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Cephalopod prey of light-mantled sooty albatross *Phoebetria palpebrata*, resource partitioning amongst Kerguelen albatrosses, and teuthofauna of the southern Indian Ocean

Yves Cherel [a,*], Colette Trouvé [a], Paco Bustamante [b]

[a] *Centre d'Etudes Biologiques de Chizé, UMR 7372 du CNRS-La Rochelle Université, 79360, Villiers-en-Bois, France*

[b] *Littoral Environnement et Sociétés (LIENSs), UMR 7266 du CNRS-La Rochelle Université, 2 rue Olympe de Gouges, 17000, La Rochelle, France*

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A B S T R A C T

The cephalopod diet of the light-mantled sooty albatross *Phoebetria palpebrata* was determined for the first time at the subantarctic Kerguelen Islands by sorting ~7000 accumulated beaks from 66 regurgitated boluses. Twenty-two taxa were identified, including four dominant squid species that are all endemic to the Southern Ocean: *Galiteuthis glacialis* (49.8% of the lower beaks) *Psychroteuthis glacialis* (18.5%), *Martialia hyadesi* (16.2%) and *Moroteuthopsis longimana* (6.9%). Beak $\delta^{13}C$ values indicated that all adult *P. glacialis*, almost all juvenile *M. longimana*, and most adult *G. glacialis* were caught in Antarctic waters, while albatrosses preyed upon juvenile *M. hyadesi* in subantarctic waters. Comparative analysis of lower beaks accumulated in food samples of Kerguelen albatrosses showed that the four main sympatric albatross species segregate primarily by species-specific foraging grounds. Light-mantled sooty albatross feed on the Antarctic *P. glacialis*, wandering albatross *Diomedea exulans* on subantarctic and subtropical histioteuthids (41.4%), and grey-headed albatross *Thalassarche chrysostoma* and black-browed albatross *T. melanophris* on subantarctic ommastrephids (69.3% and 65.7%, respectively), with black-browed albatross also preying upon neritic endemic octopuses (17.6%). Cephalopod prey of Kerguelen albatrosses highlight the abundance and importance of some squids in the functioning of the pelagic ecosystem of the southern Indian Ocean, such as ommastrephids, *M. longimana, P. glacialis, Histioteuthis atlantica, H. eltaninae*, and *G. glacialis*. Based on the diet of the light-mantled sooty albatross, *P. glacialis* appears common in high-Antarctic waters of the southern Indian Ocean, whereas the poorly known *Psychroteuthis* sp. B (Imber) is evidently present in Antarctic waters south of the Kerguelen Islands.

1. Introduction

Albatrosses are iconic seabirds most often associated with the strong winds of the southern latitudes. They are among the world's most endangered taxa of birds, with all the Southern Ocean species but one (the black-browed albatross *Thalassarche melanophris*) being classified from near threatened to critically endangered in the IUCN Red List (IUCN 2023). Many albatrosses breed on a few islands, but four species have a circumpolar breeding distribution, the wandering albatross *Diomedea exulans*, grey-headed albatross *T. chrysostoma*, black-browed albatross (together with the closely-related Campbell albatross *T. impavida*) and the light-mantled sooty albatross *Phoebetria palpebrata*. Many ecological investigations at various locations have been conducted on the wandering, grey-headed and black-browed albatrosses, while only a few studies focused on the light-mantled sooty albatross (Thomas 1982; Thomas et al., 1983; Weimerskirch and Robertson 1994; Phillips et al., 2005; Terauds and Gales 2006). The two main limitations to study of light-mantled sooty albatrosses are that they are more skittish than other species and they build their nests on steep cliffs, which are often inaccessible.

In the southern Indian Ocean, albatrosses breed in large numbers at the subantarctic Prince Edward, Crozet and Kerguelen Islands. The Kerguelen Islands host abundant populations of the four circumpolar albatrosses, which number 1,327, 6,680, 3,290 and 3-5,000 annual breeding pairs for wandering, grey-headed, black-browed and light-mantled sooty albatrosses, respectively (Weimerskirch et al., 2018). Several investigations were conducted over the last decades on the food and feeding ecology of the three former species (*e.g.*, Weimerskirch

* Corresponding author.
E-mail address: cherel@cebc.cnrs.fr (Y. Cherel).

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et al., 1988, 1997, 2015, 2020; Cherel et al., 2000, 2002, 2017), which contrast with the paucity of studies on the latter species. Anecdotal information is available on food of light-mantled sooty albatross at Kerguelen Islands (Marchant and Higgins 1990), and a few individuals have been tracked using satellite tags or light-level geolocators (GLS) (Delord et al., 2013).

Albatrosses is the group of seabirds that feed the most on cephalopods (up to 87% of the dietary intake by fresh mass; Cherel and Klages 1998; Cherel et al., 2017). Sclerotized beaks of cephalopods accumulate over weeks and months in the stomachs of albatrosses, thus allowing detailing their squid and octopus prey from large numbers of accumulated beaks (*e.g.*, Cherel et al., 2017). The importance of cephalopods in the diet of albatrosses highlights the growing body of evidence that oceanic squid species play a key role in the marine food webs of the Southern Ocean (Rodhouse and White 1995; 2013; Collins and Rodhouse 2006). The biology of Southern Ocean cephalopods is nonetheless poorly known (Cherel 2020), with the main limitations being the small number of research cruises targeting squids, together with the difficulties in collecting large specimens by nets (Rodhouse 1990). Most previous Southern Ocean oceanographic and fishery cruises had been conducted in the southwest Atlantic and western Pacific Ocean, with the result that the Indian Ocean is the less known of the three major oceans for pelagic cephalopods. A complementary and innovative tool to gather information on cephalopods is to use their predators as bio-samplers to investigate their biodiversity, biogeography, abundance and life-history traits. The method has already provided relevant information on pelagic squid and octopuses from the southern Indian Ocean (*e.g.*, Cherel and Weimerskirch, 1995; 1999; Cherel et al., 2004; Cherel 2020).

The five aims of this study were: (i) to detail for the first time the cephalopod diet of light-mantled sooty albatross at Kerguelen Islands, since cephalopods constitute a major prey group of the species elsewhere (34-77% by mass; Thomas 1982; Ridoux 1994; Cooper and Klages 1995; Connan et al., 2014); (ii) to determine in which latitudinal habitat the main cephalopod prey of light-mantled sooty albatross were caught using the carbon isotopic values of lower beaks and the well-defined latitudinal δ^{13}C gradient occurring within the Southern Ocean (Cherel and Hobson 2007; Espinasse et al., 2019); (iii) to review and update the cephalopod diet of light-mantled sooty albatross at various localities (South Georgia, Marion and Crozet Islands) to delineate similarities and site-specific differences within the Southern Ocean; (iv) to review the cephalopod diet of albatrosses at Kerguelen Islands to highlight resource partitioning and segregating mechanisms amongst sympatric albatrosses during the chick-rearing period, and (v) to use albatrosses as bio-samplers of cephalopods in the southern Indian Ocean to examine their biodiversity and abundance, because predators catch a greater diversity of large specimens than sampling gears (Rodhouse 1990).

The Southern Ocean is here defined as water masses south of the Subtropical Front (STF). The Southern Ocean can be split into three broad oceanographic zones, from South to North, the Antarctic Zone (AZ) between Antarctica and the Polar Front (PF), the Polar Frontal Zone (PFZ) between the PF and the Subantarctic Front (SAF), and the Subantarctic Zone *stricto sensu* (SAZ) between the SAF and STF (the SAZ *lato sensu* corresponds to the zone betwen the PF and STF) (Pollard et al., 2002). The oceanic zone north of the STF is the Subtropical Zone (STZ). The Kerguelen Archipelago (49°20′ S, 69°20’ E) is located near the PF, within the southern part of the PFZ of the Indian Ocean. Kerguelen Islands are surrounded by a productive and extensive peri-insular shelf, the Kerguelen Plateau, with the PF being bathymetrically diverted to flow around the plateau (Park et al., 1993; 2014).

2. Materials and methods

2.1. Study sites and sampling

A total of 66 albatross boluses regurgitated by large chicks were collected over five consecutive years (n = 19, 12, 2, 18 and 15, in 1995, 1996, 1997, 1998 and 1999, respectively) at Canyon des Sourcils Noirs (n = 49), and from nesting sites on eastern side of Grande Terre of the Kerguelen Islands, in various islands of the Golfe du Morbihan (n = 11, 4 and 2 at Mayes, Ile Haute and Guillou, respectively). Boluses were collected near nests, either at the end of the chick-rearing period and right after fledging (March–June), or early in the next breeding season near unoccupied nests (September–January), thus referring to the previous chick-rearing period. Boluses were collected because cephalopod prey identified from boluses and stomach contents compare well, and collection and analysis of boluses is therefore a simple, efficient, and noninvasive method for assessing the cephalopod diet of albatrosses (Xavier et al., 2005).

2.2. Bolus analysis

Albatross chick boluses consist of indigestible prey remains that include cephalopod beaks, lenses, spermatophores and gladii, fish bones and lenses, bird feathers, pebbles, and vegetation together with anthropogenic remains such as plastics and fishery-related items. In most cases, sclerotized cephalopod beaks were the main component of boluses, because they are retained in albatross chicks' stomachs from hatching until shortly before fledging, when it is voluntarily regurgitated (Xavier et al., 2005). Cephalopod beaks were sorted from boluses of light-mantled sooty albatrosses, cleaned and stored in 70% ethanol before subsequent analysis. Both lower and upper beaks were numbered and identified by comparison with material held in our own collection and by reference to the available literature (Clarke 1986; Imber 1992; Cherel 2020; Xavier and Cherel 2021). Species names are based on a recent review on Southern Ocean squids (Cherel 2020), which followed the Tree of Life Web Project (Tolweb, 2023), except for newly described taxa (*e.g., Taonius* spp.; Evans 2018). Lower rostral length (LRL) of squid beaks and lower hood length (LHL) of octopus beaks were measured using a Vernier calliper. Cephalopod dorsal mantle length (DML) and body mass were estimated using regression equations (Clarke 1986; Adams and Klages 1987; Rodhouse and Yeatman 1990; Lu and Williams 1994; Gröger et al., 2000; Piatkowski et al., 2001; Lu and Ickeringill 2002; Xavier and Cherel 2021). Unlike accumulated wholly darkened beaks of adult squids, most undarkened or darkening lower beaks lose their fragile wings over time in chicks' stomachs, thus precluding measuring LRL of juvenile and maturing squids, respectively.

2.3. Stable isotopes on squid beaks

Carbon and nitrogen isotopic measurements were performed on 12-15 lower beaks of the four commonest cephalopod prey of light mantled sooty albatross, namely *Galiteuthis glacialis, Martialia hyadesi, Moroteuthopsis longimana* and *Psychroteuthis glacialis*, which were sorted from boluses collected in 1996 and 1999, for a total of 25–30 beaks per species. The lack of wings precluded measuring LRL of beaks from juveniles *M. hyadesi* and *M. longimana*. Prior to analysis, samples were dried, ground to a fine powder, and ~0.3 mg sub-samples were weighed with a microbalance and packed into tin containers. Nitrogen and carbon isotope ratios were subsequently determined by a continuous flow mass spectrometer (Thermo Scientific Delta V Plus) coupled to an elemental analyser (Thermo Scientific Flash, 2000). Results are presented in the usual δ notation relative to Vienna PeeDee Belemnite and atmospheric N_2 for δ^{13}C and δ^{15}N, respectively. Normalization was done using the reference materials USGS61 and USGS63 (United States Geological Survey) based on their assigned δ^{13}C and δ^{15}N values (± standard deviation, SD), *i.e.*, -35.05 ± 0.04 and -1.17 ± 0.04‰, and -2.87 ± 0.04 and +37.83 ± 0.06‰, respectively. Replicate measurements of USGS61 and USGS63 indicate SD <0.03‰ and <0.08‰ for δ^{13}C and δ^{15}N, respectively.

The use δ^{13}C and δ^{15}N to investigate the food and feeding ecology of marine animals has been validated in the southern Indian Ocean. Tissue δ^{13}C values of consumers reflect the latitudinal δ^{13}C gradient at the base of the food web and thus indicate their latitudinal foraging habitats (Cherel and Hobson 2007; Jaeger et al., 2010), while $\delta^{15}N$ 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 $\delta^{13}C$ position of the main oceanic fronts, and thus to delineate robust isoscapes of the main foraging zones for predators. Based on $\delta^{13}C$ isoscapes (Jaeger et al., 2010) that were corrected according to beaks (+0.8‰; calculated from Hobson and Cherel 2006), the $\delta^{13}C$ position of the Polar Front was estimated at -21.7‰, meaning that $\delta^{13}C$ values less and more than -21.7‰, were considered to correspond to the Antarctic (AZ) and Subantarctic (SAZ *lato sensu*) Zones, respectively.

2.4. A review of cephalopod prey of albatrosses from Kerguelen Islands

Six albatross species breed at Kerguelen Islands, with the population of two of them, the Indian yellow-nosed albatross *Thalassarche carteri* and sooty albatross *Phoebetria fusca*, being fairly small (n = 23 and 10 breeding pairs, respectively; Weimerskirch et al., 2018). The food of yellow-nosed albatross chicks was described from a few stomach contents (Cherel et al., 2002), but no dietary information is available for sooty albatross; the two species were therefore excluded from the analysis. Cephalopod prey of the four remaining species, the wandering, grey-headed, black-browed and light-mantled sooty albatrosses were compiled from both existing literature and unpublished information (Cherel et al., 2002, 2017, this study). Accumulated beaks were sorted from chick stomach contents of wandering and grey-headed albatrosses, and from chick boluses of light-mantled sooty albatross. Cephalopod diet of black-browed albatross was studied using pooled accumulated beaks sorted from chick stomach contents at two colonies, Iles Nuageuses (Cherel et al., 2002) and Canyon des Sourcils noirs (Cherel et al., 2000), and unpublished data referring to 27 food samples collected in 2000 at the latter site.

Species names of squids from previous investigations (Cherel et al., 2000; 2002; 2017) were updated following Cherel (2020). The review focused on lower beaks only, because the upper beaks of juveniles of the two trophically important *M. hyadesi* and *Todarodes* sp. are similar, thus precluding identifying them with confidence at the species level. Their lower beaks are also closely related, but their morphology is different enough to allow identification of eroded beaks (without wings). Hence, all the lower beaks previously identified as Ommastrephidae sp. in the diet of grey-headed and black-browed albatrosses (Cherel et al., 2000; 2002) were re-examined and split into two groups corresponding to *M. hyadesi* and *Todarodes* sp.

2.5. Data analysis

All the beaks of a given cephalopod taxon from all the boluses or stomach contents were summed for a given albatross species and locality. The numerical importance (%) of each cephalopod taxon refers to the total number of beaks of that taxon over the total number of cephalopod beaks from all taxa in all food samples. Data were statistically analyzed using SYSTAT 13. Values are means ± SD.

3. Results

3.1. Light-mantled sooty albatross

A total of 6998 accumulated beaks were sorted from 66 boluses of light-mantled sooty albatross. Boluses contained no macroscopic anthropogenic items. Since 24 beaks were too eroded to be identified with confidence, beaks that were identified to the lowest possible taxon numbered 6974 (3446 and 3528 lower and upper beaks, respectively) (Table 1). Twenty-two cephalopod taxa were identified, including 21 oegopsids and one octopod. The latter was not identified to the species level, because beaks of *Graneledone gonzalezi* and *Muusoctopus thielei*, the two benthic octopuses living in Kerguelen waters, are identical (Cherel et al., 2000). The cephalopod diet of light-mantled sooty albatross was dominated by four oegopsids. The cranchiid *G. glacialis* was by far the most abundant prey (50.3% of the total number of identified beaks). The psychroteuthid *P. glacialis* ranked second (17.5%), the ommastrephid *M. hyadesi* third (see below for percentage by number of lower beaks only), and the onychoteuthid *M. longimana* fourth (6.8%). Pooled upper and lower beaks of ommastrephids amounted to 18.2% by number, and analysis of lower beaks indicated a large predominance of *M. hyadesi* over *Todarodes* sp. (16.2% versus 1.6%; Table 2). A significant number of beaks of the uncommon and still undescribed taxon *Psychroteuthis* sp.

Table 1
Numbers of accumulated cephalopod beaks identified from boluses of light-mantled sooty albatross at Kerguelen Islands in 1995–1999. Endemism and biogeography refer to the review of Cherel (2020) on Southern Ocean squids. Abbreviations: AZ, Antarctic Zone; PFZ, Polar Frontal Zone; SAZ, Subantarctic Zone *stricto sensu* (for definitions, see text).

Species	Number (n)	Number (%)	Southern Oceanendemic	Biogeography within the Southern Ocean
Ommastrephidae				
Martialia hyadesi (lower beaks)	559	8.02	yes	(AZ) + PFZ + SAZ
Todarodes sp. (lower beaks)	55	0.79	no	PFZ + SAZ
Ommastrephidae sp. (upper beaks)	657	9.42	na	na
Onychoteuthidae				
Filippovia knipovitchi	8	0.11	yes	AZ + PFZ
Moroteuthopsis longimana	471	6.75	yes	AZ + PFZ
Moroteuthopsis sp. B (Imber)	1	0.01	yes	PFZ + SAZ
Psychroteuthidae				
Psychroteuthis glacialis	1225	17.57	yes	AZ
Psychroteuthis sp. B (Imber)	75	1.08	yes	AZ + PFZ
Brachioteuthidae				
Brachioteuthis linkowskyi	1	0.01	no	PFZ + SAZ
Slosarczykovia circumantarctica	5	0.07	yes	AZ + PFZ + (SAZ)
Gonatidae				
Gonatus antarcticus	78	1.12	no	AZ + PFZ + SAZ
Octopoteuthidae				
Taningia danae	1	0.01	no	PFZ? + SAZ
Histioteuthidae				
Histioteuthis atlantica	1	0.01	no	PFZ + SAZ
Histioteuthis eltaninae	116	1.66	yes	(AZ) + PFZ + SAZ
Neoteuthidae				
Alluroteuthis antarcticus	66	0.95	yes	AZ + PFZ
Nototeuthis dimegacotyle	13	0.19	yes	PFZ + SAZ
Mastigoteuthidae				
Mastigoteuthis psychrophila	41	0.59	yes	AZ + PFZ + SAZ
Chiroteuthidae				
Chiroteuthis veranyi	14	0.20	no	AZ + PFZ + SAZ
Batoteuthidae				
Batoteuthis skolops	34	0.49	yes	AZ + PFZ + (SAZ)
Cranchiidae				
Galiteuthis glacialis	3520	50.47	yes	AZ + PFZ + (SAZ)
Mesonychoteuthis hamiltoni	1	0.01	yes	AZ + PFZ + (SAZ)
Taonius notalia	17	0.24	yes	(AZ) + PFZ + SAZ
Octopodidae				
Graneledone gonzalezi/ Muusoctopus thielei	15	0.22	yes	Kerguelen Plateau
Total	6974	100.00		
Eroded beaks	24			

Table 2
A review of accumulated cephalopod lower beaks identified from stomach contents and boluses of albatrosses at Kerguelen Islands. Only cephalopods accounting for >1% by number for one albatross species are detailed.

Species	Wandering albatross		Grey-headed albatross		Black-browed albatross		Light-mantled sooty albatross	
Sampling years	1998		1994		1994, 1995, 2000		1995, 1996, 1997, 1998, 1999	
Samples (n)	30		38		176		66	
References	Cherel et al. (2017)		Cherel et al. (2002)		Cherel et al. (2000, 2002), unpublished data		This study	
	(n)	(%)	(n)	(%)	(n)	(%)	(n)	(%)
Martialia hyadesi	100	3.8	112	8.2	652	36.7	559	16.2
Todarodes sp.	25	0.9	829	61.0	514	29.0	55	1.6
Filippovia knipovitchi	66	2.5			3	0.2	4	0.1
Moroteuthopsis longimana	268	10.1	123	9.1	23	1.3	239	6.9
Psychroteuthis glacialis	6	0.2	12	0.9			638	18.5
Psychroteuthis sp. B (Imber)			1	0.1			39	1.1
Gonatus antarcticus	46	1.7	7	0.5	12	0.7	38	1.1
Taningia danae	40	1.5			3	0.2		
Histioteuthis atlantica	799	30.1	1	0.1	2	0.1	1	0.0
Histioteuthis eltaninae	212	8.0	2	0.1	7	0.4	59	1.7
Histioteuthis miranda	40	1.5						
Alluroteuthis antarcticus	86	3.2	5	0.4	1	0.1	30	0.9
Cycloteuthis sirventi	86	3.2						
Batoteuthis skolops	36	1.4	6	0.4	34	1.9	11	0.3
Galiteuthis glacialis	326	12.3	243	17.9	177	10.0	1715	49.8
Taonius notalia	181	6.8	1	0.1			10	0.3
Taonius expolitus	56	2.1						
Teuthowenia pellucida	31	1.2						
Graneledone gonzalezi/Muusoctopus thielei	5	0.2			312	17.6	7	0.2
Other taxa	248	9.3	16	1.2	35	2.0	41	1.2
Total	2657	100.0	1358	100.0	1775	100.0	3446	100.0

B (Imber) (Cherel 2020) was present (n = 45, 1.1%; Table 1).

The loss of wings explains why only a few undarkened beaks of *M. hyadesi* and *Todarodes* sp. were measured. The loss of wings also led to an overestimation of the average size of *M. longimana*, as only a single small undarkened lower beak was measurable, while all large darkened beaks were measured (Table 3). The estimated DML and body mass of squids eaten by light-mantled sooty albatross ranged widely, from small *Histioteuthis eltaninae* (59 mm and 25 g, respectively) and *Slosarczykovia circumantarctica* (63 mm, 1.9 g) to a large adult *M. longimana* (635 mm and 6022 g). Depending on squid species, light-mantled sooty albatross fed on juveniles, immatures and/or adult specimens (lower beaks with undarkened, darkening and darkened wings, respectively; Clarke 1986). All beaks of *P. glacialis* and *Psychroteuthis* sp. B (Imber) were wholly darkened, thus indicating that albatrosses fed on adult squids. Accordingly, LRL frequency distribution of each species presented a single mode (Fig. 1). Beaks of *Psychroteuthis* sp. B (Imber) were well segregated from those of *P. glacialis* by their smaller LRL, with no size-overlap between the two squids. Beaks of *G. glacialis* showed a single LRL mode of darkened beaks of adults (93.0%), but also a significant proportion of darkening beaks (7.0%) from maturing squids (Fig. 2). A majority of beaks of *M. longimana* were from juveniles and maturing squids (77.7% *versus* 22.3% of adult beaks), while all the ommastrephid beaks were from juveniles and a few maturing specimens.

Substantial inter-annual variations and consistencies in the numerical importance of the main squid prey were found when comparing the years 1995, 1996, 1998 and 1999 (only two boluses were collected in 1997 that was thus excluded from the analysis). *G. glacialis* was always the main cephalopod prey (37.0%–68.5%), and the percentage by number of *P. glacialis* and *M. longimana* did not vary a lot from year to year (12.9%–19.5% and 4.3%–7.7%, respectively). By contrast, the numerical importance of ommastrephids (mainly *M. hyadesi*) varied greatly, from <1% in 1995 and 7.9% in 1999 to 29.5% in 1998 and 34.9% in 1996. Such large changes mostly explained year-to-year variations in the relative proportion of *G. glacialis*. Lower beaks of *Todarodes* sp. were uncommon in 1995, 1996 and 1998 (n = 0–4), but they outnumbered lower beaks of *M. hyadesi* in 1999 (n = 45 and 13, respectively). LRL of *G. glacialis* did not change statistically over years (Kruskal-Wallis H test, $H = 4.95$, $p = 0.175$), while the size of *P. glacialis* beaks varied significantly ($H = 22.23$, $p < 0.0001$). LRL was slightly larger in 1999 than in 1995, 1996 and 1998 (LRL: 7.3 ± 0.5 *versus* 7.1 ± 0.5, 7.2 ± 0.5 and 7.1 ± 0.5, n = 122 *versus* 133, 83 and 196; Conover-Inman tests for pairwise comparisons: p < 0.0001, 0.010 and <0.0001, respectively).

3.2. Stable isotopes on squid beaks

Overall, individual $\delta^{13}C$ and $\delta^{15}N$ values of lower beaks of the four main cephalopod prey of light-mantled sooty albatross at Kerguelen Islands ranged from -26.1 to -18.5‰ (a 7.7‰ difference), and from 2.3 to 9.7‰ (7.4‰), respectively. Inter-annual variations in isotopic values were not significant, or only marginally so, thus allowing pooling data from 1996 and 1999 for each squid species (Table 4). Squids were segregated by their $\delta^{13}C$ and $\delta^{15}N$ values, with each species having a species-specific isotopic niche (Fig. 3). All mean $\delta^{13}C$ values differed in the order *P. glacialis* < *M. longimana* < *G. glacialis* < *M. hyadesi*, with $\delta^{13}C$ value of *M. hyadesi* being less negative than those of the three other species (-19.2 *versus* -24.8–22.1‰). Lower beak $\delta^{15}N$ values of adult *G. glacialis* and *P. glacialis* were not statistically different (7.4-7.5‰), and they were higher than those of juvenile *M. longimana* (5.1‰) and *M. hyadesi* (2.8‰). Depending on species, mean C:N mass ratio of lower beaks ranged from 3.27 to 3.45. Such a low difference (0.18) indicates minor variations in the chemical composition of the whole accumulated beaks and, hence, that variations in chitin content cannot explain large inter-specific differences in $\delta^{15}N$ values (the higher the C:N of chitinous tissues, the higher the chitin content, and thus the higher the chitin effect that lowers $\delta^{15}N$; Cherel et al., 2009).

3.3. Sympatric albatrosses from Kerguelen Islands

A total of 9279 accumulated lower beaks were sorted from food samples of the four main albatross species breeding at Kerguelen Islands, with the number of lower beaks dependent on species, from 1365 (grey-headed albatross) to 3455 (light-mantled sooty albatross) (Table 2). Six features are notable as characterizing and differentiating the

Table 3
Measured lower rostral length (LRL) of squids and lower hood length (LHL) of octopus, and estimated dorsal mantle length (DML) and body mass of cephalopods eaten by light-mantled sooty albatross at Kerguelen Islands. Values are means ± SD with ranges in parentheses. na: not applicable.

Species	n	Measured LRL (LHL) (mm)	Estimated DML (mm)	Estimated body mass (g)
Martialia hyadesi	41	4.9 ± 0.5 (4.0-6.2)	247 ± 15 (218-285)	277 ± 56 (176-437)
Todarodes sp.	1	5.2	222	192
Filippovia knipovitchi	3	6.7 ± 0.6 (6.3-7.3)	312 ± 35 (288-352)	582 ± 193 (456-804)
Moroteuthopsis longimana (small)	1	7.5	257	407
Moroteuthopsis longimana (large)	53	13.2 ± 1.6 (10.0-17.6)	471 ± 58 (352-635)	2554 ± 1016 (1021-6022)
Psychroteuthis glacialis	560	7.2 ± 0.5 (5.8-8.6)	315 ± 49 (205-472)	542 ± 181 (197-1234)
Psychroteuthis sp. B (Imber)	39	4.8 ± 0.3 (4.1-5.5)	155 ± 13 (130-188)	93 ± 22 (54-157)
Brachioteuthis linkowskyi	1	4.5	108	4.9
Slosarczykovia circumantarctica	3	3.1 ± 0.8 (2.3-3.9)	80 ± 16 (63-96)	2.9 ± 1.0 (1.9-4.0)
Gonatus antarcticus	37	5.8 ± 0.5 (5.1-7.6)	204 ± 22 (177-282)	183 ± 65 (120-445)
Histioteuthis atlantica	1	3.5	80	98
Histioteuthis eltaninae	59	3.2 ± 0.3 (2.5-3.7)	74 ± 7 (59-87)	51 ± 13 (25-81)
Alluroteuthis antarcticus	17	5.7 ± 0.4 (4.9-6.4)	193 ± 14 (167-219)	568 ± 119 (366-800)
Nototeuthis dimegacotyle	7	3.3 ± 0.2 (2.9-3.5)	na	na
Mastigoteuthis psychrophila	17	3.8 ± 0.3 (3.3-4.2)	118 ± 2 (115-121)	21 ± 3 (17-26)
Chiroteuthis veranyi	6	6.0 ± 0.9 (4.3-6.7)	157 ± 21 (116-176)	102 ± 33 (39-135)
Batoteuthis skolops	10	3.9 ± 0.2 (3.6-4.3)	na	na
Galiteuthis glacialis	1485	5.2 ± 0.4 (3.3-6.1)	443 ± 35 (281-518)	99 ± 16 (35-139)
Taonius notalia	10	8.1 ± 1.1 (6.4-9.9)	482 ± 67 (381-598)	216 ± 64 (128-335)
Graneledone gonzalezi/Muusoctopus thielei	1	5.7	79	209
Total	2352			

cephalopod prey of albatrosses at Kerguelen Islands.

1. The food of wandering albatross included 40 different taxa, being twice as diverse as the diet of light-mantled sooty, grey-headed, and black-browed albatrosses (n = 21, 19 and 18 taxa, respectively).
2. *G. glacialis* was an important cephalopod prey of all albatrosses; it ranked first numerically for light-mantled sooty albatross (49.8%), and it accounted for 10.0-17.9% by number for the three other species (Table 2).
3. Ommastrephids (pooled beaks of *M. hyadesi* and *Todarodes* sp.) were dominant in the diet of grey-headed (69.3%) and black-browed (65.7%) albatrosses. They were also important prey of light-mantled sooty albatross (17.8%), but not for the wandering albatross (4.7%).
4. Wandering albatross fed significantly more on larger squids than the three other species (Table 5). The size-difference is large for *M. hyadesi* and *Todarodes* sp., but small for *G. glacialis*. Grey-headed, black-browed and light-mantled sooty albatrosses targeted juvenile ommastrephids, and all the four albatrosses preyed upon adult *G. glacialis*.
5. Some cephalopod taxa characterized the food of a single albatross species, as exemplified by histioteuthids (41.4% by number, mainly *H. atlantica* and *H. eltaninae*) and *Taonius notalia* (6.8%) for wandering albatross, benthic octopuses (17.6%) for black-browed albatross, and psychroteuthids (19.6%, mainly *P. glacialis*) for light-mantled sooty albatross.
6. Southern Ocean endemic cephalopods accounted for 97.0% of the total number of lower beaks sorted from food samples of light-mantled sooty albatross, a higher value than those recorded for black-browed (69.7%), wandering (50.8%) and grey-headed (38.0%) albatrosses. Conversely, squids occurring only north of the STF (as *T. expolitus* and *H. bonnellii corpuscula*) amounted to 3.2% by number in the diet of wandering albatross, while none was found in food samples of the three other albatrosses.

4. Discussion

At the Kerguelen Islands, cephalopod diet of light-mantled sooty

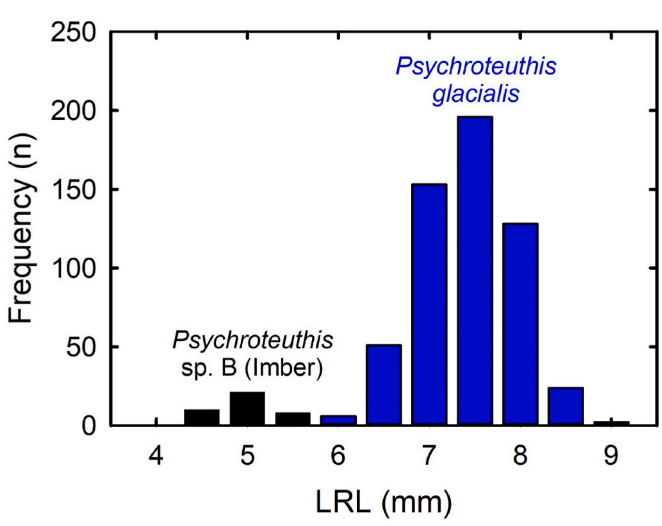

Fig. 1. Length-frequency distribution of lower rostral length (LRL) of adult *Psychroteuthis glacialis* (blue) and *Psychroteuthis* sp. B (Imber) (black) eaten by light-mantled sooty albatross at Kerguelen Islands.

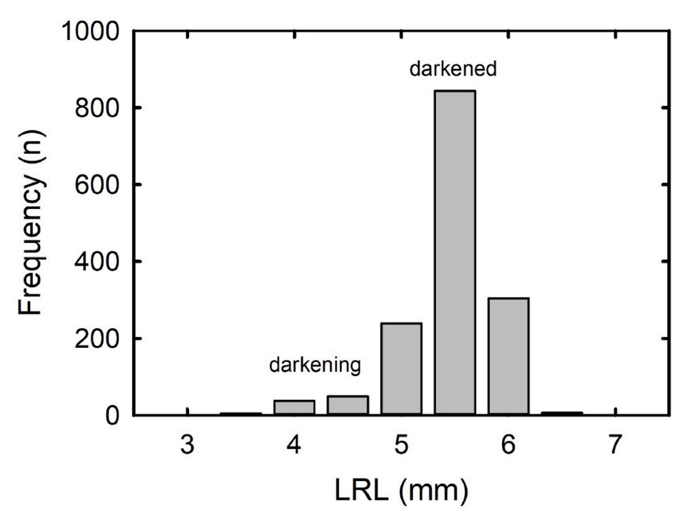

Fig. 2. Length-frequency distribution of lower rostral length (LRL) of *Galiteuthis glacialis* eaten by light-mantled sooty albatross at Kerguelen Islands.

Table 4
Size and isotopic values of lower beaks of four representative squid prey of light-mantled sooty albatross at Kerguelen Islands in 1996 and 1999. Values are means ± SD with ranges in parentheses. Values in columns sharing the same superscript letters are not statistically significant at p <0.05. LRL: lower rostral length, na: not applicable (beaks of juvenile squids without wings, thus precluding measuring LRL).

Species	Both years	1996	1999	Comparison between years
				Mann-Whitney U tests
Martialia hyadesi (n)	25	13	12	
LRL (mm)	na	na	na	na
δ^{13}C (‰)	-19.2 ± 0.5^{a}	-19.3 ± 0.4^{a} (-20.3, -19.0)	-19.0 ± 0.4^{a} (-19.7, -18.5)	*U = 46.0, p = 0.082*
δ^{15}N (‰)	2.8 ± 0.3^{a}	2.8 ± 0.3^{a} (2.5, 3.4)	2.8 ± 0.2^{a} (2.3, 3.3)	*U = 80.5, p = 0.892*
C:N mass ratio	3.45 ± 0.10^{a}	3.45 ± 0.12^{a} (3.29, 3.67)	3.44 ± 0.07^{a} (3.33, 3.55)	*U = 73.5, p = 0.806*
Moroteuthopsis longimana (n)	30	15	15	
LRL (mm)	na	na	na	na
δ^{13}C (‰)	-23.7 ± 1.2^{b}	-23.3 ± 1.3^{b} (-25.8, -20.0)	-24.1 ± 0.9^{b} (-25.4, -21.7)	***U = 163.0, p = 0.036***
δ^{15}N (‰)	5.1 ± 0.6^{b}	5.2 ± 0.6^{b} (4.0, 6.0)	4.9 ± 0.6^{b} (3.4, 6.2)	*U = 144.0, p = 0.191*
C:N mass ratio	3.27 ± 0.08^{b}	3.25 ± 0.09^{b} (3.14, 3.44)	3.29 ± 0.07^{b} (3.17, 3.45)	*U = 67.5, p = 0.062*
Psychroteuthis glacialis (n)	30	15	15	
LRL (mm)	7.2 ± 0.5	7.1 ± 0.5 (6.2, 7.7)	7.3 ± 0.5 (6.4, 8.1)	*U = 101.5, p = 0.648*
δ^{13}C (‰)	-24.8 ± 0.8^{c}	-24.5 ± 0.8^{c} (-25.4, -23.1)	-25.0 ± 0.8^{c} (-26.1, -23.1)	*U = 148.0, p = 0.141*
δ^{15}N (‰)	7.4 ± 1.1^{c}	7.5 ± 1.3^{c} (5.8, 9.7)	7.2 ± 0.8^{c} (6.0, 8.6)	*U = 122.0, p = 0.694*
C:N mass ratio	3.37 ± 0.06^{c}	3.34 ± 0.04^{c} (3.26, 3.44)	3.39 ± 0.07^{a} (3.28, 3.57)	***U = 44.0, p = 0.004***
Galiteuthis glacialis (n)	30	15	15	
LRL (mm)	5.3 ± 0.2	5.4 ± 0.2 (4.9, 5.8)	5.3 ± 0.2 (5.0, 5.6)	*U = 147.5, p = 0.146*
δ^{13}C (‰)	-22.1 ± 0.8^{d}	-22.3 ± 0.9^{d} (-25.2, -21.0)	-22.0 ± 0.6^{d} (-23.1, -20.6)	*U = 87.0, p = 0.290*
δ^{15}N (‰)	7.5 ± 0.5^{c}	7.7 ± 0.6^{c} (6.2, 8.4)	7.4 ± 0.3^{c} (6.8, 7.8)	***U = 171.5, p = 0.014***
C:N mass ratio	3.33 ± 0.09^{d}	3.33 ± 0.05^{c} (3.23, 3.40)	3.33 ± 0.12^{b} (3.21, 3.67)	*U = 141.0, p = 0.236*
Comparison between species	*Kruskal-Wallis tests and Conover-Inman tests for all pairwise comparisons*			
δ^{13}C (‰)	***H = 90.61 , p <0.0001***	***H = 43.66, p <0.0001***	***H = 46.78, p <0.0001***	
δ^{15}N (‰)	***H = 94.31, p <0.0001***	***H = 47.09, p <0.0001***	***H = 46.25, p <0.0001***	
C:N mass ratio	***H = 47.56, p <0.0001***	***H = 25.08, p <0.0001***	***H = 24.44, p <0.0001***	

albatross is essentially based on four oceanic squids. Elsewhere, light-mantled sooty albatross also feeds on a few squid species, which, with the exception of *Gonatus antarcticus* at South Georgia, are all endemic to the Southern Ocean. Albatross species at the Kerguelen Islands segregate by their cephalopod prey, with light-mantled sooty albatross being the only species feeding to a large extent on the Antarctic squid *P. glacialis*. Prey of Kerguelen albatrosses provide additional information on the southern Indian Ocean cephalopods by complementing the initial description of the Kerguelen teuthofauna that was conducted using prey of bony fish and sharks living in slope waters surrounding the archipelago (Cherel and Duhamel 2004; Cherel et al., 2004; 2011). The large foraging range of albatrosses increased the spatial coverage from which samples are available from Antarctica to the subtropics, and hence, the number of species and knowledge about their biogeography, abundance, and importance within pelagic trophic webs.

4.1. Light-mantled sooty albatross

At the Kerguelen Islands, light-mantled sooty albatross fed on 22 taxa, with four species of oceanic squids being overwhelmingly important, in a decreasing numerical order: *G. glacialis* > *P. glacialis* ~ *M. hyadesi* > *M. longimana*. The four species are endemic to the Southern Ocean (Cherel 2020) and, overall, endemic cephalopods accounted for 97% of the lower beaks (16 taxa), while no beaks from cephalopods living only in subtropical waters north of the STF were identified. Elsewhere, light-mantled sooty albatross prey upon 11-25 cephalopod taxa, with endemic species of the Southern Ocean accounting for 91-98% by number of lower beaks. As at Kerguelen Islands, birds from South Georgia, Marion and Crozet Islands feed mainly on a few squid species (n = 4–6, >5% by number), which make up 87-94% of lower beaks (Table 6). At the species level, four features are notable to characterize the cephalopod diet of light-mantled sooty albatross.

1. Adult *G. glacialis* is the most abundant squid prey everywhere (43-60%), including Heard and Macquarie Islands (Green et al., 1998). The only exception is Marion Island, where *G. glacialis* ranked second (24%).
2. Adult *P. glacialis* ranked second at South Georgia, Crozet and Kerguelen Islands (15-20%), but, surprisingly, not at Marion Island where it is negligible (2%).
3. Juvenile *M. longimana* (11-12%) and adult *Batoteuthis skolops* (7%) are significant cephalopod prey at Marion and Crozet Islands, which are both located within the PFZ of the southern Indian Ocean.
4. Some squids characterize the cephalopod diet of light-mantled sooty albatross at a single locality, such as adult *H. eltaninae* (25%) and *Alluroteuthis antarcticus* (15%) at Marion Island, and juvenile *M. hyadesi* (16%) at Kerguelen Islands.

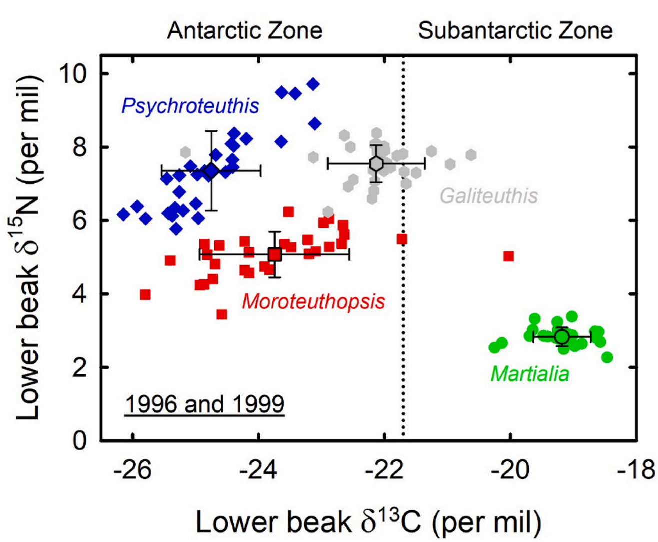

Fig. 3. Individual and mean (± SD) isotopic values of lower beaks of the four main squid prey of light-mantled sooty albatross at Kerguelen Islands, namely adult *Galiteuthis glacialis* (grey), juvenile *Martialia hyadesi* (green), juvenile *Moroteuthopsis longimana* (red) and adult *Psychroteuthis glacialis* (blue). Vertical dotted line is the isotopic estimations of the Polar Front that delineates the Antarctic Zone and Subantarctic Zone *lato sensu* (see text).

Table 5
Measured lower rostral length (LRL) and associated statistics of the main squid prey of albatrosses at Kerguelen Islands. Values are means ± SD with numbers of specimens and ranges of values in parentheses. Values in columns sharing the same superscript letters are not statistically significant at p <0.05 (Conover-Inman tests for all pairwise comparisons).

Species	*Martialia hyadesi*	*Todarodes* sp.	*Galiteuthis glacialis*
Wandering albatross	(36) 6.0 ± 0.8 (4.4-7.7)[a]	(7) 6.3 ± 0.5 (5.7-7.1)[a]	(322) 5.4 ± 0.3 (3.8-6.3)[a]
Grey-headed albatross	(21) 4.9 ± 0.5 (3.5-5.9)[b]	(243) 5.2 ± 0.4 (3.3-6.5)[b]	(217) 5.3 ± 0.3 (3.6-6.0)[b]
Black-browed albatross	(256) 4.6 ± 0.4 (3.9-7.9)[c]	(196) 5.2 ± 1.0 (3.8-10.9)[c]	(184) 5.2 ± 0.3 (4.3-6.0)[b]
Light-mantled sooty albatross	(41) 4.9 ± 0.5 (4.0-6.2)[b]	(1) 5.2	(1485) 5.2 ± 0.4 (3.3-6.1)[b]
Kruskal-Wallis tests	***H* = 93.03 , *p* <0.0001**	***H* = 28.09 , *p* <0.0001**	***H* = 117.03 , *p* <0.0001**

Overall, the cephalopod diet of light-mantled sooty albatross was studied at breeding sites located within the AZ (South Georgia, Heard) and the PFZ (Marion, Crozet, Kerguelen, Macquarie). No detailed dietary information is available from subantarctic New Zealand islands (Auckland, Campbell and Antipodes) that are located in northern warmer waters of the SAZ *stricto sensu*, and which therefore merit further investigation (but see Imber 1991 for limited data from Campbell Island).

At the Kerguelen Islands, lower beak $\delta^{13}C$ values indicated that all *P. glacialis*, almost all *M. longimana*, and most *G. glacialis* were caught by light-mantled sooty albatross within the AZ, while *M. hyadesi* showed subantarctic isotopic values (Fig. 3). This is in general agreement with the known biogeography of the squids. *P. glacialis* is the only endemic species of the AZ, while the northern boundary of *M. longimana* and *G. glacialis* is the SAF, and *M. hyadesi* occurs primarily in subantarctic waters (Cherel 2020). Beak $\delta^{13}C$ values thus highlight the importance of foraging in cold waters for the light-mantled sooty albatross. Indeed, at-sea distribution of the species during the breeding period extends from the SAF (although few were seen north of Kerguelen Islands) south to the pack-ice within the southern Indian Ocean. Light-mantled sooty albatrosses are abundant at high latitudes during the summer months, where they have been observed feeding in the Prydz Bay area, over oceanic Antarctic waters (62-64°S) and the continental slope (Weimerskirch et al., 1986, Stahl et al., Te Papa Museum, Wellington, unpublished data).

4.2. Sympatric albatrosses

Comparative analysis of the cephalopod diet showed that albatrosses from Kerguelen Islands, as in South Georgia (Croxall and Prince 1994), segregate by their species-specific diversity of cephalopod prey and the relative importance of prey species and size. A single squid, the cranchiid *G. glacialis* accounts for ≥10% by number of the lower beaks for every albatross species, thus highlighting its nutritional importance in the diet of top predators from the Southern Ocean (Xavier and Croxall 2007; Cherel 2020). By contrast, other cephalopod prey exemplified three segregating mechanisms amongst sympatric albatrosses. First, good flying manoeuvrability and diving performance are the likely explanations for the importance of ommastrephids (*e.g., M. hyadesi*) in the diet of black-browed, grey-headed and light-mantled sooty albatrosses. Since juvenile *M. hyadesi* live in large aggregations near the sea surface (O'Sullivan et al., 1983; Nolan et al., 1998; Rodhouse and Boyle 2010), catching them alive requires diving ability that have been recorded in black-browed, grey-headed and light-mantled sooty albatrosses, but not in wandering albatross (Prince et al., 1994; Bentley et al., 2021; Guilford et al., 2022). Second, competitive exclusion (social dominance) resulting from large body size and aggressive behaviour (Weimerskirch et al., 1986) explains why wandering albatross scavenges more on large adult cephalopods (*e.g.,* adult *M. longimana*) than the three other albatrosses. Third, and as previously suggested (Weimerskirch et al., 1988; Cherel et al., 2002), partitioning of feeding zones and foraging range are the main segregating mechanism amongst the community of albatrosses breeding at Kerguelen Islands.

1. The presence of the Kerguelen endemic benthic octopus *M. thielei* in the diet of black-browed albatross (Cherel et al., 2000; 2002) indicates foraging in neritic and upper slope waters surrounding the archipelago. Conversely, the near-absence of benthic octopus prey shows that wandering, grey-headed and light-mantled sooty albatrosses quickly transit through the peri-insular Kerguelen shelf back

Table 6
A review of accumulated cephalopod lower beaks identified from stomach contents and boluses of light-mantled sooty albatrosses at various localities of the Southern Ocean. Beaks from Crozet Islands refer to those from Ridoux (1994), which were pooled with accumulated beaks sorted from ten stomach contents collected in 1997 (unpublished data). Only cephalopods accounting for >1% by number at one locality are detailed. Species names of squids from previous investigations were updated following Cherel (2020). Abbreviations: AZ, Antarctic Zone; PFZ, Polar Frontal Zone (for definitions, see text).

Localities	South Georgia		Marion		Crozet		Kerguelen	
Oceanic zone	northern AZ, Atlantic		PFZ, Indian		PFZ, Indian		southern PFZ, Indian	
References	Prince and Morgan(1987)		data from Cooper and Klages (1995)		Ridoux (1994), unpublished data		This study	
	(n)	(%)	(n)	(%)	(n)	(%)	(n)	(%)
Martialia hyadesi	na	6.0	3	0.4	2	0.2	559	16.2
Todarodes sp.							55	1.6
Filippovia knipovitchi	na	1.2	45	5.4	11	1.1	4	0.1
Moroteuthopsis longimana	na	1.6	96	11.5	104	10.5	239	6.9
Onykia robsoni			20	2.4				
Psychroteuthis glacialis	na	19.9	17	2.0	146	14.7	638	18.5
Psychroteuthis sp. B (Imber)			1	0.1	6	0.6	39	1.1
Gonatus antarcticus	na	8.4	14	1.7	9	0.9	38	1.1
Histioteuthis eltaninae	na	0.8	207	24.8	97	9.8	59	1.7
Alluroteuthis antarctica	na	1.5	122	14.6	21	2.1	30	0.9
Batoteuthis skolops			57	6.8	68	6.9	11	0.3
Galiteuthis glacialis	na	59.8	199	23.9	504	50.9	1715	49.8
Unidentified Oegopsida			11	1.3	2	0.2		
Other taxa	na	0.8	42	5.0	20	2.0	59	1.7
Total	1162	100.0	834	100.0	990	100.0	3446	100.0

and forth from their nesting sites to more distant foraging grounds during the breeding period.

2. The numerical importance of *P. glacialis* in the diet of light-mantled sooty albatross indicates that it feeds more in high-Antarctic waters than other species, which is consistent with light-mantled sooty albatross having the most southerly distribution of all albatrosses (ACAP 2012), including south of the Kerguelen Plateau (Stahl et al., unpublished data).
3. The large diversity of cephalopod prey of wandering albatross reflects a large foraging range from high latitudes (*e.g.,* the AZ endemic *P. glacialis*) to the subtropics (*e.g., H. bonnellii corpuscula, T. expolitus*), with wandering albatross being the only Kerguelen albatross foraging significantly within the STZ during breeding (but see Cherel et al., 2002 for the rare nesting yellow-nosed albatross).

The use of cephalopod prey as bio-indicators of albatross feeding habitats defined a species-specific spatial pattern that is confirmed by observations at sea and satellite- and GLS-tracking of breeding adults from Kerguelen Islands. Wandering albatross forages over a large latitudinal range encompassing the AZ, PFZ, SAF *sensu stricto* and STZ (Pinaud and Weimerskirch 2007; Corbeau et al., 2021), black-browed albatross favours outer shelf and slope waters (Weimerskirch et al., 1997; Cherel et al., 2000), while the closely-related grey-headed albatross primarily targets oceanic subantarctic and Antarctic waters (Weimerskirch et al., 1988), and breeding light-mantled sooty albatross forages from the PFZ south to the pack ice (Delord et al., 2013). Such an overall spatial segregating pattern amongst the main circumpolar breeding albatrosses was also recorded at other localities, *e.g.,* South Georgia (Prince et al., 1998), Marion (Carpenter-Kling et al., 2020), Crozet (Pinaud and Weimerskirch 2007; Delord et al., 2013), Heard (Lawton et al., 2008) and Macquarie (Cleeland et al., 2019) islands. More detailed information is still needed on two species from Kerguelen Islands, since (i) electronic tracking devices have not been deployed on grey-headed albatross due to remoteness of colonies (Weimerskirch et al., 1989; 2018), and (ii) light-mantled sooty albatross has not been tracked during the mid- and late-chick rearing periods (Delord et al., 2013).

4.3. Teuthofauna of the southern Indian Ocean

Using Patagonian toothfish *Dissostichus eleginoides*, porbeagle *Lamna nasus* and sleeper shark *Somniosus antarcticus* as bio-samplers, the teuthofauna of Kerguelen slope waters includes 37 species of cephalopods (31 squids, one sepiolid, and three pelagic and two benthic octopuses; Cherel et al., 2011, unpublished data). Black-browed albatross did not add species to the list, which is in agreement with its feeding habitat that overlaps with the Patagonian toothfish fishing zone. Including the foraging grounds of grey-headed and light-mantled sooty albatrosses expands the study area to oceanic subantarctic and Antarctic waters, with *P. glacialis* being the single new relevant species. Cephalopod prey of light-mantled sooty albatross indicates that adult *P. glacialis* is abundant in high-Antarctic waters of the southern Indian Ocean. Indeed, juvenile *P. glacialis* had been collected with nets at latitudes >56°S south of Kerguelen Islands, with the largest specimens occurring from ~62°S to the Antarctic shelf break (Lu and Williams 1994; Lin et al., 2020). As usual, no adult squid was caught by nets, thus highlighting the usefulness of predators to provide information on large cephalopods (Rodhouse 1990). Within that context, the number of fully darkened beaks of adult *Psychroteuthis* sp. B (Imber) that were sorted from boluses of light-mantled sooty albatross is remarkable, since beaks of this poorly-known species were rarely identified (Imber 1992; Cherel 2020). It indicates that *Psychroteuthis* sp. B (Imber) occurs in Antarctic waters south of the Kerguelen Islands. Finally, cephalopod prey of wandering albatross considerably increased the list of cephalopods eaten by albatrosses by adding 15 species that live north of Kerguelen Islands, on either side of the STF or north of it, including histioteuthids that form the bulk of the sperm whale diet within the STZ of the Indian Ocean (Cherel 2021).

Cephalopod prey of Kerguelen albatrosses highlight the abundance and importance of some squids in the functioning of the pelagic ecosystem of the southern Indian Ocean, such as ommastrephids, *M. longimana, P. glacialis, H. eltaninae*, and *G. glacialis*. Oceanic squids including juvenile ommastrephids, *M. knipovichi*, *G. antarcticus* and *G. glacialis* occupy the ecological niche of epipelagic fish that are absent in the Southern Ocean (Rodhouse and White 1995). As predators, squids are key organisms in the transfer of energy from the pelagic to the bentho-pelagic environment where most large immatures and adults live *e.g.*, onychoteuthids*, P. glacialis* (Lu and Williams 1994; Cherel and Weimerskirch 1999). As prey, they participate in the carbon export from marine ecosystems to the atmosphere as carbon dioxide expired by air-breathing predators (Cherel and Duhamel 2003), and they constitute a major vector of some toxic contaminants to top predators (*e.g.,* cadmium; Bustamante et al., 1998). Since albatrosses catch their prey at the surface or subsurface, adult deep-sea squids eaten by the birds are likely dead or dying adults that rise to the surface after reproduction, *e.g.,* cranchiids, gonatids, histioteuthids and onychoteuthids (Nesis et al., 1998; Nesis 1999; Lynnes and Rodhouse 2002; Quetglas et al., 2010). The diet of Kerguelen light-mantled sooty albatross adds adult psychroteuthids (both *P. glacialis* and *Psychroteuthis* sp. B (Imber)) to the list, thus solving the issue about whether *P. glacialis* is a "floater" or a "sinker" species (Croxall and Prince 1994; Rodhouse 2013). Adult *P. glacialis* likely constitutes a predictable food source for albatrosses in Antarctic slope waters where they form near-bottom aggregations (Lu and Williams 1994; Collins and Rodhouse 2006).

In agreement with previous isotopic measurements (*e.g.,* Cherel and Hobson 2005; Alvito et al., 2015; Guerreiro et al., 2015), the large range of lower beak $\delta^{15}N$ values indicate that squids had different trophic positions and fed on prey from various trophic levels within the pelagic ecosystem of the southern Indian Ocean. Correcting the chitin effect (+3.8‰ for *P. glacialis*; Cherel and Hobson 2005) translates the beak $\delta^{15}N$ values to 6.7‰ (*M. hyadesi*), 8.9‰ (*M. longimana*) and 11.2-11.4‰ (*P. glacialis* and *G. glacialis*). These estimated $\delta^{15}N$ values suggest that (i) juvenile *M. hyadesi* fed more on crustaceans in the southern Indian Ocean than in the Southwest Atlantic, where mesopelagic fish dominates the diet over swarming crustaceans (Collins and Rodhouse 2006); (ii) juvenile *M. longimana* preyed upon crustaceans and fish (Filippova 2002) rather than crustaceans alone (Nemoto et al., 1988), and (iii) adult *G. glacialis* and *P. glacialis* fed on high-trophic level prey, *e.g.,* fish

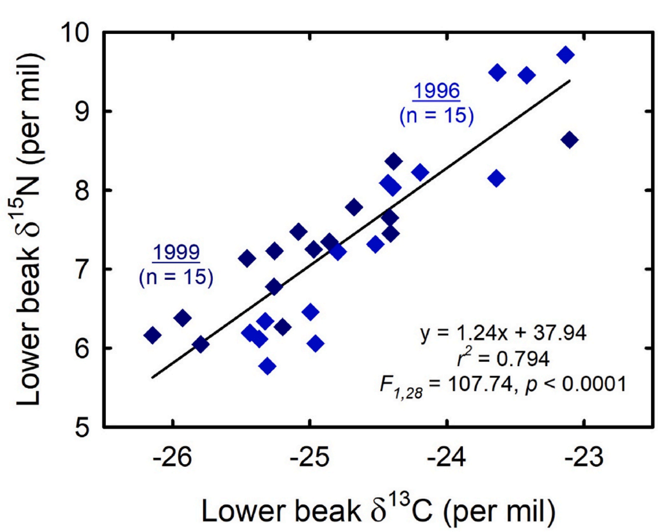

Fig. 4. Linear regression of lower beaks $\delta^{15}N$ *versus* $\delta^{13}C$ values of adult *Psychroteuthis glacialis* eaten by light-mantled sooty albatross from Kerguelen Islands.

and/or squid. No information is available on the diet of adult *G. glacialis* and *P. glacialis*, but stomach content analysis showed that juvenile *G. glacialis* feed on macrozooplankton and juvenile *P. glacialis* on Antarctic krill and fish (Nemoto et al., 1988; Lu and Williams 1994; Filippova 2002; Collins and Rodhouse 2006). Interestingly, $\delta^{15}N$ values of *P. glacialis* were strongly and positively related to $\delta^{13}C$ values (Fig. 4). The linear regression indicates either concomitant changes in $\delta^{13}C$ and $\delta^{15}N$ baselines at the Antarctic shelf break, or, more probable, an increase in the trophic position of adult *P. glacialis* with decreasing latitude of the Indian Ocean. The large 3.7‰ $\delta^{15}N$ difference corresponds to more than a trophic level and suggests a dietary shift from a crustacean-based diet in the South to a fish/squid-based diet in northern Antarctic waters, an hypothesis that need further investigation by sampling this trophically important squid at various localities of the AZ.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests Yves CHEREL reports financial support was provided by Centre National de la Recherche Scientifique. Yves CHEREL reports a relationship with French Polar Institute Paul Emile Victor that includes: funding grants.

Data availability

Data will be made available on request.

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