



Species-specific foraging strategies and segregation mechanisms of sympatric Antarctic fulmarine petrels throughout the annual cycle

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Determining the year-round distribution and behaviour of birds is necessary for a better understanding of their ecology and foraging strategies. Petrels form an important component of the high-latitude seabird assemblages in terms of species and individuals. The distribution and foraging ecology of three sympatric fulmarine petrels (Southern Fulmar *Fulmarus glacialoides*, Cape Petrel *Daption capense* and Snow Petrel *Pagodroma nivea*) were studied at Adélie Land, East Antarctica, by combining information from miniaturized saltwater immersion geolocators and stable isotopes from feathers. During the breeding season at a large spatial scale (c. 200 km), the three species overlapped in their foraging areas located in the vicinity of the colonies but were segregated by their diet and trophic level, as indicated by the different chick $\delta^{15}\text{N}$ values that increased in the order Cape Petrel < Southern Fulmar < Snow Petrel. During the non-breeding season, the three fulmarines showed species-specific migration strategies along a wide latitudinal gradient. Snow Petrels largely remained in ice-associated Antarctic waters, Southern Fulmars targeted primarily the sub-Antarctic zone and Cape Petrels migrated further north. Overall, birds spent less time in flight during the non-breeding period than during the breeding season, with the highest percentage of time spent sitting on the water occurring during the breeding season and at the beginning of the non-breeding period before migration. This activity pattern, together with the $\delta^{13}\text{C}$ values of most feathers, strongly suggests that moult of the three fulmarine petrels occurred at that time in the very productive high Antarctic waters, where birds fed on a combination of crustaceans and fish. The study highlights different segregating mechanisms that allow the coexistence of closely related species, specifically, prey partitioning during the breeding season and spatial segregation at sea during the non-breeding season.

Keywords: activity, *Daption capense*, *Fulmarus glacialoides*, moult, *Pagodroma nivea*, seabirds, stable isotopes, tracking.

Determining the year-round distribution and behaviour of birds is of paramount importance for a better understanding of their ecology, foraging strategies and conservation. This is particularly true for seabirds, which typically undertake large-scale

movements between their breeding grounds and foraging areas at sea during the non-breeding period. In several seabird species, dispersal during the non-breeding period may even encompass several ocean basins with different ecological constraints and potential threats (Shaffer *et al.* 2006, Egevang *et al.* 2010). One of the main characteristics of the Southern Ocean is the huge numbers of seabirds

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that forage in sub-Antarctic and Antarctic waters. A well-defined community of seabirds breeds along the Antarctic Continent, with additional species visiting high-Antarctic waters to feed on Antarctic krill and other resources during the summer months (Croxford 1984, Ainley *et al.* 1994). Species of this community are generally pagophilic in their distribution, being consistently associated with sea-ice or its boundaries at least during the austral summer (Ainley *et al.* 2003). Climate change is rapidly affecting various components of Antarctic ecosystems, including sea-surface temperature and sea-ice conditions (Sokolov & Rintoul 2009b, Constable *et al.* 2014). Climate change can affect the number and demography of seabirds (Barbraud & Weimerskirch 2003), probably through trophic mechanisms (Croxford *et al.* 2002, Jenouvrier *et al.* 2005, Chambers *et al.* 2013).

Fulmarine petrels form an important component of the high-latitude seabird assemblages in terms of numbers of species and individuals (Ainley *et al.* 1994, Veit & Hunt 1991, Woehler *et al.* 2010). Their foraging strategies remain poorly known apart from observations at-sea (vessel-based data), which form the basis of our knowledge on their distribution (Griffiths 1983, Ainley *et al.* 1994, Woehler *et al.* 2010). At-sea surveys have shown the primary importance of sea-ice and krill abundance on the spatial foraging distribution of fulmarine petrels, including the Southern Fulmar *Fulmarus glacialisoides*, Cape Petrel *Daption capense* and Snow Petrel *Pagodroma nivea* (Ribic *et al.* 2008, 2011, Warren *et al.* 2009, Joiris *et al.* 2013). The species vary in the degree of association with sea-ice, from the highly ice-affiliated Snow Petrel, to the intermediate Southern Fulmar, to the more open-water Cape Petrel (Veit & Hunt 1991, Ainley *et al.* 1992, Ribic *et al.* 2011). During the breeding season, seabirds are central place foragers and their foraging distance is strongly constrained by the terrestrial location of their nests. This may lead to potentially intense intra- and inter-specific competition for key food resources in surrounding waters. At the end of the breeding season, Procellariiformes typically migrate from the colony to distant non-breeding areas, where foraging constraints due to nest-site provisioning are lower than those typically experienced during the breeding period (Phillips *et al.* 2009, Jaeger *et al.* 2013, Quillfeldt *et al.* 2013, Weimerskirch *et al.* 2014). To the best of our knowledge, few tracking data are available on Southern Fulmar

(Jenouvrier *et al.* 2015) and no tracking data are available on Snow Petrel and Cape Petrel, thus precluding determination of their foraging grounds during and outside the breeding season. To date, their wintering ranges have been inferred from at-sea sightings and ring recoveries, which suggest that fulmarine petrels are resident (Snow Petrel), move further north within the Southern Ocean (Southern Fulmar), or reach warmer waters and occasionally the Northern Hemisphere (Cape Petrel) (Murphy 1964, Warham 1990, del Hoyo *et al.* 1996). However, at-sea observations do not give any indication of the colony of origin, age and status of the birds.

Miniaturized saltwater immersion geolocators or Global Location Sensor (GLS) loggers have revolutionized our understanding of the distribution of many bird species (Wilson *et al.* 1992, Afanasyev 2004), including medium to small petrels (Shaffer *et al.* 2006, Quillfeldt *et al.* 2015). However, knowledge is still very limited for fulmarine petrel populations endemic to Antarctica. Using GLS loggers deployed on 55 adult birds, the main goal of the present study was to describe and compare the distribution of three fulmarine petrels that breed sympatrically in Adélie Land (East Antarctica) during their annual cycle. Our four objectives were (1) to identify and compare intra- and inter-specific at-sea distribution during the breeding and non-breeding periods, (2) to study migration patterns and (3) to analyse the at-sea activity in relation to the periods of the year, namely during both the breeding and the non-breeding periods that include the moulting period. In the three studied species, moult of flight feathers is known to begin at the end of the breeding cycle and to continue at-sea afterwards (Beck 1969, Marchant & Higgins 1990). Therefore (4) the isotopic niche of Southern Fulmar, Cape Petrel and Snow Petrel was investigated to provide complementary information on their moulting habitats ($\delta^{13}\text{C}$) and dietary habits ($\delta^{15}\text{N}$) in order to better define potential segregating mechanisms allowing coexistence of closely related seabird species.

METHODS

Study site and species

The study was carried out at Ile des Pétrles (66°40'S, 140°01'E) located in the Pointe Géologie archipelago, Adélie Land, East Antarctica. The

archipelago holds a large population of seabirds (c. 57 000 breeding pairs), including Southern Fulmar (c. 50 breeding pairs), Cape Petrel (c. 550 breeding pairs) and Snow Petrel (c. 1100 breeding pairs) (Micol & Jouventin 2001, CEBC CNRS unpublished data). Snow Petrel breeds in crevices and clefts under boulders, whereas Southern Fulmar and Cape Petrel breed in open nests built on flat rocks or gravel. The breeding season of the three species is highly synchronized and lasts approximately 5 months (Murphy 1964, Beck 1970). Adult birds arrive at the colonies in late October to copulate; they then depart to sea for a 1.5- to 3.5-week pre-laying exodus before females lay a single egg in early December (Mougin 1967, Isenmann 1970, Isenmann & Trawa 1970). Chicks hatch in late January and fledge in late February–March (Isenmann & Trawa 1970, Mougin 1967). Male and female birds alternate incubation duties, performing foraging trips lasting a few days (3–4 days for Snow Petrel; Isenmann & Trawa 1970). Chicks are left alone at the nest after they have acquired thermal independence at 1–2 weeks of age (Mougin 1967). Adults leave the colony in March. Unlike Southern Fulmar and Cape Petrel, Snow Petrel adults visit the colony during a post-breeding period (c. 15 days) in May (Marchant & Higgins 1990). Overall, the three species feed on a wide variety of prey including cephalopods, crustaceans and fish (Ridoux & Offredo 1989, Marchant & Higgins 1990). They are mostly surface feeders that catch prey by surface diving and surface seizing (Harper *et al.* 1985, Ridoux & Offredo 1989, Marchant & Higgins 1990). In Adélie Land, food of the chicks consists mainly of fish and crustaceans; Snow Petrels feed primarily on fish, and Southern Fulmars and Cape Petrels prey more on crustaceans (Ridoux & Offredo 1989).

Geolocator data and processing

To characterize the at-sea distribution of the three species during their breeding and non-breeding periods, we used GLS loggers (British Antarctic Survey, Cambridge, UK). GLS loggers (Mk14 Southern Fulmars in 2007/08, Mk18-H Southern Fulmars and Cape Petrels in 2010/11 and 2011/12 or Mk18-L Snow Petrels in 2010/11 and 2011/12) were mounted on metal leg rings and weighed 1.5 g (Mk14, Mk18-L) or 1.9 g (Mk18-H), i.e. 0.1–0.5% of the bird's body mass (mean value for Southern Fulmars 0.23%, for Cape Petrels 0.41%

and for Snow Petrels 0.38%), well below the recommended threshold of 3% body mass (Phillips *et al.* 2003). A detailed study found no evidence for any substantial impact of GLS used in our study on a smaller seabird species (Thin-billed Prion *Pachyptila belcheri*): (1) breeding performance was unaffected in the season of attachment or following recovery, (2) eco-physiological measurements suggested that adults adapted to the higher load and (3) the similarity in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of blood and feathers of instrumented adults and control birds indicated that feeding ecology was unaffected (Quillfeldt *et al.* 2012). Furthermore, for Snow Petrel we monitored the growth rate of chicks for control vs. equipped adults (results not reported here) and found that the growth parameters were similar. Seventy-six GLS were deployed on adults during the 2007/08 (10 Southern Fulmars), 2010/11 (10 Southern Fulmars, 10 Cape Petrels, 10 Snow Petrels) and 2011/12 (16 Southern Fulmars, 20 Snow Petrels) breeding seasons, during the brooding or chick-rearing stage. The sex of the birds was unknown except for Snow Petrels (four females, 21 males). Sixty GLS (27 Southern Fulmars, six Cape Petrels and 27 Snow Petrels) were recovered 1–2 years after deployment. The proportion of GLS-equipped animals recaptured was 70% for Southern Fulmars, 60% for Cape Petrels and 87% for Snow Petrels. The high recovery rate of individuals was in accordance with the estimated probability of capture in the colonies (Chastel *et al.* 1993, Jenouvrier *et al.* 2003). Data were successfully downloaded from 55 GLS (24 Southern Fulmars, six Cape Petrels and 25 Snow Petrels). The three species were tracked simultaneously during only one breeding season (2010/11), and only one species (Southern Fulmar) was tracked during the 3-year study. The sample sizes were too small to allow testing for between-year differences, but the pattern in distribution of species appeared to be consistent over the breeding season (results not reported here).

GLS allows the estimation of latitude and longitude from daylight measurements over extended periods, although with a relatively poor precision (186 ± 114 km; Phillips *et al.* 2004), as well as precise estimation of activity (Wilson *et al.* 1992, Phillips *et al.* 2004). Loggers measured daylight level intensity every 60 s and recorded the maximum light intensity for each 5 min (each 10 min for Mk14). Thresholds in the light curves were

used to determine sunrise and sunset. An internal clock allows the estimation of latitude based on day length and longitude based on the timing of local midday with respect to Universal Time (Afanasyev 2004). In addition to light, GLS loggers also recorded saltwater immersion every 3 s and stored the sum of immersion events for each 10-min period.

Daylight data recorded by GLS were analysed using a standardized procedure for flying species (Phillips *et al.* 2004) to provide two locations per day. Location fixes were calculated using BASTRAK software (provided by British Antarctic Survey). It was not possible to estimate locations when birds experienced continuous daylight in December and January at high latitudes (from the Antarctic Circle at 67°S to the Antarctic continent). As the breeding status of tracked birds was not monitored after deployment, life-cycle stages were assigned based on the recorded dates of each species observed during 2000–2015 in Adélie Land (Table 1). For each bird, locations were assigned to the breeding stages (pre-breeding, chick-rearing (post-brood)) or non-breeding period. We removed unrealistic positions from the GLS data (1) when daylight curves showed major interferences at dawn or dusk, (2) when unrealistic flight speeds were estimated (McConnell *et al.* 1992, maximum speed threshold = 80 km/h) and (3) when positions were recorded 2 weeks before and after the equinoxes (20/21 March and 22/23 September) (Wilson *et al.* 1992). Locations were only available for the pre-breeding, chick-rearing (post-brood) and overwintering periods. The point locations in each dataset were then twice-smoothed (Phillips *et al.* 2004, Catry *et al.* 2011) and were converted into residence time distribu-

tions using time spent per square (TSS). Using GLS locations of the birds, the TSS was defined as the proportion of time spent by each bird within a 2° cell. TSS-based methods have been extensively used to convert tracking data to gridded distributions (Péron *et al.* 2010, Louzao *et al.* 2011, Pedersen *et al.* 2011, Péron *et al.* 2012). The TSS was calculated separately for each period and species.

Residence time was calculated using the *trip-Grid* function (TRIP package, Sumner 2012) in R (R Core Team 2015), which creates a grid of time spent from each individual track by exact cell crossing methods, weighted by the time between locations for separate trip events, and then calculates the time spent in each spatial unit. Then, we assigned the corresponding percentage of time spent in relation to the total trip duration. The 2° cell size (7200 cells) was chosen on the basis of the mean accuracy of GLS locations. The TSS values for each combination of period/species were then normalized (0–1) to be comparable and combined so as to have residence time distributions. The TSS distribution allows the occurrence distribution (presence/pseudo-absence data) for each period/species to be estimated. Spatial overlap between species ('hotspots') was estimated using a multiple-criterion approach with sequential filtering (Williams 1998). The overlap index was obtained by selecting grid cells where more than one species was present, calculated by summing the TSS (top-scoring of 5%) of the three species by grid cell (Prendergast *et al.* 1993).

The raw immersion data had values from 0 (no immersion or dry, in flight or sitting on the ground or sea ice) to 200 (permanently immersed in sea water or wet), indicating the number of 3-s periods during 10-min blocks when the sensor was

Table 1. Timing of the breeding season for Southern Fulmars, Cape Petrels and Snow Petrels recorded during the period 2000–2015 at Pointe Géologie. Values are mean dates (earliest–latest).

	First observation ^a	Arrival ^b	Laying ^b	Hatching ^b	Thermal emancipation ^b	Fledging
Southern Fulmar	12/10 (23/9–21/10)	28/10 (7/10–28/11)	8/12 (19/11–25/12)	26/1 (17/1–10/2)	9/2 (31/1–28/2)	17/3 (4/3–1/4)
Cape Petrel	9/10 (19/9–23/10)	23/10 (21/10–1/11)	2/12 (26/11–12/12)	18/1 (7/1–26/1)	25/1 (18/1–30/1)	4/3 (18/2–19/3)
Snow Petrel ^c	26/9 (2/9–22/10)	5/11 (17/10–13/11)	8/12 (29/11–15/12)	20/1 (8/1–29/1)	23/1 (18/1–1/2)	6/3 (16/2–20/3)

^aDate of first observation at the Pointe Géologie. ^bFirst arrival, egg-laying, hatching and thermal independence of the chick (indicating the end of the brooding period) dates recorded at the breeding colony (Barbraud & Weimerskirch 2006). ^cPerform post-breeding visit to the colony during late April–beginning of May.

immersed in saltwater. The mean percentage of time spent on the water (wet; immersion data > 0) was calculated daily during the breeding and non-breeding periods to provide information on seasonal variation in resting and foraging behaviour. Conversely, the time spent dry is generally interpreted as bird on land in the colony, sitting on ice or flying, and thus not feeding. Nonetheless, this might be only partially true for Snow Petrels, which are known to feed by ice-gleaning or pattering on the sides of icebergs (Marchant & Higgins 1990). Consequently, dry time was not necessarily related to flying time in this species. During chick-rearing (post-brood), after careful examination of raw light and immersion data, it was not possible to identify time spent at the colony. This potential bias is probably small during this stage (compared with incubation for instance), as the adults spent little time at the colony at this stage. Additionally, the proportion of time spent entirely immersed (10-min blocks with values of 200) over the total daily time spent on the water was calculated daily (hereafter referred to as resting time). This value was then used to identify locations where birds exhibited low levels of activity (high values of resting). Immersion data were also used to estimate the percentage of time spent on the sea surface during the day and at night (based on local sunset and sunrise times derived by analysis of the daylight curves in *TransEdit2-BAS-TRAK*). The duration of daylight and darkness each day (consecutive light and dark period) was assessed directly from the daylight data.

Spatial and statistical analyses were performed using R 3.2.1 (R Core Team 2015). Estimates are presented as means \pm 1 sd. General linear models were used to model mean daily proportion of time spent wet (sitting on water – model GLM1 using the ‘LME4’ package; Bates *et al.* 2015; see Supporting Information Table S1). Species and stage (independent variables) were included as fixed effects. General linear mixed-effects models (model GLMM2; Table S1) were used to model the daily proportion of time spent wet during 24 h (using the ‘NLME’ package; Pinheiro *et al.* 2013) during the non-breeding period. Species and month (independent variables) were included as fixed effects. Because not all combinations of variables were available (i.e. not all species had data for each month during the non-breeding period; Fig. 4a) we formed a subset of the original dataset (subset of months from April to September) to fit the full mixed model with interactions and ran-

dom effects. General linear mixed-effects models (models GLMM 3–5; Table S1) were used to model the daily proportion of time spent wet during the non-breeding period. Month and time of day (daylight or darkness) were included as a fixed effect. For models GLMM 2–5, the individual was fitted as a random effect to account for pseudo-replication, as the same individual could provide several values. Response variables were visually tested for normality (through Q-Q plots) and homoscedasticity (using Cleveland dotplots; Zuur *et al.* 2010) before each statistical test. The error structure approached the normal distribution, and therefore a Gaussian family was selected for all models. Models including all combinations of variables were then tested and ranked using their Akaike information criterion (AIC) values and Akaike weights following the Information-theoretic Approach (Burnham & Anderson 2002). The model with the lowest AIC was considered to be that receiving most support from the data. Two models separated by a difference in AIC values of < 2 were assumed to fit the data equally well.

Feather collection, moult and stable isotopes

The isotopic method was validated in the southern Indian Ocean, with $\delta^{13}\text{C}$ values of seabirds indicating the latitude of their foraging habitat (Cherel & Hobson 2007, Jaeger *et al.* 2010) and their $\delta^{15}\text{N}$ values increasing with trophic level (Cherel *et al.* 2010). Hence, the isotopic values of fulmarine petrels were determined during both the breeding and the adult moulting periods using body feathers collected from chicks and breeding adults, respectively. Feathers contain information about the diet at the time they were grown, because keratin is inert after synthesis (Hobson & Clark 1992, 1993, Bearhop *et al.* 2002). Seabird chicks moult completely and body feathers grow almost synchronously towards the end of the chick-rearing period in summer (Phillips & Hamer 2000). Unlike chicks, breeding adults have a protracted moult over several weeks to months; hence, the precise timing of synthesis of a given body feather is not known. In Antarctic fulmarine petrels, body moult is a gradual process extending over at least 4 months in summer and autumn. It begins during incubation, but most feathers grow in the weeks following the completion of breeding (Beck 1969, Marchant & Higgins 1990).

Body feathers from fulmarine petrels were collected during the 2006/07 austral summer, when 10–11 breeding adults and well-feathered chicks per species were sampled in December and February, respectively. For all species, several ($n = 4–6$) whole body feathers per individual were pulled out from the lower back and stored dry in sealed plastic bags until analysis. As the main goal of the present work was to depict the isotopic habitat at the species level, potential effects of individuals were not considered, and consequently only a single body feather per individual was analysed (Jaeger *et al.* 2009). Prior to isotopic analysis, single body feathers were cleaned of surface lipids and contaminants using a 2 : 1 chloroform : methanol solution for 2 min followed by two successive methanol rinses. They were then oven-dried for 48 h at 50 °C. Every whole feather was homogenized by cutting it with scissors into small fragments and a subsample of *c.* 0.3 mg was packed into tin containers for stable isotope analysis. The relative abundance of carbon and nitrogen isotopes was determined with a continuous flow mass spectrometer (Delta V Advantage with a ConFlo IV interface, Thermo Scientific, Bremen, Germany) coupled to an elemental analyser (Flash EA 1112, Thermo Scientific, Milan, Italy). Results are presented in the usual δ notation relative to Vienna PeeDee Belemnite and atmospheric N_2 for $\delta^{13}C$ and $\delta^{15}N$, respectively. Replicate measurements of internal laboratory standards (acetanilide) indicated measurement errors $< 0.15\%$ for both $\delta^{13}C$ and $\delta^{15}N$ values.

RESULTS

At-sea distribution

Geolocation data indicated a common migratory strategy for each species; birds migrated from the breeding grounds in March (Figs 1–3). Snow Petrels and Southern Fulmars travelled westwards and northwards, whereas Cape Petrels moved northwards from the breeding colony to winter at lower latitudes.

Breeding period

The distribution during the breeding period was only available during the early and late breeding stages (pre-breeding and chick-rearing periods) due to continuous daylight during the mid-breeding period (December and January). A greater resi-

dence time (greater value of time spent per square) of Southern Fulmars, Cape Petrels and Snow Petrels was observed in the vicinity of the breeding colonies, well south of the Southern Antarctic Circumpolar Current Front (Supporting Information Fig. S1). The three species overlapped in distribution during the breeding period (mean latitude Southern Fulmar: $-64.2 \pm 3.2^\circ S$; Cape Petrel: $-62.2 \pm 1.3^\circ S$ and Snow Petrel: $-65.2 \pm 1.0^\circ S$; Figs 2 & 3a, Supporting Information Fig. S4; Table 1).

Timing of migration, migration pattern and non-breeding period

Outside the breeding season, the at-sea distribution of the three fulmarine species ranged across 30° of latitude and 200° of longitude in the southern Indian Ocean (Figs 1 & 2; $40–70^\circ S$, $30^\circ W–170^\circ E$). The widest latitudinal range was observed for Cape Petrels, which spent most of the non-breeding period in the sub-Antarctic waters of the Tasman Sea and off New Zealand. The widest longitudinal range was observed for Southern Fulmars and Snow Petrels, which spent the non-breeding period in Antarctic and sub-Antarctic waters in the southern Indian and Atlantic Oceans. During the non-breeding period, the overlap in distribution of the species was mainly restricted to the Commission for the Conservation of Antarctic Marine Living Resources area (CCAMLR, subarea 58.4.1), specifically to a unique post-breeding area, in the Mawson Sea, between the Knox Coast and Banzare Coast (Fig. 3b & Supporting Information Fig. S2; $110–126^\circ E$, $60–66^\circ S$). All three species left the breeding colony in mid-March (Table 2) and most individuals moved westward (Figs 2 & S2).

Later departure dates of Snow Petrels correspond to adults that transiently return to the colony in autumn during a post-breeding visit, after which all the individuals departed for migration, with most of them spending some time in an area at *c.* $120^\circ E$. All Snow Petrels migrated westward in the southern Indian Ocean, with four individuals reaching the southern Atlantic Ocean. All left their overwintering areas in late September (median date: 24 September, range: 26 August–16 November) and were back at the breeding sites in October (median date: 14 October, range: 25 September–17 November). Southern Fulmars also migrated westward to the southern Indian Ocean basin after breeding. They spent time at high latitudes, as Snow Petrels do (Figs 1 & 2), but they

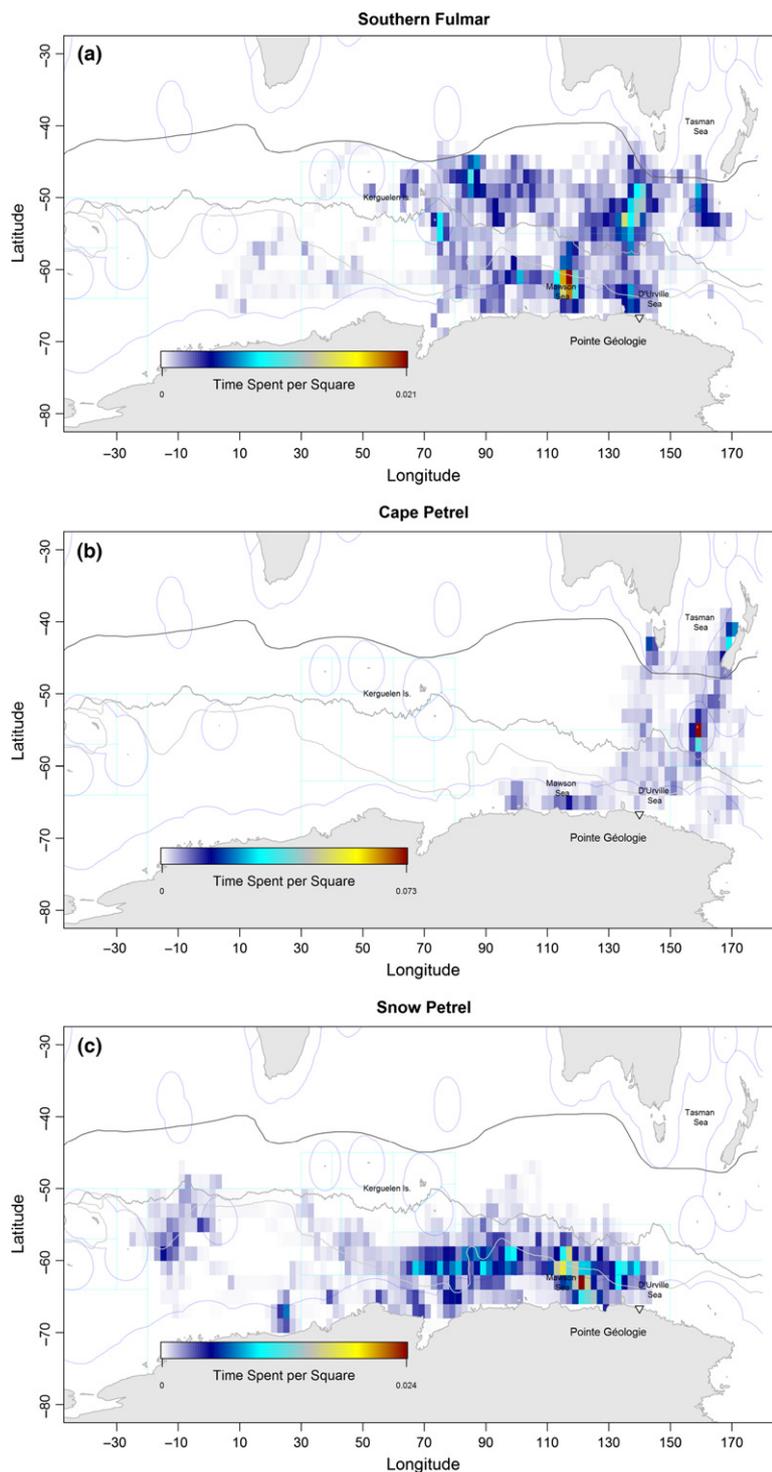


Figure 1. Distributions of sympatric fulmarine petrels tracked using geolocators (per cent of time of residence spent in each cell) during the non-breeding period: (a) Southern Fulmar, (b) Cape Petrel and (c) Snow Petrel. Oceanographic frontal structures are shown: the South Subtropical Front (dark grey line), Polar Front (grey line) and Southern Antarctic Circumpolar Current Front (light grey line) (Belkin & Gordon 1996 (updated 2003), Sokolov & Rintoul 2009a). Boundaries of CCAMLR (Commission for the Conservation of Antarctic Marine Living Resources) (light blue lines) and of Exclusive Economic Zones (dark blue lines) are also shown. The black inverted triangle indicates the breeding colony

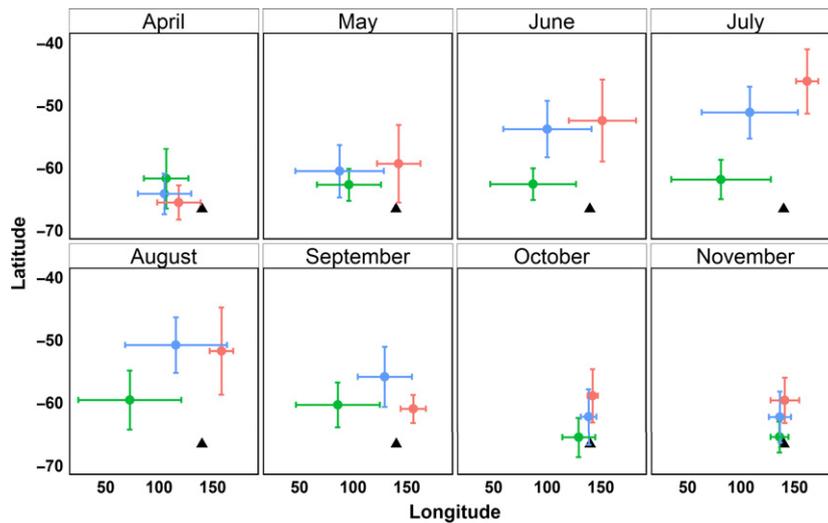


Figure 2. Mean latitudes and longitudes of fulmarine petrels during the non-breeding period (blue: Southern Fulmar, red: Cape Petrel and green: Snow Petrel). Values are means \pm 1 sd.

overwintered at lower latitudes than Snow Petrels (Figs 1, 2 & S2, Table 2). They remained over the Australian-Antarctic Basin (Kerguelen-Heard and McDonald Plateau and north of Adélie Land), where they reached the southeast Indian Ridge. All Southern Fulmars departed from the wintering grounds in October (median date: 14 October, range: 26 September–12 November) and were back at the colony in late October/early November (median date: 23 October, range: 9 October–19 November; Figs 2 & S2). The third species, Cape Petrel, migrated in similar southerly areas (90–120°E) during the post-breeding period. Cape Petrels overwintered at more northerly latitudes than the two other species (Exclusive Economic Zones of New Zealand and Australia: South New Zealand, South Tasmania and Macquarie area), and remained latitudinally segregated from Southern Fulmars and Snow Petrels from June to August. All Cape Petrels left their wintering areas in October (median date: 11 October, range: 4 October–4 November) and were back at the colony in late October/early November (median date: 27 October, range: 18 October–6 November; Figs 1, 2 & S2).

Activity patterns

The three species shared a similar activity pattern overall: the proportion of time spent wet was greater during the non-breeding than the breeding

period (Fig. 4, Supporting Information Tables S1 and S2). During the non-breeding period the daily proportion of time spent wet differed between species and months (average 22–69%; Supporting Information Tables S1 and S3, Fig. 5a). Interestingly, the proportion of time spent wet by Southern Fulmars and Cape Petrels was greater at the end of the breeding period and at the beginning of the non-breeding period (up to average values of 45 and 69%, respectively, in March–April; Supporting Information Tables S1, S4 and S5, Fig. 5b, c). In contrast, the proportion of time spent on the water by Snow Petrels reached a smaller peak at a later date (31% in July–August; Supporting Information Tables S1 and S6, Fig. 5d). Activity levels differed between day and night within seasons (Fig. 5b–d). The proportions of time spent wet (max. 62% for Cape Petrels) were lower during the night than during the day whatever the period (max. 75% for Cape Petrels; Fig. 5, Tables S1, S4, S5 and S6).

Resting time

The daily proportions of resting time were not homogeneously distributed throughout the tracking period (Fig. S3). The proportion of resting time by Southern Fulmars and Cape Petrels was greater at the end of the breeding period and at the beginning of the non-breeding period (up to average values of 6%, in April). The spatial distribution of resting activity revealed differences in

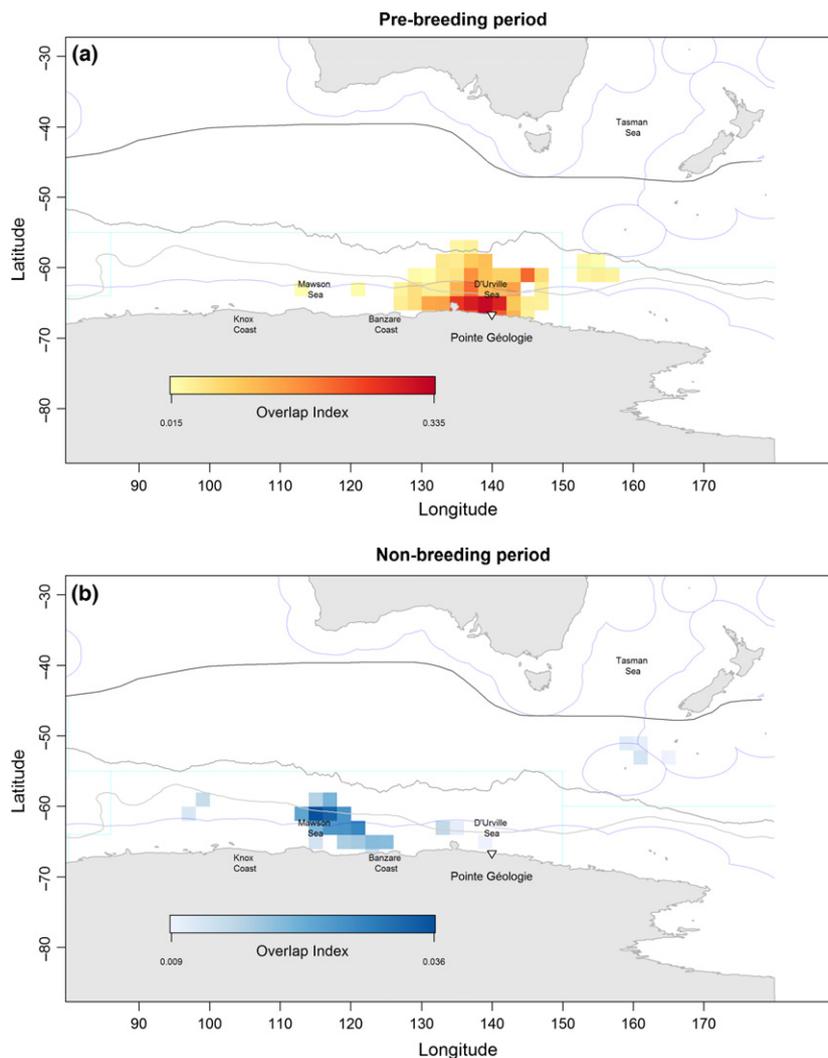


Figure 3. Hotspots of sympatric fulmarine petrels tracked using geolocators (distribution overlap of species-specific top-scoring 5% of time spent per square corresponds to the values of the upper quartile for cells with at least two species; see Methods) during (a) pre-breeding and (b) non-breeding periods. Oceanographic frontal structures are shown: the South Subtropical Front (dark grey line), Polar Front (grey line) and Southern Antarctic Circumpolar Current Front (light grey line) (Sokolov & Rintoul 2009a, updated 2003). Boundaries of CCAMLR (light blue lines) and of Exclusive Economic Zones (dark blue lines) are also shown. The black inverted triangle indicates the breeding colony

spatial distribution of the three species (Fig. S3). These sectors corresponded to the areas where the three species overlapped in distribution, mainly during the early non-breeding period (Figs 2 & 3b). The highest concentration of resting time was principally restricted to an area located in the Mawson Sea during the early non-breeding period.

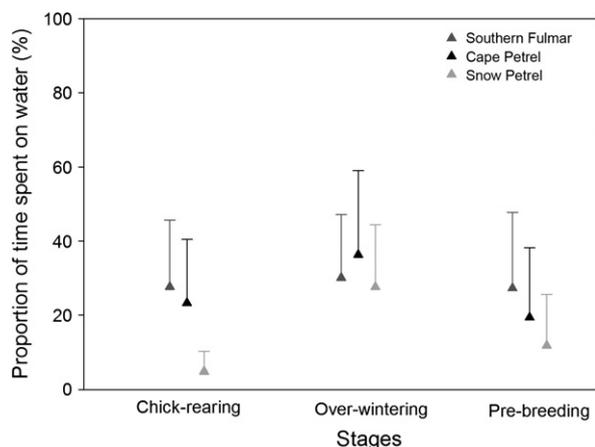
Stable isotopes

Body feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of chicks and breeding adults encompassed relatively small and

large ranges, amounting to differences of 1.6‰ (mean values from -24.7 to -23.1 ‰) and 3.5‰ (8.8–12.3‰), respectively (Fig. 6). In univariate analyses, both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values differed significantly across groups (ANOVA, $F_{5,55} = 7.11$ and 9.18, respectively, both $P < 0.0001$). In chicks, *post-hoc* Tukey's HSD multiple comparison tests showed that Cape Petrels and Snow Petrels had significantly different $\delta^{13}\text{C}$ values ($P < 0.0001$), and that the three species differed in their $\delta^{15}\text{N}$ values (all $P \leq 0.039$). In contrast to chicks, breeding adults did not segregate by their stable isotope

Table 2. Mean characteristics of foraging areas of Southern Fulmars, Cape Petrels and Snow Petrels during the breeding and non-breeding periods (values are means \pm 1 sd).

	Breeding period			Non-breeding period		
	Southern Fulmar ($n = 24$)	Cape Petrel ($n = 6$)	Snow Petrel ($n = 25$)	Southern Fulmar ($n = 21$)	Cape Petrel ($n = 6$)	Snow Petrel ($n = 24$)
Latitude range ($^{\circ}$ S)	49–71	60–63	52–71	53–68	41–71	51–71
Mean latitude ($^{\circ}$ S)	64.2 ± 3.2	62.2 ± 1.3	65.2 ± 1.0	57.3 ± 4.4	54.7 ± 1.65	61.2 ± 2.8
Longitude range	72 $^{\circ}$ E–160 $^{\circ}$ E	134 $^{\circ}$ E–145 $^{\circ}$ E	10 $^{\circ}$ W–140 $^{\circ}$ E	11 $^{\circ}$ W–169 $^{\circ}$ E	94 $^{\circ}$ E–178 $^{\circ}$ E	11 $^{\circ}$ W–134 $^{\circ}$ E
Mean longitude ($^{\circ}$ E)	139.3 ± 3.7	140.9 ± 3.8	124.6 ± 8.6	100.2 ± 37.7	147.9 ± 6.9	85.7 ± 40.4
Mean range (km)	1257 ± 603	1557 ± 547	2648 ± 1054	3402 ± 1429	4247 ± 961	2664 ± 1500
Maximal range (km)	2986	2527	4978	7269	5727	6314
Mean bathymetry	-1448 ± 1392	-2569 ± 460	-827 ± 724	-3149 ± 1073	-2382 ± 947	-3613 ± 852
Median departure date	23/3 (10/3–3/4)	7/3 (6/3–17/3)	10/3 (30/1–2/4)	–	–	–

**Figure 4.** Activity patterns (proportion of time spent on water) calculated from geolocator-immersion loggers for breeding adults of three Antarctic fulmarine species: average daily activity pattern during breeding: pre-breeding and chick-rearing (post-brood) and non-breeding (over-wintering) periods. Values are means \pm 1 sd.

values (all $P > 0.05$). Chicks and adults of each species showed no significant $\delta^{13}\text{C}$ differences (all $P > 0.05$), but feather $\delta^{15}\text{N}$ values were lower and higher in chicks than in adults of Cape Petrels and Snow Petrels, respectively ($P = 0.049$ and 0.002).

DISCUSSION

The complementary use of spatial, activity and isotopic data highlights the year-round foraging strategies of high-Antarctic seabirds and sheds light on the mechanisms that allow the coexistence of

closely related fulmarine petrels. Southern Fulmars, Cape Petrels and Snow Petrels segregated during the breeding season primarily by feeding at different trophic levels, whereas during the non-breeding period they differed in their migratory movements and wintering areas. However, each method suffers its own biases and this study had one main limitation. The location accuracy of GLS loggers (186 ± 114 km; Phillips *et al.* 2004) precludes the collection of spatial information at small spatial scales. Thus, we cannot form clear conclusions about the spatial segregation between species during the breeding season. The method is at its best for depicting large-scale movements, but is of more limited use when birds are central-place foragers and feed at short distances from the colonies. Finally, between-year differences could not be investigated and we cannot exclude that species and year effect may be partly confounded. Clearly, more tracking investigations using satellite or GPS tags are needed to better define petrel foraging areas during the incubation and chick-rearing periods (e.g. Jenouvrier *et al.* 2015).

Trophic segregation during the breeding period

During the breeding season, the three petrels overlapped in time and space, as illustrated by areas with the greatest residence times. Given that during breeding their movements were restricted to small spatial scales, it cannot be excluded that they might segregate spatially, but at a scale that was simply not detectable by the method used here

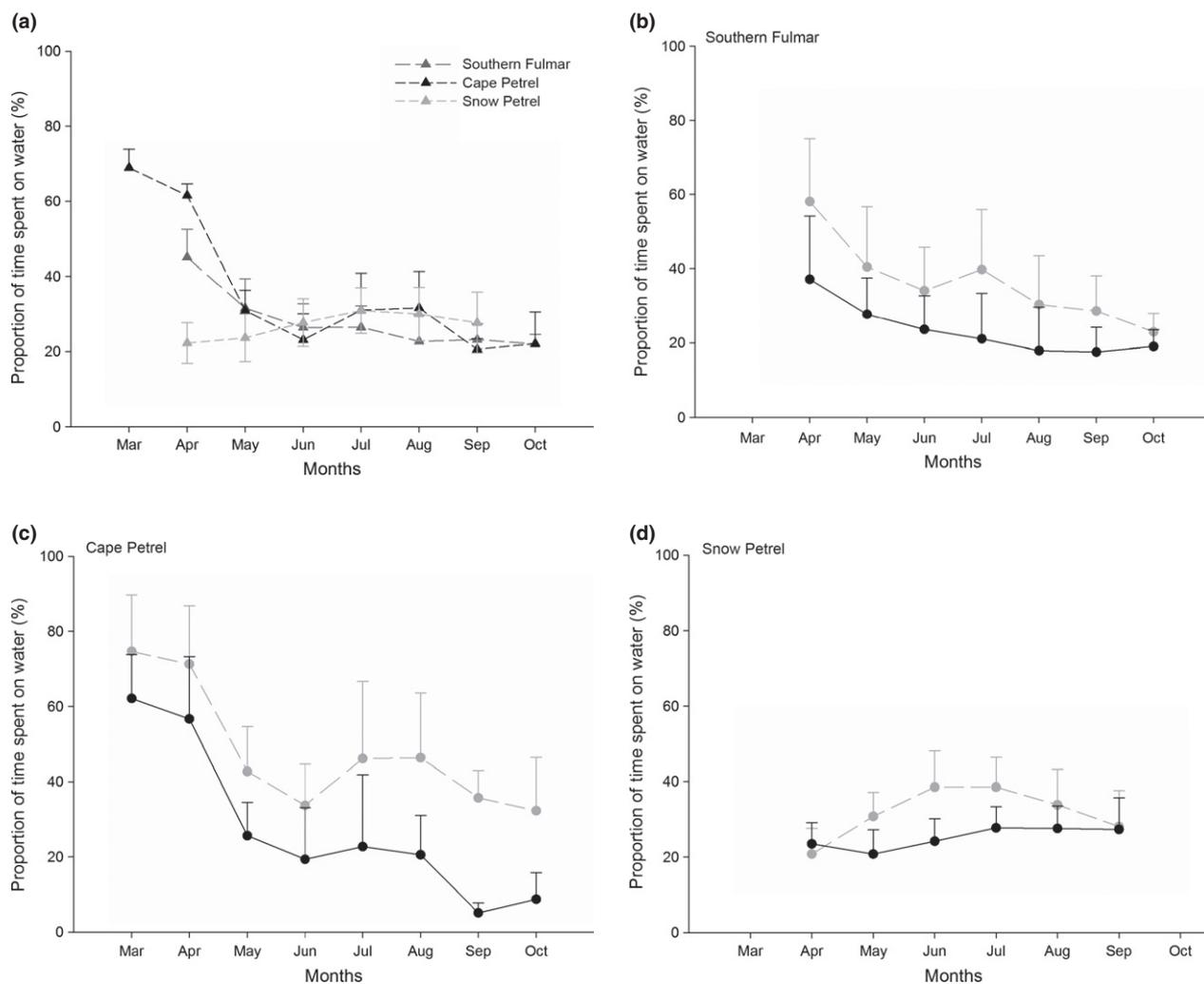


Figure 5. Activity patterns (proportion of time spent on water) calculated from geolocator-immersion loggers for breeding adults of three Antarctic fulmarine species: average daily activity pattern with time (a) and during daytime (grey) and darkness (black) for (b) Southern Fulmars, (c) Cape Petrels and (d) Snow Petrels. Values are means \pm 1 sd.

due to poor GLS accuracy. Overall, Southern Fulmars, Cape Petrels and Snow Petrels foraged mainly in high Antarctic waters in the vicinity of the colonies in summer. Accordingly, the low feather $\delta^{13}\text{C}$ values of chicks are typical of marine organisms feeding in the high-Antarctic pelagic habitat (Hodum & Hobson 2000, Cherel 2008, Cherel *et al.* 2011). Adult Southern Fulmars satellite tracked during breeding foraged in the vicinity of the colony (200–600 km) where they target shelf slopes areas (1000–3000 m depth) with a pack-ice concentration of *c.* 20% (Jenouvrier *et al.* 2015). However, some individuals of all three species foraged several thousand kilometres away (Fig. S1, Table 2), which may reflect the pre-lay-

ing exodus at the beginning of the breeding cycle or the behavioural shift of failed breeders afterwards.

Interestingly, feather $\delta^{15}\text{N}$ values of chicks indicated trophic separation among the petrel species, with $\delta^{15}\text{N}$ values increasing in the order Cape Petrels < Southern Fulmars < Snow Petrels, and the overall $\delta^{15}\text{N}$ difference encompassing a full trophic level (3.4‰). This segregation contrasts with the only other available isotopic investigation on Antarctic fulmarine petrels, which indicated a more limited $\delta^{15}\text{N}$ range (1.0‰) among species at Hop Island, East Antarctica (Hodum & Hobson 2000). In Adélie Land, the low Cape Petrel and high Snow Petrel $\delta^{15}\text{N}$ values are close to those of

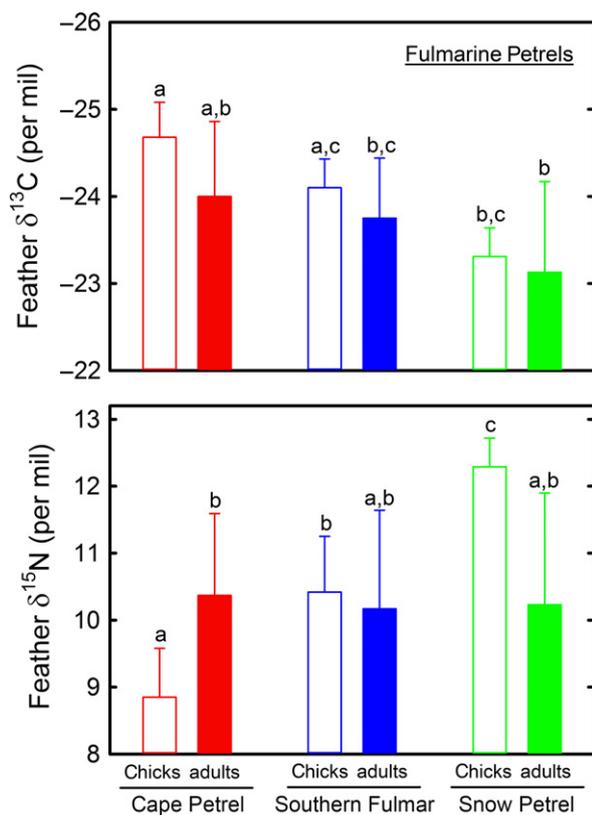


Figure 6. Body feather $\delta^{13}\text{C}$ (upper panel) and $\delta^{15}\text{N}$ (lower panel) values of chicks and breeding adults of sympatric fulmarine petrels from Adélie Land. Values not sharing the same superscript letter are significantly different. Values are means \pm 1 sd.

the primarily crustacean-eater Adélie Penguin *Pygoscelis adeliae* and primarily fish-eater Emperor Penguin *Aptenodytes forsteri*, respectively (Offredo & Ridoux 1986, Ridoux & Offredo 1989, Chérel 2008). Consequently, the intermediate $\delta^{15}\text{N}$ value of Southern Fulmar suggests that birds are feeding on a mixture of crustaceans and fish. Stomach content analysis showed that Southern Fulmar chicks were fed with fish and euphausiids, while the staple food of Snow Petrel chicks was fish (Ridoux & Offredo 1989). However, Cape Petrel chicks were fed with fish and euphausiids (Ridoux & Offredo 1989), which did not fit well the $\delta^{15}\text{N}$ indication of a crustacean-based diet. Such a discrepancy may result from a differential temporal integration between the methods (dietary snapshot vs. feather growth period) and/or from inter-annual changes in food availability (1982 vs. 2007). Elsewhere, Cape Petrels breeding in Antarctica feed predominantly either on crustaceans (Green 1986, Arnould

& Whitehead 1991, Soave *et al.* 1996) or on crustaceans and fish (Creet *et al.* 1994, Coria *et al.* 1997), thus highlighting the foraging plasticity of the species.

Spatial segregation during the non-breeding period

One of the main findings of this study is the almost complete spatial segregation at sea of the three petrels during the non-breeding period (Fig. 2). All the individuals migrated far away from the breeding colonies but showed species-specific and contrasting overwintering strategies along well-marked spatial gradients. Longitudinally, Snow Petrels moved to the western Indian Ocean (occasionally reaching the Atlantic Ocean), whereas Cape Petrels migrated eastward into the Pacific Ocean and Southern Fulmars foraged in the eastern Indian Ocean. Latitudinally, Snow Petrels essentially remained in Antarctic waters (south of the Polar Front) including both the Seasonal Ice Zone and also the Permanent Open Ocean Zone further north. In contrast, Southern Fulmars and Cape Petrels favoured warmer waters in the middle of the austral winter (June–August); both species foraged in the sub-Antarctic Zone and Cape Petrels crossed the Subtropical Front to reach subtropical and even tropical waters. The latitudinal segregation of the GLS-equipped petrels is in general agreement with vessel-based observations of birds of unknown origin, age and status (Marchant & Higgins 1990). Cape Petrels are widespread within the Southern Hemisphere, and Southern Fulmars are also widely distributed, whereas Snow Petrels, a pack-ice-affiliated species, are virtually confined to cold waters ($\leq 1^\circ\text{C}$) (Murphy 1964). The last two species breed only in the Antarctic Zone, whereas the first has a more widespread northern breeding distribution ($44\text{--}70^\circ\text{S}$) that includes sub-Antarctic islands (Brooke 2004). This wide latitudinal breeding range indicates the need to track Cape Petrels from different colonies, populations and marine areas in order to get a synoptic view of the wintering strategies of the species (e.g. Weimerskirch *et al.* 2015).

Activity patterns and moult

Three main features characterized the activity patterns of fulmarine petrels, here quantified by the proportion of time spent on water, presumably

resting: (1) birds were more active during than outside the breeding period; (2) they were generally less active during the day than at night; and (3) Southern Fulmar and Cape Petrel, but not Snow Petrel, showed a pronounced peak of inactivity in autumn (March–April). Less time spent on water during the chick-rearing than the non-breeding period is likely to be due to numerous commuting flights between foraging grounds and colony to feed the chick, compared with non-breeding birds that are no longer under breeding constraints. An identical seasonal activity pattern has been recorded in other petrel species (Pinet *et al.* 2011, Rayner *et al.* 2012) and in albatrosses (Mackley *et al.* 2010). Hence, more resting time during the non-breeding period may occur regardless of the species, the wintering zones and the prey consumed, suggesting that it is a common feature among seabirds. It also indicates that birds readily meet their energy demands during the non-breeding period. During the non-breeding period, the petrels spent more time on water during the day and were thus more active at night, which concurs with the little information available for petrels (Mackley *et al.* 2011, Pinet *et al.* 2011, Rayner *et al.* 2012). The greater night-time activity of petrels suggests that they exploit nocturnally available prey (Brooke & Prince 1991) during non-breeding, a hypothesis that needs to be tested using bio-logging.

The proportion of time spent on water by Southern Fulmars and Cape Petrels was remarkably high during the day and at night in March–April, indicating low flight activity at the end of the breeding cycle and the beginning of the non-breeding period before birds initiated their migration. Similarly, the highest values of proportion of resting were reported in April for these two species. Interestingly, the resting peak corresponds to the moulting period of fulmarine petrels, which are known to initiate feather growth during the breeding period (Beck 1969, Marchant & Higgins 1990). Consequently, it is likely that the prolonged period of relative flightlessness of Southern Fulmars and Cape Petrels was a direct consequence of the loss of several old flight feathers while the new ones were still too small to be used efficiently. This time overlap between two events (chick-rearing and moult) was explained by the high abundance of food at the end of the short summer and autumn in high-Antarctica (Beck 1969). Surprisingly, although Snow Petrels also moult at that time of the year during a ‘moult

exodus’ (Beck 1969, 1970), they did not present any concomitant resting peak at the sea surface. Snow Petrels had a stronger association with ice than other petrels (Ainley *et al.* 1994) and the species is often observed sitting on sea ice and icebergs (Ainley *et al.* 1993). Hence, the most likely explanation for the lack of sea surface resting peak in autumn in Snow Petrels is that they spent a large amount of time resting on the ice while moulting, a behaviour that cannot be distinguished from flight activity by the wet/dry activity recorders.

A final notable finding of the work is that the spatial overlap index delineated an oceanic area located at high latitudes west of Adélie Land, which was used by all three species. The time spent in this area corresponds to the autumnal resting peak of Southern Fulmars and Cape Petrels and, hence, to the zone where they probably moulted. Thus, after breeding, petrels resumed feather growth in the same moulting area before departing with a new plumage for different species-specific wintering zones. The low and similar feather $\delta^{13}\text{C}$ values of adult birds indicated that the three species grew feathers in pelagic Antarctic waters, and not further north. In contrast to the breeding period, however, adult moult was not marked by any trophic separation among the petrels. Instead, their feather $\delta^{15}\text{N}$ values were not different and showed a similarly wide range of values within each species, meaning that the populations were isotopically generalists and relied on different prey from different trophic levels during moult (most likely Antarctic krill, mid-water fish and possibly squid). This moulting area should be considered a hotspot for these species’ conservation. It therefore constitutes a previously unknown hotspot of marine resources (Raymond *et al.* 2015), highlighting the usefulness of tracking marine consumers to gather relevant information on remote marine zones of biological interest (Bost *et al.* 2009).

CONCLUSION

During the summer breeding period, Southern Fulmars, Cape Petrels and Snow Petrels all foraged in high-Antarctic waters in the vicinity of their breeding colonies. Accordingly, the low feather $\delta^{13}\text{C}$ values of chicks are typical of the high-Antarctic pelagic habitat. Interestingly, feather $\delta^{15}\text{N}$ values of chicks depicted trophic segregation at that time, with feather $\delta^{15}\text{N}$ values increasing in

the order Cape Petrels < Southern Fulmars < Snow Petrels. One of the main findings of the study is the almost complete spatial segregation at sea of the three petrels during the non-breeding period. All the individuals migrated far away from the breeding colonies but showed species-specific and contrasting overwintering strategies along well-marked spatial gradients. Three main features characterized the activity patterns of the petrels: (1) birds were more active during than outside the breeding period; (2) they were generally less active during the day than at night; and (3) Southern Fulmars and Cape Petrels, but not Snow Petrels, showed a pronounced peak of inactivity in autumn (March–April). The spatial overlap index delineated an oceanic area located west of Adélie Land. This area was used by all species, and by Southern Fulmars and Cape Petrels probably for moulting their flight feathers.

Despite their low conservation threat status (all are listed as Least Concern according to IUCN 2015), fulmarine petrels face a range of threats in the marine environment, including direct interactions with fisheries (Brothers *et al.* 2010, Favero *et al.* 2011, Richard *et al.* 2011), contamination from pollutants (Tartu *et al.* 2015), over-fishing of prey species and climate change (Barbraud *et al.* 2011). The areas of high use identified in this study highlighted that CCAMLR was the management organization with the greatest responsibility, given the overlap between the species distribution at sea and the CCAMLR jurisdiction zone. CCAMLR is a well-known exemplar ecosystem-based management organization which has implemented successful bycatch mitigation measures. However, a significant part of the high-use areas by these fulmarine petrels extends beyond CCAMLR boundaries, highlighting the need to implement similar mitigation measures by other regional fisheries management organizations.

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REFERENCES

- Afanasyev, V. 2004. A miniature daylight level and activity data recorder for tracking animals over long periods. *Mem. Natl Inst. Polar Res.* **58**: 227–233.
- Ainley, D.G., Ribic, C.A. & Fraser, W.R. 1992. Does prey preference affect habitat choice in Antarctic seabirds? *Mar. Ecol. Prog. Ser.* **90**: 207–221.
- Ainley, D.G., Ribic, C.A. & Spear, L.B. 1993. Species–habitat relationships among antarctic seabirds: a function of physical or biological factors? *Condor* **95**: 806–816.
- Ainley, D.G., Ribic, C.A. & Fraser, W.R. 1994. Ecological structure among migrant and resident seabirds of the Scotia-Weddell confluence region. *J. Anim. Ecol.* **63**: 347–364.
- Ainley, D.G., Tynan, C.T. & Stirling, I. 2003. Sea-ice: a critical habitat for polar marine mammals and birds. In Thomas, D.N. & Dieckmann, G.S. (eds) *Sea-Ice: An Introduction to Its Physics, Biology, Chemistry and Geology*. 240–266. London: Blackwell Science.
- Arnould, J.P.Y. & Whitehead, M.D. 1991. The diet of Antarctic petrels, Cape petrels and Southern Fulmars rearing chicks in Prydz Bay. *Antarct. Sci.* **3**: 19–27.
- Barbraud, C. & Weimerskirch, H. 2003. Climate and density shape population dynamics of a marine top predator. *Proc. R. Soc. Lond. Ser. B* **270**: 2111–2116.
- Barbraud, C. & Weimerskirch, H. 2006. Antarctic birds breed later in response to climate change. *Proc. Natl Acad. Sci. USA* **103**: 6248–6315.
- Barbraud, C., Rivalan, P., Inchausti, P., Nevoux, M., Rolland, V. & Weimerskirch, H. 2011. Contrasted demographic responses facing future climate change in Southern Ocean seabirds. *J. Anim. Ecol.* **80**: 89–100.
- Bates, D., Maechler, M., Bolker, B. & Walker, S. 2015. Fitting linear mixed-effects models Using lme4. *J. Statist. Software* **67**: 1–48.
- Bearhop, S., Waldron, S., Votier, S.C. & Furness, R.W. 2002. Factors that influence assimilation rates and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. *Physiol. Biochem. Zool.* **75**: 451–458.
- Beck, J.R. 1969. Food, moult and age of first breeding in the Cape pigeon, *Daption capensis* Linnaeus. *Br. Antarct. Surv. Bull.* **21**: 33–44.
- Beck, J.R. 1970. Breeding seasons and moult in some smaller Antarctic petrels. In Holdgate, M.W. (ed.) *Antarctic Ecology*. 542–550. London: Academic Press.
- Belkin, I.M. & Gordon, A.L. 1996. Southern Ocean fronts from the Greenwich meridian to Tasmania. *J. Geophys. Res.* **101**: 3675–3696.
- Bost, C.-A., Thiebot, J.-B., Pinaud, D., Chérel, Y. & Trathan, P.N. 2009. Where do penguins go during the inter-breeding period? Using geolocation to track the winter dispersion of the Macaroni Penguin. *Biol. Lett.* **5**: 473–476.
- Bretagnolle, V. 1988. Cycles de présence et rythmes d'activité chez cinq espèces de pétrels antarctiques. *L'Oiseau et R.F.O.* **58**: 44–58.

- Brooke, M. 2004. *Albatrosses and Petrels across the World*. Oxford: Oxford University Press.
- Brooke, M.D.L. & Prince, P.A. 1991. Nocturnality in seabirds. *Proc. Int. Ornithol. Congr.* **20**: 1113–1121.
- Brothers, N., Duckworth, A.R., Safina, C. & Gilman, E.L. 2010. Seabird bycatch in pelagic longline fisheries is grossly underestimated when using only haul data. *PLoS ONE* **5**: e12491.
- Burnham, K.P. & Anderson, D.R. 2002. *Model Selection and Multimodel Inference: A Practical Information-theoretic Approach*. New York: Springer.
- Catry, I., Dias, M.P., Catry, T., Afanasyev, V., Fox, J., Franco, A.M. & Sutherland, W.J. 2011. Individual variation in migratory movements and winter behaviour of Iberian Lesser Kestrels *Falco naumanni* revealed by geolocators. *Ibis* **153**: 154–164.
- Chambers, L.E., Altwegg, R., Barbraud, C., Barnard, P., Beaumont, L.J., Crawford, R.J.M., Durant, J.M., Hughes, L., Keatley, M.R., Low, M., Morellato, P.C., Poloczanska, E.S., Ruoppolo, V., Vanstreels, R.E.T., Woehler, E.J. & Wolfaardt, A.C. 2013. Phenological changes in the southern hemisphere. *PLoS ONE* **8**: e75514.
- Chastel, O., Weimerskirch, H. & Jouventin, P. 1993. High annual variability in reproductive success and survival of an antarctic seabird, the snow petrel *Pagodroma nivea*. *Oecologia* **94**: 278–285.
- Cherel, Y. 2008. Isotopic niches of Emperor and Adélie penguins in Adélie Land, Antarctica. *Mar. Biol.* **154**: 813–821.
- Cherel, Y. & Hobson, K.A. 2007. Geographical variation in carbon stable isotope signatures of marine predators: a tool to investigate their foraging areas in the Southern Ocean. *Mar. Ecol. Prog. Ser.* **329**: 281–287.
- Cherel, Y., Fontaine, C., Richard, P. & Labat, J.P. 2010. Isotopic niches and trophic levels of myctophid fishes and their predators in the Southern Ocean. *Limnol. Oceanogr.* **55**: 324–332.
- Cherel, Y., Koubbi, P., Giraldo, C., Penot, F., Tavernier, E., Moteki, M., Ozouf-Costaz, C., Causse, R., Chartier, A. & Hosie, G. 2011. Isotopic niches of fishes in coastal, neritic and oceanic waters off Adélie Land, Antarctica. *Polar Sci.* **5**: 286–297.
- Constable, A.J., Melbourne-Thomas, J., Corney, S.P., Arrigo, K.R., Barbraud, C., Barnes, D.K., Bindoff, N.L., Boyd, P.W., Brandt, A., Costa, D.P., Davidson, A.T., Ducklow, H.W., Emmerson, L., Fukuchi, M., Gutt, J., Hindell, M.A., Hofmann, E.E., Hosie, G.W., Iida, T., Jacob, S., Johnston, N.M., Kawaguchi, S., Kokubun, N., Koubbi, P., Lea, M.A., Makhado, A., Massom, R.A., Meiners, K., Meredith, M.P., Murphy, E.J., Nicol, S., Reid, K., Richerson, K., Riddle, M.J., Rintoul, S.R., Smith, W.O., Southwell, C., Stark, J.S., Sumner, M., Swadling, K.M., Takahashi, K.T., Trathan, P.N., Welsford, D.C., Weimerskirch, H., Westwood, K.J., Wienecke, B.C., Wolf-Gladrow, D., Wright, S.W., Xavier, J.C. & Ziegler, P. 2014. Climate change and Southern Ocean ecosystems. I: how changes in physical habitats directly affect marine biota. *Glob. Change Biol.* **20**: 3004–3025.
- Coria, N.R., Soave, G.E. & Montalti, D. 1997. Diet of Cape Petrel *Daption capense* during the post-hatching period at Laurie Island, South Orkney Islands, Antarctica. *Polar Biol.* **18**: 236–239.
- Creet, S., van Franeker, J.A., Van Spanje, T.M. & Wolff, W.J. 1994. Diet of the Pintado Petrel *Daption capense* at King George Island, Antarctica, 1990/91. *Mar. Ornithol.* **22**: 221–229.
- Croxall, J.P. 1984. Seabirds. In Laws, R.M. (ed.) *Antarctic Ecology*, vol. 2. 534–616. London: Academic Press.
- Croxall, J.P., Trathan, P.N. & Murphy, E.J. 2002. Environmental change and Antarctic seabird populations. *Science* **297**: 1510–1514.
- Egevang, C., Stenhouse, I.J., Phillips, R.A., Petersen, A., Fox, J.W. & Silk, J.R.D. 2010. Tracking of Arctic terns *Sterna paradisaea* reveals longest animal migration. *Proc. Natl Acad. Sci. USA* **107**: 2078–2081.
- Favero, M., Blanco, G., Garcia, G., Copello, S., Pon, J.P.S., Frere, E., Quintana, F., Yorio, P., Rabuffetti, F., Canete, G. & Gandini, P. 2011. Seabird mortality associated with ice trawlers in the Patagonian shelf: effect of discards on the occurrence of interactions with fishing gear. *Anim. Conserv.* **14**: 131–139.
- Green, K. 1986. Food of the Cape pigeon (*Daption capense*) from Princess Elizabeth Land, East Antarctica. *Notornis* **33**: 151–154.
- Griffiths, A.M. 1983. Factors affecting the distribution of the Snow Petrel (*Pagodroma nivea*) and the Antarctic Petrel (*Thalassoica antarctica*). *Ardea* **71**: 145–150.
- Harper, P.C., Croxall, J.P. & Cooper, J. 1985. A guide to foraging methods used by marine birds in antarctic and subantarctic seas. *Biomass Handbook* **24**: 1–22.
- Hobson, K.A. & Clark, R.G. 1992. Assessing avian diets using stable isotopes I: turnover of ^{13}C in tissues. *Condor* **94**: 181–188.
- Hobson, K.A. & Clark, R.G. 1993. Turnover of ^{13}C in cellular and plasma fractions of blood: implications for non destructive sampling in avian dietary studies. *Auk* **110**: 638–641.
- 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. *Mar. Ecol. Prog. Ser.* **198**: 273–281.
- del Hoyo, J., Elliott, A. & Sargatal, J. 1996. *Handbook of the Birds of the World*, Vol. 3. Barcelona: Lynx Edicions.
- Isenmann, P. 1970. Note sur la biologie de reproduction comparée des damiers du Cap *Daption capensis* aux Orcades du sud et en Terre Adélie. *L'Oiseau et R.F.O.* **40**: 135–141.
- Isenmann, P. & Trawa, G. 1970. Contribution à la biologie de reproduction du Pétrel des Neiges (*Pagodroma nivea* Forster). Le problème de la petite et de la grande forme. *L'Oiseau et R.F.O.* **40**: 99–134.
- IUCN. 2015. *IUCN Red List of Threatened Species. Version 2015.3*. Available at: <http://www.iucnredlist.org> (accessed 7 October 2015).
- Jaeger, A., Blanchard, P., Richard, P. & Cherel, Y. 2009. Using carbon and nitrogen isotopic values of body feathers to infer inter- and intra-individual variations of seabird feeding ecology during moult. *Mar. Biol.* **156**: 1233–1240.
- Jaeger, A., Lecomte, V.J., Weimerskirch, H., Richard, P. & Cherel, Y. 2010. Seabird satellite tracking validates the use of latitudinal isoscapes to depict predators' foraging areas in the Southern Ocean. *Rapid Commun. Mass Spectrom.* **24**: 3456–3460.

- Jaeger, A., Jaquemet, S., Phillips, R.A., Wanless, R.M., Richard, P. & Cherel, Y. 2013. Stable isotopes document inter- and intra-specific variation in feeding ecology of nine large southern Procellariiformes. *Mar. Ecol. Prog. Ser.* **490**: 255–266.
- Jenouvrier, S., Barbraud, C. & Weimerskirch, H. 2003. Effects of climate variability on the temporal population dynamics of southern fulmars. *J. Anim. Ecol.* **72**: 576–587.
- Jenouvrier, S., Barbraud, C. & Weimerskirch, H. 2005. Long-term contrasted responses to climate of two Antarctic seabird species. *Ecology* **86**: 2889–2903.
- Jenouvrier, S., Péron, C. & Weimerskirch, H. 2015. Extreme climate events and individual heterogeneity shape life history traits and population dynamics. *Ecol. Monogr.* **85**: 605–624.
- Joiris, C.R., Humphries, G.R.W. & De Broyer, A. 2013. Seabirds encountered along return transects between South Africa and Antarctica in summer in relation to hydrological features. *Polar Biol.* **36**: 1633–1647.
- Louzao, M., Pinaud, D., Peron, C., Delord, K., Wiegand, T. & Weimerskirch, H. 2011. Conserving pelagic habitats: seascape modelling of an oceanic top predator. *J. Appl. Ecol.* **48**: 121–132.
- Mackley, E.K., Phillips, R.A., Silk, J.R.D., Wakefield, E.D., Afanasyev, V., Fox, J.W. & Furness, R.W. 2010. Free as a bird? Activity patterns of albatrosses during the nonbreeding period. *Mar. Ecol. Prog. Ser.* **406**: 291–303.
- Mackley, E.K., Phillips, R.A., Silk, J.R.D., Wakefield, E.D., Afanasyev, V. & Furness, R.W. 2011. At-sea activity patterns of breeding and nonbreeding White-chinned Petrels *Procellaria aequinoctialis* from South Georgia. *Mar. Biol.* **158**: 429–438.
- Marchant, S. & Higgins, P.J. 1990. *Handbook of Australian, New Zealand and Antarctic birds*, Vol. 1, 126–134. Marchant, S. & Higgins, P. J. (eds) Melbourne, Vic: Oxford University Press.
- McConnell, B.J., Chambers, C. & Fedak, M.A. 1992. Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern Ocean. *Antarct. Sci.* **4**: 393–398.
- Micol, T. & Jouventin, P. 2001. Long-term population trends in seven Antarctic seabirds at Pointe Géologie (Terre Adélie). Human impact compared with environmental change. *Polar Biol.* **24**: 175–185.
- Mougin, J.L. 1967. Etude écologique des deux espèces de fulmars le Fulmar atlantique (*Fulmarus glacialis*) et le Fulmar antarctique (*Fulmarus glacialisoides*). *L'Oiseau et R.F.O.* **37**: 57–103.
- Murphy, R.C. 1964. Systematics and distribution of Antarctic petrels. In Carrick, R., Holdgate, M. & Prevost, J. (eds) *Biologie Antarctique*: 349–358. Paris: Hermann.
- Offredo, C. & Ridoux, V. 1986. The diet of Emperor Penguins *Aptenodytes forsteri* in Adélie Land, Antarctica. *Ibis* **128**: 409–413.
- Pedersen, M.W., Patterson, T.A., Thygesen, U.H. & Madsen, H. 2011. Estimating animal behavior and residency from movement data. *Oikos* **120**: 1281–1290.
- Péron, C., Delord, K., Phillips, R.A., Charbonnier, Y., Marteau, C., Louzao, M. & Weimerskirch, H. 2010. Seasonal variation in oceanographic habitat and behaviour of White-chinned Petrels *Procellaria aequinoctialis* from Kerguelen Island. *Mar. Ecol. Prog. Ser.* **416**: 267–284.
- Péron, C., Weimerskirch, H. & Bost, C.-A. 2012. Projected poleward shift of king penguins' (*Aptenodytes patagonicus*) foraging range at the Crozet Islands, southern Indian Ocean. *Proc. R. Soc. Lond. Ser. B* **279**: 2515–2523.
- Phillips, R.A. & Hamer, K.C. 2000. Postnatal development of northern fulmar chicks, *Fulmarus glacialis*. *Physiol. Biochem. Zool.* **73**: 597–604.
- Phillips, R.A., Xavier, J.C., Croxall, J.P. & Burger, A.E. 2003. Effects of satellite transmitters on albatrosses and petrels. *Auk* **120**: 1082–1090.
- Phillips, R.A., Silk, J.R.D., Croxall, J.P., Afanasyev, V. & Briggs, D.R. 2004. Accuracy of geolocation estimates for flying seabirds. *Mar. Ecol. Prog. Ser.* **266**: 265–272.
- Phillips, R., Bearhop, S., McGill, R. & Dawson, D. 2009. Stable isotopes reveal individual variation in migration strategies and habitat preferences in a suite of seabirds during the nonbreeding period. *Oecologia* **160**: 795–806.
- Pinet, P., Jaquemet, S., Pinaud, D., Weimerskirch, H., Phillips, R.A. & Le Corre, M. 2011. Migration, wintering distribution and habitat use of an endangered tropical seabird, Barau's Petrel *Pterodroma baraui*. *Mar. Ecol. Prog. Ser.* **423**: 291–302.
- Pineiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team. 2013. *nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-117*. Available at: <http://CRAN.R-project.org/package=nlme> (accessed 15 September 2015).
- Prendergast, J.R., Quinn, R.M., Lawton, J.H., Eversham, B.C. & Gibbons, D.W. 1993. Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature* **365**: 335–337.
- Quillfeldt, P., McGill, R.A.R., Furness, R.W., Mostl, E., Ludynia, K. & Masello, J.F. 2012. Impact of miniature geolocation loggers on a small petrel, the Thin-billed Prion *Pachyptila belcheri*. *Mar. Biol.* **159**: 1809–1816.
- Quillfeldt, P., Masello, J.F., Navarro, J. & Phillips, R.A. 2013. Year-round distribution suggests spatial segregation of two small petrel species in the South Atlantic. *J. Biogeogr.* **40**: 430–441.
- Quillfeldt, P., Cherel, Y., Delord, K. & Weimerskirch, H. 2015. Cool, cold or colder? Spatial segregation of prions and blue petrels is explained by differences in preferred sea surface temperatures. *Biol. Lett.* **11**: 4, 20141090.
- R Core Team 2015. R: A Language and Environment for Statistical Computing. Vienna: R Foundation for Statistical Computing, <https://www.R-project.org>
- Raymond, B., Lea, M.A., Patterson, T., Andrews-Goff, V., Sharples, R., Charrassin, J.B., Cottin, M., Emmerson, L., Gales, N., Gales, R., Goldsworthy, S.D., Harcourt, R., Kato, A., Kirkwood, R., Lawton, K., Ropert-Coudert, Y., Southwell, C., van den Hoff, J., Wienecke, B., Woehler, E.J., Wotherspoon, S. & Hindell, M.A. 2015. Important marine habitat off east Antarctica revealed by two decades of multi-species predator tracking. *Ecography* **38**: 121–129.
- Rayner, M.J., Taylor, G.A., Gummer, H.D., Phillips, R.A., Sagar, P.M., Shaffer, S.A. & Thompson, D.R. 2012. The breeding cycle, year-round distribution and activity patterns of the endangered Chatham Petrel (*Pterodroma axillaris*). *Emu* **112**: 107–116.
- Ribic, C.A., Chapman, E., Fraser, W.R., Lawson, G.L. & Wiebe, P.H. 2008. Top predators in relation to bathymetry,

- ice and krill during austral winter in Marguerite Bay, Antarctica. *Deep-Sea Res. II* **55**: 485–499.
- Ribic, C.A., Ainley, D.G., Ford, R.G., Fraser, W.R., Tynan, C.T. & Woehler, E.J.** 2011. Water masses, ocean fronts, and the structure of Antarctic seabird communities: putting the eastern Bellingshausen Sea in perspective. *Deep-Sea Res. II* **58**: 1695–1709.
- Richard, Y., Abraham, E.R. & Filippi, D.** 2011. *Assessment of the risk to seabird populations from New Zealand commercial fisheries. Final Res.* Report for research projects IPA2009–19 and IPA2009–20. Unpublished report held by Ministry for Primary Industries, Wellington.
- Ridoux, V. & Offredo, C.** 1989. The diets of five summer breeding seabirds in Adélie Land, Antarctica. *Polar Biol.* **9**: 137–145.
- Shaffer, S.A., Tremblay, Y., Weimerskirch, H., Scott, D., Thompson, D.R., Sagar, P.M., Moller, H., Taylor, G.A., Foley, D.G., Block, B.A. & Costa, D.P.** 2006. Migratory shearwaters integrate oceanic resources across the Pacific Ocean in an endless summer. *Proc. Natl Acad. Sci. USA* **103**: 12799–12802.
- Soave, G.E., Coria, N.R. & Montalti, D.** 1996. Diet of the Pintado Petrel *Daption capense* during the late incubation and chick-rearing periods at Laurie Island, South Orkney Islands, Antarctica, January–February 1995. *Mar. Ornithol.* **24**: 35–37.
- Sokolov, S. & Rintoul, S.R.** 2009a. Circumpolar structure and distribution of the Antarctic Circumpolar Current fronts: 1. Mean circumpolar paths. *J. Geophys. Res. Oceans* **114**: C11018.
- Sokolov, S. & Rintoul, S.R.** 2009b. Circumpolar structure and distribution of the Antarctic Circumpolar Current fronts: 2. Variability and relationship to sea surface height. *J. Geophys. Res. Oceans* **114**: C11019.
- Tartu, S., Angelier, F., Wingfield, J., Bustamante, P., Labadie, P., Budzinski, H., Weimerskirch, H., Bustnes, J. & Chastel, O.** 2015. Corticosterone, prolactin and egg neglect behavior in relation to mercury and legacy POPs in a long-lived Antarctic bird. *Sci. Total Environ.* **505**: 180–188.
- Veit, R.R. & Hunt, G.L. Jr** 1991. Broad-scale density and aggregation of pelagic birds from a circumnavigational survey of the antarctic ocean. *Auk* **108**: 790–800.
- Warham, J.** 1990. *The Petrels: Their Ecology and Breeding Systems.* London: Academic Press.
- Warren, J.D., Santora, J.A. & Demer, D.A.** 2009. Submesoscale distribution of Antarctic krill and its avian and pinniped predators before and after a near gale. *Mar. Biol.* **156**: 479–491.
- Weimerskirch, H., Chereil, Y., Delord, K., Jaeger, A., Patrick, S.C. & Riotte-Lambert, L.** 2014. Lifetime foraging patterns of the wandering albatross: life on the move!. *J. Exp. Mar. Biol. Ecol.* **450**: 68–78.
- Weimerskirch, H., Tarroux, A., Chastel, O., Delord, K., Chereil, Y. & Descamps, S.** 2015. Population-specific wintering distributions of adult south polar skuas over three oceans. *Mar. Ecol. Prog. Ser.* **538**: 229–237.
- Williams, P.H.** 1998. Key sites for conservation: area-selection methods for biodiversity. In Mace, G., Balmford, A. & Ginsberg, J.R. (eds) *Conservation in a Changing World: Integrating Process into Priorities for Action*: 211–249. Cambridge: Cambridge University Press.
- Wilson, R.P., Ducamp, J.J., Rees, G., Culik, B.M. & Niekamp, K.** 1992. Estimation of location: global coverage using light intensity. In Priede, I.M.S.S. (ed.) *Wildlife Telemetry: Remote Monitoring and Tracking of Animals*: 131–134. Chichester: Ellis Horward.
- Woehler, E.J., Raymond, B., Boyle, A. & Stafford, A.** 2010. Seabird assemblages observed during the BROKE-West survey of the Antarctic coastline (30 degrees E–80 degrees E), January–March 2006. *Deep-Sea Res. II* **57**: 982–991.
- Zuur, A.F., Ieno, E.N. & Elphick, C.S.** 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* **1**: 3–14.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Distributions of sympatric fulmarine petrels tracked using geolocators (per cent of time of residence spent in each cell) during breeding period, (1) pre-breeding (left panel) and (2) chick-rearing (post-brood; right panel) of (a) Southern Fulmar, (b) Cape Petrel, and (c) Snow Petrel.

Figure S2. Monthly spatial distribution of fulmarine petrels.

Figure S3. Spatial distribution of proportion of resting time (mean) of sympatric fulmarine petrels tracked using geolocators during non-breeding: (a) Southern Fulmar, (b) Cape Petrel and (c) Snow Petrel.

Figure S4. Hotspots of sympatric fulmarine petrels tracked using geolocators (distribution overlap of species-specific top-scoring 5% of time spent per square corresponds to the values of the upper quartile for cells with at least two species; see Material and Methods section) during chick-rearing period (post-brood).

Table S1. Detailed list of the analyses performed (Generalized Linear Mixed Models with a random factor ‘individual’, except when mentioned*).

Table S2. Fixed-effect parameters of generalized linear model of the variation of the activity pattern (mean daily proportion of time spent wet) for Southern Fulmar (SOFU), Cape Petrel (CAPE) and Snow Petrel (SNPE).

Table S3. Fixed-effect parameters of generalized linear mixed model of the variation of the activity pattern (daily proportion of time spent wet) for Southern Fulmar (SOFU), Cape Petrel (CAPE),

and Snow Petrel (SNPE) during the non-breeding period.

Table S4. Fixed-effect parameters of generalized linear mixed model of the variation of the activity pattern (proportion of time spent wet) for Southern Fulmar during the non-breeding period.

Table S5. Fixed-effect parameters of generalized linear mixed model of the variation of the activity

pattern (proportion of time spent wet) for Cape Petrel during the non-breeding period.

Table S6. Fixed-effect parameters of generalized linear mixed model of the variation of the activity pattern (proportion of time spent wet) for Snow Petrel during the non-breeding period.