



HAL
open science

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

Charles-André Bost, Karine Delord, Yves Cherel, Colin Miskelly, Alice Carravieri,
Paco Bustamante, J. P. Y. Arnould, Aymeric Fromant

► **To cite this version:**

Charles-André Bost, Karine Delord, Yves Cherel, Colin Miskelly, Alice Carravieri, et al.. Foraging trips and isotopic niche of chick-rearing South Georgian diving petrels from the Kerguelen Islands. *Marine Ecology Progress Series*, 2022, 689, pp.169-177. <10.3354/meps14029>. <hal-03651876>

HAL Id: hal-03651876

<https://hal.science/hal-03651876v1>

Submitted on 6 Sep 2022

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



HAL Authorization

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

C.A. Bost¹, K. Delord¹, Y. Cherel¹, C.M. Miskelly², A. Carravieri¹, P. Bustamante^{4,5}, J.P.Y.
Arnould³, A. Fromant^{1,3}

¹ Centre d'Études Biologiques de Chizé, UMR 7372 du CNRS-La Rochelle Université, 405
route de Prissé-la-Charrière, 79360 Villiers-en-Bois, France

² Museum of New Zealand Te Papa Tongarewa, PO Box 467, Wellington 6140, New Zealand

³ School of Life and Environmental Sciences, Deakin University, 221 Burwood Hwy,
Burwood, VIC 3125, Australia

⁴ Littoral Environnement et Sociétés (LIENSs), UMR 7266 CNRS - La Rochelle Université, 2
rue Olympe de Gouges, 17000 La Rochelle, France

⁵ Institut Universitaire de France (IUF), 1 rue Descartes 75005 Paris, France

Corresponding author: charly.bost@cebc.cnrs.fr

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 of 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 are still lacking. The detailed at-sea movements and the trophic niche of the South Georgian diving petrel *Pelecanoides 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 shallower resource allows South Georgian diving petrels to cope with its high commuting costs, and to segregate spatially from the sympatric common diving petrel during the breeding season.

KEYWORDS: at-sea distribution, trophic niche, Procellariiform, *Pelecanoides georgicus*, Southern Ocean

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 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 (BirdLife International 2021, Guinet et al. 1996), information on the movements and foraging areas of diving petrels are 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, Cherel 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 (SGDP, *Pelecanoides georgicus*) and common diving petrels (CDP, *P. urinatrix*) 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 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 miniaturised global positioning system (GPS) data loggers and measured their isotopic niche - 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: i) that SGDP depend on productive, pelagic areas where they feed efficiently on energetic macrozooplankton (Schaafsma et al. 2018), and ii) that these areas were reached by directional, fast commuting trips to offshore waters.

MATERIALS AND METHODS

Study area

Fieldwork was carried out during three breeding seasons (2016: 8-11 January; 2018: 12-17 January; 2019: 9-15 January) 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 two 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 Kerguelen Islands host large populations of marine predators (Barbraud et al. 2020), including large sympatric populations of CDP and SGDP (Weimerskirch et al. 1989).

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 tag 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 days (the chick-rearing period lasts 44-52 days; Jouventin et al. 1985).

A total of 32 breeding SGDP were fitted with a nanoFix-GEO miniaturized GPS, Pathtrack Ltd, Otley, United-Kingdom). The sampling interval of GPS fixes was 5 min. The loggers were attached to the base of two to three tail feathers using waterproof Tesa tape (Tesa 4651; Beiersdorf AG, Germany). The total mass of the loggers ranged between 1.2 to 2.6 g, i.e. corresponding to $2.0 \pm 0.19\%$ of the birds' body mass (130 ± 16 g). SGDP were weighed (± 2 g; Pesola) 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, burrows were visually checked using the vertical position (or not) of small sticks at their opening. 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 common diving petrel (Fromant et al. 2021).

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):

$$\text{Speed threshold} = 2 * (\text{Drift Speed} * \text{Average Flight Speed}) / (\text{Drift Speed} + \text{Average Flight Speed})$$

For SGDP, the speed threshold was $9.1 \text{ km}\cdot\text{h}^{-1}$, with a drift speed of $5 \text{ km}\cdot\text{h}^{-1}$ (Petalas et al. 2021), and average flight speed of $50 \text{ km}\cdot\text{h}^{-1}$. 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 to 225 km) were used to select continuous flying bouts, and speed was averaged for each flying bout ($50 \pm 11 \text{ km}\cdot\text{h}^{-1}$). 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).

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 two to four weeks 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 was 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 the Bayesian standard ellipses areas (SEA_B) on 10^5 replicates was used to measure the overlap of the isotopic niches between years (Jackson et al. 2011).

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 (GLMM) using the package *glmmADMB* (Bolker et al. 2012). Year, distance to the colony, sea surface temperature (SST), chlorophyll-a concentration, and bathymetry were considered as fixed effects, with the individual bird added as a random effect (Table S1). SST, chlorophyll-a and bathymetry have been shown to 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 analyses of variance (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 standard deviation.

RESULTS

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

Forty trips were recorded during the three studied seasons. All the tracks were complete excepted during one season (2016, $n = 9$ incomplete trips, Table 1, Figure 1). All the tracked SGDP performed direct, long-distance trips toward the south of the Kerguelen Archipelago, to the vicinity of the APF (Figure 1). The mean duration of foraging trips was about one day, ranging between 26 to 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 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 two and three hours 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, Supplementary Figure 1). 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.

Changes in travelling speed

Flight speed analysis revealed three distinct phases during the trips: firstly, an outward phase (i) (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: 32-93 km·h⁻¹, for the first 5% of the trip; Figure 2). Flying speeds then gradually decreased until they fell below the threshold value (9.1 km·h⁻¹, see methods) between commuting and foraging. This corresponded to the beginning of the central phase (ii), 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 foraging locations were recorded (Figure 2, Figure S2). Then, during the inward phase (iii) (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 (Figure 2). Their flying speed gradually increased until stabilizing at 40-60 km·h⁻¹ up to 6 h before arrival, after which flying speeds slowly decreased until arrival at their burrows (Figure 2).

Foraging area

The central phase of the trip corresponded roughly to an area located between the northern and southern boundaries of the APF (Figure 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 km²), 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 sea surface temperature (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 $P < 0.001$, Tables S1 and 2).

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).

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 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 the 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 a 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, Bost et al. 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 has 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 three years of the study. 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, the sympatric inshore forager CDP feed their chicks with a barely-digested crustacean-based diet that includes mainly the amphipod *Themisto gaudichaudii* and the large copepod *Paraeuchaeta antarctica*. These two 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, Fromant & Bost pers. obs).

Differences in diving abilities could be a major factor explaining such strong differences in foraging areas between the two sibling species of diving petrels. By foraging at the distant APF, the smaller SGPD 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 seems 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. unpubl. data). At-sea energy expenditure of SGDP is high as indicated by the doubly labelled water method (4.1 time Standard Metabolic Rates: 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 twice 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) should provide fascinating insights about i) the processes that determine their preferential habitat use, ii) how the mesoscale dynamics of frontal structures drive their at-sea foraging strategies, and iii) 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).

Acknowledgements. The French Polar Institute IPEV (Program IPEV 394 C.A Bost & 109 C. Barbraud) funded this study. We thank the IPEV logistic staff (Y. Le Meur, R. Bellec, and the Geners of the 66-67-68 missions on Kerguelen Islands) for their full support and help in the

field. Special thanks to Samuel Perroteau, Julien Fleureau, Uéline Courcoux-Caro, Tobie Getti and Emile Brisson-Curadeau for invaluable help with field work and Y. Eizenberg for helpful comments and corrections on the ms. We are grateful to G. Guillou from the “Plateforme analyses isotopiques” of LIENSs for running stable isotope analyses. Thanks are due to the Contrat de Projet Etat-Région (CPER) and the Fonds Européen de Développement Régional (FEDER) for funding the isotope-ratio mass spectrometers of LIENSs laboratory. The Institut Universitaire de France (IUF) is acknowledged for its support to P. Bustamante as a Senior Member. The ethics committee of IPEV approved all field procedures.

LITERATURE CITED

- Amélineau F, Grémillet D, Bonnet D, Le Bot T, Fort J (2016) Where to forage in the absence of sea ice? Bathymetry as a key factor for an Arctic seabird. *PloS ONE* 11(7): e0157764
- Bailleul F, Charrassin JB, Monestiez P, Roquet F, Biuw M, Guinet C (2007) Successful foraging zones of southern elephant seals from Kerguelen Islands in relation to oceanographic conditions. *Phil Trans Roy Soc B* 362: 2169–2181
- Barbraud C, Delord K, Bost CA, Chaigne A, Marteau C, Weimerskirch H (2020) Population trends of penguins in the French Southern Territories. *Polar Biol* 43: 835–850
- Bearhop S, Waldron S, Votier SC, Furness RW (2002) Factors that influence assimilation rates and fractionation of nitrogen and carbon stable isotopes in avian blood and feathers. *Physiol Biochem Zool* 75(5): 451–458
- BirdLife International (2021) IUCN Red List for birds
- Bocher P, Cherel Y, Hobson KA (2000) Complete trophic segregation between South Georgian and common diving petrels during breeding at Iles Kerguelen. *Mar Ecol Prog Ser* 208: 249–264
- Bocher P, Cherel Y, Labat JP, Mayzaud P, Razouls S, Jouventin P (2001) Amphipod-based food web: *Themisto gaudichaudii* caught in nets and by seabirds in Kerguelen waters, southern Indian Ocean. *Mar Ecol Prog Ser* 223: 261–276
- Bocher P, Cherel Y, Alonzo F, Razouls S, Labat JP, Mayzaud P, Jouventin P (2002) Importance of the large copepod *Paraeuchaeta antarctica* (Giesbrecht, 1902) in coastal waters and the diet of seabirds at Kerguelen, Southern Ocean. *J Plankton Res* 24: 1317–1333

- Bolker B, Skaug H, Magnusson A, Nielsen A (2012) Getting started with the *glmmADMB* package. <http://glmmadmb.r-forge.r-project.org/glmmADMB.pdf>
- Bost CA, Georges JY, Guinet C, Cherel Y, Pütz K, Charrassin JB, Handrich Y, Zorn T, Lage J, Le Maho Y (1997) Foraging habitat and food intake of satellite tracked king penguins during the austral summer at Crozet archipelago. *Mar Ecol Prog Ser* 150: 21–33
- Bost CA, Zorn T, Le Maho Y, Duhamel G (2002) Feeding of diving predators and diel vertical migration of prey: king penguin diet versus trawl sampling at Kerguelen islands. *Mar Ecol Prog Ser* 227: 51–62
- Bost CA, Cotté C, Bailleul F, Cherel Y, Charrassin JB, Guinet C, Ainley DG, Weimerskirch H (2009) Importance of Southern Ocean fronts for seabird and marine mammals. *J Mar Syst SIOF* 79: 363–376
- Cherel Y, Hobson KA, Hassani S (2005) Isotopic discrimination between food and blood and feathers of captive penguins: implications for dietary studies in the wild. *Physiol Biochem Zool* 78(1): 106–115
- Cherel Y, Hobson KA (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 JP (2010) Isotopic niches and trophic levels of myctophid fishes and their predators in the Southern Ocean. *Limnol Oceanogr* 55: 324–332
- Cherel Y, Connan M, Jaeger A, Richard P (2014) Seabird year-round and historical feeding ecology: blood and feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values document foraging plasticity of small sympatric petrels. *Mar Ecol Prog Ser* 505: 267–280
- Delord K, Barbraud C, Bost CA, Cherel Y, Guinet C, Weimerskirch H (2013) Atlas of top predators from French Southern Territories in the Southern Indian Ocean. The National Center for Scientific Research France - CNRS-CEBC UMR7372 UMS3462
- Domalik A, Hipfner JM, Studholme KR, Crossin GT, Green DJ (2018) At-sea distribution and fine-scale habitat use patterns of zooplanktivorous Cassin's auklets during the chick-rearing period. *Mar Biol* 165: 1–15
- Dunphy BJ, Vickers SI, Zhang J, Sagar RL, Landers TJ, Bury SJ, Hickey AJ, Rayner MJ (2020) Seabirds as environmental indicators: foraging behaviour and ecophysiology of common diving petrels (*Pelecanoides urinatrix*) reflect local-scale differences in prey availability. *Mar Biol* 167(4): 1–2

- Fromant A, Schumann N, Dann P, Cherel Y, Arnould JPY (2020a) Trophic niches of a seabird assemblage in Bass Strait, south-eastern Australia. *Peerj* 8: e8700
- Fromant A, Miskelly CM, Arnould JPY, Bost CA (2020b) Artificial burrows as a tool for long-term studies of diving petrels. *Polar Biol* 43(5): 435–442
- Fromant A, Delord K, Bost CA, Eizenberg YH, Botha JA, Cherel Y, Bustamante P, Gardner BR, Brault-Favrou M, Lec'hvien A, Arnould JPY (2021) Impact of extreme environmental conditions: foraging behaviour and trophic ecology responses of a diving seabird. *Prog Oceanogr* 198: 102676
- Fromant A, Arnould JP, Delord K, Sutton GJ, Carravieri A, Bustamante P, Miskelly CM, Kato A, Brault-Favrou M, Cherel Y, Bost CA (2022) Year-round niche segregation in two sympatric sibling seabirds: the common and South Georgian diving petrels from Kerguelen Islands. *Oecologia*, 199(3): 537–548
- Guinet C, Cherel Y, Ridoux V, Jouventin P (1996) Consumption of marine resources by seabirds and seals in Crozet and Kerguelen waters: changes in relation to consumer biomass 1962–1985. *Antarct Sci* 8: 23–30
- Guinet C, Dubroca L, Lea MA, Goldsworthy S, Cherel Y, Duhamel G, Bonnadona F, Donnay JP (2001) Spatial distribution of foraging in female Antarctic fur seals (*Arctocephalus gazella*) in relation to oceanographic factors: a scale-dependent approach using geographic information systems. *Mar Ecol Prog Ser* 219: 251–264
- Hunt Jr GL, Mehlum F, Russell RW, Irons D, Decker MB, Becker PH (1999) Physical processes, prey abundance, and the foraging ecology of seabirds. In: Adams NJ, Slotow RH (eds) *Proc 22th International Ornithological Congress, Durban*, p 2040–2056
- Jackson AL, Inger R, Parnell AC, Bearhop S (2011) Comparing isotopic niche widths among and within communities: SIBER—Stable Isotope Bayesian Ellipses in R. *J Anim Ecol* 80(3): 595–602
- Jaeger A, Lecomte VJ, 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
- Jakubas D, Wojczulanis-Jakubas K, Iliszko LM, Kidawa D, Boehnke R, Błachowiak-Samołyk K, Stempniewicz L (2020) Flexibility of little auks foraging in various oceanographic features in a changing Arctic. *Sci Rep* 10: 8283
- Jouventin P, Mougin JL, Stahl JC, Weimerskirch H (1985) Comparative biology of the burrowing petrels of the Crozet islands. *Notornis* 27: 327–220

- Kim, YS, Orsi AH (2014) On the variability of Antarctic Circumpolar Current Fronts inferred from 1992–2011 altimetry. *J Phys Oceanogr* 44: 3054–3071
- Navarro J, Votier SC, Aguzzi J, Chiesa JJ, Forero MG (2013) Ecological segregation in space, time and trophic niche of sympatric planktivorous petrels. *PLoS ONE* 8(4): e62897
- McGowan JA (1986) The biogeography of pelagic ecosystems. UNESCO Tech Pap Mar Sci 49: 191–200
- Pakhomov EA (1993) Macroplankton of the waters contiguous to the Kerguelen Archipelago. In: Duhamel G (ed) Campagnes SKALP 1987 et 1988 aux îles Kerguelen à bord des navires ‘SKIF’ et ‘KALPER’. Institut Français pour la Recherche et la Technologie Polaires, les Rapports des campagnes à la mer 93–01: 104–112
- Park YH, Roquet F, Durand I, Fuda JL (2008) Large-scale circulation over and around the Northern Kerguelen Plateau. *Deep Sea Res Part II Top Stud Oceanogr* 55: 566–581
- Park YH, Durand I, Kestenare E, Rougier G, Zhou M, d’Ovidio F, Cotté C, Lee JH (2014) Polar Front around the Kerguelen Islands: An up to-date determination and associated circulation of surface/subsurface waters. *J Geophys Res Oceans* 119: 6575–6592
- Péron C, Weimerskirch H, Bost CA (2012) Predicting king penguins (*Aptenodytes patagonicus*) foraging distribution over the next century. *Proc Royal Soc B* 279: 2515–2523
- Petalas C, Lazarus T, Lavoie RA, Elliott KH, Guigueno MF (2021) Foraging niche partitioning in sympatric seabird populations. *Sci Rep* 11: 2493
- R Core Team (2021) R: A language and environment for statistical computing. R Foundation for statistical computing, Vienna, Austria
- Rayner MJ, Taylor GA, Gaskin C, Dunphy BJ (2017) Seasonal activity and unpredicted polar front migration of northern New Zealand common diving petrels (*Pelecanoides urinatrix*). *Emu* 117(3): 290–298
- Razouls S, De Bove´e F, Delille D, Fiala M, Mayzaud P (1997) Temporal variability of bacteria, phytoplankton and zooplankton assemblages of the sub-Antarctic Morbihan Bay (Kerguelen Archipelago). In: Battaglia B, Valencia V, Wlaton DWH (eds) Antarctic communities: species, structure and survival. Cambridge University Press, Cambridge, p 86–92
- Razouls S, Du Réau G, Guillot P, Maison J, Jeandel C (1998) Seasonal abundance of copepod assemblages and grazing pressure in the Kerguelen Island area (Southern Ocean). *J Plank Res* 20: 1599–1614

- Reisinger RR, Raymond B, Hindell MA, et al. (2018) Habitat modelling of tracking data from multiple marine predators identifies important areas in the Southern Indian Ocean. *Divers Distrib* 24: 535–550
- Ricklefs RE, Roby DD, Williams JB (1986) Daily energy expenditure of adult Leach's storm-petrels during the nesting cycle. *Physiol Zool* 59: 649–660
- Roby DD, Ricklefs RE (1986) Energy expenditure in adult least auklets and diving petrels during the chick-rearing period. *Physiol Zool* 59(6): 661–678
- Schaafsma FL, Cherel Y, Flores H, van Franeker JA, Lea MA, Raymond B, van de Putte AP (2018) Review: the energetic value of zooplankton and nekton species of the Southern Ocean. *Mar Biol* 165: 1–35
- Thiers L, Delord K, Bost CA, Guinet C, Weimerskirch H (2017) Important marine sectors for the top predator community around Kerguelen Archipelago. *Polar Biol* 40: 365–378
- van Franeker JA, van den Brink NW, Bathmann UV, Pollard RT, de Baar HJ, Wolff WJ (2002) Responses of seabirds, in particular prions (*Pachyptila* sp.), to small-scale processes in the Antarctic Polar Front. *Deep Sea Research Part II. Topical Studies Oceanogr* 49(18): 3931–3950
- Venables H, Meredith MP, Atkinson A, Ward P (2012) Fronts and habitat zones in the Scotia Sea. *Deep Sea Research Part II. Topical Studies Oceanogr* 59: 14–24
- Warham J (1996) *The behaviour, population biology and physiology of the petrels*, Academic Press
- Weimerskirch H, Zotier R, Jouventin P (1989) The avifauna of the Kerguelen Islands. *Emu* 89: 15–29
- Weimerskirch H (1997) Foraging strategies of southern albatrosses and their relationship with fisheries. In: Robertson G, Gales R. (eds) *Albatross biology and conservation*. Surrey Beatty and Sons, Sydney, Australia, p 168–179
- Weimerskirch H (2007) Are seabirds foraging for unpredictable resources? *Deep Sea Res II* 54: 211–223
- Zhang J, Rayner M, Vickers, Landers T, Sagar R, Stewart J, Dunphy B (2019) GPS telemetry for small seabirds: using hidden Markov models to infer foraging behaviour of common diving petrels (*Pelecanoides urinatrix urinatrix*). *Emu* 119: 126–137
- Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. *Ecol Evol* 1: 3–14

Table 1. Summary of foraging trip metrics (mean \pm SD) for GPS-equipped South Georgian diving petrels (*P. georgicus*) from Ile des 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 (a or b) are significantly different (Mann-Whitney *U* test: $P < 0.05$)

Year	2016	2018	2019
Number of trips (n complete); individuals (N)	n = 9 (0) N = 9	n = 21 (8) N = 16	n = 10 (7) N = 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

* All the tracks were incomplete in 2016.

Table 2. Mean environmental variables (\pm SD) along commuting and foraging areas of GPS-equipped South Georgian diving petrels (*P. georgicus*) from Ile aux Cochons (Kerguelen Islands) during the chick-rearing period. Data from the three years were pooled. SST = sea surface temperature; Chl-a = chlorophyll-a concentration.

	Bathymetry (m)	SST ($^{\circ}$ C)	Chl-a (mg.m ³)
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

Table 3. Whole blood $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of South Georgian diving petrels (*P. 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 (a or b) 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)

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

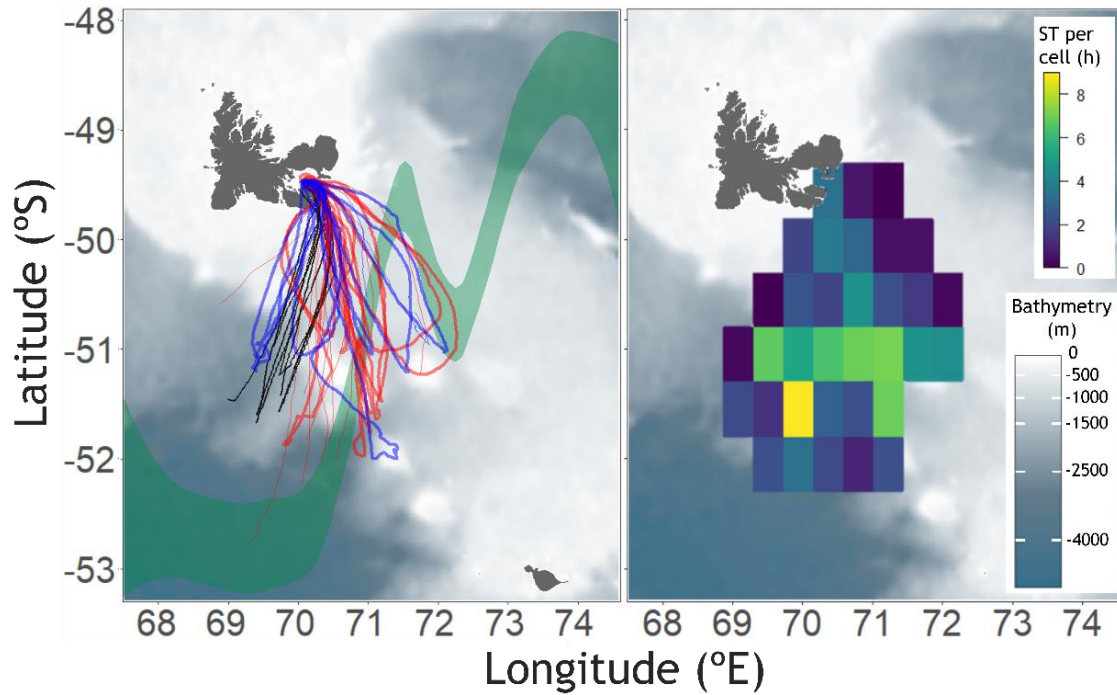


Fig. 1. At-sea distribution of tracked South Georgian diving petrels (*P. georgicus*) from Ile aux Cochons (Kerguelen Islands) during the chick-rearing period. Left panel: Foraging tracks recorded in January 2016 (black, nine trips from nine individuals), January 2018 (red, 21 trips from 16 individuals) and January 2019 (blue, 10 trips from seven 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 and Orsi 2014). Right panel: at-sea standardised time (ST) spent foraging ($9.1 \text{ km}\cdot\text{h}^{-1}$; see Materials & Methods) in area within 0.5° cell by instrumented birds during the chick-rearing period.

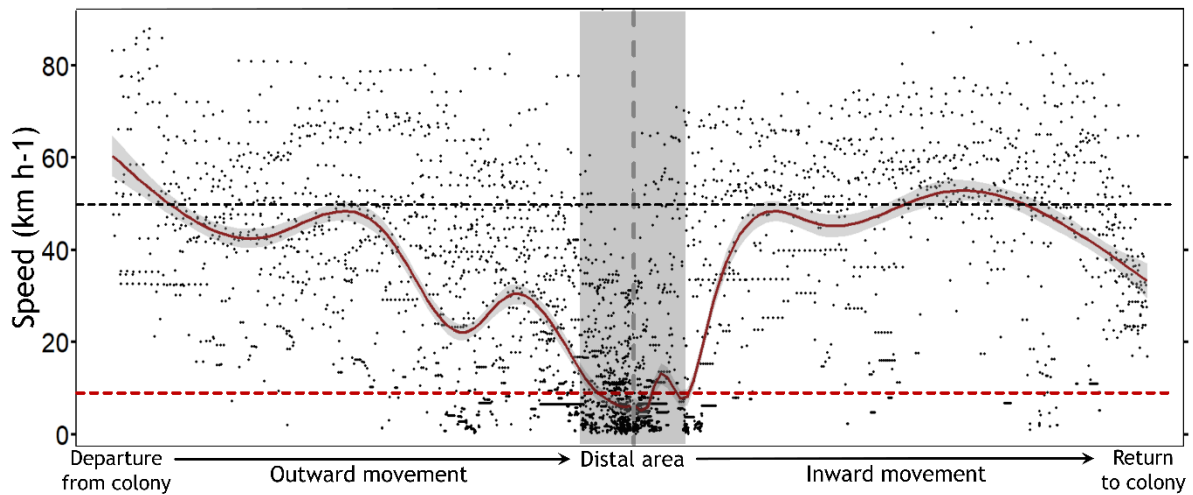


Fig. 2. Relationship between distance from the colony and flight speed of chick-rearing South Georgian diving petrels (*P. georgicus*) during foraging trips (full trips only). For each trip, the distance from the colony was standardised as the proportion of the maximal distance from the colony (distance between colony and distal point). The distal point represents the farthest location from the colony reached during each trip. The shaded area corresponds to the 10% most distant area (standardised per trip). The black dotted line corresponds to the mean flying speed of the birds in commuting ($50 \text{ km}\cdot\text{h}^{-1}$) and the red dotted line to the speed threshold determined to identify foraging behaviour ($9.1 \text{ km}\cdot\text{h}^{-1}$; see Materials & Methods)

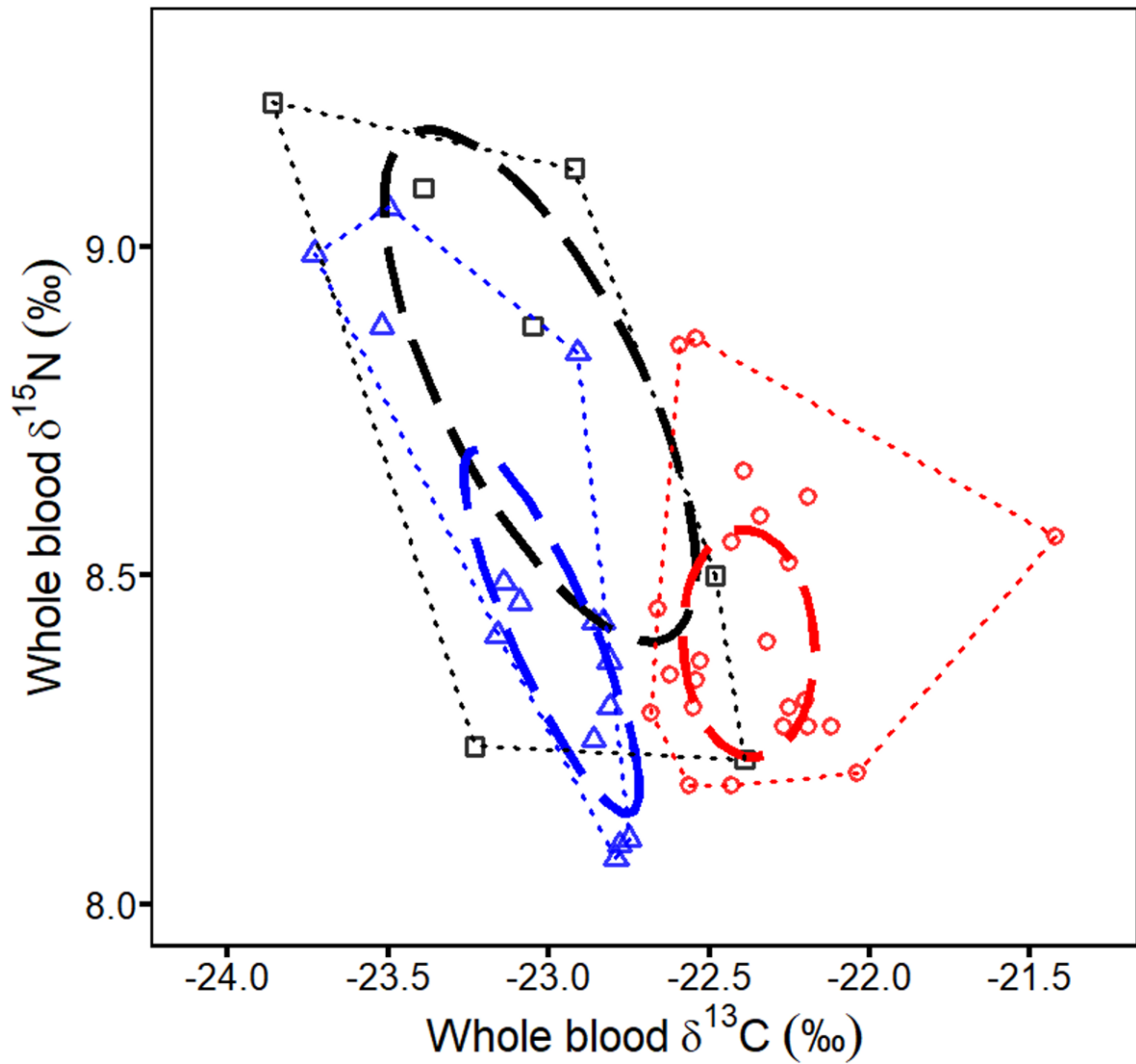


Fig. 3. Whole blood $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of South Georgian diving petrels (*P. georgicus*) from Ile aux Cochons (Kerguelen Islands) during the chick-rearing period. Black squares = January 2016 (n = 7); red circles = January 2018 (n = 23); blue triangles = January 2019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

SUPPLEMENTARY DATA

Table S1. Results of GLMM models explaining the instantaneous speed of South-Georgian diving petrels from Kerguelen Islands. Explanatory variables (Dist_colony = distance from the colony; SST = sea surface temperature; Chl-a = chlorophyll-a concentration; Bathy = bathymetry), Akaike Information Criterion (AIC), Delta AIC (difference in AIC compared to the best model) and Log-likelihood are given for each model. Models are ranked according to their respective AIC value

Models	AIC	Delta AIC	Log-likelihood	Nagelkerke Pseudo R ²
Speed ~ Dist_colony + SST + Chl-a + Bathy	21662.8	0	-10824.4	0.42
Speed ~ Dist_colony + SST	21671.1	8.2	-10828.5	0.41
Speed ~ Dist_colony	21727.4	64.6	-10859.7	0.40
Speed ~ SST	22431.7	768.9	-11211.9	0.21
Speed ~ Bathy	22500.9	838.1	-11246.5	0.19
Speed ~ Chl-a	22848.9	1186.1	-11420.4	0.06
Speed ~ Year	23008.7	1345.9	-11500.3	< 0.01
Speed ~ 1	23010.6	1347.8	-11502.3	0

Table S2. Degree of isotopic niche overlap (%) among years. The overlap between two ellipses is calculated based on the maximum likelihood fitted ellipses (Jackson et al. 2011)

Year	2016	2018	2019
2016	-	25.8	29.5
2018		-	18.4
2019			-

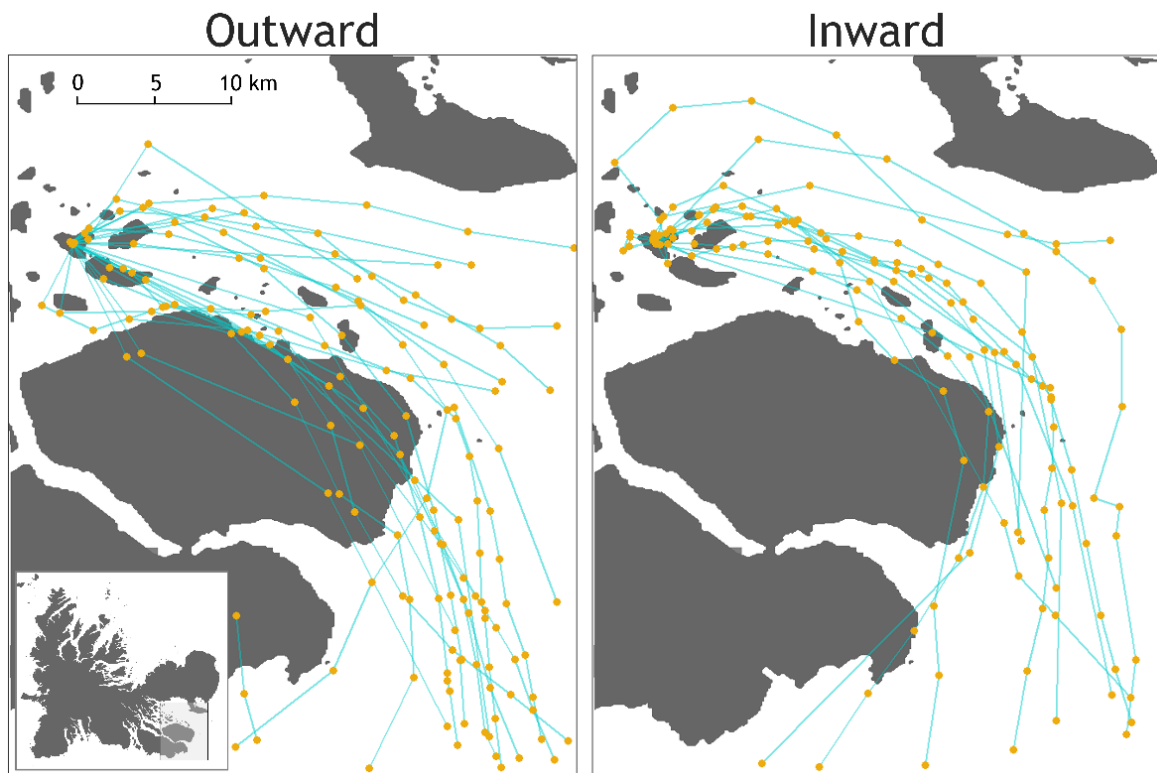


Fig. S1. Outward and inward movements of South Georgian diving petrels (*P. georgicus*) close to their colony showing the flight paths direction in relation to land and marine areas.

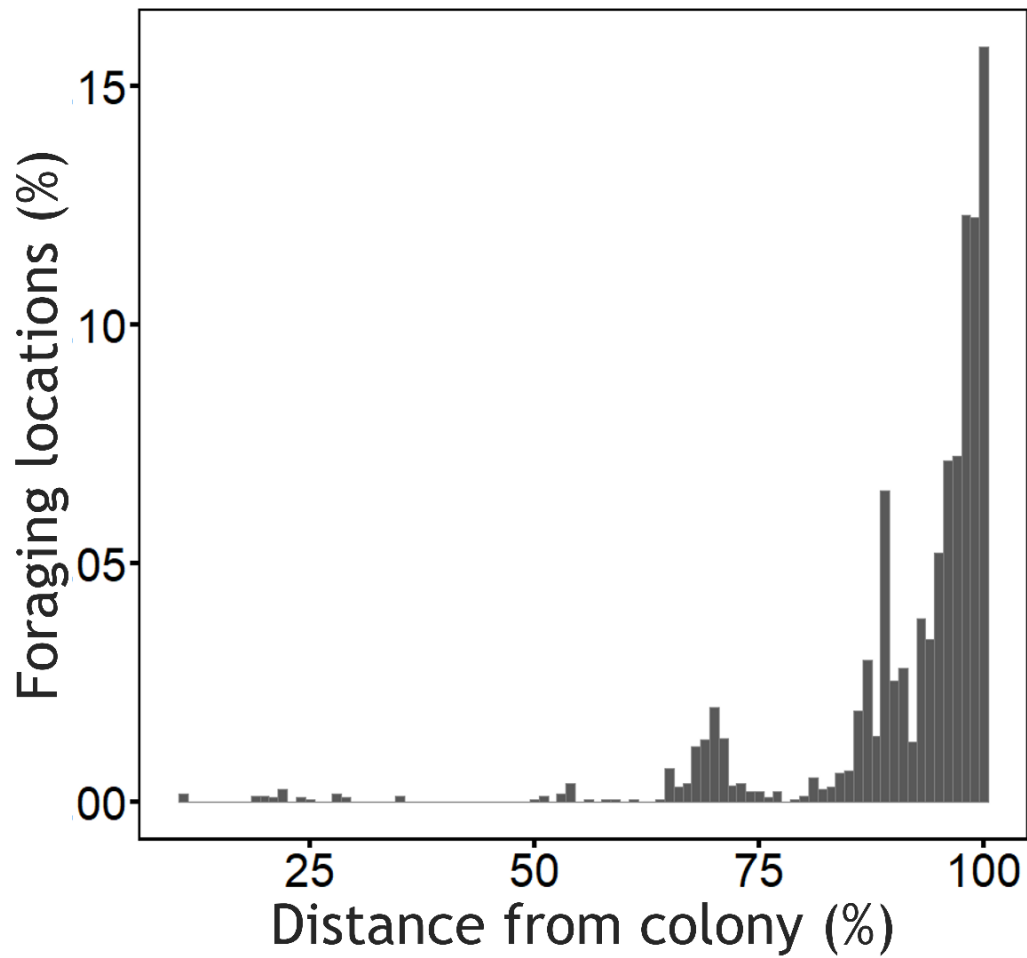


Fig. S2. Distribution of foraging locations ($< 9.1 \text{ km}\cdot\text{h}^{-1}$) along the maximum range gradient from the colony (0% = colony location; 100% distal point). For each trip, the distance from the colony was standardised by dividing the distance from the colony by the maximal distance from the colony (distance between colony and distal point). The distal point represents the farthest location from the colony reached during each trip.