounced in our study species during chick-rearing when sample sizes were higher (Table 1). During chick-rearing, these species exhibit central-place foraging because they are constrained to forage close to the colonies to provision their chicks regularly, resulting in higher physiological work rates of adults (Hodum & Weathers, 2003). The fact that we found no individual specialization during chick-rearing indicates that Antarctic petrels, cape petrels and southern fulmars behaved as generalist individuals.

4.3 | Interspecific overlap in foraging habitat preferences

As discussed above, we found significant interspecific overlap in UD during the entire breeding season and no individual specialization in foraging sites or environmental space. As a likely consequence of using the same foraging areas, response curves of GAMs to identify the effect of environmental covariates on the foraging probability of the different species were also very similar. For example, foraging probability was highest in all three species at sea ice concentrations of approximately 30%–40%—which translates to breaking up sea ice and edges of the polynya, where seabirds have access to krill and fish that seek shelter under the ice.

However, we were surprised to find no set of one or few best environmental covariates to consistently explain foraging behaviour (as compared to other studies which used similar methodology; Carneiro et al., 2016; Clay et al., 2017). Instead, the best environmental covariate to predict foraging behaviour was highly variable among trips, and also among trips of the same individuals, while for most models (and thus for most trips), at least one environmental covariate resulted in a reasonable to good model fit (Figure S4.1). We can conclude from this that the birds target a range of different foraging areas with contrasting conditions, possibly dictated by mobile prey swarms, using their capacity to assess foraging conditions along

the foraging trip rather than necessarily targeting a specific location to forage in. This would match with their apparent generalist foraging behaviour at the individual level, with no individual specialization on either foraging locations or environmental conditions (see above).

In addition, birds may respond to environmental features that are either different to those included here as covariates in our models, or respond at a finer spatial or temporal scale than data are available due to the coarse nature of satellite-derived data. This is in line with the concept of mobile prey fields shaping foraging opportunities for seabirds in the highly variable Antarctic environment—which on the other hand comes with the remaining possibility that species segregated in their foraging behaviour at spatial or temporal scales that could not be captured in this study. The challenge therefore in further interpreting the results from our study is to understand what drives the seabirds' foraging decisions and how they successfully interpret signals from their environment to make a profitable living in such a highly dynamic landscape.

5 | CONCLUSIONS

In the highly productive, yet spatio-temporally variable Antarctic environment, flexibility is the key to finding (mobile) prey. Being a generalist under these conditions would therefore seem advantageous, even though this increases the potential for competition within and among sympatrically breeding species. In the case of our study at Prydz Bay, high productivity of the ecosystem may facilitate the here observed spatial, temporal and trophic overlap among and within species. It remains open how productivity in the sea ice zone will be affected by current and future climate change and whether these generalist foragers will be able to adapt to any changes in the underlying distribution and abundance of their prey.

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AUTHORS' CONTRIBUTIONS

L.E., C.S., N.D., J.C. and M.E. conceived and designed the study. N.D., L.E. and H.A. conducted the fieldwork. M.D.S. and L.E. processed the environmental covariate data. N.D. and L.N.M. analysed the data. All authors contributed to the writing of the paper and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Biologging and stable isotope data are publically available through the Australian Antarctic Data Centre: https://data.aad.gov.au/metadata/records/AAS_4087_Fulmarine_petrel_tracking_study_Hop_Island_2015_16

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REFERENCES

- Aarts, G., MacKenzie, M., McConnell, B., Fedak, M., & Matthiopoulos, J. (2008). Estimating space-use and habitat preference from wildlife telemetry data. *Ecography*, 31, 140–160. <https://doi.org/10.1111/j.2007.0906-7590.05236.x>
- Araújo, M. S., Bolnick, D. I., & Layman, C. A. (2011). The ecological causes of individual specialisation. *Ecology Letters*, 14, 948–958. <https://doi.org/10.1111/j.1461-0248.2011.01662.x>
- Araújo, M. S., Guimarães, P. R., Svanbäck, R., Pinheiro, A., Guimarães, P., dos Reis, S. F., & Bolnick, D. I. (2008). Network analysis reveals contrasting effects of intraspecific competition on individual vs. population diets. *Ecology*, 89, 1981–1993. <https://doi.org/10.1890/07-0630.1>
- Arrigo, K. R., & Dijken, G. L. V. (2003). Phytoplankton dynamics within 37 Antarctic coastal polynya systems. *Journal of Geophysical Research*, 108, 3271. <https://doi.org/10.1029/2002JC001739>
- Barbraud, C., Delord, K., & Weimerskirch, H. (2015). Extreme ecological response of a seabird community to unprecedented sea ice cover. *Royal Society Open Science*, 2, 140456. <https://doi.org/10.1098/rsos.140456>
- Barbraud, C., Rivalan, P., Inchausti, P., Nevoux, M., Rolland, V., & Weimerskirch, H. (2011). Contrasted demographic responses facing future climate change in Southern Ocean seabirds. *Journal of Animal Ecology*, 80, 89–100. <https://doi.org/10.1111/j.1365-2656.2010.01752.x>
- Bates, D., Maechler, M., & Bolker, B. (2011). *lme4: Linear mixed-effects models using Eigen and Eigen4*. R package version 0.999375-42. Retrieved from <http://CRAN.R-project.org/package=lme4>.
- Bearhop, S., Adams, C. E., Waldron, S., Fuller, R. A., & MacLeod, H. (2004). Determining trophic niche width: A novel approach using stable isotope analysis. *Journal of Animal Ecology*, 73, 1007–1012.
- Beck, J. R. (1969). Food, moult and age of first breeding in the cape pigeon, *Daption capensis* Linnaeus. *British Antarctic Survey Bulletin*, 21, 33–44.
- Bertolin, M. L., & Casaux, R. (2019). Diet overlap among top predators at the South Orkney Islands, Antarctica. *Polar Biology*, 42, 371–383. <https://doi.org/10.1007/s00300-018-2428-9>
- Bestley, S., Raymond, B., Gales, N. J., Harcourt, R. G., Hindell, M. A., Jonsen, I. D., ... Cox, M. J. (2018). Predicting krill swarm characteristics important for marine predators foraging off East Antarctica. *Ecography*, 41, 996–1012. <https://doi.org/10.1111/ecog.03080>
- Birt, V. L., Birt, T. P., Goulet, D., Cairns, D. K., & Montevecchi, W. A. (1987). Ashmole's Halo – Direct evidence for prey depletion by a seabird. *Marine Ecology Progress Series*, 40, 205–208. <https://doi.org/10.3354/meps040205>
- Bivand, R., & Lewin-Koh, N. (2016). *mapproj: Tools for reading and handling spatial objects*. R package version 0.8-39. Retrieved from <https://cran.r-project.org/web/packages/mapproj/>
- Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., & Forister, M. L. (2003). The ecology of individuals: Incidence and implications of individual specialization. *The American Naturalist*, 161, 1–28. <https://doi.org/10.1086/343878>
- Bonnet-Lebrun, A.-S., Phillips, R. A., Manica, A., & Rodrigues, A. S. L. (2018). Quantifying individual specialization using tracking data: A case study on two species of albatrosses. *Marine Biology*, 165, 152. <https://doi.org/10.1007/s00227-018-3408-x>
- Cagnacci, F., Boitani, L., Powell, R. A., & Boyce, M. S. (2010). Animal ecology meets GPS-based radiotelemetry: A perfect storm of opportunities and challenges. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 365, 2157–2162.
- Calenge, C. (2006). The package adehabitat for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling*, 197, 516–519. <https://doi.org/10.1016/j.ecolmodel.2006.03.017>
- Carboneras, C. (1992). Order Procellariiformes, Family Procellariidae (Petrels and Shearwaters). In J. del Hoyo, A. Elliott, & J. Sargatal (Eds.), *Handbook of the birds of the world* (pp. 197–278). Barcelona, Spain: Lynx Edicions.
- Carneiro, A. P. B., Manica, A., Clay, T. A., Silk, J. R. D., King, M., & Phillips, R. A. (2016). Consistency in migration strategies and habitat preferences of brown skuas over two winters, a decade apart. *Marine Ecology Progress Series*, 553, 267–281. <https://doi.org/10.3354/meps11781>
- Cavalieri, D. J., & Parkinson, C. L. (2008). Antarctic sea ice variability and trends, 1979–2006. *Journal of Geophysical Research*, 113, C07004. <https://doi.org/10.1029/2007JC004564>
- Ceia, F., Phillips, R., Ramos, J., Cherel, Y., Vieira, R., Richard, P., & Xavier, J. (2012). Short- and long-term consistency in the foraging niche of wandering albatrosses. *Marine Biology*, 159, 1581–1591. <https://doi.org/10.1007/s00227-012-1946-1>
- Clavel, J., Julliard, R., & Devictor, V. (2011). Worldwide decline of specialist species: Toward a global functional homogenization? *Frontiers in Ecology and Evolution*, 9, 222–228. <https://doi.org/10.1890/080216>
- Clay, T. A., Phillips, R. A., Manica, A., Jackson, H. A., & Brooke Mde, L. (2017). Escaping the oligotrophic gyre? The year-round movements, foraging behaviour and habitat preferences of Murphy's petrels. *Marine Ecology Progress Series*, 579, 139–155. <https://doi.org/10.3354/meps12244>
- Coplen, T. B. (2011). Guidelines and recommended terms for expression of stable-isotope-ratio and gas-ratio measurement results. *Rapid Communications in Mass Spectrometry*, 25, 2538–2560. <https://doi.org/10.1002/rcm.5129>
- Cowie, R. J. (1977). Optimal foraging in great tits (*Parus major*). *Nature*, 268, 137. <https://doi.org/10.1038/268137a0>
- Dehnhard, N., Eens, M., Sturaro, N., Lepoint, G., Demongin, L., Quillfeldt, P., & Poisbleau, M. (2016). Is individual consistency in body mass and reproductive decisions linked to individual specialization in foraging behavior in a long-lived seabird? *Ecology and Evolution*, 6, 4488–4501. <https://doi.org/10.1002/ece3.2213>
- Delord, K., Pinet, P., Pinaud, D., Barbraud, C., De Grissac, S., Lewden, A., ... Weimerskirch, H. (2016). Species-specific foraging strategies and segregation mechanisms of sympatric Antarctic fulmarine petrels throughout the annual cycle. *Ibis*, 158, 569–586. <https://doi.org/10.1111/ibi.12365>

- Descamps, S., Tarroux, A., Chereil, Y., Delord, K., Godø, O. R., Kato, A., ... Varpe, Ø. (2016). At-sea distribution and prey selection of Antarctic petrels and commercial krill fisheries. *PLoS ONE*, *11*, e0156968. <https://doi.org/10.1371/journal.pone.0156968>
- Emmerson, L., & Southwell, C. (2008). Sea ice cover and its influence on Adélie penguin reproductive performance. *Ecology*, *89*, 2096–2102. <https://doi.org/10.1890/08-0011.1>
- Fieberg, J., & Kochanny, C. O. (2005). Quantifying home-range overlap: The importance of the utilization distribution. *Journal of Wildlife Management*, *69*, 1346–1359. [https://doi.org/10.2193/0022-541X\(2005\)69\[1346:QHOTIO\]2.0.CO;2](https://doi.org/10.2193/0022-541X(2005)69[1346:QHOTIO]2.0.CO;2)
- Fontaine, C., Collin, C. L., & Dajoz, I. (2008). Generalist foraging of pollinators: Diet expansion at high density. *Journal of Ecology*, *96*, 1002–1010. <https://doi.org/10.1111/j.1365-2745.2008.01405.x>
- Forero, M. G., Bortolotti, G. R., Hobson, K. A., Donazar, J. A., Bertellotti, M., & Blanco, G. (2004). High trophic overlap within the seabird community of Argentinean Patagonia: A multiscale approach. *Journal of Animal Ecology*, *73*, 789–801. <https://doi.org/10.1111/j.0021-8790.2004.00852.x>
- Freeman, E. A., & Moisen, G. (2008). PresenceAbsence: An R package for presence-absence model analysis. *Journal of Statistical Software*, *23*, 1–31.
- Freeman, R., Dennis, T., Landers, T., Thompson, D., Bell, E., Walker, M., & Guilford, T. (2010). Black petrels (*Procellaria parkinsoni*) patrol the ocean shelf-break: GPS tracking of a vulnerable Procellariiform seabird. *PLoS ONE*, *5*, e9236. <https://doi.org/10.1371/journal.pone.0009236>
- Futuyma, D. J., & Moreno, G. (1988). The evolution of ecological specialization. *Annual Review of Ecology and Systematics*, *19*, 207–233.
- Garriga, J., Palmer, J. R. B., Oltra, A., & Bartumeus, F. (2016). Expectation-maximization binary clustering for behavioural annotation. *PLoS ONE*, *11*, e0151984. <https://doi.org/10.1371/journal.pone.0151984>
- Gaston, A. J., Ydenberg, R. C., & Smith, G. E. J. (2007). Ashmole's Halo and population regulation in seabirds. *Marine Ornithology*, *35*, 119–126.
- Gladics, A. J., Suryan, R. M., Brodeur, R. D., Segui, L. M., & Filliger, L. Z. (2014). Constancy and change in marine predator diets across a shift in oceanographic conditions in the Northern California Current. *Marine Biology*, *161*, 837–851. <https://doi.org/10.1007/s00227-013-2384-4>
- Guyot, C., Arlettaz, R., Korner, P., & Jacot, A. (2017). Temporal and spatial scales matter: Circannual habitat selection by bird communities in vineyards. *PLoS ONE*, *12*, e0170176. <https://doi.org/10.1371/journal.pone.0170176>
- Harris, J. W., & Woehler, E. J. (2004). Can the important bird area approach improve the Antarctic protected area system? *Polar Record*, *40*, 97–105. <https://doi.org/10.1017/S0032247403003322>
- Hobson, K. A., & Clark, R. G. (1992). Assessing avian diets using stable isotopes I. Turnover of ^{13}C in tissues. *Condor*, *94*, 181–188.
- Hodum, P. J. (2002). Breeding biology of high-latitude Antarctic fulmarine petrels (Procellariidae). *Journal of Zoology*, *256*, 139–149. <https://doi.org/10.1017/S0952836902000171>
- Hodum, P. J., & Hobson, K. A. (2000). Trophic relationships among Antarctic fulmarine petrels: Insights into dietary overlap and chick provisioning strategies inferred from stable-isotope ($\delta\text{N-15}$ and $\delta\text{C-13}$) analyses. *Marine Ecology Progress Series*, *198*, 273–281.
- Hodum, P. J., & Weathers, W. W. (2003). Energetics of nestling growth and parental effort in Antarctic fulmarine petrels. *Journal of Experimental Biology*, *206*, 2125–2133. <https://doi.org/10.1242/jeb.00394>
- Hutchinson, G. E. (1957). Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, *22*, 415–427. <https://doi.org/10.1101/SQB.1957.022.01.039>
- Jackson, A. L., Inger, R., Parnell, A. C., & Bearhop, S. (2011). Comparing isotopic niche widths among and within communities: SIBER – Stable Isotope Bayesian Ellipses in R. *Journal of Animal Ecology*, *80*, 595–602. <https://doi.org/10.1111/j.1365-2656.2011.01806.x>
- Jarvis, T., Kelly, N., Kawaguchi, S., van Wijk, E., & Nicol, S. (2010). Acoustic characterisation of the broad-scale distribution and abundance of Antarctic krill (*Euphausia superba*) off East Antarctica (30–80°E) in January–March 2006. *Deep Sea Research Part II: Topical Studies in Oceanography*, *57*, 916–933. <https://doi.org/10.1016/j.dsr2.2008.06.013>
- Jenouvrier, S., Péron, C., & Weimerskirch, H. (2015). Extreme climate events and individual heterogeneity shape life-history traits and population dynamics. *Ecological Monographs*, *85*, 605–624. <https://doi.org/10.1890/14-1834.1>
- Kassen, R. (2002). The experimental evolution of specialists, generalists, and the maintenance of diversity. *Journal of Evolutionary Biology*, *15*, 173–190. <https://doi.org/10.1046/j.1420-9101.2002.00377.x>
- Krebs, J. (1977). Optimal foraging: Theory and experiment. *Nature*, *268*, 583–584. <https://doi.org/10.1038/268583a0>
- Layman, C. A., & Allgeier, J. E. (2012). Characterizing trophic ecology of generalist consumers: A case study of the invasive lionfish in the Bahamas. *Marine Ecology Progress Series*, *448*, 131–141. <https://doi.org/10.3354/meps09511>
- Layman, C. A., Arrington, D. A., Montaña, C. G., & Post, D. M. (2007). Can stable isotope ratios provide for community-wide measures of trophic structure? *Ecology*, *88*, 42–48. [https://doi.org/10.1890/0012-9658\(2007\)88\[42:CSIRPF\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2007)88[42:CSIRPF]2.0.CO;2)
- Louzao, M., Becares, J., Rodriguez, B., Hyrenbach, K., Ruiz, A., & Arcos, J. (2009). Combining vessel-based surveys and tracking data to identify key marine areas for seabirds. *Marine Ecology Progress Series*, *391*, 183–197. <https://doi.org/10.3354/meps08124>
- MacArthur, R. H. (1958). Population ecology of some warblers of northeastern coniferous forests. *Ecology*, *39*, 599–619. <https://doi.org/10.2307/1931600>
- Marchant, S., & Higgins, P. J. (1990). *Handbook of Australian, New Zealand and Antarctic birds*. Melbourne, Vic, Australia: Oxford University Press
- Massom, R. A., & Stammerjohn, S. E. (2010). Antarctic sea ice change and variability – Physical and ecological implications. *Polar Science*, *4*, 149–186. <https://doi.org/10.1016/j.polar.2010.05.001>
- Morrison, M. L., Marcot, B., & Mannan, W. (2006). *Wildlife-habitat relationships: Concepts and applications* (3rd ed.). Washington, DC: Island Press.
- Navarro, J., Votier, S. C., Aguzzi, J., Chiesa, J. J., Forero, M. G., & Phillips, R. A. (2013). Ecological segregation in space, time and trophic niche of sympatric planktivorous petrels. *PLoS ONE*, *8*, e62897. <https://doi.org/10.1371/journal.pone.0062897>
- Newsome, S. D., Martinez del Rio, C., Bearhop, S., & Phillips, D. L. (2007). A niche for isotopic ecology. *Frontiers in Ecology and the Environment*, *5*, 429–436. [https://doi.org/10.1890/1540-9295\(2007\)5\[429:ANFIE\]2.0.CO;2](https://doi.org/10.1890/1540-9295(2007)5[429:ANFIE]2.0.CO;2)
- Nicol, S. (2006). Krill, currents, and sea ice: *Euphausia superba* and its changing environment. *BioScience*, *56*, 111–120. [https://doi.org/10.1641/0006-3568\(2006\)056\[0111:KCASIE\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2006)056[0111:KCASIE]2.0.CO;2)
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., ... Wagner, H. (2018). *vegan: Community ecology package*. R package version 2.5-3. Retrieved from <http://CRAN.R-project.org/package=vegan>
- Patrick, S. C., Bearhop, S., Grémillet, D., Lescroël, A., Grecian, W. J., Bodey, T. W., ... Votier, S. C. (2014). Individual differences in searching behaviour and spatial foraging consistency in a central place marine predator. *Oikos*, *123*, 33–40. <https://doi.org/10.1111/j.1600-0706.2013.00406.x>
- Phillips, R. A., Lewis, S., González-Solís, J., & Daunt, F. (2017). Causes and consequences of individual variability and specialization in foraging and migration strategies of seabirds. *Marine Ecology Progress Series*, *578*, 117–150. <https://doi.org/10.3354/meps12217>
- Pianka, E. R. (1981) Competition and niche theory. In R. M. May (ed.) *Theoretical ecology* (pp. 167–196). Oxford, UK: Blackwell.

- Quillfeldt, P., McGill, R. A. R., Masello, J. F., Poisbleau, M., van Noordwijk, H., Demongin, L., & Furness, R. W. (2009). Differences in the stable isotope signatures of seabird egg membrane and albumen – Implications for non-invasive studies. *Rapid Communications in Mass Spectrometry*, 23, 3632–3636. <https://doi.org/10.1002/rcm.4286>
- R Core Team (2018). *R: A Language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from <http://www.R-project.org/>.
- Raymond, B., Lea, M.-A., Patterson, T., Andrews-Goff, V., Sharples, R., Charrassin, J.-B., ... Hindell, M. A. (2015). Important marine habitat off east Antarctica revealed by two decades of multi-species predator tracking. *Ecography*, 38, 121–129. <https://doi.org/10.1111/ecog.01021>
- Scheffer, A., Bost, C. A., & Trathan, P. N. (2012). Frontal zones, temperature gradient and depth characterize the foraging habitat of king penguins at South Georgia. *Marine Ecology Progress Series*, 465, 281–297. <https://doi.org/10.3354/meps09884>
- Scheffer, A., Trathan, P. N., Edmonston, J. G., & Bost, C.-A. (2016). Combined influence of meso-scale circulation and bathymetry on the foraging behaviour of a diving predator, the king penguin (*Aptenodytes patagonicus*). *Progress in Oceanography*, 141, 1–16. <https://doi.org/10.1016/j.pocean.2015.10.005>
- Schoener, T. W. (1974). Resource partitioning in ecological communities. *Science*, 185, 27–39. <https://doi.org/10.1126/science.185.4145.27>
- Sládeček, M., Vozabulová, E., Šálek, M. E., & Bulla, M. (2019). Diversity of incubation rhythms in a facultatively uniparental shorebird – The northern lapwing. *Scientific Reports*, 9, 4706. <https://doi.org/10.1038/s41598-019-41223-z>
- Smetacek, V., & Nicol, S. (2005). Polar ocean ecosystems in a changing world. *Nature*, 437, 362–368. <https://doi.org/10.1038/nature04161>
- Southwell, C., Emmerson, L., Takahashi, A., Barbraud, C., Delord, K., & Weimerskirch, H. (2017). Large-scale population assessment informs conservation management for seabirds in Antarctica and the Southern Ocean: A case study of Adélie penguins. *Global Ecology and Conservation*, 9, 104–115. <https://doi.org/10.1016/j.gecco.2016.12.004>
- Spreen, G., Kaleschke, L., & Heygster, G. (2008). Sea ice remote sensing using AMSR-E 89-GHz channels. *Journal of Geophysical Research*, 113, C02S03–00. <https://doi.org/10.1029/2005JC003384>
- Stephens, D. W., & Krebs, J. (1986). *Foraging theory*. Princeton, NJ: Princeton University Press.
- Sumner, M. D. (2017). *raadtools: Tools for synoptic environmental spatial data*. R package version 0.4.0.9001. Retrieved from <https://github.com/AustralianAntarcticDivision/raadtools>
- Switzer, P. V. (1993). Site fidelity in predictable and unpredictable habitats. *Evolutionary Ecology*, 7, 533–555. <https://doi.org/10.1007/BF01237820>
- Thiebot, J. B., Chérel, Y., Trathan, P. N., & Bost, C. A. (2012). Coexistence of oceanic predators on wintering areas explained by population-scale foraging segregation in space or time. *Ecology*, 93, 122–130. <https://doi.org/10.1890/11-0385.1>
- Turner, T. F., Collyer, M. L., & Krabbenhoft, T. J. (2010). A general hypothesis-testing framework for stable isotope ratios in ecological studies. *Ecology*, 91, 2227–2233. <https://doi.org/10.1890/09-1454.1>
- van de Pol, M., Brouwer, L., Ens, B. J., Oosterbeek, K., & Tinbergen, J. M. (2010). Fluctuating selection and the maintenance of individual and sex-specific diet specialization in free-living oystercatchers. *Evolution*, 64, 836–851. <https://doi.org/10.1111/j.1558-5646.2009.00859.x>
- van Rij, J., Wieland, M., Baayen, R., & van Rijn, H. (2017). *itsadug: Interpreting time series and autocorrelated data using GAMMs*. R package version 2.3. Retrieved from <https://cran.r-project.org/web/packages/itsadug/index.html>
- Vander Zanden, M. J., Clayton, M. K., Moody, E. K., Solomon, C. T., & Weidel, B. C. (2015). Stable isotope turnover and half-life in animal tissues: A literature synthesis. *PLoS ONE*, 10, e0116182. <https://doi.org/10.1371/journal.pone.0116182>
- Wakefield, E. D., Cleasby, I. R., Bearhop, S., Bodey, T. W., Davies, R. D., Miller, P. I., ... Hamer, K. C. (2015). Long-term individual foraging site fidelity—Why some gannets don't change their spots. *Ecology*, 96, 3058–3074. <https://doi.org/10.1890/14-1300.1>
- Weimerskirch, H. (2007). Are seabirds foraging for unpredictable resources? *Deep Sea Research Part II: Topical Studies in Oceanography*, 54, 211–223. <https://doi.org/10.1016/j.dsr2.2006.11.013>
- Weimerskirch, H., Bertrand, S., Silva, J., Bost, C., & Peraltilla, S. (2012). Foraging in Guanay cormorant and Peruvian booby, the major guano-producing seabirds in the Humboldt Current System. *Marine Ecology Progress Series*, 458, 231–245. <https://doi.org/10.3354/meps09752>
- Weimerskirch, H., Le Corre, M., Jaquemet, S., & Marsac, F. (2005). Foraging strategy of a tropical seabird, the red-footed booby, in a dynamic marine environment. *Marine Ecology Progress Series*, 288, 251–261. <https://doi.org/10.3354/meps288251>
- Wilson, R. P. (2010). Resource partitioning and niche hyper-volume overlap in free-living Pygoscelid penguins. *Functional Ecology*, 24, 646–657. <https://doi.org/10.1111/j.1365-2435.2009.01654.x>
- Woehler, E. J., Raymond, B., & Watts, D. J. (2003). Decadal-scale seabird assemblages in Prydz Bay, East Antarctica. *Marine Ecology Progress Series*, 251, 299–310. <https://doi.org/10.3354/meps251299>
- Wood, S. (2016). *package "mgcv"*. R package version 1.8-17. Retrieved from <http://cran.r-project.org/web/packages/mgcv/>.

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