



Foraging trips and isotopic niche of chick-rearing South Georgian diving petrels from the Kerguelen Islands

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ABSTRACT: Seabirds are central place foragers, relying on prey that is patchily distributed and of variable predictability. Species travelling at a high energetic cost are more strongly dependent on spatially predictable prey. This is the case for diving petrels *Pelecanoides* spp., which are small Procellariiformes that feed by pursuit diving and travel by flapping constantly. Despite their abundance and importance as zooplankton consumers, information on the foraging strategy of diving petrels is still lacking. The detailed at-sea movements and the trophic niche of the South Georgian diving petrel *P. georgicus* was investigated for the first time using miniaturized GPS and the stable isotope method, respectively. Overall, South Georgian diving petrels from the Kerguelen Islands performed unexpected, direct and long-distance trips (mean foraging range: 191–217 km) to the Antarctic Polar Front, south of the archipelago. This foraging ground is a productive and predictable area, where the birds stopped and fed at the distal part of their trip. Blood isotopic values indicate that the tracked birds fed consistently on macrozooplankton. Such a distant oceanic feeding strategy contrasts with the coastal foraging patterns of the closely related common diving petrel *P. urinatrix*. Commuting to a more distant but easily accessible resource allows South Georgian diving petrels to cope with their high commuting costs, and to segregate spatially from the sympatric common diving petrel during the breeding season.

KEY WORDS: At-sea distribution · Trophic niche · Procellariiformes · *Pelecanoides georgicus* · Southern Ocean

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1. INTRODUCTION

In the ocean, physical processes determine the hydrological structure and hence the distribution of marine resources and of their predators (McGowan 1986, Hunt et al. 1999). Oceanic seabirds are generally considered to rely on patchy resources with a variable predictability, both spatially and temporally. Species unable to fly (penguins) or those flying at a high energetic cost by constant flapping of wings (e.g.

auks, cormorants, diving petrels) are much more dependent on spatially predictable prey than gliding species that travel huge distances at a low cost, such as albatrosses and most petrels (Weimerskirch 2007).

Diving petrels are small, short-winged procellariiform seabirds of the Southern Hemisphere; they have a high wing loading, a fast flapping flight and feed by pursuit diving (Warham 1996, Navarro et al. 2013). Despite their abundance and their important role in food webs as zooplankton consumers (Guinet

et al. 1996, BirdLife International 2021), information on the movements and foraging areas of diving petrels is largely lacking. Furthermore, how these small planktivorous species manage to trophically segregate within the genus *Pelecanoides* and with the numerous other species of small petrels remains poorly known. Until recently, knowledge of the foraging ecology of diving petrels was mainly based on at-sea surveys, dietary analyses and stable isotopes (Bocher et al. 2000, Chérel et al. 2014, Fromant et al. 2020a). Miniaturization of data loggers now allows tracking these species during the breeding season (Navarro et al. 2013, Rayner et al. 2017, Zhang et al. 2019, Dunphy et al. 2020, Fromant et al. 2021). However, no previous studies have been undertaken in the southern Indian Ocean, where several million pairs of South Georgian diving petrels *P. georgicus* (SGDP) and common diving petrels *P. urinatrix* (CDP) breed within the Kerguelen Archipelago (Weimerskirch et al. 1989). In this locality, dietary studies indicated a complete trophic segregation, with SGDP feeding mostly on euphausiids and small copepods, while CDP prey upon hyperiids and large copepods (Bocher et al. 2000).

In the present study, our aim was to investigate for the first time the foraging strategy of SGDP during the breeding season at the Kerguelen Islands. We sought to assess where SGDP foraged during the chick-rearing period, and how their feeding niche differed from that of the closely related CDP. To address these questions, we investigated the movements of breeding birds using miniaturized global positioning system (GPS) data loggers and measured their isotopic niche, as a proxy of the trophic niche, using the stable isotope method ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) on blood samples collected from the tracked birds. Based on the short duration of foraging trips at this time of the breeding cycle (1–2 d at sea; Bocher et al. 2000), their costly and direct flight, and previous information on diet and at-sea surveys, we predicted: (1) that SGDP depend on productive, pelagic areas where they feed efficiently on energetic macrozooplankton (Schaafsma et al. 2018), and (2) that these areas were reached by directional, fast-commuting trips to offshore waters.

2. MATERIALS AND METHODS

2.1. Study area

Fieldwork was carried out during 3 breeding seasons (8–11 January 2016; 12–17 January 2018; 9–15 January 2019) on Ile aux Cochons (49.476° S,

70.049° E), an island free of introduced mammals that is located in the enclosed Golfe du Morbihan, Kerguelen Archipelago (7215 km²), southern Indian Ocean. The 2 most prominent oceanic fronts in the area are the Antarctic Polar Front (APF) and the Fawn Trough Current (FTC), which are part of the Antarctic Circumpolar Current. The APF is a major hydrological discontinuity, which marks the boundary between southern cold waters of Antarctic origin and the northern warmer subantarctic waters (Park et al. 2014). The FTC is a strong current along the southern limit of the Kerguelen Plateau (Park et al. 2008). The bathymetry of the Kerguelen Plateau leads to an upwelling of the cold Winter Water flow along the Eastern Kerguelen Plateau shelf break (Park et al. 2008), which produces high primary productivity downstream of the Plateau. These favourable conditions combined with the archipelago's isolation within the Southern Ocean explain why the Kerguelen Islands host large populations of marine predators (Barbraud et al. 2020), including large sympatric populations of CDP and SGDP (Weimerskirch et al. 1989).

2.2. Fieldwork

In order to track the movements of breeding adult SGDP, 20 to 35 burrows containing chicks were studied each year. The nesting chamber within each burrow was accessed via a study hole dug into the access tunnel 30–50 cm in front of the chamber (this distance from the chamber minimised disturbance during capture of adults feeding their chicks) (Fromant et al. 2020b). The logger deployments took place during the night, which facilitated the deployment of GPS tags on parent birds that had just been relieved by their partners and were ready to go to sea (see Fromant et al. 2021). The age of the chicks ranged from 1 to >35 d (the chick-rearing period lasts 44–52 d; Jouventin et al. 1985).

A total of 32 breeding SGDP were fitted with a nanoFix-GEO miniaturized GPS (Pathtrack). The sampling interval of GPS fixes was 5 min. The loggers were attached to the base of 2–3 tail feathers using waterproof Tesa tape (Tesa 4651; Beiersdorf). The total mass of the loggers ranged between 1.2 and 2.6 g, i.e. corresponding to $2.0 \pm 0.19\%$ (mean \pm SE) of the birds' body mass (130 ± 16 g). SGDP were weighed (± 2 g; Pesola Precision Scale) before release. During instrumentation, biometric measurements were restricted to body mass, to minimise stress associated with handling.

Recapture of the equipped SGDP took place on their return to the colony on the following night(s), after confirmation of the partner's presence in the burrow. To determine whether a changeover had taken place without disturbing birds, small sticks were placed vertically at the opening of the burrows and visually checked to see if they had been knocked down. A blood sample (<0.3 ml) was collected from the brachial vein for stable isotope analysis and molecular sexing. Handling time at deployment (banding, weighing and device attachment) and recapture (device removal, measurements, blood sampling) was usually less than 5 min. After removing the device from the bird's tail, the following biometric measurements were taken: wing length (± 1 mm; ruler), bill length and tarsus length (± 0.1 mm; Vernier calliper) and body mass (± 2 g, Pesola Precision Scale). For logistical reasons, it was not possible to assess the impact of logger attachment on trip duration. However, no breeding failure occurred during GPS deployments. In addition, no significant effect of handling and GPS attachment has been reported on trip duration and chick growth rate of the similar sized CDP (Fromant et al. 2021).

2.3. Track analysis

To study the at-sea distribution of SGDP, we used a time-in-area approach to look at the influence of environmental variables on the time birds spent in an area (Bost et al. 1997, Delord et al. 2013, Domalik et al. 2018). For each bird, we calculated the time spent foraging in each visited $0.5 \times 0.5^\circ$ cell. To identify foraging/resting state (hereafter foraging, see Fromant et al. 2021), a conservative instantaneous speed threshold method was used following Petalas et al. (2021):

$$\text{Speed Threshold} = 2 \times (\text{Drift Speed} \times \text{Average Flight Speed}) / (\text{Drift Speed} + \text{Average Flight Speed}) \quad (1)$$

For SGDP, the speed threshold was 9.1 km h^{-1} , with a drift speed of 5 km h^{-1} (Petalas et al. 2021), and average flight speed of 50 km h^{-1} . Average flight speed was estimated from the analysis of 15 flying bouts (with regular fixes) using raw data. Regular distance between location points over large distances (45–225 km) were used to select continuous flying bouts, and speed was averaged for each flying bout ($50 \pm 11 \text{ km h}^{-1}$). Values equal or lower than the speed threshold were considered to represent foraging. This threshold was in the same range as for the

little auk *Alle alle*, a species with similar body size and wing-flapping frequency (Amélineau et al. 2016, Jakubas et al. 2020).

2.4. Stable isotopes

The stable isotope method has been widely applied in the southern Indian Ocean, with $\delta^{13}\text{C}$ values of seabirds indicating their latitudinal foraging habitats (Cherel & Hobson 2007, Jaeger et al. 2010) and their $\delta^{15}\text{N}$ values increasing with trophic level (Cherel et al. 2010). The isotopic niche of chick-rearing SGDP was investigated by measuring $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of whole blood, which represent a dietary integration period of 2–4 wk before sampling (Bearhop et al. 2002). Blood samples were freeze-dried, ground to powder, and homogenized, before subsamples were weighed with a microbalance and packed in tin cups. The relative abundance of carbon and nitrogen isotopes was determined with a continuous-flow mass spectrometer (Thermo Scientific Delta V Advantage) coupled to an elemental analyser (Thermo Scientific Flash EA 1112). Isotopic results are presented in the δ notation relative to Vienna PeeDee Belemnite and atmospheric N_2 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. Replicate measurements of internal laboratory standards (acetanilide) indicate measurement errors $< 0.10\%$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. The consistently low C:N mass ratio (< 4.0) verified that the low lipid content of whole blood did not necessitate lipid extraction (Cherel et al. 2005). The isotopic niche position and width were compared between years using the ellipse area-based metrics of the 'SIBER' package (Jackson et al. 2011). The isotopic niche was estimated by the 40% standard ellipse area corrected for small sample size (SEA_C), and Bayesian standard ellipses areas (SEA_B) on 10^5 replicates were used to measure the overlap of the isotopic niches between years (Jackson et al. 2011).

2.5. Statistical analysis

All statistical analyses were conducted in the R statistical environment 4.0.0 (R Core Team 2021). To investigate the flying speed (proxy of foraging behaviour) of SGDP, we generated multiple generalized linear mixed models (GLMMs) using the package 'glmmADMB' (Bolker et al. 2012). Year, distance to the colony, sea surface temperature (SST), chlorophyll *a* (chl *a*) concentration and bathymetry were considered as fixed effects, with the individual bird added as

a random effect (Table S1 in the Supplement at www.int-res.com/articles/suppl/m689p169_supp.pdf). SST, chl *a* and bathymetry potentially influence marine predator habitat use (Péron et al. 2012, Reisinger et al. 2018) and were downloaded from Copernicus (<http://marine.copernicus.eu/>). For all models, a Gaussian family was selected (error structure approached the normal distribution), all combinations of variables were then tested and ranked based on their Akaike's Information Criterion (AIC), and the global models were checked to ensure normality and homoscedasticity of the residuals (Zuur et al. 2010) before further statistical tests. Inter-annual differences of trip parameters and isotopic values were quantified using ANOVA or Welch's ANOVA, and post-hoc tests were conducted using *t*-tests (parametric), or Kruskal-Wallis and Mann-Whitney *U*-tests (non-parametric) depending on data distribution. Data were first checked for normality (Shapiro-Wilk test) and equality of variances (Levene test). Estimates are presented as means \pm SD.

3. RESULTS

3.1. At-sea movements and patterns of departure from and return to the breeding colony

Forty trips were recorded during the 3 studied seasons. All tracks were complete except during 1 season (2016, $n = 9$ incomplete trips; Table 1, Fig. 1). All tracked SGDP performed direct, long-distance trips toward the south of the Kerguelen Archipelago, to the vicinity of the APF (Fig. 1). The mean duration of foraging trips was about 1 d, ranging between 26 and 30 h, without significant inter-year differences (Mann-Whitney *U*-test: $U = 24.5$, $p = 0.728$; Table 1). The mean maximum foraging distance ranged from 191 to 217 km, with a corresponding total distance travelled ranging from 478 to 572 km, depending on years (Table 1). SGDP travelled farther on average

Table 1. Summary of foraging trip metrics (mean \pm SD) for GPS-equipped South Georgian diving petrels *Pelecanoides georgicus* from Ile aux Cochons (Kerguelen Islands) during the chick-rearing period. Total distance travelled, trip duration, time spent foraging and time between sunset and return were determined using complete trips only. For each parameter, values not sharing the same superscript letter are significantly different (Mann-Whitney *U*-test: $p < 0.05$). All tracks were incomplete in 2016

	2016	2018	2019
Number of trips (n complete)	9 (0)	21 (8)	10 (7)
Number of individuals	9	16	7
Maximum foraging distance (km)	199 \pm 30 ^a	217 \pm 77 ^a	191 \pm 56 ^a
Total distance travelled (km)	–	572 \pm 146 ^a	478 \pm 100 ^a
Trip duration (h)	–	30.3 \pm 12.4 ^a	25.9 \pm 8.7 ^a
Time spent foraging (h; speed <9.1 km h ⁻¹)	–	14.0 \pm 9.7 ^a	11.9 \pm 5.2 ^a
Time between departure and sunrise (h)	3.4 \pm 1.5 ^{ab}	2.4 \pm 0.4 ^a	3.6 \pm 1.2 ^b
Time between sunset and return (h)	–	3.0 \pm 0.7 ^a	3.0 \pm 0.5 ^a
Mass at deployment (g)	117 \pm 10 ^a	122 \pm 10 ^a	127 \pm 15 ^a
Mass at retrieval (g)	128 \pm 14 ^a	130 \pm 12 ^a	136 \pm 16 ^a

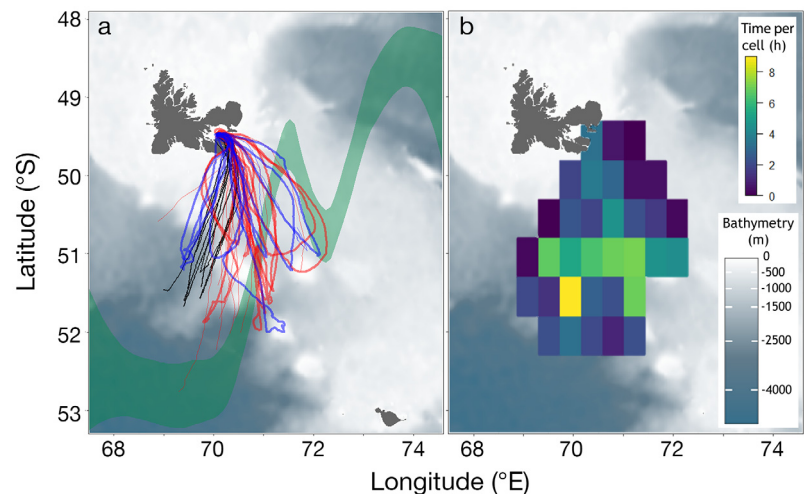


Fig. 1. At-sea distribution of tracked South Georgian diving petrels *Pelecanoides georgicus* from Ile aux Cochons (Kerguelen Islands) during the chick-rearing period. (a) Foraging tracks recorded in January 2016 (black, 9 trips from 9 individuals), January 2018 (red, 21 trips from 16 individuals) and January 2019 (blue, 10 trips from 7 individuals). Thick lines correspond to full trips (January 2018 = 8; January 2019 = 7). The green area corresponds to the average position of the Antarctic Polar Front (APF) determined from vertical profile characteristics of frontal sea surface height signatures (Venables et al. 2012, Kim & Orsi 2014). (b) Time spent foraging (9.1 km h⁻¹; see Section 2) within a 0.5° grid cell by instrumented birds during the chick-rearing period

in 2018 than during 2016 and 2019, although the difference was not significant (Table 1). All equipped birds left their burrows at the same time, i.e. between 2 and 3 h before sunrise, with a significant difference between 2018 and 2019 (Mann-Whitney

U -test: $U = 25.5$, $p = 0.006$). The return to the burrows followed a very similar pattern irrespective of year, i.e. 3 h after sunset (Table 1). Many departing birds crossed the land in the south of the archipelago (at night), flying at a minimum altitude of 250–300 m to reach the open sea (45% of outward trips; Fig. S1). Similarly, a minority of the tracks (21%) indicated that some birds directly crossed a portion of land before returning to the islet where the colony is located within the enclosed Golfe du Morbihan.

3.2. Changes in travelling speed

Flight speed analysis revealed 3 distinct phases during the trips: (1) an outward phase (mean duration: 6.8 h, i.e. 25.6% of the trip), at the beginning of which SGDP moved rapidly during their first hours of flight with the highest recorded speeds (mean speed = 59 km h^{-1} , range: $32\text{--}93 \text{ km h}^{-1}$, for the first 5% of the trip; Fig. 2). Flying speeds then gradually decreased until they fell below the threshold value (9.1 km h^{-1} , see Section 2.3) between commuting and foraging. This corresponded to the beginning of (2) the central phase, at the most distal part of the foraging trip during which the lowest velocity values were recorded. The birds spent the majority of their time at sea during the central phase (mean duration: 13.6 h, i.e. 49.2% of the trip) during which 72% of for-

aging locations were recorded (Fig. 2; Fig. S2). Then, during (3) the inward phase (mean duration: 6.1 h, i.e. 23.0% of the trip), the birds quickly set off again towards the north, heading directly to the breeding colony with few stops (Fig. 2). Their flying speed gradually increased until stabilizing at $40\text{--}60 \text{ km h}^{-1}$ up to 6 h before arrival, after which flying speeds slowly decreased until arrival at their burrows (Fig. 2).

3.3. Foraging area

The central phase of the trip corresponded roughly to an area located between the northern and southern boundaries of the APF (Fig. 1), where, accordingly, the highest value of time spent per sector occurred (Fig. 1b). This oceanic area was quite limited in size (about $42\,000 \text{ km}^2$), and corresponded to slope waters at the southern part of the Kerguelen shelf. The preferred model explaining the behaviour of SGDP (instantaneous speed) included a strong effect of distance from the colony and SST (Table S1). The model indicated that SGDP foraged in colder and deeper waters than those that were crossed during the outward and inward transit phases, and that primary productivity was significantly lower (Mann-Whitney U -test: all $p < 0.001$, Table 2; Table S1).

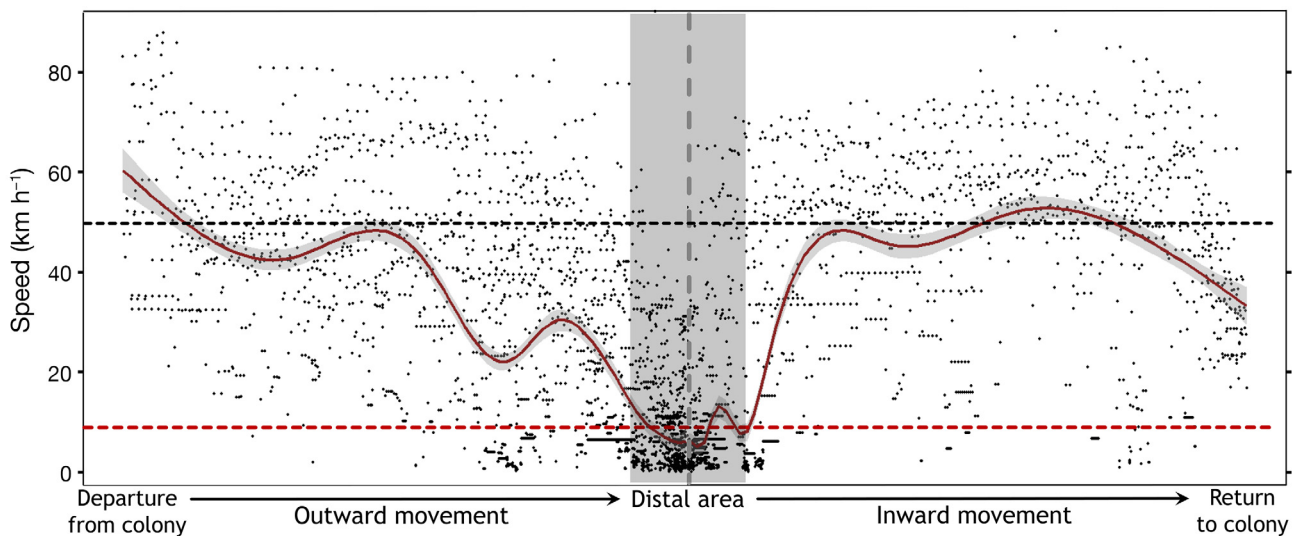


Fig. 2. Relationship between distance from the colony and flight speed of chick-rearing South Georgian diving petrels *Pelecanooides georgicus* during foraging trips (full trips only). The full red line corresponds to the data fitted with a generalized additive mixed model (\pm SE in shaded gray). For each trip, the distance from the colony corresponds to the proportion of the maximal distance from the colony (distance between colony and distal point). The distal point represents the farthest location from the colony reached during each trip (gray vertical dashed line). The shaded gray central bar corresponds to the 10% most distant area (standardised per trip). The horizontal black dashed line corresponds to the mean flying speed of the birds in commuting (50 km h^{-1}) and the horizontal red dashed line to the speed threshold determined to identify foraging behaviour (9.1 km h^{-1} ; see Section 2)

Table 2. Mean environmental variables (\pm SD) along commuting and foraging areas of GPS-equipped South Georgian diving petrels *Pelecanoides georgicus* from Ile aux Cochons (Kerguelen Islands) during the chick-rearing period. Data from the 3 studied seasons were pooled. SST: sea surface temperature

	Bathymetry (m)	SST ($^{\circ}$ C) (mg m $^{-3}$)	Chl <i>a</i>
Commuting	-726 \pm 710	4.60 \pm 0.73	0.47 \pm 0.58
Foraging	-1316 \pm 820	4.11 \pm 0.26	0.29 \pm 0.13

3.4. Stable isotopes

Whole-blood $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of chick-rearing SGDP averaged -22.7 ± 0.5 and 8.5 ± 0.3 ‰ ($n = 45$), respectively. Variances were overall low either between individuals or between years, and the isotopic niches overlapped between all years (Table S2). Blood $\delta^{15}\text{N}$ values were not significantly different amongst years (Table 3). In contrast, $\delta^{13}\text{C}$ values were lower in 2018 than in 2016 and 2019 (Mann-Whitney *U*-test: $p < 0.01$), but the isotopic difference was low (0.6‰). The areas of both the convex hulls and SEA_c were 2–3 times larger in 2016 than in 2018 and 2019 (Fig. 3).

4. DISCUSSION

Two broad types of foraging trips have been described amongst seabirds (Weimerskirch 1997, 2007). ‘Looping’ movement describes a trip where the bird does not return to the colony from the same

Table 3. Whole blood $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of South Georgian diving petrels *Pelecanoides georgicus* from Ile aux Cochons (Kerguelen Islands) during the chick-rearing period. Values are means \pm SD with the number of individuals given in brackets. Values not sharing the same superscript letter are significantly different (*t*-test: $p < 0.05$). More birds were blood sampled than tracked in 2018 and 2019. This difference is due to failed deployments (failed device or defaults in programming). SEA_c : standard ellipses corrected for sample size

	2016	2018	2019
Blood $\delta^{13}\text{C}$ (‰)	-23.0 ± 0.5^a (7)	-22.4 ± 0.3^b (23)	-23.0 ± 0.3^a (15)
Blood $\delta^{15}\text{N}$ (‰)	8.8 ± 0.4^a (7)	8.4 ± 0.2^a (23)	8.5 ± 0.3^a (15)
SEA_c (‰ 2)	0.63	0.18	0.19
Convex hull (‰ 2)	0.84	0.53	0.38

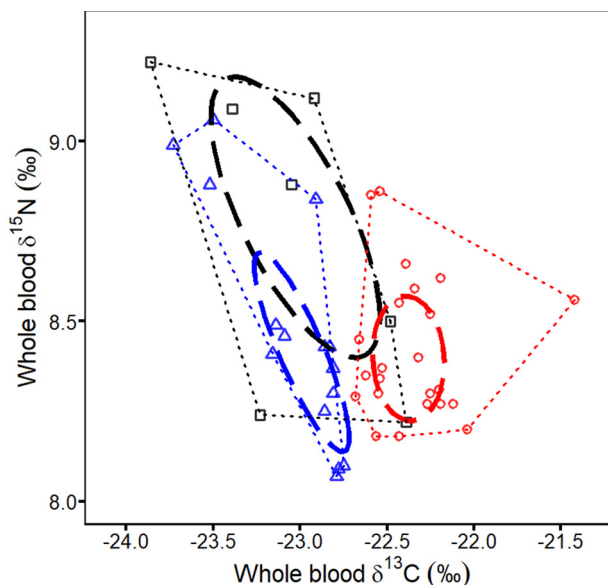


Fig. 3. Whole blood $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of South Georgian diving petrels *Pelecanoides georgicus* from Ile aux Cochons (Kerguelen Islands) during the chick-rearing period. Black squares = January 2016 ($n = 7$); red circles = January 2018 ($n = 23$); blue triangles = January 2019 ($n = 15$). Dashed ellipses represent the standard ellipses corrected for sample size (SEA_c ; 40% probability of containing a subsequently sampled datum regardless of sample size; Jackson et al. 2011). Thin dashed lines correspond to the total convex hull (isotopic niche width)

direction as the outward phase. ‘Commuting’ movement is where the bird leaves the colony with a particular bearing, and keeps this bearing while flying rapidly until it reaches a particular area where it increases its turning rate, and eventually decreases its flight speed. After a certain time, the bird returns in a direct flight path to the breeding colony (e.g. Amélineau et al. 2016, Domalik et al. 2018). Looping trips suggest that individuals search for unpredictable resources during the whole trip, stopping and feeding when they find prey items, whereas commuting trips suggest that the birds ‘know’ where to find predictable food, probably from experience (Weimerskirch 2007).

Our study shows SGDP typically perform commuting, long-distance (but short-duration) trips during the chick-rearing period. All tracked birds travelled to the APF, where they stopped at the distal part of their trip. This area within the APF appears to be very favourable for foraging SGDP, as the birds travelled fast to maximize their foraging time there and returned to the colony with few stops. Thus, at-sea movements of SGDP during chick rearing indicate profitable offshore prey stocks over the southern

limit of the shelf, near the APF. The consistency of SGDP foraging in such a restricted but distant area, from one summer to another, indicates the presence of a consistent, reliable food source.

Consistency of foraging within a same area should be strongest when prey availability is predictable (Weimerskirch 2007). Indeed, the APF is a major foraging ground with predictable resources for many marine predators (Bost et al. 2009), especially at Kerguelen Islands (Antarctic fur seals *Arctocephalus gazella*: Guinet et al. 2001; elephant seal *Mirounga leonina*: Bailleul et al. 2007; king penguin *Aptenodytes patagonicus*: Bost et al. 2002, 2009, Thiers et al. 2017). Mesoscale features at this front are known for concentrating prey because of enhanced productivity and physical forcing (Pakhomov 1993, Park et al. 2014). The spatial coherence of the APF persists enough to allow the development of large zooplankton stocks at an energetically relevant threshold for avian predators (van Franeker et al. 2002). The lower primary productivity in the petrels' foraging area compared with values recorded in the transit area is surprising, as high primary productivity can be expected in association with the APF (Pakhomov 1993). This unexpected result must be interpreted with caution. It likely results from the exceptionally high values of primary productivity that characterize the enclosed Golfe du Morbihan (Razouls et al. 1997), around the study colony, which induces a bias in the calculation of the mean primary productivity in the petrels' transit area. Similar foraging strategies toward a predictable feeding area have been reported in the Arctic for other small seabirds with high flying costs, such as auks (Amélineau et al. 2016, Domalik et al. 2018). However, none of these small flapping flight species has shown such extensive travel distances with continuous flight as those performed by SGDP.

Blood $\delta^{13}\text{C}$ values of SGDP agree well with a foraging habitat at the APF, with the average value being identical to the $\delta^{13}\text{C}$ estimation of the boundary between the Subantarctic and Antarctic Zones at -22.5‰ (Cherel & Hobson 2007). The blood $\delta^{15}\text{N}$ values indicate that the tracked SGDP fed consistently on low-trophic level prey during the 3 studied seasons. Feeding on macrozooplankton by SGDP is consistent with a previous dietary study at the Kerguelen Islands based on prey determination from regurgitates. During the chick-rearing period, SGDP feed their chicks with a well-digested crustacean-based diet dominated by the euphausiid *Thysanoessa macroura/vicina* and the copepod *Calanoides acutus*, with little inter-annual variations (Bocher et al. 2000).

Interestingly, CDPs, which are sympatric inshore foragers, feed their chicks with a barely digested crustacean-based diet that includes mainly the amphipod *Themisto gaudichaudii* and the large copepod *Paraeuchaeta antarctica*. These 2 prey are extremely abundant within the Golfe du Morbihan (Bocher et al. 2001, 2002). In contrast, prey items of SGDP foraging offshore are oceanic macrozooplankton species (Pakhomov 1993), which are abundant in offshore sub-surface waters around Kerguelen Islands and especially at the APF (Pakhomov 1993, Razouls et al. 1998). The lack of foraging activity of tracked SGDP within the productive Golfe du Morbihan is in agreement with at-sea records in Kerguelen coastal areas where, unlike CDP, no feeding concentrations of SGDP occur (Weimerskirch et al. 1989, A. Fromant & C. A. Bost pers. obs).

Differences in diving abilities could be a major factor explaining such strong differences in foraging areas between the 2 sibling species of diving petrels. By foraging at the distant APF, the smaller SGDP would have access to more accessible macrozooplankton prey at shallower depth compared to the Golfe du Morbihan where prey are present at deeper depths (Bocher et al. 2001). Indeed, at Kerguelen, SGDP seem to dive less deeply than the larger CDP, as suggested by pilot studies using capillary depth gauges (26 vs. 33 m, respectively; Bocher et al. 2000), which has been recently confirmed using time-depth recorders (Fromant et al. 2022). At-sea energy expenditure of SGDP is high as indicated by the doubly labelled water method ($4.1\times$ higher than the standard metabolic rate: Roby & Ricklefs 1986). This is a consequence of the high energy requirements for flapping flight and pursuit diving, while surface-feeding and gliding species of similar body size have lower energy expenditures (about $2\times$ less; Roby & Ricklefs 1986, Ricklefs et al. 1986). Thus, commuting to a distant but shallower and predictable resource would be an efficient feeding strategy allowing SGDP to cope with high-energy requirements during breeding, and result in a complete spatial segregation in feeding areas with the CDP during the breeding season.

Further studies using miniaturized tags and investigating the trophic and foraging behaviour between SGDP and CDP (Navarro et al. 2013, Fromant et al. 2022) should provide fascinating insights about (1) the processes that determine their preferential habitat use, (2) how the mesoscale dynamics of frontal structures drive their at-sea foraging strategies and (3) the potential mechanisms of niche divergence. The dependence of SGDP on the APF, which may be

influenced by current environmental changes, could have strong implications for its breeding populations, as already described for other Southern Ocean predators (Péron et al. 2012).

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