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Diet of the soft-plumaged petrel (*Pterodroma mollis*) at Kerguelen Islands and a review of the food of gadfly petrels (*Pterodroma* spp.) worldwide

Yves Cherel[1] · **Pierrick Bocher**[2]

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Abstract
Little is known on the food and feeding ecology of the soft-plumaged petrel *Pterodroma mollis*, which is the single gadfly petrel *Pterodroma* spp. with a circumpolar breeding distribution within the Southern Ocean. Our primary goal was to describe its diet at Kerguelen Islands, which is the southernmost breeding locality of the species. Soft-plumaged petrels fed on fish (71% by mass), and secondarily on crustaceans (22%), while cephalopods (7%) and other items (< 1%) were minor dietary components. Eight-hundred and sixty prey were identified from the pooled 33 food samples, with the 2 hyperiid amphipods *Cyllopus magellanicus* (48%) and *Themisto gaudichaudii* (35%) being the main food items by number. Owing to their larger size than crustaceans, mesopelagic fishes were the main prey by mass, with myctophids being the most important fish family in terms of both abundance (68% of the fish) and diversity (10 species). Prey distribution indicated that soft-plumaged petrels foraged primarily in oceanic subantarctic waters to feed their chicks. The oceanic life style of gadfly petrels was then highlighted by a review of their diet worldwide (20 species, 26 studies). Gadfly petrels prey mainly upon mesopelagic fishes (chiefly myctophids) and squids with their relative proportions depending on species and localities. Crustaceans are minor food items for tropical species, but they form a significant part of the food of the small- and medium-sized petrels that live in temperate and cold waters. The review underlines the need for more well-designed investigations on this globally endangered group of seabirds, since dietary information is available for only 57% of the 35 species of gadfly petrels.

Keywords Fish · Food · Myctophidae · Procellariiformes · Seabirds · Southern Ocean · Squid · Tropics

Introduction

The avifauna of the Southern Ocean (water masses south of the Subtropical Front) includes five breeding gadfly petrels *Pterodroma* spp., excluding four additional species that breed on islands located in fringing waters of the Subtropical Front in the Pacific New Zealand (Brooke 2004). The five species breed on subantarctic islands with no breeding sites located south of the Polar Front. Two petrels are endemic from either the Atlantic (the Atlantic petrel *P. incerta*) or the Pacific (the mottled petrel *P. inexpectata*), while the three remaining species have a larger distribution and occur sympatrically in the Indian Ocean. They breed at the subantarctic Crozet and Kerguelen Islands, with the large white-headed *P. lessonii* and great-winged *P. macroptera* petrels being summer and winter breeders, respectively, while the medium-sized soft-plumaged petrel *P. mollis* only breeds in summer (Brooke 2004).

Little is known about the basic biology of the soft-plumaged petrel, including its food and feeding ecology (Marchant and Higgins 1990; Brooke 2004). Bio-logging has not been used on the species and, apart from data from feathers of a single individual (Thiébot et al. 2010), no other stable isotope information is available to our knowledge. The soft-plumaged petrel forages over oceanic waters where it feeds mostly by surface seizing, with scavenging having been reported occasionally (Marchant and Higgins 1990;

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✉ Yves Cherel
cherel@cebc.cnrs.fr

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

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

Ridoux 1994; Brooke 2004). Its diet was investigated twice using the conventional method of stomach content analysis, with additional anecdotal information (Marchant and Higgins 1990). Soft-plumaged petrels preyed mainly upon cephalopods and crustaceans with the former being the more important on Marion Island (Schramm 1986) and the latter dominating at Crozet Islands (Ridoux 1994). However, the number of analyzed food samples was low, only a few items were identified to the species level, and squid names are now out-of-date (Cherel 2020).

The primary goal of the present work was to describe the diet of the soft-plumaged petrel at the southernmost breeding site of the species (Kerguelen Islands; Weimerskirch et al. 1989), with an emphasis on prey determination. The second aim was to briefly review the food of gadfly petrels to make an easy access of the scattered literature to marine scientists and seabird biologists. *Pterodroma* is the most diverse genus of procellariiform seabirds with 35 species foraging in all water masses but the high Arctic (Brooke 2004; Harrison et al. 2021). Procellariiformes are among the world's most endangered taxa of birds, with 25 (74%) of gadfly petrels classified from near threatened to critically endangered in the IUCN Red list (IUCN 2021). Hence, understanding their prey requirements and dietary flexibility is important for the effective conservation and management of gadfly petrels. The previous review on the diet and feeding ecology of Procellariiformes that included gadfly petrels was published 35 years ago (Prince and Morgan 1987) and it listed the food of six *Pterodroma* petrels only. Since many species were investigated over the last decades (e.g., Spear et al. 2007), a new synthesis is now needed to better understand the trophic role of gadfly petrels in the World Ocean.

Materials and methods

Fieldwork and food analysis

The study was conducted at Ile Foch (48° 56′ S, 69° 22′ E), a large remote island free of introduced mammals, which is located in the north-eastern part of the subantarctic Kerguelen Islands (southern Indian Ocean). The Kerguelen Islands are located close to the Polar Front, i.e., in the southern part of the Polar Frontal Zone, which is the oceanographic zone between the Subantarctic Front in the north and the Polar Front in the south (Park et al. 1993).

Thirty-three stomach contents were collected from adult birds that were either attracted by light or caught in a mist net at night when they came back to the colony to feed their single chick during the period 08–22 February 1999. Since soft-plumaged petrels vomit when handled, food samples were spontaneous regurgitations, but birds were subsequently up-ended over a plastic bucket and their stomach and throat were gently massaged to complete the collection of as much as possible material. Then, birds were weighed using a Pesola spring balance. The breeding cycle of the soft-plumaged petrel at Kerguelen Islands was not investigated (Weimerskirch et al. 1989), but hatching occurs in early February at the nearby Crozet Islands (Jouventin et al. 1985). Hence, fieldwork occurred at the beginning of the chick-rearing period, which was checked in the field by the finding of small chicks in burrows.

Food samples were all returned deep-frozen (− 20 °C) to the laboratory in France for analysis, which followed Cherel et al. (2000). Each sample was weighed (total mass) and thawed overnight over a sieve so that the liquid fraction (including stomach oil) was separated from the solid fraction (accumulated and fresh items) and collected in a graduated tube. Both fractions were weighed and the volume of stomach oil from the liquid fraction was measured. Accumulated items are hard parts with no flesh attached that accumulate over time; they included a few much-eroded cephalopod beaks, gladii and spermatophores, cephalopod and fish lenses, and plant remains. Accumulated items were sorted from the solid fraction and weighed. Fresh items (solid fraction minus accumulated items) were divided into broad prey groups (crustaceans, cephalopods, fish and others), which were weighed to calculate their proportion by mass in the diet. Species identification of prey relied on the examination of exoskeletons for crustaceans, sclerotized beaks for cephalopods, and otoliths and bones for fish. Special care was made to use all fish hard parts recovered in stomach contents (bones, otoliths and teeth), with an emphasis on some distinctive bones (premaxilla, maxilla, dentary, articular, parasphenoid, opercle, vertebrae and caudal skeleton) 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). Oegopsida sp. A refers to the presence of large cephalopod eye lenses that were barely digested, but with no corresponding flesh or beak remains in the samples, thus precluding species identification (Cherel et al. 2002a, b; Connan et al. 2007).

Items were identified by comparison with material held in our own collection and by reference to the available literature, including Boltovskoy (1999) for crustaceans, Clarke (1986) and Xavier and Cherel (2021) for cephalopods, and Williams and McEldowney (1990) and Duhamel et al. (2005) for fish. Lower rostral length (LRL) of squid beaks, and length of uneroded or slightly eroded otoliths (OL) of fish were measured to the nearest 0.1 mm with a vernier caliper. Cephalopod dorsal mantle length (ML), fish standard or total length (SL or TL), and prey mass were estimated using regression equations (Williams and McEldowney 1990; Saunders et al. 2021; Xavier and Cherel 2021, authors' unpublished data). Food samples were generally highly digested, thus precluding measuring most prey items and, hence, precluding the estimation of reconstituted mass of each prey taxon in the overall diet.

Three dietary metrics were used to describe the petrel food. (i) The proportion by fresh mass: the total mass of each broad prey group was expressed as a proportion of the total fresh mass in all the samples. (ii) The frequency of occurrence was the total number of samples in which a given prey item appears expressed as a proportion of the total number of food samples. (iii) The percentage by number: the number of each prey item was recorded for each food sample and the total number of each prey item was expressed as a proportion of the total number of prey items in all the samples. Each prey taxon was numbered by counting diagnostic items in each food sample. Values are means ± SD.

Literature review

All the available literature were reviewed up to August 2021. We first looked at general articles and books on Procellariiformes (Prince and Morgan 1987; Marchant and Higgins 1990; Brooke 2004), and then at the detailed dietary investigations on gadfly petrels (Table 1). We focused on studies that quantified the proportion by mass of the main prey groups (crustaceans, cephalopods, fish and others), because percentage by mass is the best dietary index to relate predators to the fluxes of energy and mass that characterize ecosystem dynamics. Such percentages also allow estimating predators' trophic level and help interpreting their nitrogen isotopic values that correspond to the food they assimilated. Therefore, studies that did not quantify the mass proportions, but detailed only prey items and their frequency of occurrence and numerical importance were not included in Table 1 (e.g., Simons 1985; Imber et al. 1995; Bester et al. 2011; Perez et al. 2019). When needed, the mass proportion of prey groups was calculated by totalizing the original data detailing the importance by mass of each food item (e.g., Spear et al. 2007).

Results

Body mass of adult soft-plumaged petrels averaged ~ 300 g (Table 2), which is in agreement with the values previously reported in the scientific literature (Marchant and Higgins 1990), including measurements of Kerguelen birds (Weimerskirch et al. 1989).

Overall diet

The mean mass of the 33 food samples was 31.5 g (Table 2), which included almost equally a solid fraction (56.4% by mass) and a liquid fraction (42.6%). Orange stomach oil was found in 17 (52%) food samples with an average oil volume of 6 ml; most of the remaining 16 samples showed traces of stomach oil, either orange or yellowish. The solid fraction of all the samples contained fresh items, and accumulated items occurred in 23 samples. Small pieces of fishing line ($n = 2$) and blue/green plastic ($n = 1$) were found in three food samples.

Eight-hundred and sixty prey were identified from the pooled stomach contents (Table 3). Fresh items amounted to most (96.4% by mass) of the solid fraction (Table 2). Fish ranked first by mass (71%) and crustaceans second (22%), with cephalopods being a minor prey group (7%). Fish predominated by mass in 23 (70%) individual food samples, crustaceans in 9 (27%), and cephalopods in a single sample (3%). Fish and crustaceans were found in 29 (88%) and 28 (85%) food samples, while the occurrence of cephalopods is much lower (30%, $n = 10$). In contrast to the analysis by mass and owing to their small size relative to fish, crustaceans (88.7%) overall dominated by number over fish (8.7%), cephalopods (1.3%), and other items (1.3%). The mean number of prey taxa per sample was 4.4 ± 2.0 and ranged from one to eight.

Crustaceans

Amphipoda numerically dominated the whole diet (84.9% by number) and, hence, the crustacean diet (95.7%). They included the two dominant hyperiids *Cyllopus magellanicus* and *Themisto gaudichaudii* that occurred in 30% and 64% of the food samples and amounted to 54.3% and 39.3% of the crustacean prey, respectively. Other minor, but significant crustacean items were the subantarctic krill *Euphausia vallentini*, the shrimp *Pasiphaea scotiae* and the gammarid *Eurythenes obesus*. We highlight three other crustacean taxa: (i) an ectoparasite praniza larval stage of an unknown species of gnathiid isopod, (ii) a specimen of the poorly known mesoparasite pennellid *Sarcotretes eristaliformis*, and (iii) one rarely recorded eryoneicus megalopa larval stage of the polychelid *Stereomastis suhmi* (Table 3). Zooplanktonic prey were not measured due to digestion, but the maximal known length of the two main crustacean species, *C. magellanicus* and *T. gaudichaudii* is 17 and 28 mm, respectively (Vinogradov 1999), thus indicating they were small prey.

Fish

The fish diet of the soft-plumaged petrel was dominated by myctophids (68.0% of the total number of fish prey), with nototheniids ranking second (10.7%) and melamphaids third (6.7%). Ten different species of myctophids were eaten by the birds, with *Electrona carlsbergi*, *E. subaspera*, *Gymnoscopelus microlampas* and *Protomyctophum choriodon* (together with the gempylid *Paradiplospinus gracilis*) being

Table 1 Worldwide review of the diet of gadfly petrels (*Pterodroma* spp.) as percentages by mass of the main prey groups

Species Harrison et al. (2021)	Size (cm), body mass (g) Brooke (2004)	Sampling locality	Sampling years	Food samples	Number of samples	Percentages by mass				References
						Fish	Cephalopods	Crustaceans	Others	
Tropical waters										
Defilippi's petrel (*P. defilippiana*)	26, 159	Tropical Pacific	1983–1991	Stomach contents	7	94.2	5.4	0.2	0.2	Spear et al. (2007)[a]
Stejneger's petrel (*P. longirostris*)	26, 143	Tropical Pacific	1983–1991	Stomach contents	46	95.4	3.6	0.1	0.9	Spear et al. (2007)[a]
Black-winged petrel (*P. nigripennis*)	30, 154–185	Tropical Pacific	1983–1991	Stomach contents	88	92.7	7.2	0.0	0.1	Spear et al. (2007)[a]
Bonin petrel (*P. hypoleuca*)	30, 176	Hawaii	1979–1980	Induced regurgitations	144	62.7	28.0	9.3	0.0	Harrison et al. (1983)
Gould's petrel (*P. leucoptera*)	30, 159–184	Tropical Pacific	1983–1991	Stomach contents	135	89.6	10.2	0.1	0.1	Spear et al. (2007)[a]
Phoenix petrel (*P. alba*)	35, 284	Christmas	1963–1964	Spontaneous regurgitations	95	14	78	2	6	Ashmole and Ashmole (1967)[b]
		Tropical Pacific	1983–1991	Stomach contents	21	33.3	66.6	0.1	0.0	Spear et al. (2007)[a]
Herald/Henderson petrel (*P. heraldica/atrata*)	37, 277	Tropical Pacific	1983–1991	Stomach contents	13	74.3	25.6	0.0	0.1	Spear et al. (2007)[a]
Trindade petrel (*P. arminjoniana*)	37	Tropical Atlantic	2006–2007	Spontaneous regurgitations	26	28.3	71.7	< 0.1	< 0.1	Leal et al. (2017)
Kermadec petrel (*P. neglecta*)	38, 369–509	Tropical Pacific	1983–1991	Stomach contents	11	47.7	52.3	0.0	0.0	Spear et al. (2007)[a]
Murphy's petrel (*P. ultima*)	40, 375–435	Tropical Pacific	1983–1991	Stomach contents	8	57.7	42.3	0.0	0.0	Spear et al. (2007)[a]
Galapagos petrel (*P. phaeopygia*)	43, 387–429	Galapagos	1984–1986	Spontaneous regurgitations	80	37	46	17	0	Imber et al. (1992)[a]
Juan Fernandez petrel (*P. externa*)	43, 428	Tropical Pacific	1983–1991	Stomach contents	204	54.3	45.7	0.0	0.0	Spear et al. (2007)[a]
White-necked petrel (*P. cervicalis*)	43, 414–445	Tropical Pacific	1983–1991	Stomach contents	12	83.9	16.0	0.1	0.0	Spear et al. (2007)[a]
Temperate and polar waters										
Cook's petrel (*P. cookii*)	26, 164–193	New Zealand	1972–1975	Induced regurgitations	25	31	44	24	1	Imber (1996)
Soft-plumaged petrel (*P. mollis*)	34, 312	Marion	1980	Stomach contents	9	1	89	10	0	Schramm (1986)
		Crozet	1981–1982	Spontaneous regurgitations	12	0.0	15.7	77.8	6.5	Ridoux (1994)[a]
		Kerguelen	1999	Induced regurgitations	33	71.2	6.5	21.9	0.4	This study
Mottled petrel (*P. inexpectata*)	35, 329	New Zealand	no data	Spontaneous regurgitations	69	42	20	30	8	Imber (1991)

Table 1 (continued)

Species Harrison et al. (2021)	Size (cm), body mass (g) Brooke (2004)	Sampling locality	Sampling years	Food samples	Number of samples	Percentages by mass				References
						Fish	Cephalopods	Crustaceans	Others	
Great-winged petrel (*P. macroptera*)	41, 587	Marion	1979	Stomach contents	21	4	90	6	0	Schramm (1986)
			1991	Stomach flushing	50	38.7	58.8	2.5	0.0	Cooper and Klages (2009)
		Crozet	1981	Spontaneous regurgitations	27	4.2	63.7	32.1	0.0	Ridoux (1994)[a]
Grey-faced petrel (*P. gouldi*)	41, 668	New Zealand	1971	Spontaneous regurgitations	85	28	58	12	2	Imber (1973)
Atlantic petrel (*P. incerta*)	43, 522	Gough	1979	Spontaneous regurgitations	13	17	70	13	0	Williams and Imber (1982)
			1989–1990	Spontaneous regurgitations	59	11.0	86.7	0.9	1.4	Klages and Cooper (1997)
White-headed petrel (*P. lessonii*)	43, 574–698	Kerguelen	2001–2003	Stomach flushing	56	67.9	26.0	5.5	0.6	Authors' unpublished data

[a]Percentages by reconstituted mass

[b]Percentages by volume

Table 2 Birds' body mass and composition of the food from stomach contents of adult soft-plumaged petrels during the early chick-rearing period at Kerguelen Islands

Parameters	*n*	1999 (*n* = 33) Mean ± SD (range)
Body mass (g)	27	299 ± 24 (245–340)
Total food mass (g)	33	31.5 ± 15.3 (10.8–67.4)
Liquid fraction (g)	33	13.7 ± 8.3 (3.6–40.2)
Stomach oil (ml)	17	6.2 ± 6.6 (0.5–25.0)
Solid fraction (g)	33	17.8 ± 9.2 (5.1–35.7)
Accumulated items (g)	23	0.93 ± 1.70 (0.04–8.11)
Fresh items (g)	33	17.1 ± 8.8 (4.8–34.3)
Crustaceans (g)	28	4.4 ± 7.2 (< 0.1–31.3)
Cephalopods (g)	10	3.7 ± 7.2 (0.1–23.9)
Fish (g)	29	13.9 ± 10.2 (< 0.1–33.5)
Others (g)	7	0.3 ± 0.7 (< 0.1–1.9)
Overall composition:		
Crustaceans (%)		21.9
Cephalopods (%)		6.5
Fish (%)		71.2
Others (%)		0.4

Stomach oil and accumulated items were found in 17 and 23 food samples, respectively

the main fish prey (Table 3). Unexpectedly, two species of the benthic nototheniids *Gobionotothen acuta* and *Lepidonotothen mizops* occurred in three food samples. The estimated length and mass of most fish were in the range 70–150 mm and 5–25 g, respectively, with a maximum of 201 mm and 32 g for a specimen of the rattail *Macrourus carinatus* (Table 4).

Cephalopods and other items

Cephalopods were difficult to identify, with half of the fresh remains being not associated with the corresponding beaks, and almost all accumulated items being too eroded pieces of beaks. Nevertheless, three squid species were positively determined, namely fresh *Galiteuthis glacialis* and *Mastigoteuthis psychrophila*, and one pair of accumulated beaks of *Histioteuthis macrohista*. Other food items were an unidentified carrion in one food sample, and *Salpa thompsoni*, the commonest salp from the Southern Ocean (Pakhomov et al. 2006), which was found in 18% of the samples (Table 3).

Literature review

Twenty-six investigations on 20 taxa quantified the diet by mass of gadfly petrels (Table 1). Two petrels were studied twice, the Phoenix *P. alba* and Atlantic petrels (Ashmole and Ashmole 1967; Williams and Imber 1982; Klages and Cooper 1997; Spear et al. 2007), and three dietary studies were conducted on two species, the soft-plumaged and great-winged petrels (Schramm 1986; Cooper and Klages 2009; Ridoux 1994, present study). The three investigations on the soft-plumaged petrel showed contrasted results, with crustaceans dominating at the Crozet Islands, cephalopods at Marion Island, and fish at Kerguelen Islands (Table 1).

Overall, cephalopods and fish dominated the food of gadfly petrels in an almost equal number of studies (50% and 46%, *n* = 13 and 12, respectively), and crustaceans in a single one (4%). Conversely, cephalopods, fish, crustaceans and others were found to be negligible prey (< 5% by mass) in 1, 4, 14 and 23 dietary investigations, respectively (Table 1). The diet of *Pterodroma* petrels is contrasted according to their biogeography. Tropical species feed more on fish than cold-water species, with seven (50%, *n* = 14) versus two (17%, *n* = 12) studies showing a predominance of fish (> 60% by mass). Moreover, fish was found as a minor item (< 5% by mass) in four Southern Ocean investigations versus none in the tropics. On the other hand, crustaceans were more important prey in the Southern Ocean than in tropical seas, since they were minor items in only two (17%) versus 12 (86%) studies conducted in those two oceanic areas, respectively (Table 1, Fig. 1).

Discussion

The present study adds substantial information about the diet of the understudied soft-plumaged petrel. It is the first dietary study conducted at the Kerguelen Islands, which are a significant breeding locality for the species in the southern Indian Ocean (Weimerskirch et al. 1989). It detailed hundreds of food items at the species level, thus contrasting with previous investigations (Schramm 1986; Ridoux 1994). The spontaneous regurgitations were collected opportunistically, but the presence of accumulated items in most of the samples indicate that they were nearly complete, thus allowing relevant comparison with other works.

The food of the soft-plumaged petrel at Kerguelen Islands

At Kerguelen Islands, the soft-plumaged petrel fed mainly on fish and secondarily on crustaceans, while cephalopod was a minor dietary component by mass. Unlike Kerguelen birds, petrels from Marion and Crozet Islands targeted primarily cephalopod and crustaceans, respectively, during the chick-rearing period (Schramm 1986; Ridoux 1994). Food analysis of Marion Island samples followed a different procedure with fresh and accumulated items being pooled, with the latter forming the bulk of cephalopod remains, thus explaining the higher proportion of cephalopods at that locality (Schramm 1986). Otherwise, there is no obvious explanation

Table 3 Frequency of occurrence, numbers, and known distribution of prey items identified from stomach contents ($n = 33$) of adult soft-plumaged petrels during the early chick-rearing period at Kerguelen Islands

Species	Occurrence		Number		Known distribution		References
	n	%	*n*	%	Horizontal	Vertical	
Crustaceans							
Euphausiacea							
Euphausia vallentini	4	12.1	11	1.28	Neritic, oceanic	Epi-mesopelagic	Cuzin-Roudy et al. (2014)
Decapoda							
Pasiphaea scotiae	6	18.2	7	0.81	Oceanic	Meso-abyssopelagic	Basher and Costello (2014)
Stereomastis suhmi (eryoneicus larva)	1	3.0	1	0.12	Oceanic	Meso-bathypelagic	Tiefenbacher (1994)
Mysida							
Neognathophausia gigas	1	3.0	1	0.12	Oceanic	Meso-abyssopelagic	Petryashov (2014)
Pseudochalaraspidum hanseni	1	3.0	1	0.12	Oceanic	Meso-bathypelagic	as *Chalaraspis alata*, Fage (1941)
Isopoda							
Gnathiidae (praniza larva)	1	3.0	1	0.12	Fish ectoparasite		Smit and Davies (2004)
Unidentified Isopoda	2	6.1	2	0.23			
Amphipoda							
Eurythenes obesus	8	24.2	12	1.40	Oceanic	Meso-abyssopelagic	Vinogradov (1999)
Cyllopus magellanicus	10	30.3	414	48.14	Oceanic	Epi-mesopelagic	Zeidler and de Broyer (2014)
Hyperia spinigera	1	3.0	1	0.12	Oceanic	Epi-abyssopelagic	Vinogradov (1999)
Themisto gaudichaudii	21	63.6	300	34.88	Neritic, oceanic	epipelagic	Bocher et al. (2001)
Vibilia antarctica	2	6.1	2	0.23	Oceanic	Epi-bathypelagic	Zeidler and de Broyer (2014)
Unidentifiable Hyperiidae	1	3.0	1	0.12			
Copepoda							
Rhincalanus gigas	1	3.0	1	0.12	Oceanic	Epi-bathypelagic	
Paraeuchaeta sp.	1	3.0	1	0.12			
Sarcotretes eristaliformis	1	3.0	2	0.23	Mesoparasite of mesopelagic fish		Cherel and Boxshall (2004)
Unidentifiable Crustacea	5	15.2	5	0.58			
Cephalopods							
Cranchiidae							
Galiteuthis glacialis	1	3.0	2	0.23	Oceanic	Meso-bathypelagic	Cherel (2020)
Mastigoteuthidae							
Mastigoteuthis psychrophila	1	3.0	1	0.12	Oceanic	Meso-bathypelagic	Cherel (2020)
Oegopsida sp. A (eyes)	3	9.1	3	0.35			
Unidentifiable Oegopsida	5	15.2	5	0.58			
Fish							
Myctophidae							
Electrona antarctica	1	3.0	1	0.12	Oceanic	Mesopelagic	Duhamel et al. (2005)
Electrona carlsbergi	7	21.2	7	0.81	Oceanic	Mesopelagic	Duhamel et al. (2005)
Electrona subaspera	4	12.1	6	0.70	Oceanic	Mesopelagic	Duhamel et al. (2005)
Gymnoscopelus microlampas	4	12.1	5	0.58	Oceanic	Mesopelagic	Duhamel et al. (2005)
Gymnoscopelus nicholsi	1	3.0	2	0.23	Oceanic	Mesopelagic	Duhamel et al. (2005)
Unidentifiable *Gymnoscopelus*	4	12.1	4	0.47			
Metelectrona ventralis	1	3.0	1	0.12	Oceanic	Mesopelagic	Duhamel et al. (2005)
Protomyctophum andriashevi	1	3.0	1	0.12	Oceanic	Mesopelagic	Duhamel et al. (2005)
Protomyctophum bolini	2	6.1	2	0.23	Oceanic	Mesopelagic	Duhamel et al. (2005)
Protomyctophum choriodon	6	18.2	12	1.40	Oceanic	Mesopelagic	Duhamel et al. (2005)
Protomyctophum normani	1	3.0	1	0.12	Oceanic	Mesopelagic	Duhamel et al. (2005)
Unidentifiable Myctophidae	8	24.2	9	1.05			
Macrouridae							
Macrourus carinatus	2	6.1	2	0.23	Oceanic	Benthopelagic	Duhamel et al. (2005)

Table 3 (continued)

Species	Occurrence		Number		Known distribution		References
	n	%	*n*	%	Horizontal	Vertical	
Melamphaidae							
Melamphaes microps	2	6.1	2	0.23	Oceanic	Meso-bathypelagic	Duhamel et al. (2005)
Poromitra atlantica	1	3.0	1	0.12	Oceanic	Meso-bathypelagic	as *P. crassiceps*, Duhamel et al. (2005)
Sio nordenskjöldii	1	3.0	1	0.12	Oceanic	Meso-bathypelagic	Duhamel et al. (2005)
Unidentifiable Melamphaidae	1	3.0	1	0.12			
Nototheniidae							
Gobionotothen acuta	2	6.1	3	0.35	Neritic	Demersal	Duhamel et al. (2005)
Lepidonotothen mizops	2	6.1	5	0.58	Neritic	Demersal	Duhamel et al. (2005)
Gempilidae							
Paradiplospinus gracilis	4	12.1	4	0.47	Oceanic	Mesopelagic	Duhamel et al. (2005)
Unidentifiable Osteichthyes	5	15.2	5	0.58			
Others							
Salpa thompsoni	6	18.2	10	1.16	Neritic, oceanic	Epi-mesopelagic	Hunt et al. (2011)
Carrion	1	3.0	1	0.12			
Total	33	100.0	860	100.00			

Table 4 Ranges of values in measured otolith length (OL) and lower rostral length (LRL), estimated length [fish standard (SL) or total length (TL) for *Macrourus carinatus*, and squid mantle length (ML)], and estimated mass of fish and squid prey of adult soft-plumaged petrels during the early chick-rearing period at Kerguelen Islands

Taxa	Number	Measured OL or LRL (mm)	Estimated length SL/TL or ML (mm)	Estimated mass (g)
Fish				
Electrona carlsbergi	3	3.7–4.0	93–97	11–13
Electrona subaspera	3	2.2–4.0	56–108	3.0–24
Gymnoscopelus microlampas	2	4.5–5.1	116–136	20–29
Metelectrona ventralis	1	3.2	No equation	No equation
Protomyctophum choriodon	4	2.1–2.2	72–76	4.7–5.4
Protomyctophum normani	1	2.3	No equation	No equation
Macrourus carinatus	2	4.4–5.5	157–201	14–32
Melamphaes microps	2	6.6	No equation	No equation
Poromitra atlantica	1	5.0	No equation	No equation
Gobionotothen acuta	3	4.0–4.3	129–139	19–25
Lepidonotothen mizops	5	2.1–3.6	68–108	2.7–14
Squid				
Histioteuthis macrohista	1	3.5	53	99
Mastigoteuthis psychrophila	1	3.6	117	20

for the differences between Crozet and Kerguelen Islands, but they may be related to (i) different breeding grounds (although both are located within the Polar Frontal Zone of the southern Indian Ocean), (ii) different sampling years (spanning nearly 2 decades), (iii) too short sampling periods to assess temporal variations, and (iv) the relatively small number of stomach contents. These contrasted results highlight how poorly known is the food and feeding ecology of the soft-plumaged petrel, which need to be further investigated by combining various complementary methods such as food samples, stable isotopes and bio-logging.

Fishes formed the bulk of the food of the soft-plumaged petrel at Kerguelen Islands, with myctophids being the most important fish prey in terms of both abundance and diversity. At low latitudes of the Southern Ocean, myctophids play an equivalent role as Antarctic krill (*Euphausia superba*) at high latitudes, being eaten by a large variety of predators, including petrels, penguins and fur seals (Cherel et al. 2010). Most of the myctophid species eaten by the petrels are known to occur in the subantarctic zone (Hulley 1990), which, together with the offshore distribution of almost all prey items (Table 3), indicate that soft-plumaged petrels

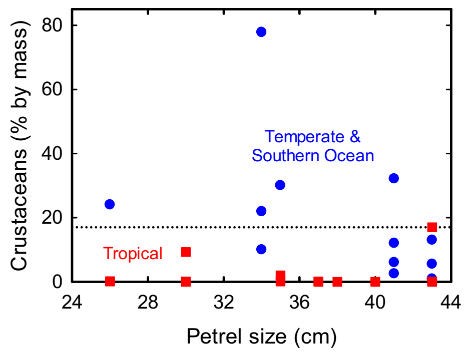

Fig. 1 Relationship between mass proportions of crustaceans in their diet and the size of gadfly petrels breeding in the tropics (red) and in temperate and cold waters of the Southern Ocean (blue). The reference line corresponds to the highest mass percentage of crustaceans (17%) in the diet of a tropical species (the Galapagos petrel)

foraged primarily in oceanic subantarctic waters to feed their chicks. The presence of melamphaid prey was another relevant feature, because fish of that family live in the lower mesopelagic and below (Duhamel et al. 2005), thus occurring generally in small numbers in the diet of Southern Ocean seabirds (Cherel et al. 2002a, b). Soft-plumaged petrels also preyed opportunistically upon a few neritic and slope-associated fish that occur in Kerguelen waters (Duhamel et al. 2005), but how Procellariiformes catch demersal and deep-sea organisms still remains a mystery (Cherel et al. 2000).

The diet of the soft-plumaged petrel was numerically dominated by two crustaceans, the hyperiid amphipod *Cyllopus magellanicus* and *Themisto gaudichaudii*. The latter is an important component of the macrozooplankton community at Kerguelen Islands, where it is one of the main prey for planktivorous seabirds, including small petrels and penguins (Bocher et al. 2001). The former sometimes form small concentrations, often with *T. gaudichaudii* (Vinogradov et al. 1996), thus explaining its presence in significant numbers, but not as a main prey, in the diet of Kerguelen seabirds (Cherel et al. 2002a, b). Larger crustaceans as *Eurythenes obesus*, *Neognathophausia gigas* (as *Gnathophausia gigas*) and *Pasiphaea scotiae* (as *P. longispina* and probably *Parapasiphae* sp.) were previously recorded in small numbers in the diet of soft-plumaged petrels elsewhere (Schramm 1986; Ridoux 1994) and of other Kerguelen Procellariiformes that feed in oceanic waters (Cherel et al. 2002a, b; Delord et al. 2010). The commonest cephalopod remains in food samples of soft-plumaged petrels were large eyes that were barely digested (the so-called “Oegopsida sp. A”). Such isolated cephalopod eyes were previously found in stomach contents of other petrels at Kerguelen (Cherel et al. 2002a, b; Connan et al. 2007), and, interestingly, of the tropical Phoenix petrel (Ashmole and Ashmole 1967). It is likely that eyes were opportunistically scavenged from dead or dying cephalopods too large to swallow whole, as was the largest and heaviest prey, one *Histioteuthis macrohista* weighing 100 g that corresponded to about one-third of the body mass of the birds.

Only three anthropogenic items were found in the spontaneous regurgitations (partial stomach content), which is consistent with the low number of plastic particles ingested by the soft-plumaged petrel when dissecting the proventriculus and gizzard (whole stomach content; Ryan 1987). They were probably collected as floating objects, since the main petrel foraging method is surface-seizing (Brooke 2004). The lack of fishery-related items, including bait remains, is in agreement with *Pterodroma* petrels showing little interest in ships (Cherel et al. 1996, but see Warham 1990). Hence, both food analysis and the birds’ behavior indicate that gadfly petrels are generally not at risk to be killed by fisheries, a major difference with large Procellariiformes, as albatrosses and *Procellaria* petrels (Weimerskirch et al. 2000).

The food of gadfly petrels *Pterodroma* spp.

Overall, gadfly petrels prey mainly upon fish and cephalopods with their relative proportions depending on species and localities (Table 1). An important feature is that most prey are micronektonic fishes and squids, thus highlighting the high-sea foraging habits of *Pterodroma* species. Mesopelagic fishes dominate the world total fishes biomass (Irigoien et al. 2014), with myctophids ranking first in oceanic waters (Catul et al. 2011). Accordingly, myctophids constitute consistently the main fish items of both tropical (Harrison et al. 1983; Spear et al. 2007) and cold-water (Imber 1973, 1996; Williams and Imber 1982; Schramm 1986; Klages and Cooper 1997; Cooper and Klages 2009; Bester et al. 2011) species of gadfly petrels. Hence, the diet of the soft-plumaged petrel at Kerguelen Islands reinforces the importance of myctophids to oceanic seabirds (Spear et al. 2007; Watanuki and Thiébot 2018). Surprisingly, the studied gadfly petrels did not prey significantly upon epipelagic cephalopods as ommastrephids (flying squids), but, instead upon meso- and bathypelagic species of squids. For example, the abundant warm-water ommastrephid *Sthenoteuthis oualaniensis* is rarely caught by gadfly petrels, while it is the main cephalopod prey of most other tropical seabirds. The two exceptions are the Bonin *P. hypoleuca* and Phoenix petrels that feeds substantially on *S. oualaniensis* (Ashmole and Ashmole 1967; Harrison et al. 1983; Spear et al. 2007), while the previous record of the species as the main cephalopod prey of the Galapagos petrel *P. phaeopygia* (Imber et al. 1992) results from beak misidentification of a cranchiid (likely *Cranchia scabra*) as *S. oualaniensis* (YC unpublished data). How gadfly petrels feed on mesopelagic organisms is not well understood, but both the nocturnal habits of the birds together with prey upward migration at night likely explain in part the importance of myctophids and squids in their diets (Spear et al. 2007).

Temperate and Southern Ocean gadfly petrels, including the soft-plumaged petrel, feed more on crustaceans than most tropical species (Fig. 1). They primarily target euphausiids and hyperiid amphipods (Imber 1996, present study) that form dense aggregations. Hence, the almost lack of swarming macrozooplanktonic crustaceans in the tropics likely explain the marked dietary difference between warm- and cold-waters gadfly petrels. The consumption of crustaceans seems inversely related to the birds' size, since the small- and medium-sized petrels generally include more crustaceans in their food than the largest species (Fig. 1). This illustrates well the seabird community structure within the Southern Ocean, which shows a general increase of trophic position with increasing procellariiforms' size, with small species targeting primarily crustaceans (e.g., prions, storm-petrels, diving petrels; Ridoux 1994; Bocher et al. 2000; Cherel et al. 2002a, YC unpublished data). Interestingly, most cold-water gadfly petrels favor subantarctic waters and thus do not feed significantly at high latitudes where the abundant Antarctic krill (*Euphausia superba*) forms the staple food of many seabirds and marine mammals. Exceptions are the mottled petrel that forage in open Antarctic waters southward to the ice-edge during the breeding season, and the white-headed petrel that has been recorded foraging just north of the pack-ice (Jouventin et al. 1988; Marchant and Higgins 1990; Brooke 2004; Taylor et al. 2020).

Our knowledge of the food habits of gadfly petrels increased significantly over the last decades from 6 to 20 species (Prince and Morgan 1987, this study). However, it is still largely incomplete with dietary information being available for only 57% of the 35 living species of the genus *Pterodroma*. Moreover, the investigations overall suffer from methodological drawbacks, including (i) a too small number of food samples, with $n < 15$ in 31% ($n = 8$) of the 26 studies (Table 1), (ii) an opportunistic collection of incomplete food samples from handled birds (e.g., Ashmole and Ashmole 1967; Imber et al. 1992; Klages and Cooper 1997), (iii) a too small number of food items identified to the species level (Williams and Imber 1982; Ridoux 1994) or no prey identification at all (Imber 1991), and (iv) out-of-date prey identification that are now difficult to interpret due to taxonomical changes and initial misidentifications (Imber 1973, Schramm 1986, details in Cherel 2020). Moreover, some dietary studies were performed decades ago thus questioning their ability to depict the current feeding habits of gadfly petrels in a rapidly changing marine environment. Consequently, the review underlines the need for more well-designed dietary investigations on this globally endangered group of seabirds. As a starting point, we consequently recommend: (i) to collect food samples from recently fed large chicks to determine fresh prey composition, species and size, and to complete the work with the analysis of accumulated cephalopod beaks, (ii) to validate on those chicks the promising and non-invasive metabarcoding-based dietary analysis of feces (McInnes et al. 2017; Carreiro et al. 2020), (iii) to generalize the DNA method on breeding and non-breeding adults and on immature gadfly petrels when present on land, and (iv) to complement those direct methods using trophic markers, as lipids of stomach oil (Connan et al. 2007), and stable isotopes on blood and feathers of various petrel age-classes (Cherel et al. 2014).

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Author contributions Fieldwork was performed by PB. Food samples and the dietary data were analyzed by YC who wrote the first draft of the manuscript. Both the authors commented on previous versions of the manuscript, and they read and approved the final 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 have no relevant financial or non-financial interests to disclose.

Ethics 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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