



Diet, isotopic niche, and spatial distribution of the white-headed petrel (*Pterodroma lessonii*) at Kerguelen Islands

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Abstract

The subantarctic white-headed petrel is unique amongst Procellariidae by its biennial breeding frequency. Its food and feeding ecology is poorly known with limited available bio-logging data and no dietary and isotopic information. Our goal was to detail its prey species and isotopic niche at Kerguelen Islands, which is the most important breeding site in the Indian Ocean. Analysis of stomach contents ($n=56$) indicated chicks were fed on fish (68% by mass) and secondarily on cephalopods (26%), whilst crustaceans were minor dietary components. Mesopelagic fishes were the main prey, with myctophids and melamphaid being the most important fish family in terms of both abundance (50% and 15% of the fish, respectively) and diversity (10 and three species). Prey distribution indicated that petrels foraged primarily in subantarctic waters and secondarily further south to feed their chicks, which is corroborated by the lower blood $\delta^{13}\text{C}$ values of fledglings ($n=10$) than incubating adults ($n=9$). Body feather $\delta^{13}\text{C}$ values ($n=45$) indicate that adult white-headed petrels moulting over different latitudinal habitats, from the subtropics to Antarctica where $\delta^{15}\text{N}$ values showed they fed on low trophic-level prey (most likely Antarctic krill). Indeed, three geolocator-tracked birds ranged widely, from the mid-Atlantic (18° W) to the eastern Indian Ocean (110° E) and from the warmer Subtropical Zone (19% of the locations), across the Subantarctic Zone (58%) to the colder Antarctic Zone (23%). Neither fishery-related items nor plastic debris were found in chick food samples, thus indicating no significant interactions with human activities, which is a key positive issue for the conservation of white-headed petrels.

Keywords Fish · Food · Myctophidae · Procellariiformes · Seabirds · Southern ocean · Squid

Introduction

The gadfly petrels (*Pterodroma* spp.) is the most diverse genus of procellariiform seabirds, with 35 species living in all water masses of the World Ocean, but the high-Arctic (Brooke 2004; Harrison et al. 2021). Five species breed within the Southern Ocean (water masses south of the Subtropical Front), including two species that reproduce in localized areas, the Atlantic petrel *P. incerta* in the Atlantic, and the mottled petrel *P. inexpectata* in the Pacific. The remaining three species have a larger distribution, the medium-sized soft-plumaged petrel *P. mollis* has a circumpolar breeding distribution, the great-winged petrel *P. macroptera* breeds in both the Atlantic and Indian Oceans,

and the white-headed petrel *P. lessonii* in the Indian and Pacific Oceans. Hence, the three species are sympatric in the subantarctic Indian Ocean at the Crozet and Kerguelen Archipelagoes. The two large *Pterodroma* petrels segregate temporally, since the great-winged petrel breeds in winter (egg-laying late May–June), whilst the white-headed petrel reproduces during the summer months (egg-laying late November–December) (Marchant and Higgins 1990; Brooke 2004).

The key breeding areas of white-headed petrels are located in the western Pacific, with at least 100,000 pairs reproducing at the Antipodes and Auckland Islands (Brooke 2004). The species is unique amongst procellariids by its biennial breeding frequency. Most successful breeders skip breeding the next year, (Zotier 1990; Chastel 1995), a life-history trait that the species shares with several albatrosses (Diomedeidae). Where adult white-headed petrels forage during the long inter-breeding and breeding periods was unknown until the recent use of bio-logging to examine their at-sea movements (Taylor et al. 2020). Geolocators (GLS)

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revealed that birds from the Auckland Islands cover a huge oceanic area both longitudinally (from the western Indian to the mid-Pacific) and latitudinally (from the subtropics to Antarctica) during their biennial cycle. In contrast to spatial ecology, minimum information is available on the food of the white-headed petrel, with no detailed dietary study to identify its prey items, and no isotopic data to document its at-sea habitats ($\delta^{13}\text{C}$) and diet/trophic position ($\delta^{15}\text{N}$) (but see Blévin et al. 2013 for chicks).

The goal of the present work was to combine methods to depict the food and feeding ecology of the white-headed petrel from the subantarctic Kerguelen Archipelago, which is the most important breeding site of the species in the Indian Ocean (20,000–50,000 annual breeding pairs; Weimerskirch et al. 1989). Food was examined by collecting stomach contents from chicks over three consecutive years, which allowed determining the main prey groups and prey items of the species (e.g. Cherel et al. 2002a). The stable isotope method was used on blood and feathers to depict the isotopic niche as a proxy of the trophic niche of adult birds during the breeding and inter-breeding periods, respectively (e.g. Cherel et al. 2008). Finally, white-headed petrels were GLS tracked to investigate their at-sea distribution and activity over the long inter-breeding period (e.g. Cherel et al. 2016). Few studies of a single seabird used all these methods towards one goal in understanding its foraging behaviour.

Materials and methods

White-headed petrels were studied at Mayes Island, Kerguelen Archipelago ($49^{\circ} 28' \text{S}$, $69^{\circ} 57' \text{E}$). Breeding adults arrive at the colonies in late August–September to display and copulate before departing to sea for an 80-day pre-laying exodus (mid-October to mid-November). Females lay a single egg in late November–early December, hatching occurs at the end of January, and chicks fledge in May–early June (Barré 1976; Jouventin et al. 1985; Zotier 1990; Brooke 2004; Taylor et al. 2020). White-headed petrels are considered dispersive or migratory, with successful birds skipping the next breeding season, which means they are mostly away from the colonies during a ~15-months period that includes two successive winters and one summer (Zotier 1990; Chastel 1995; Taylor et al. 2020).

Dietary sampling and analysis

Dietary studies were conducted over three consecutive years, with 20, 28, and eight stomach contents collected during the study period (late February–early April) 2001, 2002, and 2003, respectively. The 56 food samples were taken from randomly selected chicks after successive weighings (at dusk, midnight, and dawn) indicating they were fed

recently. Samples were obtained by up-ending chicks over a plastic bucket and massaging the stomach and throat. If needed, chicks were flushed one time using the offloading technique (Wilson 1984). Collection of a single meal has no detrimental effects in terms of survival and development on procellariform chicks (Phillips 2006). Food samples were all returned deep-frozen (-20°C) to the laboratory in France for analysis.

Each sample was thawed, drained, and weighed (solid fraction; Cherel et al. 2000). Accumulated items, including cephalopod beaks, were subsequently sorted and weighed. Beaks can persist in predator stomachs for weeks and even months, thus overemphasizing the importance of cephalopods in seabird diets (Xavier et al. 2005). Following Cherel and Klages (1998), accumulated beaks (without flesh attached) were consequently analysed separately from fresh items. Fresh items (solid fraction minus accumulated items) were divided into broad prey classes (fish, cephalopods, crustaceans, and others), which were weighed to calculate their proportion by mass in the diet. Species identification of prey relied almost totally on the examination of otoliths and bones for fish, sclerotized beaks for cephalopods, and exoskeletons for crustaceans. Special care was made to use all fish hard parts recovered in stomach contents (bones, otoliths, scales, teeth), with an emphasis on some distinctive bones to identify items to the lowest possible taxon. In the same way, the morphology of both lower and upper beaks was used to determine cephalopod prey (Cherel et al. 2000; Xavier et al. 2011). Items were identified by comparison with material held in our own collection and by reference to the available literature, including Williams and McElroy (1990), and Duhamel et al. (2005) for fish, Boltovskoy (1999) for crustaceans, and Xavier and Cherel (2021) for cephalopods. Species names of cephalopods followed a recent review on Southern Ocean squids that includes taxonomic revisions conducted over the last decades (Cherel 2020).

Stable isotopes and moult

Ten randomly chosen incubating adults of unknown sex and large chicks near fledging were caught in burrows in December and late March–early April, respectively, during two breeding cycles (2002/2003 and 2007/2008). All birds were feather sampled and they were also blood sampled in 2007/2008. Six whole body feathers were pulled out from the lower back of each bird and stored dry in sealed individual plastic bags. A 1-ml blood sample was taken from a wing vein using a heparinized syringe. Seventy percent ethanol was added to whole blood, because this preservation method does not alter the isotopic composition of tissues (Hobson et al. 1997). Blood samples were stored at -20°C until analysis. Feathers were cleaned to remove surface

contaminants using a 2:1 chloroform:methanol solution followed by two methanol rinses. They were then oven dried for 48 h at 50 °C and cut into small pieces. Whole blood was freeze-dried and powdered. Tissue sub-samples were weighed with a microbalance, packed in tin containers, and nitrogen and carbon isotope ratios were subsequently determined by a continuous flow mass spectrometer (Thermo Scientific Delta V Advantage) coupled to an elemental analyser (Thermo Scientific Flash 2000). Results are presented in the usual δ notation relative to Vienna PeeDee Belemnite and atmospheric N₂ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively. Replicate measurements of internal laboratory standards (caffeine) indicate measurement errors <0.10‰ and <0.15‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively.

The isotopic method was validated in the southern Indian Ocean. Tissue $\delta^{13}\text{C}$ values of consumers reflect the latitudinal $\delta^{13}\text{C}$ gradient at the base of the food web and thus indicate their latitudinal foraging habitats (Cherel and Hobson 2007; Jaeger et al. 2010b), whilst $\delta^{15}\text{N}$ values change according to their trophic position in the increasing order planktivorous species < piscivorous species < fish and squid eaters (Cherel et al. 2010). The isotopic consumer data allowed estimating the $\delta^{13}\text{C}$ position of the main oceanic fronts within the southern Indian Ocean and thus to delineate robust isoscapes of the main foraging zones for top predators, depending on the targeted tissues. Based on blood (feather) $\delta^{13}\text{C}$ isoscapes, values less than –22.5‰ (–21.2‰), –22.5 to –19.7‰ (–21.2 to –18.3‰), and greater than –19.7‰ (–18.3‰) were considered to correspond to the Antarctic (AZ), Subantarctic (SAZ) and Subtropical (STZ) Zones, respectively (Cherel and Hobson 2007; Jaeger et al. 2010b). Isoscapes differ for blood and feathers due to tissue-related isotopic differences, with feathers (keratin) being ^{13}C enriched when compared to blood (Cherel et al. 2014).

Blood and feathers are the main collected avian tissues because they record trophic information at different and complementary time scales and can be sampled easily and nondestructively on live individuals. Blood and feathers from breeding birds allow investigating their feeding strategies during the breeding and inter-breeding periods, respectively (Cherel et al. 2008), since reproduction and moult are largely separated in time in many species due to energetic constraints (Murphy and King 1991). Blood is a metabolically active tissue whose isotopic values reflects diet during the days/weeks before sampling, whereas feather $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values correspond to the period of feather growth because keratin is metabolically inert after synthesis (Hobson and Clark 1992, 1993; Bearhop et al. 2002). A major difference between chick and adult moult of body feathers in Procellariiformes is that all chick body feathers grow almost simultaneously, thus showing low intra-individual isotopic variation (Phillips and Hamer 2000; Carravieri et al. 2014),

whilst adult body feather moult is protracted over the inter-breeding period (Battam et al. 2010; Bugoni et al. 2015; Cherel et al. 2016). Hence, isotopic values of white-headed petrels were measured on a single chick feather, but isotopic measurement was performed on four different body feathers of adults sampled in December 2007 to better depict their moulting foraging habitats (Jaeger et al. 2009, 2010a).

Geolocators and spatial distribution

Tracking data were used to characterize the at-sea distribution of adults during their breeding and non-breeding periods. GLS (Mk 14, British Antarctic Survey, Cambridge) were deployed during the breeding season 2008/2009 on 10 breeding adults. Loggers were mounted on plastic or metal leg bands and weighed 1.5 g, i.e. ~0.25% of the birds' body mass, well below the recommended threshold of 3% body mass (Phillips et al. 2003). Three GLS were recovered 1–7 years after deployment (2009/2010, 2010/2011, and 2015/2016), with a total recorded period of 12, 22, and 24 months, respectively. Two birds failed to fledge a chick the season of deployment. The proportion of GLS-equipped individuals recaptured was 30%. This slow recovery rate might be partly explained by the biennial breeding strategy of the white-headed petrel, with 87% of successful breeders returning to breed 2 years or more later (Chastel 1995). Birds were not sexed (the white-headed petrel is sexually monomorphic).

GLS allows estimating the latitude and longitude from daylight measurements over extended periods, but with a relatively low accuracy (186 ± 114 km); it also records precise activity information from a wet/dry sensor (Wilson et al. 1992; Afanasyev 2004; Phillips et al. 2004). GLS sampled daylight level intensity every 1 min and recorded the maximum value every 10 min. Thresholds in the light curves were used to determine the timings of sunrise and sunset. An internal clock estimates latitude based on day length and longitude based on the timing of local midday with respect to Universal Time (Wilson et al. 1992; Afanasyev 2004). Daylight data were processed using standardized procedure for flying species to provide two locations per day (Phillips et al. 2004). Location fixes were calculated using BASTrak software (Fox 2009). As nests were not monitored daily during the study period, breeding stage and phenology were estimated on a combination of visual examination of movements and activity patterns. Outward migration started from the first directional movement (followed by several consecutive days with directional flight) away the breeding colony, whilst the final non-breeding location was the last location in the non-breeding area before a sustained period of directional movement towards the breeding colony. The first visit to the breeding colony was determined as the first period of at least one night and one day dry spent in the burrow

after the arrival date within the breeding area. The wintering period was defined as the period from the end of the outward migration in February to April to the onset of the return migration in the following August to October.

In addition to light, geolocators recorded salt water immersion every 3 s and stored the sum of immersion events for each 10-min bout. The raw immersion data ranged from 0 (no immersion or dry, in flight or sitting on the ground) to 200 (permanently immersed in sea water or wet), indicating the number of 3-s periods during 10-min blocks when the sensor was immersed in saltwater. The mean percentage of time spent on the water (wet; immersion data > 0) was calculated daily during the non-breeding period to provide information on resting and foraging behaviour. Conversely, the time spent dry is generally interpreted as bird on land in the colony or flying. 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-BASTrack). The duration of daylight and darkness each day (consecutive light and dark period) was assessed directly from the daylight data.

Data analysis

Prey frequency of occurrence (%) refers to the number of food samples in which a given prey was identified over the total number of food samples, and the numeric frequency (%) corresponds to the total number of a given prey in all the samples over the total number of prey items in all the samples.

General linear mixed-effects models (GLMMs), fitted in the glmmTMB package (Zuur et al. 2010; Douma and Weedon 2019), were used to model activity patterns (daily proportion of time spent on the water). We considered the period of time available for all individuals (from the departure to the colony to October 2009). Month and time elapsed since departure from the colony (in month) were included as independent fixed effects. To account for pseudo-replication, individual identity was fitted as a random effect, as the same individual contributed several values. Response variables were visually tested for normality (through $Q-Q$ plots) and homoscedasticity (using Cleveland dotplots; Zuur et al. 2010). A beta family (link = “log”) used for analysing proportion data (Douma and Weedon 2019) was selected for all models. Models were tested and ranked using the Akaike Information Criterion (AIC) values and Akaike weights following the Information-Theoretic Approach (Burnham & Anderson 2002). The model with the lowest AIC was considered the best model. Two models separated by a difference in AIC values < 2 were assumed to fit the data similarly.

To describe graphically the pattern of daily proportion of time spent on water, a generalized additive model (GAM)

was fitted separately for each individual using the gam package (Hastie 2015). Spatial and statistical analyses for spatial distribution and activity were performed using QGIS (QGIS Development Team 2020) and R 3.5.2 (R Core Team 2021). Diet and isotopic data were statistically analysed using SYSTAT 13. Values are means \pm SD.

Results

Chick food

The mean mass of the solid fraction of the 56 stomach samples of white-headed petrel chicks was 51 g, which includes mostly fresh remains (97.4%) and a few accumulated items (2.6%). Overall, the chick diet was dominated by fish, which accounted for 67.8% by fresh mass, and cephalopods ranked second (26.0%). Crustaceans were minor items (5.5%) and other various organisms were negligible (0.6%). In terms of individual food samples, fish was the main prey group by fresh mass in 66.1% ($n=37$) of the stomachs, cephalopods in 23.2% ($n=13$), and crustaceans in 8.9% ($n=5$). Inter-annual variations were not statistically significant (Table 1). Neither fishery-related items nor plastic debris were found in the samples.

A total of 324 fresh prey items from 46 species or prey categories were recovered from the 56 dietary samples (Table 2). Items included 121 (37.4%) fish, 83 (25.6%) cephalopods, 109 (33.6%) crustaceans, and 11 (3.4%) other organisms. Fish occurred in 53 (94.6%) of the samples. At the family level, the fish diet was dominated by myctophids (50% of the fish prey, 10 species, 60 individuals), followed by melamphaid (15% of the fish prey, three species, 18 individuals). Other common prey items were macrourids, the gempylid *Paradiplospinus gracilis* and the paralepidid *Magnisudis prionosa*. Crustaceans were found in 47 (83.9%) of the stomach contents, but owing to their small size, they were not important by mass. The two main crustacean species were the hyperiid amphipod *Themisto gaudichaudii* and the larger Natantia *Pasiphaea scotiae*. Unidentified carrion occurred in two samples, and a few specimens of the tunicate *Salpa thompsoni* were found in four stomach contents.

Fresh remains of cephalopods occurred in 29 (51.8%) samples, but only two of them were identified to the species level (Table 2). The main cephalopod items were non-eroded eyes that were previously called “Oegopsida sp. A” (Cherel et al. 2002a, b; Connan et al. 2007; Cherel and Bocher 2022). The analysis of accumulated beaks increased substantially the number of cephalopod prey (Table 3), which, together with fresh items, included 17 taxa, all oegopsids. White-headed petrels fed mostly on six squid species, by decreasing order of importance: *Galiteuthis glacialis* (25.5% of the total number of accumulated beaks), *Gonatus antarcticus*

Table 1 Composition of the food of white-headed petrel chicks over three consecutive years at Mayes Island, Kerguelen Archipelago

Parameters	Total (n=56)	2001 (n=20)	2002 (n=28)	2003 (n=8)	Statistics (Kruskal–Wallis) 2001, 2002, 2003
Solid fraction (g)	51.4±28.6 (56)	59.0±34.3 (20)	45.3±23.2 (28)	53.3±29.1 (8)	H=1.283, p=0.527
Fresh items (g)	50.0±28.4 (56)	58.4±33.8 (20)	44.0±22.6 (28)	50.0±30.5 (8)	H=1.434, p=0.488
Fish (g)	35.9±32.8 (53)	46.9±41.4 (19)	28.4±23.8 (28)	36.1±34.0 (6)	H=1.278, p=0.528
Cephalopods (g)	25.2±22.0 (29)	25.8±22.4 (9)	24.4±24.8 (14)	26.0±17.4 (6)	H=0.199, p=0.905
Crustaceans (g)	3.3±9.3 (47)	2.5±7.0 (16)	3.8±11.3 (25)	3.2±6.5 (6)	H=0.104, p=0.949
Others (g)	1.7±2.2 (10)	3.4±3.2 (2)	0.6±0.6 (5)	2.5±3.1 (3)	H=3.385, p=0.184
Overall composition					
Fish (%)	67.9	76.1	64.4	54.1	
Cephalopods (%)	26.0	19.9	27.7	39.1	
Crustaceans (%)	5.5	3.4	7.7	4.9	
Others (%)	0.6	0.6	0.2	1.9	

Values are means ± SD, with numbers of samples in parentheses

(19.6%), *Moroteuthopsis longimana* (13.7%), *Histioteuthis eltaninae* (10.5%), *Todarodes* sp. (6.5%), and *Batoteuthis skolops* (5.9%).

Stable isotopes

Overall, feather stable isotope values between the two sampling years were marginally or not significantly different in both adults and chicks (Mann–Whitney; adults: $U=158.5$ and 172.0 , $p=0.652$ and 0.935 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively; chicks: $U=8.0$ and 40.0 , $p=0.001$ and 0.450 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively). Hence, stable isotope values of body feathers from the two years were pooled in further analysis. Feather values were significantly different between chicks and adults, with chicks having lower $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values with less variance than adults (-21.5 ± 0.6 and $-19.4\pm2.1\text{\%}$, 12.3 ± 0.3 and $12.7\pm1.5\text{\%}$, $U=807.5$ and 699.5 , respectively, both $p<0.0001$). Whole-blood $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were also significantly lower in large chicks than in incubating adults of white-headed petrels (Table 4).

The feather $\delta^{13}\text{C}$ estimation of the Subtropical and Polar Fronts allowed delineating the main latitudinal moulting ranges of adult white-headed petrels. Of the 45 body feathers (two years pooled), 33.3%, 57.8%, and 8.9% grew within the STZ, SAZ, and AZ, respectively, with the latter group showing lower $\delta^{15}\text{N}$ values (13.5 ± 0.6 , 12.8 ± 0.6 , and $8.5\pm0.6\text{\%}$, respectively) (Fig. 1). Isotopic values of their four body feathers indicated that, amongst the nine 2007 adults, three moulted in a single zone (one and two within the STZ and SAZ, respectively), five moulted within two zones (four within the STZ and SAZ and one within the SAZ and AZ), and one bird moulted within the three zones.

Light records and at-sea distribution

Overall, the three GLS-tracked white-headed petrels from Kerguelen Islands ranged widely at sea, both longitudinally (from 18°W to 110°E) and latitudinally (30°S to 65°S). They foraged from the mid-Atlantic to the eastern Indian Ocean and from the warmer STZ (19% of the locations), across the SAZ (58%) to the colder AZ (23%). The three birds favoured the SAZ during both the breeding and inter-breeding periods, but they tended to forage more in the AZ and less in the STZ during the breeding period than the inter-breeding period (Tables 5 and S1). The overall distribution included areas over the Southwest Indian Ridge (southeast off South Africa; $42^\circ\text{06}'\text{S } 41^\circ\text{33}'\text{E}$), north of the Prince Edward Islands ($46^\circ\text{53}'\text{S } 37^\circ\text{45}'\text{E}$), and over the Kerguelen Plateau ($50^\circ\text{48}'\text{S } 72^\circ\text{11}'\text{E}$) and the Southeast Indian Ridge ($47^\circ\text{50}'\text{S } 101^\circ\text{13}'\text{E}$) (Figs. 2 and 3).

Early in the breeding season, two individuals (#3138 and #3152) first briefly visited their burrows before departing from the colony for a long pre-laying exodus period (46 and 56 days, Table S2) either westward of Kerguelen Islands or over the Del Cano Rise located midway between the Crozet and Prince Edward Islands. During the breeding season (late September to April), the distribution at sea of white-headed petrels was centred over both a large area surrounding the Kerguelen Plateau and the Southeast Indian Ridge (at $\sim 50^\circ\text{S}$, $\sim 75^\circ\text{E}$). At the end of the breeding attempt, the two failed breeders (#3138 and #3150) exhibited a short (3–5 days) outward migration, whilst the successful breeder (#3152) showed a dispersive behaviour with no well-defined outward movement.

During the inter-breeding period, the distribution extended widely, from the southern Atlantic Ocean, a few hundred kilometres south of Gough Island and across the Indian Ocean to the West of Australia at the Southeast Indian

Table 2 Frequency of occurrence, numbers, and known distribution of prey items identified from stomach contents (n=56) of white-headed petrel chicks from Kerguelen Islands

Species	Occurrence		Number		Known distribution			References
	(n)	(%)	(n)	(%)	Horizontal	Vertical	Southern Ocean endemic	
Fish	53	94.6	121	37.35				
Microstomatidae								
<i>Nansenia antarctica</i>	3	5.4	3	0.93	Oceanic	Meso-bathypelagic	Yes	Duhamel et al. (2005)
Paralepididae								
<i>Magnisudis prionosa</i>	7	12.5	7	2.16	Oceanic	Meso-bathypelagic	No	Duhamel et al. (2005)
Myctophidae								
<i>Electrona carlsbergi</i>	10	17.9	15	4.63	Oceanic	Mesopelagic	Yes	Duhamel et al. (2005)
<i>Electrona subaspera</i>	3	5.4	4	1.23	Oceanic	Mesopelagic	Yes	Duhamel et al. (2005)
<i>Gymnoscopelus bolini</i>	1	1.8	1	0.31	Oceanic	Mesopelagic/epibenthic	Yes	Duhamel et al. (2005)
<i>Gymnoscopelus fraseri</i>	2	3.6	2	0.62	Oceanic	Mesopelagic	Yes	Duhamel et al. (2005)
<i>Gymnoscopelus microlampas</i>	4	7.1	5	1.54	Oceanic	Mesopelagic/epibenthic	Yes	Duhamel et al. (2005)
<i>Gymnoscopelus piabilis</i>	3	5.4	6	1.85	Oceanic	Mesopelagic/epibenthic	Yes	Duhamel et al. (2005)
Unidentifiable <i>Gymnoscopelus</i>	2	3.6	2	0.62				
<i>Krefftichthys anderssoni</i>	4	7.1	4	1.23	Oceanic	Mesopelagic	Yes	Duhamel et al. (2005)
<i>Protomyctophum andriashevi</i>	1	1.8	1	0.31	Oceanic	Mesopelagic	Yes	Duhamel et al. (2005)
<i>Protomyctophum bolini</i>	4	7.1	4	1.23	Oceanic	Mesopelagic	Yes	Duhamel et al. (2005)
<i>Protomyctophum choriodon</i>	5	8.9	5	1.54	Oceanic	Mesopelagic	Yes	Duhamel et al. (2005)
Unidentifiable <i>Protomyctophum</i>	1	1.8	1	0.31				
Unidentifiable Myctophidae	10	17.9	10	3.09				
Muraenolepididae								
<i>Muraenolepis marmoratus</i>	1	1.8	1	0.31	Neritic, oceanic	Benthopelagic	Yes	Duhamel et al. (2005)
Macrouridae								
<i>Coryphaenoides</i> sp.	2	3.6	2	0.62				
<i>Macrourus carinatus</i>	6	10.7	7	2.16	Oceanic	Benthopelagic	No	Duhamel et al. (2005)
Unidentifiable Macrouridae	1	1.8	1	0.31				
Melamphaidae								
<i>Melamphaes microps</i>	6	10.7	7	2.16	Oceanic	Meso-bathypelagic	No	Duhamel et al. (2005)
<i>Poromitra atlantica</i>	3	5.4	3	0.93	Oceanic	Meso-bathypelagic	No	as <i>P. crassiceps</i> , Duhamel et al. (2005)
<i>Sio nordenskjöldii</i>	6	10.7	8	2.47	Oceanic	Meso-bathypelagic	No	Duhamel et al. (2005)
Channichthyidae								
<i>Champscephalus gunnari</i>	1	1.8	1	0.31	Neritic	Semi-pelagic	Yes	Duhamel et al. (2005)
Gempylidae								
<i>Paradiplospinus gracilis</i>	10	17.9	10	3.09	Oceanic	Meso-bathypelagic	Yes	Duhamel et al. (2005)
Unidentifiable Osteichthyes	11	19.6	11	3.40				

Table 2 (continued)

Species	Occurrence		Number		Known distribution			References
	(n)	(%)	(n)	(%)	Horizontal	Vertical	Southern Ocean endemic	
Cephalopods	29	51.8	83	25.62				
Brachioteuthidae								
<i>Slosarczykvia circumantarctica</i>	1	1.8	1	0.31	Oceanic	Epi-mesopelagic	Yes	Cherel (2020)
Ommastrephidae								
<i>Todarodes</i> sp.	1	1.8	1	0.31				
Oegopsida sp. A (lenses)	21	37.5	74	22.84				
Unidentifiable Oegopsida	7	12.5	7	2.16				
Crustaceans	47	83.9	109	33.64				
Euphausiacea								
<i>Euphausia superba</i>	2	3.6	2	0.62	Neritic, oceanic	Epi-mesopelagic	Yes	Cuzin-Roudy et al. (2014)
Unidentifiable <i>Euphausia</i>	1	1.8	1	0.31				
Decapoda								
<i>Pasiphaea scotiae</i>	26	46.4	30	9.26	Oceanic	Meso-abyssopelagic	Yes	Basher and Costello (2014)
Mysida								
<i>Gnathophausia zoea</i>	1	1.8	1	0.31	Oceanic	Meso-abyssopelagic	No	Petryashov (2014)
<i>Neognathophausia gigas</i>	1	1.8	1	0.31	Oceanic	Meso-abyssopelagic	No	Petryashov (2014)
Unidentifiable Gnathophausiidae	5	8.9	5	1.54				
Isopoda								
Unidentified Isopoda	2	3.6	2	0.62				
Amphipoda								
<i>Eurythenes gryllus</i>	2	3.6	2	0.62	Oceanic	Benth-meso-abyssopelagic	No	Vinogradov (1999)
<i>Eurythenes obesus</i>	5	8.9	5	1.54	Oceanic	Benth-meso-abyssopelagic	No	Vinogradov (1999)
<i>Themisto gaudichaudii</i>	26	46.4	51	15.74	Neritic, oceanic	Epipelagic	No	Vinogradov (1999)
Unidentifiable Amphipoda	2	3.6	2	0.62				
Copepoda								
<i>Lophoura</i> sp.	1	1.8	1	0.31				
<i>Sarcotretes eristaliformis</i>	1	1.8	1	0.31				
Unidentifiable Crustacea	5	8.9	5	1.54				
Others	10	17.9	11	3.40				
Carriion	2	3.6	2	0.62				
<i>Salpa thompsoni</i>	4	7.1	5	1.54	Oceanic	Epi-mesopelagic	Yes	Henschke et al. (2018, 2021)
Unidentifiable gelatinous plankton	4	7.1	4	1.23				
Total			324	100.00				

Ridge (Figs. 2 and 3). Each bird visited successively different sectors within this vast oceanic area, depending on the duration of the inter-breeding period, which was shorter

(~ 7 months) for the failed breeder (#3138) that began a new breeding attempt later on the same calendar year (Fig. 2, upper right panel) and longer (~ 17 to 18 months) for the two

Table 3 Cephalopod prey of white-headed petrels identified from accumulated beaks sorted from chick food samples ($n=56$) from Kerguelen Islands

Species	Upper beaks (n)	Lower beaks (n)	Total		Southern Ocean endemic (Cherel 2020)
			(n)	(%)	
Ommastrephidae					
<i>Todarodes</i> sp.	7	3	10	6.54	
Unidentifiable Ommastrephidae	1	0	1	0.65	
Onychoteuthidae					
<i>Moroteuthopsis longimana</i>	11	10	21	13.73	Yes
Psychroteuthidae					
<i>Psychroteuthis</i> sp. B (Imber)	3	1	4	2.61	Yes
Brachioteuthidae					
<i>Brachioteuthis linkovskiyi</i>	1	0	1	0.65	No
Gonatidae					
<i>Gonatus antarcticus</i>	18	12	30	19.61	No
Histioteuthidae					
<i>Histioteuthis atlantica</i>	2	2	4	2.61	No
<i>Histioteuthis elongata</i>	8	8	16	10.46	Yes
Neoteuthidae					
<i>Alluroteuthis antarcticus</i>	3	2	5	3.27	Yes
Mastigoteuthidae					
<i>Mastigoteuthis psychrophila</i>	3	3	6	3.92	Yes
Batoteuthidae					
<i>Batoteuthis skolops</i>	6	3	9	5.88	Yes
Chiroteuthidae					
<i>Chiroteuthis mega</i>	1	0	1	0.65	No
<i>Chiroteuthis veranyi</i>	2	1	3	1.96	No
Cranchiidae					
<i>Galiteuthis glacialis</i>	19	20	39	25.49	Yes
<i>Taonius notalia</i>	0	1	1	0.65	Yes
<i>Teuthowenia pellucida</i>	0	1	1	0.65	No
Unknown Oegopsida	0	1	1	0.65	
Total	85	68	153	100.00	
Eroded beaks	68	95	163		

other birds (#3150 and #3152) that skipped the next breeding season (Fig. 2, middle and lower right panels). Interestingly, both light and activity data indicated that the two latter petrels returned briefly to their burrows (two visits of 1 or 2 days) in October–November 2009 at the beginning of the breeding season they skipped.

Activity recorders and the birds' behaviour

The small number of GLS-tracked white-headed petrels together with their different breeding statuses precluded detailed analysis of the birds' behaviour over the species biennial cycle. Despite these limitations, a common pattern seems to emerge for the two individuals that were tracked during more than a year (Fig. 4). The daily proportion of time spent on water varied according to time elapsed since departure to the colony and to the month of

the year (Tables S3 and S4). Two birds (#3150 and #3152) had a first period of four months after leaving the colony where the daily proportion of time on water increased, whilst one failed breeder (#3138) left the colony earlier and showed an increase during the first month at sea (Fig. 4). When focusing on the first winter months (April to September 2009), the daily proportion of time spent on water varied from ~26% in May to ~65% in July. Whilst the time elapsed since departure from the colony explains a part of the variation of the daily proportion of time spent on water, the highest values seem to be reached in July, August, and September (Fig. S1, Table S4), thus suggesting that the moult of flight feathers occurred at that time. A similar pattern occurred during both the day and night, but white-headed petrels consistently spent more time on water during the night than during the day (Fig. S1).

Table 4 Isotopic values of white-headed petrels from Kerguelen Islands

Groups	Sampling date	Tissue	Individuals (n)	Feathers (n)	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	C:N mass ratio
Incubating adults	December 2007	Whole blood	9	na	-21.8 ± 0.6 (−22.3, −20.6)	12.4 ± 0.3 (12.0, 12.8)	3.51 ± 0.25 (3.32, 4.10)
Large chicks	March 2008	Whole blood	10	na	-23.4 ± 0.2 (−23.7, −23.2)	11.4 ± 0.2 (11.1, 11.9)	3.57 ± 0.10 (3.43, 3.72)
<i>Two-sample t test</i>					<i>t = 7.83, p < 0.0001</i>	<i>t = 9.03, p < 0.0001</i>	<i>t = −0.733, p = 0.473</i>
Incubating adults	December 2002	Body feathers	10	10	-19.5 ± 1.5 (−22.5, −17.1)	12.6 ± 1.6 (8.3, 13.7)	3.16 ± 0.03 (3.12, 3.20)
	December 2007	Body feathers	9	35	-19.4 ± 2.3 (−26.8, −16.7)	12.7 ± 1.4 (7.8, 14.7)	3.14 ± 0.01 (3.11, 3.17)
Large chicks	April 2003	Body feathers	10	10	-21.9 ± 0.5 (−22.6, −21.0)	12.2 ± 0.2 (12.0, 12.5)	3.20 ± 0.02 (3.18, 3.22)
	March 2008	Body feathers	10	10	-21.1 ± 0.4 (−21.5, −20.5)	12.3 ± 0.4 (11.6, 12.9)	3.15 ± 0.04 (3.12, 3.26)
<i>Kruskal-Wallis test</i>					<i>H = 27.24,</i> <i>p < 0.0001</i>	<i>H = 12.72,</i> <i>p = 0.005</i>	<i>H = 27.22, p < 0.0001</i>
Incubating adults	Both years	Body feathers	19	45			
STZ				15	-17.4 ± 0.5	13.5 ± 0.6	
SAZ				26	-19.7 ± 0.6	12.8 ± 0.6	
AZ				4	-24.7 ± 1.8	8.5 ± 0.6	
<i>Kruskal-Wallis test</i>					<i>H = 33.87,</i> <i>p < 0.0001</i>	<i>H = 18.21,</i> <i>p < 0.0001</i>	

Values are means \pm SD with ranges in parentheses

AZ Antarctic zone; SAZ subantarctic zone; STZ subtropical zone

Significant differences are in bold italics

Discussion

This study is the first to detail the diet of the white-headed petrel and to investigate its food and feeding ecology using the stable isotope method, thus allowing detailing both its prey items and its complex moulting habitats, respectively. Two limitations are that food, tissue sampling, and at-sea data were collected on different years, and only three birds equipped with GLS were retrieved. However, we are confident that the results represent the normal biology of the species because inter-annual variations in both food items (three consecutive years) and isotopic values (two years) were negligible.

Chick diet

The food of the white-headed petrel was virtually unknown, because the previous anecdotal information was based on the opportunistic examination of either partial regurgitates from handled birds or the digestive tract from dead specimens (Barré 1976; Imber 1983; Zotier 1990). This opportunistic sampling resulted in an overestimation of the dietary importance of cephalopods due to the consistent finding of accumulated beaks in the birds' stomachs. By contrast, our study emphasizes that white-headed petrels feed primarily

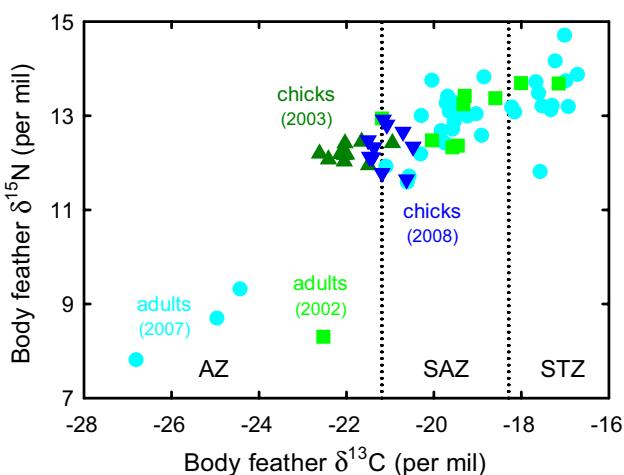


Fig. 1 Body feather isotopic values of white-headed petrels during the 2002/2003 (incubating adults, green squares; large chicks, dark green triangles up) and 2007/2008 (incubating adults, cyan circles; large chicks, blue triangles down) breeding cycles. A single-body feather was measured on chicks and on the 2002 adults, but four body feathers were used on 2007 adults. Vertical reference-dotted lines correspond to the feather isotopic estimation of the Polar and Subtropical Fronts (Jaeger et al. 2010b). AZ Antarctic Zone; SAZ Subantarctic Zone; STZ subtropical Zone

Table 5 Number of GLS locations and the corresponding time spent in various water masses by white-headed petrels from the Kerguelen Islands

Periods	Antarctic Zone		Subantarctic Zone		Subtropical Zone	
	(n)	(%)	(n)	(%)	(n)	(%)
Breeding	177	30.4	344	59.0	62	10.6
Inter-breeding	414	21.1	1128	57.4	424	21.6
Both	591	23.2	1472	57.7	486	19.1

Data from the three tracked adult birds were pooled

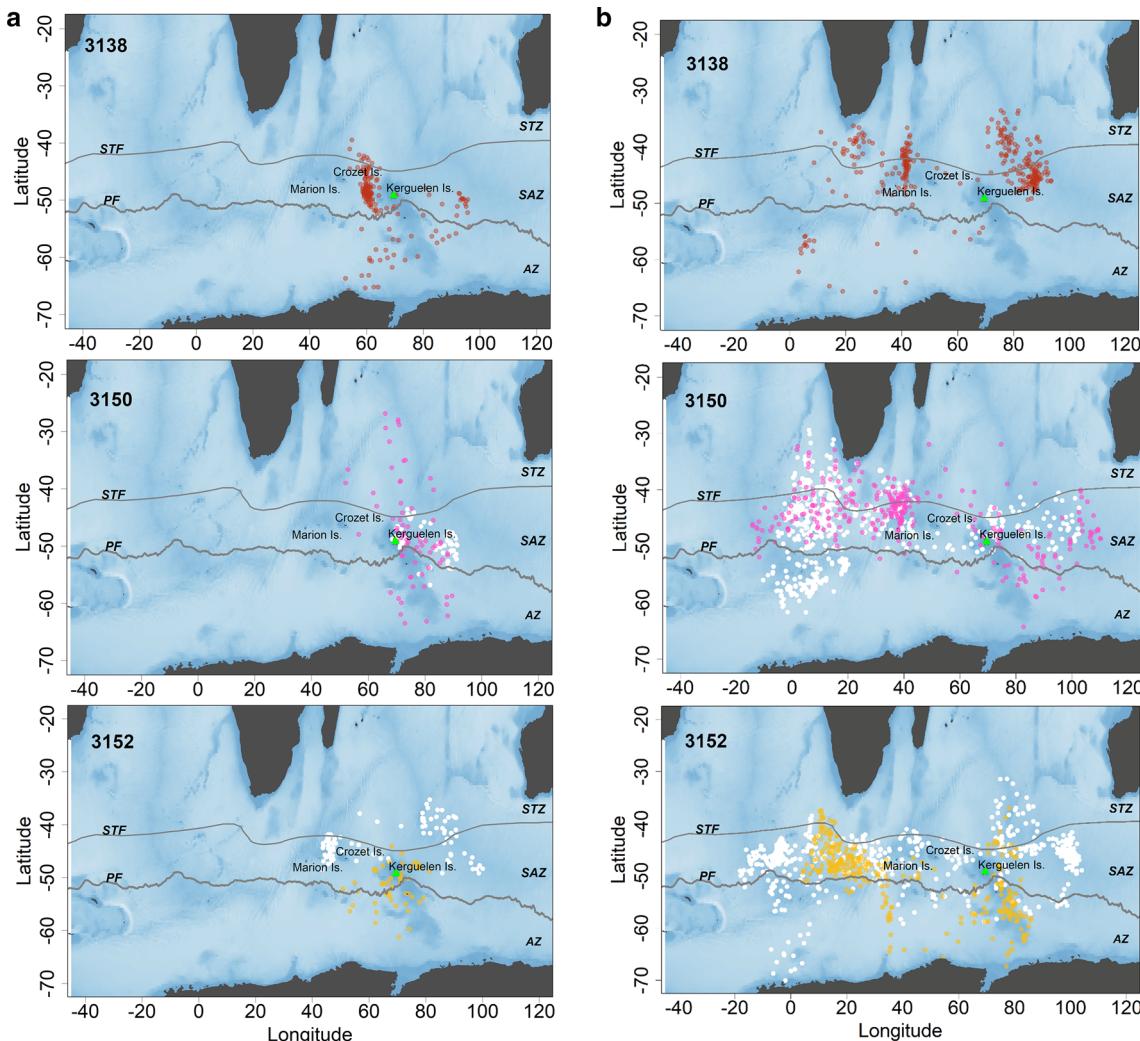


Fig. 2 Distribution at sea of three GLS-tracked white-headed petrels from the Kerguelen Islands during both the breeding (left panels, **a**) and non-breeding (right panels, **b**) periods. Each individual is showed with a different colour during the first year of tracking; locations of the second year are in white. Breeding colony (green triangle) is

indicated. The main frontal structures, the Subtropical Front (STF) and Polar Front (PF), are showed by grey lines (Belkin and Gordon 1996; Sokolov and Rintoul 2009). They delineate the following oceanic zones, from north to south, the Subtropical (STZ), Subantarctic (SAZ), and Antarctic (AZ) Zones

their chick with fish, which was the main component of the diet estimated by fresh items mass over the three consecutive years of the study period. Cephalopods ranked second, whilst crustaceans are minor items. Fish predominated by mass in a majority of the food samples, but owing to their large size, they only accounted for 37% of the total number

of prey, followed by crustaceans (34%) and cephalopods (26%).

With the exception of a single prey item (the icefish *Champscephalus gunnari*), all the food sources were oceanic species (Table 2), with a large majority of pelagic organisms and a few benthopelagic fish living in slope

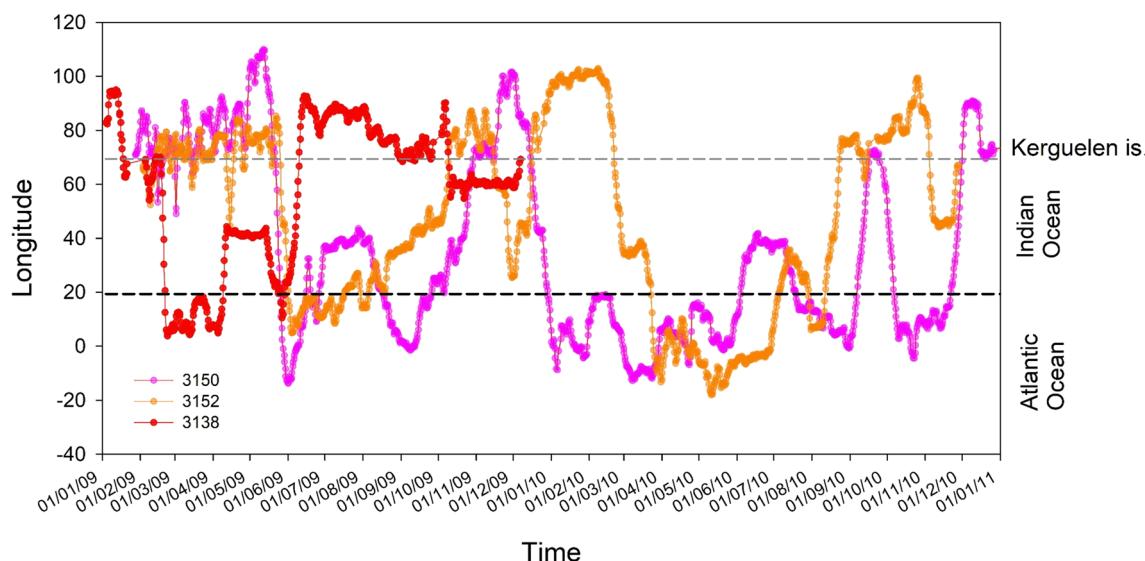


Fig. 3 Year-round longitudinal position of three GLS-tracked white-headed petrels from the Kerguelen Islands. Each individual is showed with a different colour. Horizontal-dashed lines represent the location

of the breeding colony and the spatial limit between the Indian and Atlantic Oceans

waters (e.g. macrourids). The diet of white-headed petrels was dominated by mesopelagic fish, with myctophids ranking first and melamphaids second in terms of both species diversity and prey number (10 and three species, 50% and 15% of the fish prey, respectively). Hence, the study emphasizes the great importance of myctophids in the diet of oceanic seabirds worldwide (Watanuki and Thiébot 2018), including gadfly petrels *Pterodroma* spp. (Spear et al. 2007; Cherel and Bocher 2022). The presence of significant numbers of melamphaids is more unusual as those deep-sea fish are rarely reported in the diet of seabirds (Ridoux 1994; Spear et al. 2007). However, the consistent identification of melamphaids as prey of procellariids breeding at Kerguelen and Crozet Islands indicates they are not rare prey items in the western Indian Ocean (Cherel et al. 2002a; Connan et al. 2007; Cherel and Bocher 2022), thus suggesting they were previously underestimated elsewhere in the Southern Ocean. White-headed petrels fed also significantly on cephalopods, all oceanic squids (Cherel 2020), which highlight the importance of both squid and fish in the diet of gadfly petrels worldwide (review in Cherel and Bocher 2022). Crustaceans constitute a minor prey group for the large-sized white-headed petrel, which is in agreement with crustaceans being only significant food items of small- and medium-sized *Pterodroma* species foraging in temperate and cold waters of the Southern Hemisphere (Cherel and Bocher 2022).

Almost all prey species of the white-headed petrel are known to live in the Southern Ocean, including endemic species of fish (e.g. *Gymnoscopelus* spp.), squids (e.g. *Galiteuthis glacialis*, *Moroteuthopsis longimana*), and crustaceans

(e.g. the Antarctic krill *Euphausia superba*) (Tables 2 and 3). Consequently, a combination of information (food items, tracking, at-sea distribution, and isotopes) corroborates that the species forages primarily in oceanic waters of the SAZ and AZ during the chick-rearing period (Jouventin et al. 1988; Taylor et al. 2020, Stahl et al. unpublished data, this study). No dietary data are available from the great-winged petrel from Kerguelen Islands, but prey biogeography indicates that the third species of sympatric gadfly petrels, the soft-plumaged petrel, forages primarily in oceanic waters of the SAZ, but not the AZ, during the chick-rearing period (Cherel and Bocher 2022). Soft-plumaged and white-headed petrels feed primarily on mesopelagic fish, but, owing to its smaller size, soft-plumaged petrel prey more on crustaceans and less on squids than the white-headed petrel. The commonest cephalopod remains in food samples of both species were large eyes that were barely digested (the so-called “Oegopsida sp. A”), which were likely scavenged from dead or dying cephalopods too large to swallow whole (Cherel and Bocher 2022, this study).

Stable isotopes, breeding cycle, and moult

Isotopic values of white-headed petrels highlight their oceanic habitat during breeding. The low blood and feather $\delta^{13}\text{C}$ values of large chicks indicate a diet based on mixed subantarctic and Antarctic prey. Indeed, white-headed petrels occur at sea mainly at 48–56° S and to the ice edge in the western Indian Ocean during the chick-rearing period (Stahl et al. unpublished data). Accordingly, a few digested specimens of the high-Antarctic endemic Antarctic krill were identified

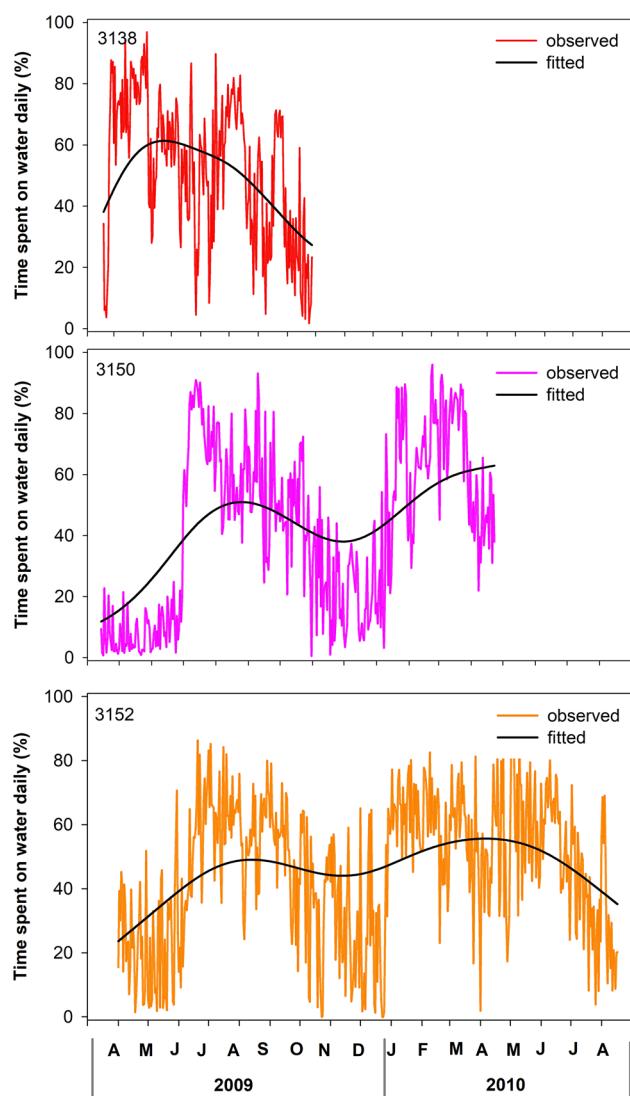


Fig. 4 Daily proportion of time spent on the water (observed data and values fitted using GAM) during the complete GLS-tracking period of three adult white-headed petrels from the Kerguelen Islands

in some food samples. In contrast to chick values, the higher adult blood $\delta^{13}\text{C}$ values suggest that, in early breeding and incubation, breeders did not forage at high latitudes but favoured feeding within the SAZ. Again, this is in agreement with both tracking and at-sea observations with birds foraging north of 50° S at that time (Stahl et al. unpublished data). The relatively high blood $\delta^{15}\text{N}$ values correspond well with a mesopelagic fish and squid-based diets, with the 1‰ higher value in adults than in chicks likely resulting from the combination of a low proportion of lower trophic-level prey in the chick food (e.g. Antarctic krill; Cherel 2008) and of a decreasing $\delta^{15}\text{N}$ baseline with latitudes (Jaeger et al. 2010b).

Feathers of adult white-headed petrels showed higher mean values and variances than chick feathers. Adult $\delta^{13}\text{C}$ values indicate moulting body feathers within the Southern

Ocean and north of it, within the STZ, where the slightly higher $\delta^{15}\text{N}$ values again suggest a fish and squid-based diet. In contrast, the very low $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of a few body feathers highlight a dietary shift to low trophic-level prey, most likely Antarctic krill, when birds moulted in high Antarctica. Moulted body feathers in different latitudinal habitats were previously described within and between individuals of various Southern Ocean Procellariiformes (Jaeger et al. 2010a, 2013; Mills et al. 2021). Body feathers show a larger range of isotopic values than flight feathers, thus illustrating the more protracted moult of body feathers than flight feathers in Procellariiformes (Warham 1996; Cherel et al. 2016).

In most species, new feathers are synthesized during the inter-breeding period, with a transient flight impairment due to wing moult being associated with a peak in the proportion of time spent on water during the post-breeding or, more rarely, the pre-breeding period (Cherel et al. 2016). The activity and geolocation data of the three white-headed petrels from the Kerguelen Islands suggest a wing moult right after breeding in both the SAZ (61% of the locations) and STZ (31%) (Figs. S1 and S2). This timing agrees with an expected post-breeding wing moult (Warham 1967) and the disappearance of white-headed petrels from Kerguelen waters during July–August together with the at-sea observations of moulting birds within the STZ at that time (Stahl et al. unpublished data). Whether white-headed petrels renew their flight feathers during a single inter-breeding period merits further investigations, because biennial breeding albatrosses renew the whole set of primaries and secondaries either during one or two consecutive inter-breeding periods, depending on species and/or their previous breeding success (Prince et al. 1997).

The presence of feathers in burrows previously suggested that body moult of white-headed petrels occurs not only during the inter-breeding period but also during the beginning of the breeding cycle (Warham 1967). This unusual timing is questionable, however, because (i) the birds themselves were not examined to check both their breeding status and moulting pattern (Warham 1967), (ii) Warham (1967) expected an annual breeding cycle, but white-headed petrels are biennial breeders, meaning that successful breeders have plenty of time to renew their plumage during their long inter-breeding period, and (iii) the birds that skipped breeding attempts returned to their burrows just briefly at the start of the breeding season they are about to skip (Taylor et al. 2020, this study). At that time, they are likely in moult, thus probably explaining the presence of body feathers in some burrows.

At-sea distribution

The low accuracy of our tracking data associated with GLS (Phillips et al. 2004) is balanced by the wide range

of white-headed petrels during both the breeding and inter-breeding periods (Taylor et al. 2020, this study). However, a better knowledge of the at-sea distribution and foraging behaviour of the species at Kerguelen Islands requires more tracked individuals of known age and sex coupled with feather and blood sampling for isotopic analyses. Despite this limitation, the study provides the first information on the foraging ecology of the poorly-known white-headed petrel from the Indian Ocean, which can be compared with the recent GLS tracking of birds from the Pacific Ocean (Taylor et al. 2020). The most relevant features are the following. (i) Latitudinally, adult birds from both populations foraged in oceanic waters from ~30° S to the ice edge, but they overall favour the SAZ over the STZ and AZ, with the former and latter zones being more used during the inter-breeding and breeding periods, respectively. (ii) Longitudinally, the at-sea distribution of the two populations overlaps greatly within the Indian Ocean. Breeding petrels from the Auckland Islands spatially overlap with Kerguelen birds during their long-range pre-laying exodus, and the distribution of non-breeding Auckland petrels overlap with the breeding distribution of Kerguelen birds. (iii) Noticeably, however, only Kerguelen birds move west in the eastern Atlantic and only Auckland birds forage in the western Pacific. Interestingly, the tracked individuals did not distribute in most of the Atlantic and Pacific Oceans, thus suggesting that birds observed in those areas might not be adults during their ‘sabbatical’ year as previously suggested, but most probably immatures (Brooke 2004). (iv) Tracking data from the two populations fit well with the known at-sea distribution of white-headed petrels (Marchant and Higgins 1990; Brooke 2004, Stahl et al. unpublished data), with the main limitation that visual observations gave no information about the breeding origin and status of the recorded individuals.

Procellariiform seabirds are at risk to interact directly with commercial fisheries and to ingest anthropogenic debris at the sea surface (Wilcox et al. 2015; Dias et al. 2019). The oceanic habits of the white-headed petrel are likely to minimize its interactions with neritic and slope fisheries, but they do not exclude potential detrimental effects of oceanic fisheries in the subtropics. However, like other gadfly petrels (Warham 1990), the species has little interest in ships and it was not consequently recorded in the incidental capture of seabirds by fishing vessels in Kerguelen waters (Cherel et al. 1996; Weimerskirch et al. 2000; Delord et al. 2005) and elsewhere (Petyt 1995; Brothers et al. 2010). Accordingly, neither fishery-related items nor plastic debris were found in food samples and in the colony, thus indicating no significant interactions of white-headed petrels with human activities, which is a key positive issue for its conservation at sea.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00300-022-03092-7>.

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Author contributions YC, HW, CB, and KD conceived and designed the research, KD analysed the GLS data, YC analysed food samples and stable isotopes data and drafted the manuscript. All authors edited, read, and approved the manuscript.

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Data availability The dataset generated during the current study is available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors declare that they have no conflict of interest to disclose.

Ethical approval Fieldwork was approved by the Conseil des Programmes Scientifiques et Technologies Polaires (CPST) of the Institut Polaire Français Paul Emile Victor (IPEV), and procedures and animal manipulations were approved by the Animal Ethics Committee of IPEV.

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