



Dietary evidence of trophic segregation between Campbell albatross *Thalassarche impavida* and grey-headed albatross *T. chrysostoma* at subantarctic Campbell Island

Yves Cherel¹ · Susan M. Waugh^{1,2,3}

Received: 26 May 2023 / Accepted: 2 August 2023

© The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2023

Abstract

Diet and trophic relationships of New Zealand albatrosses are poorly known, while comprehensive information on their feeding ecology are needed in an ecological and evolutionary context, but also for effective conservation management. Here, food samples of the sympatric Campbell albatross *Thalassarche impavida* and grey-headed albatross *T. chrysostoma* were collected at subantarctic Motu Ihupuku Campbell Island to (1) detail their prey items, (2) investigate segregating mechanisms allowing co-existence, and (3) look at potential overlaps between albatrosses and human activities. Chick food of the two albatrosses overlapped greatly in terms of the most consumed prey species but segregated in terms of prey groups. The most abundant item was epipelagic young-of-the-year *Micromesistius australis*, a species that is commercially-exploited when adult. The myctophid *Electrona carlsbergi* and various macrourids constituted other significant fish prey, while juveniles of *Moroteuthopsis ingens* and *Martialia hyadesi* were the main squid prey. Campbell albatross fed their chicks more on fish (79% vs. 27% by mass) and grey-headed albatross more on cephalopods (67% vs. 18%). Albatrosses also segregated by their foraging habitats, with Campbell albatross favoring neritic prey and grey-headed albatross oceanic prey from colder waters. A few plastic debris and no fishery-related items were found in food samples, indicating limited interactions with human activities at the time of sample collection. However, the nutritional importance of naturally-caught juvenile *M. australis* for albatrosses has to be taken into account for a sustainable management of the resource, its predators and the trawl fishery targeting adult fish.

Keywords Cephalopods · Fish · Fishery · *Micromesistius australis* · Seabirds · Southern blue whiting · Southern Ocean

Responsible Editor: Vitor H. Paiva.

This work is dedicated to Peter Prince (1948–1998) from the British Antarctic Survey who died suddenly one year after the fieldwork at Campbell Island in 1997.

✉ 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 BirdLife International, The David Attenborough Building, Pembroke Street, Cambridge CB2 3QZ, UK

³ National Institute of Water and Atmospheric Research Ltd, 10 Kyle Street, Riccarton, Christchurch 8011, New Zealand

Introduction

Albatrosses are among the world's most endangered taxa of birds, with all but one of the 22 species classified from Near Threatened to Critically Endangered in the IUCN Red List (IUCN 2023). Most albatrosses (18 species) breed on scattered remote islands and archipelagoes throughout the Southern Ocean and fringing subtropical waters. Eight species are endemic to New Zealand, which comprise three *Dio-medea* species, and three medium-sized and two small *Thalassarche* species including Campbell albatross *T. impavida*. Campbell albatross were formerly described as a subspecies of black-browed albatross *T. melanophris*, but are now considered a separate species (Burg and Croxall 2001; Burg et al. 2017). Campbell albatross breeds at subantarctic Motu Ihupuku Campbell Island, where it nests in mixed colonies with another small *Thalassarche* species, the grey-headed albatross *T. chrysostoma*, which has a circumpolar breeding

distribution (ACAP 2012). Campbell and grey-headed albatrosses are classified as ‘Vulnerable’ and ‘Endangered’ in the IUCN Red List, respectively (IUCN 2023).

Although Campbell albatrosses are annual breeders and grey-headed albatrosses are biennial breeders, their reproductive cycles overlap greatly in time (ACAP 2012), thus raising the question of niche partitioning in these taxonomically closely-related species. Evolutionary biology predicts that, if trophic resources are limited, potential competitors that coexist in a community should, at the very least, exhibit niche differentiation (Begon et al. 1990). We thus hypothesized species-specific trophic segregating mechanisms allowing co-existence during breeding of these two small *Thalassarche* species, as already described on sympatric albatrosses elsewhere (e.g., Weimerskirch et al. 1986, Cherel et al. 2002). How albatrosses exploit and use marine resources also allows determining their interactions within marine ecosystems and their vulnerability to human activities. Major threats to albatrosses are fisheries bycatch, climate change, diseases, and invasive alien species (Phillips et al. 2016; Dias et al. 2019). Effects of fisheries can be either indirect through competition for marine resources, or direct through mortality resulting from collision in trawl cables and drowning when caught on longline baited hooks. Fatal interactions with fisheries are a conservation concern for Campbell albatross in New Zealand waters that are exploited by numerous finfish and squid fisheries (ACAP 2012; Burg et al. 2017), and the species continues to be in the top 20 most at-risk species for population effects of fishery mortality in the New Zealand region (Richard et al. 2020).

Comprehensive data on the food and feeding ecology of albatrosses are needed in an ecological and evolutionary context, but also for effective conservation management. In the last decades, tracking of albatrosses increased our knowledge of the movements at sea of many populations (e.g., Delord et al. 2013, Sztukowski et al. 2017, Weimerskirch et al. 2020), which contrasts with the paucity of recent investigations on their diet preferences (Cherel et al. 2017; Mills et al. 2020). Food analysis is the best way to define the key natural marine resources for the nutrition of albatrosses, and it reveals the magnitude of interactions between albatrosses and human activities, including fisheries and plastic pollution (e.g., Cherel et al. 2017, Provencher et al. 2019). Albatrosses endemic to New Zealand exemplify how albatross diet is poorly known, with a single well-designed dietary study on Buller’s albatrosses (James and Stahl 2000), and limited information, particularly in recent years, on the seven remaining endemic species (Imber and Russ 1975; West and Imber 1986; Imber 1992, 1999; Cherel et al. 1999; Waugh et al. 1999, 2017; Xavier et al. 2014; McInnes et al. 2017).

The goals of the present work were (1) to study the foraging ecology of Campbell and grey-headed albatrosses by

detailing their food, (2) to investigate inter-specific differences in the trophic niche of the two sympatric albatrosses, and (3) to look at potential overlaps between albatrosses and human activities. Food was examined by collecting stomach contents from chicks over two consecutive years (January 1996 and 1997), which allowed the determination of the main prey groups and prey items caught by adult albatrosses. The present investigation is a companion paper to three previous articles on the feeding ecology of Campbell and grey-headed albatrosses that are all based on data collected at Campbell Island during the breeding seasons of 1996 and 1997 (Cherel et al. 1999; Waugh et al. 1999, 2000).

Materials and methods

Study site, birds and sampling

Dietary studies of Campbell and grey-headed albatrosses were conducted over two consecutive years (1996 and 1997), during the same month (January), and at the same colony (Bull Rock) at Campbell Island (52° 33' S, 169° 09' E) in the western Pacific Ocean, south of New Zealand. Campbell Island is located in the Subantarctic Zone, between the Subtropical Front to the north and the Subantarctic Front to the south. The island is surrounded by an extensive and deep (400–1000 m) platform, the Campbell Plateau, with the Subantarctic Front being bathymetrically diverted southwards to flow along the plateau (Chiswell et al. 2015).

A total of 149 albatross stomach contents were collected ($n=81$ and 68 for Campbell and grey-headed albatrosses, and $n=81$ and 68 in 1996 and 1997, respectively) (Table 1). Food samples were taken from randomly-selected chicks (4–5 weeks old) after a returning parent had completed feeding them. Collection of a single meal has no detrimental effects in terms of survival and development on chicks of black-browed and grey-headed albatrosses (Phillips 2006). Samples were obtained by up-ending chicks over a plastic bucket and massaging the stomach and throat. The remoteness of the colony precluded freezing stomach contents in the field. Samples were drained, the liquid fraction (including stomach oil) was discarded, and the remaining items were preserved in isopropyl alcohol until analysis in France.

Food analysis

In the laboratory (1996–1998), each sample was drained and weighed (solid fraction; Cherel et al. 2000). Accumulated items, including cephalopod beaks, were subsequently sorted and weighed. Sclerotized beaks can persist in predator stomachs for weeks and even months, thus overemphasizing their importance in seabird diets (Xavier et al. 2005). Following Cherel and Klages (1998), accumulated beaks

Table 1 Mass and composition of chick stomach contents of Campbell and grey-headed albatrosses from Campbell Island in 1996 and 1997

	Total	Statistics (Campbell vs. grey-headed albatross)	January 1996	January 1997	Statistics (temporal changes)
Campbell albatross					
Number (n)	81		47	34	
Solid fraction (g)	187 ± 137		210 ± 160	154 ± 87	$U = 916.0$, $p = 0.263$
Accumulated items (g)	3.4 ± 4.7		4.1 ± 5.3	2.4 ± 3.6	$U = 934.0$, $p = 0.194$
Fresh items (g)	184 ± 135		206 ± 159	152 ± 86	$U = 909.0$, $p = 0.292$
Fish (g)	145 ± 140		156 ± 170	128 ± 83	$U = 754.0$, $p = 0.667$
Cephalopods (g)	33 ± 76		46 ± 90	15 ± 47	$U = 1013.0$, $p = 0.031$
Crustaceans (g)	1.8 ± 3.3		2.3 ± 4.1	1.1 ± 1.6	$U = 1056.0$, $p = 0.014$
Others, including carrion (g)	4.0 ± 14.1		1.4 ± 3.3	7.7 ± 21.1	$U = 398.0$, $p < 0.0001$
Overall composition:					
Fish (%)	78.7		75.9	84.1	na
Cephalopods (%)	18.1		22.3	10.0	na
Crustaceans (%)	1.0		1.1	0.7	na
Others, including carrion (%)	2.2		0.7	5.1	na
Accumulated beaks (g)	0.6 ± 0.8		0.8 ± 0.9	0.3 ± 0.6	$U = 1078.5$, $p = 0.007$
Accumulated beaks (n)	(67) 21 ± 25		(41) 27 ± 28	(26) 13 ± 17	$U = 699.5$, $p = 0.032$
Grey-headed albatross					
Number (n)	68		34	34	
Solid fraction (g)	193 ± 123	$U = 2570.0$, $p = 0.483$	232 ± 148	154 ± 77	$U = 757.0$, $p = 0.028$
Accumulated items (g)	5.8 ± 7.5	$U = 2168.5$, $p = 0.025$	9.1 ± 8.7	2.5 ± 3.9	$U = 906.5$, $p < 0.0001$
Fresh items (g)	187 ± 122	$U = 2599.5$, $p = 0.556$	223 ± 147	151 ± 74	$U = 734.0$, $p = 0.056$
Fish (g)	50 ± 89	$U = 4224.0$, $p < 0.0001$	60 ± 107	39 ± 65	$U = 622.0$, $p = 0.587$
Cephalopods (g)	126 ± 137	$U = 1315.0$, $p < 0.0001$	145 ± 168	106 ± 95	$U = 613.5$, $p = 0.663$
Crustaceans (g)	2.4 ± 6.8	$U = 2829.5$, $p = 0.773$	3.7 ± 9.4	1.2 ± 1.4	$U = 680.5$, $p = 0.207$
Others, including carrion (g)	8.9 ± 40.0	$U = 3818.5$, $p < 0.0001$	13.7 ± 54.2	4.1 ± 16.3	$U = 696.5$, $p = 0.056$
Overall composition					
Fish (%)	26.6	na	27.0	26.0	na
Cephalopods (%)	67.3	na	65.2	70.5	na
Crustaceans (%)	1.3	na	1.6	0.8	na
Others, including carrion (%)	4.8	na	6.2	2.7	na
Accumulated beaks (g)	1.5 ± 2.1	$U = 1959.0$, $p = 0.002$	2.3 ± 2.5	0.7 ± 1.2	$U = 886.0$, $p < 0.0001$
Accumulated beaks (n)	(59) 48 ± 55	$U = 1508.5$, $p = 0.017$	(34) 64 ± 56	(25) 27 ± 46	$U = 632.5$, $p = 0.004$

Values are means ± SD. Some stomach samples contained no accumulated items, thus explaining the lower number of samples that were used to calculate the mean number of beaks per sample. Mann–Whitney U tests were performed to compare the two sampled years and the two albatross species. Significant differences ($p < 0.05$) are highlighted in bold

na not applicable

(without flesh attached) were consequently analyzed 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 on the examination of otoliths and bones for fish, beaks for cephalopods, and exoskeletons for crustaceans. Special care was taken to use all fish hard parts recovered in stomach contents, with an emphasis on some distinctive bones (premaxilla, maxilla, dentary, articular, parasphenoid, 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 species (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 Smale et al. (1995), Duhamel et al. (2005) and Voskoboinikova and Zhukov (2021) for fish, Baker et al. (1990) and Vinogradov et al. (1996) for crustaceans, Boltovskoy (1999) for gelatinous plankton, and Xavier and Cherel (2021) for cephalopods. Every initial identification (1996–1998) was checked and, if needed, updated in 2022. Species names of cephalopods followed a recent review on Southern Ocean squids (Cherel

2020). Length of uneroded or slightly eroded otoliths (OL) and of dentary bones (ML, for mandible length) of fish, lower rostral length (LRL) of squid beaks, and lower crest length (LCL) of octopus beaks were measured with a Vernier caliper. Fish standard length (SL) and cephalopod dorsal mantle length (DML) were calculated using regression equations (Table A1).

Data analyses and statistics

The original data are presented by calculating frequency of occurrence and numerical abundance of each prey item (Duffy and Jackson 1986). 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 numerical 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.

Data were statistically analyzed using SYSTAT 13. Non-parametric Mann–Whitney *U* tests were performed to compare mass and composition of chick stomach contents, and prey size between the two sampled years and the two albatross species. Equality of proportion tests (large-sample tests) were performed to compare relative prey numbers between the two albatross species. Values are means \pm SD.

Results

A total of 15,354 fresh prey items was identified from 149 chick food samples of Campbell and grey-headed albatrosses collected in January 1996 and 1997. They included a majority of crustacean prey (80.1% by number), which constituted a minor part (1.1%) of the chick diet by fresh mass (Table 1). This mismatch between numbers and mass is mainly driven by the small size of crustaceans, with most items being ‘secondary prey’, i.e. prey of albatross prey. Hence, crustaceans were not considered in the overall prey list of the birds (Table 2), but they were detailed in a separate section (see below).

Campbell albatross

Mean mass of the solid fraction of the 81 stomach samples of Campbell albatross chicks was 187 g, which included mostly fresh remains (98.2%) and a few accumulated items (1.8%) (Table 1). The chick diet was dominated by fish, which accounted for 78.7% by fresh mass. Cephalopods ranked second (18.1%), while crustaceans (1.0%) and other organisms (2.2%) were minor items. In terms of individual food samples, fish and cephalopods were the main prey group by mass in 82.7% ($n=67$) and 17.3% ($n=14$) of the stomachs, respectively. Interannual variations did not change

the overall picture, but albatrosses fed significantly more on cephalopods in 1996 than in 1997 (Table 1). Eight pieces of plastic (from 3 to 36 mm, mostly in the range 14–27 mm) were found in seven samples (8.6%).

A total of 2283 fresh prey items from 36 species or broader taxa were recovered from the 81 chick dietary samples (Table 2). Items included 1863 (81.6%) fish, 119 (5.2%) cephalopods, and 301 (13.2%) other organisms. Fish occurred in 75 (92.6%) of the samples. At the species level, the fish diet was dominated by the gadid *Micromesistius australis* (89.1% of the fish prey). Macrourids were the most diverse fish family recorded here (at least seven species). Campbell albatross preyed upon gelatinous plankton (13.0% of the total food items), including the pyrosomatid *Pyrosoma atlanticum* and the salp *Soestia zonaria*. Finally, fresh cephalopod diet of Campbell albatrosses was dominated by two species of squids, the onychoteuthid *Moroteuthopsis ingens* (58.0% of cephalopod prey) and the ommastrephid *Martialia hyadesi* (28.6%). Analysis of accumulated beaks ($n=1431$) substantially increased the number of cephalopod prey from nine to 23 species, which included 21 oegopsids, and one benthic and one pelagic octopod (Table 3). The cephalopod diet was again dominated by *M. hyadesi* (37.3% of the total number of identified beaks) and *M. ingens* (26.2%).

Grey-headed albatross

Mean mass of the solid fraction of the 68 stomach samples of grey-headed albatross chicks was 193 g, which included fresh remains (97.0%) and accumulated items (3.0%) (Table 1). The chick diet was dominated by cephalopods, which accounted for 67.3% by fresh mass. Fish ranked second (26.6%), while crustaceans (1.3%) and other organisms (4.8%) were minor items. In terms of individual food samples, cephalopods and fish were the main prey group by mass in 63.2% ($n=43$) and 29.4% ($n=20$) of the stomachs, respectively. Interannual variations did not change the overall picture, but the average mass of stomach contents was significantly higher in 1996 than 1997. This resulted from significantly more accumulated items and more accumulated beaks, and non-significantly more fresh cephalopods and fish in 1996 than 1997 (Table 1). Seven pieces of plastic (from 15 to 31 mm) were found in seven samples (10.3%).

A total of 779 fresh prey items from 31 species or broader taxa were recovered from the 68 chick dietary samples (Table 2). Items included 566 (72.7%) fish, 184 (23.6%) cephalopods, and 29 (3.7%) other organisms. Fish and cephalopods occurred in 53 (77.9%) and 57 (83.8%) of the samples, respectively. At the species level, the fish diet was dominated by *M. australis* (80.6% of the fish prey). Fresh cephalopod prey of grey-headed albatross included two main species of squids, *M. hyadesi* (67.4% of cephalopods) and *M. ingens* (22.8%). Analysis of accumulated beaks ($n=2869$)

Table 2 Frequency of occurrence and numbers of fresh fish, cephalopods and other organisms identified from stomach contents of Campbell and grey-headed albatross chicks at Campbell Island in 1996 and 1997

Prey taxa	Campbell albatross (n = 81)				Grey-headed albatross (n = 68)				Statistics on numbers (%)
	Occurrence		Number		Occurrence		Number		
	(n)	(%)	(n)	(%)	(n)	(%)	(n)	(%)	
Fish									
Congridae									
<i>Bassanago bulbiceps/hirsutus</i>	1	1.2	1	0.04					na
Argentinidae									
<i>Argentina elongata</i>	1	1.2	1	0.04					na
Paralepididae									
<i>Magnisudis prionosa</i>					3	4.4	3	0.39	na
Myctophidae									
<i>Electrona carlsbergi</i>	13	16.0	68	2.98	5	7.4	28	3.59	Z=0.85, p=0.394
<i>Krefflichthys anderssoni</i>	1	1.2	2	0.09	3	4.4	6	0.77	Z = 3.22, p = 0.001
<i>Protomyctophum gemmatum</i>					1	1.5	1	0.13	na
Unidentifiable Myctophidae					2	2.9	5	0.64	na
Moridae									
<i>Antimora rostrata</i>					1	1.5	1	0.13	na
<i>Lepidion microcephalus</i>					1	1.5	1	0.13	na
<i>Mora moro</i>	1	1.2	1	0.04					na
<i>Notophycis marginata</i>	11	13.6	55	2.41					na
Gadidae									
<i>Micromesistius australis</i>	69	85.2	1660	72.71	35	51.5	456	58.54	Z = 7.39, p < 0.0001
Merlucciidae									
<i>Macruronus novaezelandiae</i>	1	1.2	1	0.04					na
Macrouridae									
<i>Coelorinchus aspercephalus</i>	4	4.9	4	0.18	7	10.3	10	1.28	Z = 3.96, p < 0.0001
<i>Coelorinchus fasciatus</i>	7	8.6	7	0.31					na
<i>Coelorinchus kaiyomaru</i>	1	1.2	1	0.04					na
<i>Coelorinchus oliverianus</i>	4	4.9	4	0.18	3	4.4	3	0.39	Z= 1.06, p=0.290
<i>Coryphaenoides subserrulatus</i>	2	2.5	2	0.09					na
<i>Lepidorhynchus denticulatus</i>	7	8.6	7	0.31	4	5.9	4	0.51	Z=0.83, p=0.405
<i>Macrourus carinatus</i>	1	1.2	1	0.04					na
Unidentifiable Macrouridae	7	8.6	14	0.61	5	7.4	5	0.64	Z=0.09, p=0.930
Unidentifiable Gadiformes	6	7.4	6	0.26	4	5.9	4	0.51	Z= 1.06, p=0.290
Diretmidae									
<i>Diretmus argenteus</i>					1	1.5	1	0.13	na
Congiopodidae									
<i>Alertichthys blacki</i>	1	1.2	1	0.04					na
<i>Congiopodus coriaceus/leucopaecilus</i>	5	6.2	11	0.48					na
Gempylidae									
<i>Paradiplospinus gracilis</i>					1	1.5	24	3.08	na
Osteichthyes spp. (3 species)	2	2.5	2	0.09	3	4.4	3	0.39	Z= 1.78, p=0.076
Unidentifiable fish	9	11.1	14	0.61	11	16.2	11	1.41	Z = 2.14, p = 0.032
Cephalopods									
Ommastrephidae									
<i>Martialia hyadesi</i>	14	17.3	34	1.49	44	64.7	124	15.92	Z = 15.72, p < 0.0001
Onychoteuthidae									
<i>Moroteuthopsis ingens</i>	24	29.6	69	3.02	10	14.7	42	5.39	Z = 3.06, p = 0.002
<i>Moroteuthopsis longimana</i>	4	4.9	4	0.18	1	1.5	1	0.13	Z=0.28, p=0.780

Table 2 (continued)

Prey taxa	Campbell albatross (n=81)				Grey-headed albatross (n=68)				Statistics on numbers (%)
	Occurrence		Number		Occurrence		Number		
	(n)	(%)	(n)	(%)	(n)	(%)	(n)	(%)	
Gonatidae									
<i>Gonatus antarcticus</i>					1	1.5	1	0.13	na
Histioteuthidae									
<i>Histioteuthis atlantica</i>	1	1.2	1	0.04	2	2.9	2	0.26	Z= 1.64, p=0.101
<i>Histioteuthis eltaninae</i>	2	2.5	2	0.09	1	1.5	1	0.13	Z=0.31, p=0.753
Neoteuthidae									
<i>Alluroteuthis antarcticus</i>					1	1.5	1	0.13	na
Mastigoteuthidae									
<i>Mastigoteuthis psychrophila</i>	1	1.2	1	0.04					na
Batoteuthidae									
<i>Batoteuthis skolops</i>					1	1.5	1	0.13	na
Cranchiidae									
<i>Galiteuthis glacialis</i>	1	1.2	1	0.04	2	2.9	2	0.26	Z= 1.64, p=0.101
<i>Taonius notalia</i>	1	1.2	1	0.04					na
Octopodidae									
<i>Enteroctopus zealandicus</i>	1	1.2	1	0.04					na
Unidentifiable cephalopods	5	6.2	5	0.22	9	13.2	9	1.16	Z= 3.35, p=0.001
Others									
Pyrosomatida									
<i>Pyrosoma atlanticum</i>	24	29.6	52	2.28	4	5.9	6	0.77	Z= 2.67, p=0.08
Salpida									
<i>Salpa</i> sp.	2	2.5	3	0.13					na
<i>Soestia zonaria</i>	39	48.1	201	8.80	6	8.8	9	1.16	Z= 7.29, p<0.0001
Unidentifiable Salpida	13	16.0	40	1.75	1	1.5	3	0.39	Z= 2.80, p=0.005
Carrion/unknown organisms	5	6.2	5	0.22	5	7.4	11	1.41	Z= 3.99, p<0.0001
Total			2283	100.00			779	100.00	

Equality of proportion tests (large-sample tests) were performed to compare relative prey numbers between the two albatross species. Significant differences ($p < 0.05$) are highlighted in bold

na not applicable

increased the number of cephalopod prey to 17 species, all oegopsids (Table 3). The cephalopod diet was dominated by a single species, *M. hyadesi*, which accounted for 67.5% of the total number of identified beaks.

Comparison between species

The mean mass of chick food samples was very similar for the two albatross species, but Campbell albatross fed significantly more on fish (2.9 times) and grey-headed albatross significantly more on cephalopods (3.8 times) by fresh mass (Table 1). Accordingly, food samples from grey-headed albatross included significantly more accumulated cephalopod beaks than those from Campbell albatross.

Overall, both species of albatross fed on the same prey, but in different proportions (Table 2). Fish in the diet was dominated by Gadiformes that were significantly

more numerous in the diet of Campbell albatross chicks than grey-headed albatross chicks (94.6% and 85.5% of the fish prey, respectively). Gadiform fishes included the dominant *M. australis*, together with various species of macrourids and morids. Campbell albatross fed significantly more on gelatinous plankton (*P. atlanticum* and salps) than grey-headed albatross, and both species preyed upon the same two dominant squids, with *M. ingens* predominating over *M. hyadesi* as fresh items in Campbell albatross samples, and *M. hyadesi* over *M. ingens* in grey-headed albatross samples. Accumulated beaks emphasized the importance of *M. hyadesi* in the diet of grey-headed albatross (67.5% vs. 37.3% of the beaks) and that of onychoteuthids in the diet of Campbell albatross (six species, 33.4% of the beaks vs. three species and 14.2%) (Table 3).

Table 3 Numbers of accumulated cephalopod beaks identified from stomach contents of Campbell and grey-headed albatross chicks at Campbell Island in 1996 and 1997

Cephalopod taxa	Campbell albatross		Grey-headed albatross		Statistics on numbers (%)
	(n)	(%)	(n)	(%)	
Decapoda					
Ommastrephidae					
<i>Martialia hyadesi</i>	465	37.26	1904	67.47	Z = 18.02, p < 0.0001
<i>Todarodes</i> sp.	2	0.16			na
Onychoteuthidae					
<i>Filippovia knipovitchi</i>	11	0.88	1	0.04	Z = 4.59, p < 0.0001
<i>Moroteuthopsis ingens</i>	327	26.20	75	2.66	Z = 23.21, p < 0.0001
<i>Moroteuthopsis longimana</i>	73	5.85	101	3.58	Z = 3.30, p = 0.001
<i>Moroteuthopsis</i> sp. B (Imber)	2	0.16			na
<i>Onychoteuthis aequimanus</i>	1	0.08			na
<i>Onykia robsoni</i>	3	0.24			na
Brachioteuthidae					
<i>Brachioteuthis linkowskyi</i>	3	0.24			na
Gonatidae					
<i>Gonatus antarcticus</i>	22	1.76	38	1.35	Z = 1.02, p = 0.310
Octopoteuthidae					
<i>Octopoteuthis</i> sp.	4	0.32			na
Histioteuthidae					
<i>Histioteuthis atlantica</i>	31	2.48	18	0.64	Z = 4.98, p < 0.0001
<i>Histioteuthis bonnellii corpuscula</i>			2	0.07	na
<i>Histioteuthis eltaninae</i>	72	5.77	141	5.00	Z = 1.02, p = 0.307
Neoteuthidae					
<i>Alluroteuthis antarcticus</i>	6	0.48	15	0.53	Z = 0.21, p = 0.835
<i>Nototeuthis dimegacotyle</i>	5	0.40	3	0.11	Z = 1.96, p = 0.051
Mastigoteuthidae					
<i>Mastigoteuthis psychrophila</i>	7	0.56	14	0.50	Z = 0.27, p = 0.790
Chiroteuthidae					
<i>Chiroteuthis veranyi</i>	4	0.32	1	0.04	Z = 2.39, p = 0.017
Batoteuthidae					
<i>Batoteuthis skolops</i>	149	11.94	375	13.29	Z = 1.19, p = 0.236
Cranchiidae					
<i>Galiteuthis glacialis</i>	33	2.64	125	4.43	Z = 2.72, p = 0.007
<i>Mesonychoteuthis hamiltoni</i>	2	0.16			na
<i>Taonius notalia</i>	18	1.44	4	0.14	Z = 5.22, p < 0.0001
<i>Teuthowenia pellucida</i>			2	0.07	na
Octopoda					
Octopodidae					
<i>Enteroctopus zealandicus</i>	3	0.24			na
Undetermined Octopodidae	1	0.08			na
Amphitretidae					
<i>Amphitretus thielei</i>	3	0.24	2	0.07	Z = 1.42, p = 0.155
Undetermined Octopoda	1	0.08	1	0.04	Z = 0.59, p = 0.553
Total	1248	100.00	2822	100.00	
Unidentifiable beaks (eroded)	183		47		

Equality of proportion tests (large-sample tests) were performed to compare relative prey numbers between the two albatross species. Significant differences ($p < 0.05$) are highlighted in bold

na not applicable

Crustaceans

Stomach contents of chicks of both albatross species included the same crustacean taxa, with the hyperiid amphipod *Themisto gaudichaudii* being the main item (48.3% of the total number of crustaceans) (Table 4). Both species also preyed upon the same proportion of Antarctic krill *Euphausia superba* (6.5–7.2%) and the hyperiid *Vibilia* sp. (1.0–1.2%), which are supposed to be primary and secondary

prey, respectively. However, significantly more pelagic larvae (13.7% vs. 1.3%) and *Cylopus magellanicus* (11.3% vs. 5.6%), and fewer *Euphausia vallentini* (10.9% vs. 22.1%), *Nyctiphanes australis* (2.9% vs. 8.5%) and *Nematoscelis/Thysanoessa* sp. (2.2% vs. 3.9%) were found in food samples of Campbell albatross compared to grey-headed albatross.

Table 4 Frequency of occurrence and numbers of crustaceans identified from stomach contents of Campbell and grey-headed albatross chicks at Campbell Island in 1996 and 1997

Crustacean taxa	Campbell albatross (n = 81)				Grey-headed albatross (n = 68)				Statistics on numbers (%)
	Occurrence		Number		Occurrence		Number		
	(n)	(%)	(n)	(%)	(n)	(%)	(n)	(%)	
Euphausiacea									
<i>Euphausia superba</i>	4	4.9	540	7.17	2	2.9	309	6.49	Z = 1.43, p = 0.152
<i>Euphausia vallentini</i>	14	17.3	819	10.87	13	19.1	1053	22.13	Z = 16.92, p < 0.0001
<i>Euphausia</i> sp.	10	12.3	20	0.27	7	10.3	15	0.32	Z = 0.51, p = 0.614
<i>Nematoscelis/Thysanoessa</i> sp. ^a	26	32.1	166	2.20	13	19.1	184	3.87	Z = 5.40, p < 0.0001
<i>Nyctiphanes australis</i>	4	4.9	219	2.91	5	7.4	406	8.53	Z = 13.83, p < 0.0001
Decapoda									
<i>Grimothea gregaria</i>	11	13.6	50	0.66	1	1.5	35	0.74	Z = 0.47, p = 0.639
<i>Campylonotus rathbunae</i>	1	1.2	1	0.01					na
<i>Pasiphaea scotiae</i>	7	8.6	9	0.12	22	32.4	33	0.69	Z = 5.31, p < 0.0001
Unidentified Natantia	3	3.7	4	0.05	1	1.5	1	0.02	Z = 0.86, p = 0.390
Mysida									
<i>Neognathophausia gigas</i>	7	8.6	7	0.09	17	25.0	18	0.38	Z = 3.42, p = 0.001
Isopoda									
Unidentified Flabellifera	5	6.2	6	0.08	1	1.5	1	0.02	Z = 1.33, p = 0.185
Amphipoda									
<i>Cyphocaris richardi</i>					1	1.5	1	0.02	na
<i>Eurythenes gryllus</i>					2	2.9	2	0.04	na
<i>Eurythenes obesus</i>	2	2.5	2	0.03	3	4.4	3	0.06	Z = 0.98, p = 0.328
<i>Cylopus magellanicus</i>	39	48.1	855	11.35	19	27.9	265	5.57	Z = 10.85, p < 0.0001
<i>Hyperia gaudichaudii/spinigera</i>	14	17.3	38	0.50	2	2.9	5	0.11	Z = 3.65, p < 0.0001
<i>Primno macropa</i>	1	1.2	1	0.01					na
<i>Themisto gaudichaudii</i>	72	88.9	3636	48.26	51	75.0	2299	48.32	Z = 0.06, p = 0.951
<i>Vibilia</i> sp.	20	24.7	92	1.22	9	13.2	48	1.01	Z = 1.08, p = 0.280
Unidentified Amphipoda	3	3.7	11	0.15	3	4.4	3	0.06	Z = 1.33, p = 0.184
Cirripedia									
<i>Lepas australis</i>	1	1.2	14	0.19	1	1.5	1	0.02	Z = 2.55, p = 0.011
Parasitic Copepoda	6	7.4	7	0.09	3	4.4	3	0.06	Z = 0.57, p = 0.572
Pelagic larvae ^b	30	37.0	1030	13.67	8	11.8	64	1.35	Z = 23.38, p < 0.0001
Unidentifiable crustaceans	7	8.6	7	0.09	8	11.8	9	0.19	Z = 1.44, p = 0.149
Total			7534	100.00			4758	100.00	

Equality of proportion tests (large-sample tests) were performed to compare relative prey numbers between the two albatross species. Significant differences (p < 0.05) are highlighted in bold

na not applicable

^aBilobed eyes of euphausiids

^bMainly Decapoda larvae and some Stomatopoda larvae

Prey size and age classes

All but one *M. australis* were young-of-the-year fish ($n = 1318$, $ML = 7.8 \pm 0.7$ [range: 5.2–10.7] mm, estimated $SL = 80 \pm 7$ [56–108] mm; Cohen et al. 1990). A single larger specimen was provided to grey-headed albatross chicks (19.3 mm ML, 191 mm SL) (Fig. 1). Campbell albatross fed on smaller *M. australis* than grey-headed albatross in January 1996 ($n = 472$ and 124, $ML = 7.5 \pm 0.6$ and 7.9 ± 0.5 mm, respectively; two sample t -test, $t = 6.84$, $p < 0.0001$), but not in January 1997 ($n = 588$ and 134, $ML = 8.0 \pm 0.7$ and 8.0 ± 0.8 mm; $t = 0.32$, $p = 0.746$). Campbell and grey-headed albatross fed their chicks on the same size-class of juvenile *Electrona carlsbergi* (ML , $t = 0.70$, $p = 0.486$), with an estimated SL of 53 ± 8 and 55 ± 4 mm (mature at 76–78 mm SL ; Duhamel et al. 2005), respectively. The estimated SL of *Paradiplospinus gracilis* eaten by grey-headed albatross averaged 136 ± 7 mm that corresponds again to juvenile fish (Nakamura and Parin 1993). Few measurements of otoliths and dentary bones, together

with the lack of allometric equations, precluded size estimation of other fish prey, including the larger macrourids (Table A2). However, the small otoliths and dentaries of the morid *Notophycis marginata* indicate juvenile fish (Cohen et al. 1990).

The range of smallest and largest squids were specimens of *Moroteuthopsis longimana* (a juvenile with 44 mm and 4 g estimated DML and body mass, respectively) and *Onykia robsoni* (an adult with 776 mm and 7973 g DML and body mass, respectively) caught by grey-headed and Campbell albatross, respectively. Overall, Campbell albatross preyed upon slightly smaller squids than grey-headed albatross ($n = 300$ and 749, estimated DML = 208 ± 114 and 230 ± 85 g, respectively; Mann–Whitney U test, $U = 82,881.0$, $p < 0.0001$). Both albatross species generally caught specimens of the same size classes when feeding on the same squid species, but, unlike grey-headed albatross, Campbell albatross sometimes fed on large *M. ingens* (Table A3, Figs. 2, 3). Depending on species, albatross fed on juveniles, immatures and/or adult squids (lower beaks with undarkened, darkening and darkened wings, respectively; Clarke 1986). For example, both beaks and corresponding estimated DML indicate that albatross targeted primarily juveniles of *M. ingens* (Arkhipkin and Laptikhovskiy 2010), and both immatures and maturing *M. hyadesi* (Jereb and Roper 2010).

Specimens of the salp *S. zonaria* eaten by Campbell albatross were mainly aggregate zooids, which predominated by number over a few solitary zooids.

Discussion

Previous reviews on the food of Procellariiformes highlighted the need for more dietary investigations on this endangered group of seabirds, which includes many populations breeding in New Zealand waters (Cherel and Klages 1998; McInnes et al. 2016; Cherel and Bocher 2022). The present study partly fills such knowledge gap by detailing the food niche of Campbell and grey-headed albatrosses from Campbell Island when they feed their chicks. The main limitations of the work are that food samples represent a single month each year (January 1996 and 1997), and they were collected more than 25 years ago. However, the study sets a baseline against which the effects of long-term environmental changes on trophic relationships of albatrosses can be studied across years and various conditions, essential information for evidence-based conservation planning since the use of altered or alternative habitats determines the vulnerability of organisms to anthropogenic threats (e.g., Waldron et al. 2006, McGowan et al. 2017). Climate change is already operating in the subantarctic (Favier et al. 2016; Sallée 2018), but to what extent it is driving changes in the

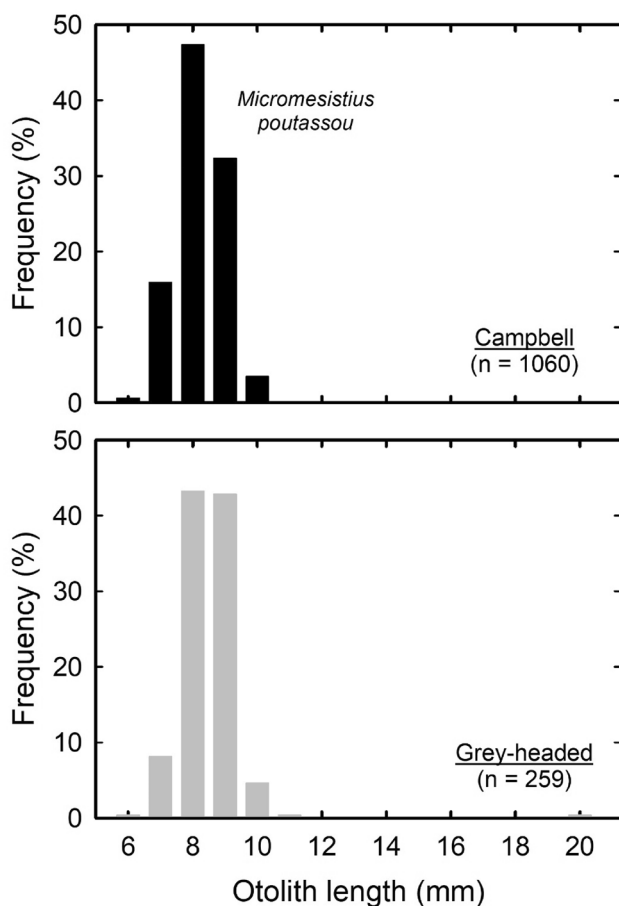


Fig. 1 Length-frequency distribution of otolith length of the gadid *Micromesistius australis* eaten by Campbell (black, upper panel) and grey-headed (grey, lower panel) albatrosses from Campbell Island

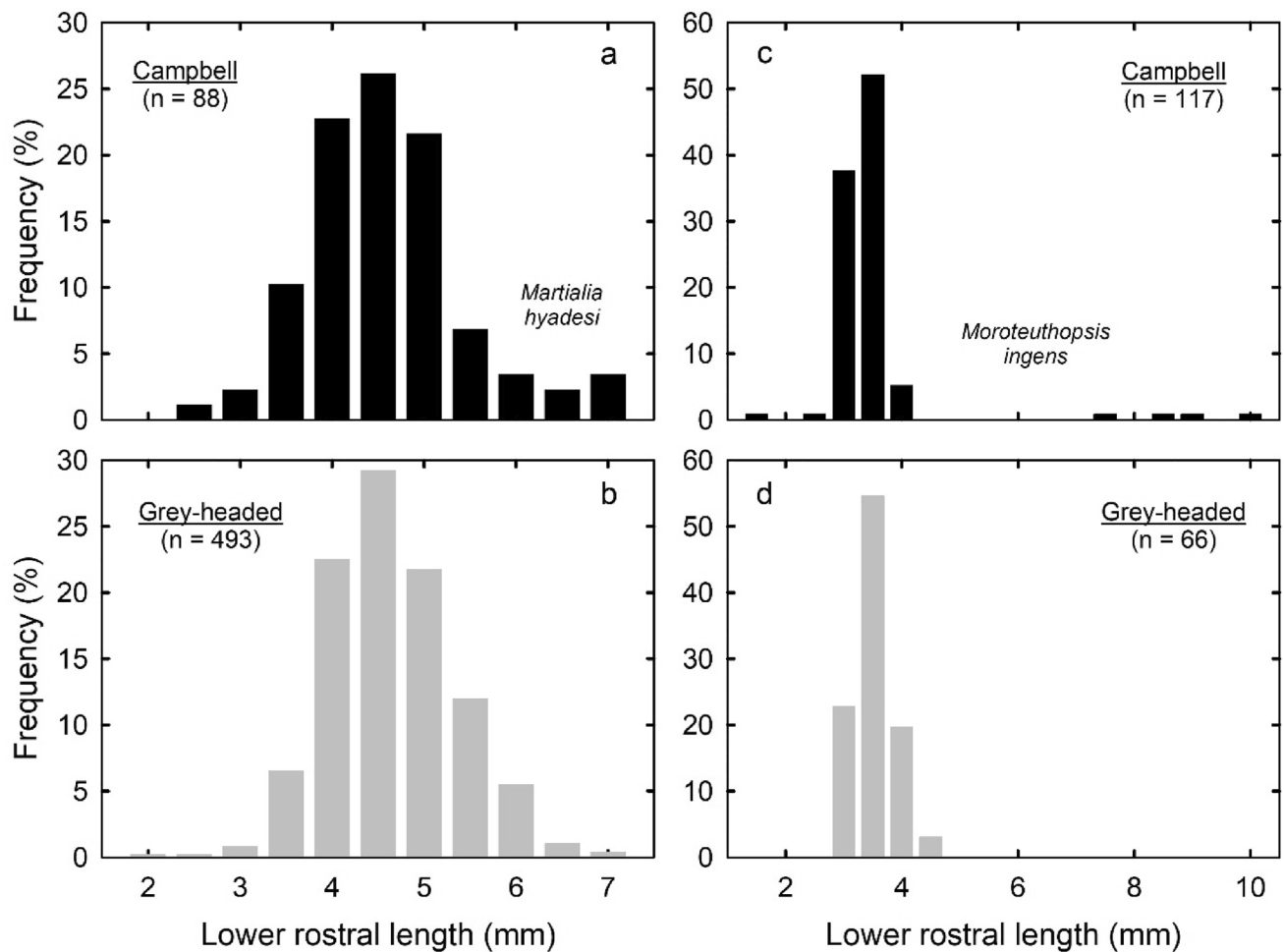


Fig. 2 Length-frequency distribution of lower rostral length of **a, b** the ommastrephid *Martialia hyadesi*, and **c, d** the onychoteuthid *Moroteuthopsis ingens* eaten by Campbell (black, upper panels) and grey-headed (grey, lower panels) albatrosses from Campbell Island

food and feeding ecology of albatrosses breeding at Campbell Island merits further investigation.

Prey of Campbell and grey-headed albatrosses

At Campbell Island, the sympatric Campbell and grey-headed albatrosses fed their chicks on the same prey groups and species. A review of the food of the Campbell/black-browed albatross complex and grey-headed albatross revealed similar chick diets where they co-exist as breeding species (Table 5). The diet is site-specific with concomitant spatial variations in the chick food of both albatrosses, which can likely be related to site-specific availability. For example, Antarctic krill is an important prey item at high latitude breeding locations (Diego Ramirez, South Georgia) (Arata and Xavier 2003; Arata et al. 2004; Mills et al. 2020), penguins characterize the chick food of albatrosses at Kerguelen Islands (Cherel et al. 2000, 2002), and gadiform fishes are the main fish prey at Campbell Island (this study). The squid

M. ingens accounted for a higher number of cephalopod prey at Campbell Island than elsewhere, as *Todarodes* sp. at Kerguelen Islands (Cherel and Weimerskirch 1995; Cherel et al. 2000, 2002), and *Gonatus antarcticus* at Diego Ramirez Islands (Arata and Xavier 2003; Arata et al. 2004).

A first dietary segregating mechanism between the two albatross species is that Campbell albatross fed their chicks more on fish and grey-headed albatross more on cephalopods. Interestingly, the same mechanism operates between black-browed and grey-headed albatrosses where they breed in sympatry (Table 5). A second segregating mechanism is related to different foraging habitats. Prey biological characteristics indicate that Campbell albatross and grey-headed albatross favour neritic and oceanic waters, respectively. Campbell albatross fed more on the fish *M. australis* and macrourids, the squid *M. ingens* and gelatinous zooplankton (*P. atlanticum*, *S. zonaria*) that are abundant over the Campbell Plateau (Anderson et al. 1998; Bagley et al. 2000; Hurst et al. 2000; Escobar-Flores

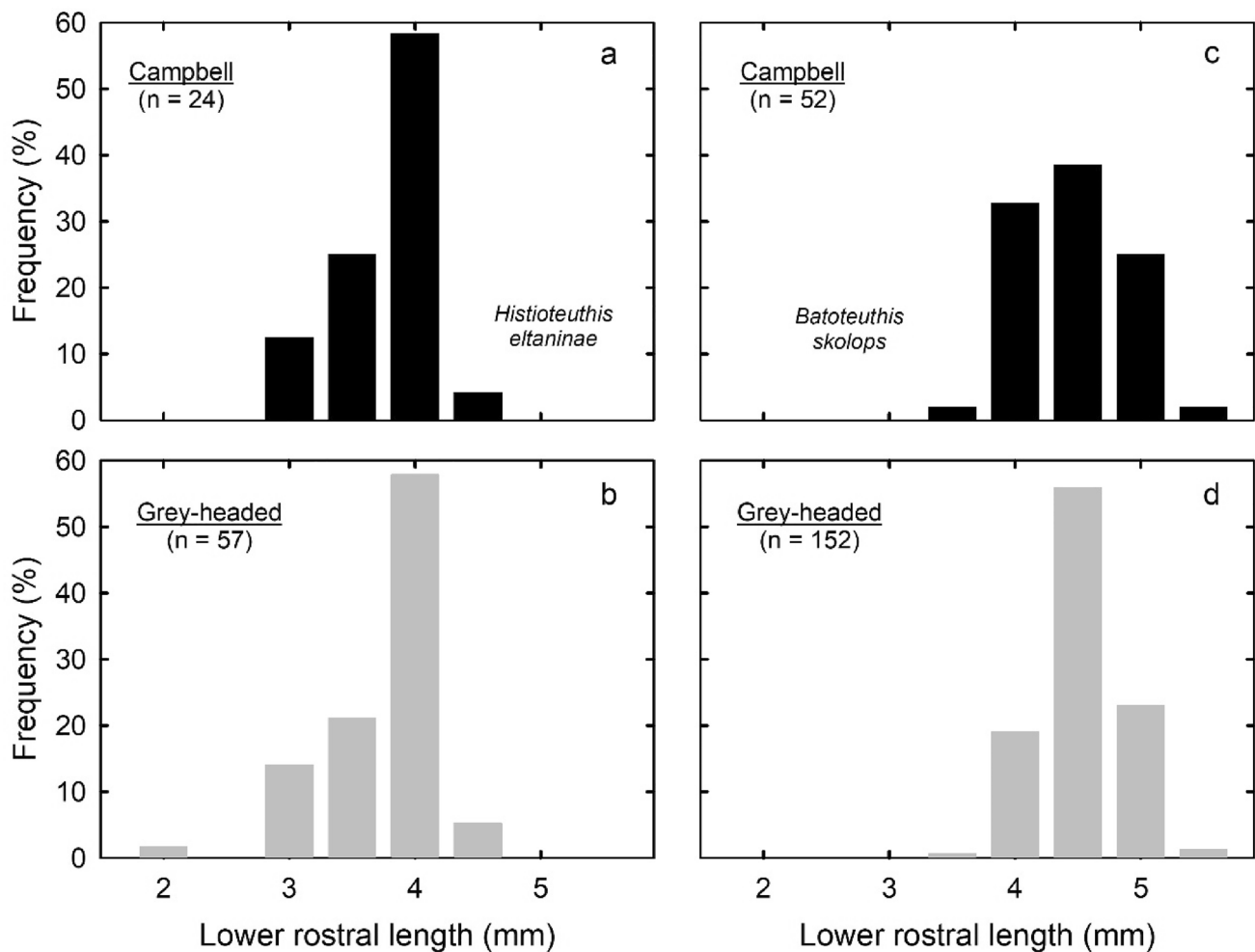


Fig. 3 Length-frequency distribution of lower rostral length of **a, b** the histoteuthid *Histoteuthis eltaninae*, and **c, d** the batoteuthid *Batoteuthis skolops* eaten by Campbell (black, upper panels) and grey-headed (grey, lower panels) albatrosses from Campbell Island

et al. 2022), while grey-headed albatross preyed more upon *M. hyadesi*, a circumpolar oceanic squid (Rodhouse 1997; Cherel 2020). In addition, some shelf-associated organisms occurred only in the chick food of Campbell albatross (e.g., *N. marginata*, congiopodids), and some oceanic items only in the food of grey-headed albatross (e.g., *Magnisudis prionosa*, *P. gracilis*). However, grey-headed albatross also fed on neritic prey (e.g., *M. australis*, macrourids), thus confirming the hypothesis that they also forage over shelf waters (Waugh et al. 1999). Indeed, simultaneous tracking of the two species during chick-rearing showed overlap in their foraging areas, but with Campbell albatross spending more time over shelf waters and grey-headed albatross foraging more over colder, oceanic waters (Waugh et al. 1999; Goetz et al. 2022). Tracking of breeding black-browed and grey-headed albatross at other sites shows the same consistent spatial pattern, with the former species favoring neritic waters and the latter oceanic waters (Cherel et al. 2000; Nel et al. 2001; Catry

et al. 2004; Wakefield et al. 2011; Cleeland et al. 2019). Hence, in terms of both dietary preference and foraging habitats during breeding, Campbell albatross at Campbell Island is ecologically equivalent to the circumpolar black-browed albatross elsewhere (Wakefield et al. 2011). It is noteworthy that Campbell albatross and black-browed albatross are phylogenetically closely related, as evidenced by the presence of fixed pairs that can rear chicks successfully, and of a few birds that are suspected to be hybrids *T. melanophris* × *T. impavida* (Moore et al. 1997, 2001; Burg et al. 2017).

Gelatinous zooplankton and crustaceans

Visual observations of albatrosses feeding on jellyfish are anecdotal (Weimerskirch et al. 1986; Harper 1987; Pages et al. 1996), and accordingly gelatinous zooplankton constitutes a minor prey group for albatrosses (Thompson 1992; Cherel and Klages 1998; Hedd and Gales 2001). An

Table 5 Review of the importance by mass of the main prey groups in the chick diet of the Campbell/black-browed albatross complex and grey-headed albatross

	Sampling years	Age	Food samples (n)	Fish (% mass)	Cephalopods (% mass)	Crustaceans (% mass)	Others (% mass)	References
Campbell albatross								
Campbell Island	1996–1997	Chicks	81	78.7	18.1	1.0	2.2	This study
Black-browed albatross								
Falkland Islands	1987, 1988, 1991	Adults	67	25.9–81.5	0.7–74.0	<0.1–9.4	0.1–8.4	Thompson (1992)
Diego Ramirez	2000–2002	Chicks	177	68.7–88.9	0.0–22.9	3.0–11.1	0.0–2.3	Arata and Xavier (2003)
South Georgia (Bird Island)	1975	Adults	138	39.5	20.6	39.9	–	Prince 1980
	1976–1977, 1980, 1986	Adults	198	28.4–40.5	13.2–37.3	27.1–41.6	0.1–4.7	Croxall et al. (1988)
	1986, 1994	Adults	81	29.5–72.4	22.9–31.1	4.7–39.4	–	Reid et al. (1996)
	1996–2017	Chicks	762	35.9	23.1	32.3	8.6	Data from Mills et al. (2020)
Crozet (Ile de l'Est)	1982	Chicks	12	Mostly	No fresh items	Minor items	No fresh items	Ridoux (1994)
Kerguelen (Canyon des Sourcils Noirs)	1994–1995	Chicks	114	73.1	9.7	<0.1	17.1	Cherel et al. (2000)
Kerguelen (Iles Nuageuses)	1994	Chicks	35	30.7	38.5	<0.1	30.8	Cherel et al. (2002)
Grey-headed albatross								
Diego Ramirez	2000–2002	Chicks	103	0.0–5.2	32.4–94.5	2.6–40.7	0.4–26.9	Arata et al. (2004)
South Georgia (Bird Island)	1975	Adults	132	34.5	49.0	16.5	–	Prince 1980
	1976–1977, 1980, 1986	Adults	204	10.5–32.3	8.7–42.3	44.1–65.5	0.1–2.4	Croxall et al. (1988)
	1986, 1994	Adults	77	13.6–60.4	37.3–70.5	2.3–15.9	–	Reid et al. (1996)
	1996–2017	Chicks	782	28.3	43.9	19.3	8.5	Data from Mills et al. (2020)
Marion and Prince Edward Islands	1985, 1987	Adults	88	58.0	34.2	3.0	4.9	Hunter and Klages (1989)
Marion Island	2006	Chicks and adults	16	59.6	20.7	0.3	19.4	Richoux et al. (2010)
	2009	Chicks and adults	19	45.8	36.5	14.5	3.2	Connan et al. (2014)
Crozet (Ile de l'Est)	1982	Chicks	12	<0.1	89.3	10.7	–	Ridoux (1994)
Kerguelen (Iles Nuageuses)	1994	Chicks	38	15.8	52.4	1.6	30.2	Cherel et al. (2002)
Campbell Island	1996–1997	Chicks	68	26.6	67.3	1.3	4.8	This study

exception is the southern Buller's albatross *Thalassarche bulleri bulleri* that preys on the same tunicates as those occurring in food samples of Campbell and grey-headed albatrosses (James and Stahl 2000, this study). *P. atlanticum* and salps were also eaten by southern royal albatross *Diomedea epomophora* (Imber 1999), thus suggesting that tunicates are common albatross prey items in southern New Zealand waters. Gelatinous zooplankton are notably difficult to identify in food samples, but stomach temperature loggers (Catry et al. 2004), DNA barcoding on scats (McInnes et al. 2017), and the presence in food samples of jellyfish- and salp-associated crustaceans (e.g., *Hyperia gaudichaudii/spinigera*, *Vibilia* sp.; Vinogradov et al. 1996) suggest they are a common prey group of grey-headed and Campbell/black-browed albatrosses.

Disentangling whether crustaceans were primary or secondary prey was challenging. The large Antarctic krill, lobster-krill *Grimothea gregaria*, *Pasiphaea scotiae*, *Neognathophausia gigas*, *Eurythenes* spp., and goose barnacle *Lepas australis* were likely primary prey that have been previously identified in dietary studies (Thompson 1992; Cherel and Klages 1998; Cherel et al. 2002; Delord et al. 2010). The presence of Antarctic krill is noteworthy because it indicates feeding in distant oceanic Antarctic waters, a foraging behaviour already described for Campbell albatross but not for the sympatric grey-headed albatross (Waugh et al. 1999). Other taxa were secondary prey as gauged by their biology (parasitic copepods of fish) or small size (pelagic larvae). Some items were more problematic because they may be either primary or secondary prey. For example, some *T. gaudichaudii* were found in large numbers and in good condition, while others were badly digested with some individuals still inside fish stomachs. Indeed, albatrosses were observed feeding on *T. gaudichaudii* and *N. australis* (Fenwick 1978), but those crustaceans also play a key role in the nutrition of fish, including *M. australis* and macrourids over the Campbell Plateau (Clark 1985; Clark et al. 1989; Jones 2008; Stevens and Dunn 2011).

Prey biology and human activities

Campbell and grey-headed albatrosses mainly fed on organisms that live in swarms. This shoaling behaviour is well documented for the myctophids *E. carlsbergi* and *Krefflichthys anderssoni* (Collins et al. 2008; Lourenço et al. 2017), the squid *M. hyadesi* (Rodhouse and Boyle 2010), the tunicates *P. atlanticum* and *S. zonaria* (Esnal 1990; Daponte et al. 2013), the hyperiids *T. gaudichaudii* and *C. magellanicus* (Vinogradov et al. 1996), and the euphausiids *E. superba*, *E. vallentini*, *N. australis* and *Nematoscelis/Thysanoessa* (Mauchline 1980). No information is available for *M. ingens*, but it is likely that juveniles form schools, because up to 12 specimens occurred in a single stomach

content from a grey-headed albatross. In the same way, a total of 2013 (up to 243 in a single sample) and 600 (up to 141) otoliths of *M. australis* were sorted from samples of Campbell and grey-headed albatrosses, respectively, thus indicating that young-of-the-year fish forms dense schools over the Campbell Plateau. Almost nothing is known about the biology of *M. australis* of that size and age, but young-of-the-year of the congeneric *M. poutassou* from the North Atlantic are epipelagic (Bailey 1982).

The main foraging strategy of Campbell and grey-headed albatrosses is surface seizing (Harper 1987; Warham 1990), but they plunge to 6 m and exceptionally to 19 m (Bentley et al. 2021; Guilford et al. 2022). Albatross feeding behaviour thus indicates that prey aggregations occurred at the sea surface or sub-surface, which concurs with the biology of some prey (Mauchline 1980; Vinogradov et al. 1996; Rodhouse and Boyle 2010), but adds new relevant information on other prey taxa. For example, data presented here suggest that the commercially-exploited *M. australis* shifts from pelagic to demersal habitats at > 8 cm SL, which is in agreement with a mode at 12 cm of fish caught during demersal research cruises in April (Hanchet and Uozumi 1996). Whether prey were caught during the day or at night remains to be determined, but there is a potential mismatch between the behaviour of prey that perform daily vertical migration to the surface at night (Saunders et al. 2014; Rodhouse and Boyle 2010), and the activity pattern of Campbell and grey-headed albatrosses that are more active during the day with a higher proportion of food consumed during daytime than nighttime (Weimerskirch and Guionnet 2002; Catry et al. 2004).

Young-of-the-year *M. australis* are major dietary items of Campbell and grey-headed albatross chicks from Campbell Island (this study), minor prey of black-browed albatross at Diego Ramirez and the Falkland Islands (Arata and Xavier 2003; Thompson 1992), and they were also identified in the diet of Magellanic penguins *Spheniscus magellanicus* (Thompson 1993), and rockhopper penguins *Eudyptes chrysocome* (Cunningham and Moors 1994). White-chinned petrels *Procellaria aequinoctialis* from South Georgia also feed on *M. australis* (Berrow and Croxall 1999), but on larger specimens than albatrosses and penguins. *M. australis* (southern blue whiting) has two separate commercially-fished populations in the Falkland-Patagonian region and southern New Zealand (Cohen et al. 1990). In New Zealand, commercial trawling occurs on winter aggregations of spawning fish, and fingerlings are not fished in summer (Fisheries New Zealand 2022), thus minimising direct interactions between breeding albatross and fishery activities (Richard et al. 2020). In the Falkland Islands, experiments from fishing boats showed that black-browed albatross feeds on discarded medium-sized *M. australis* (Thompson and Riddy 1995), but the interpretation that fingerlings are

scavenged from trawling operations (Thompson 1992) is questionable because young-of-the-year *M. australis* are natural epipelagic prey of albatrosses and penguins.

Only a few plastic debris that were likely confused with natural prey, and no fishery-related items were found in food samples of Campbell and grey-headed albatross chicks. This suggests limited interactions of parent birds with human activities in the summers of 1996 and 1997. Accordingly, a synthesis of seabird bycatch records ($n=9966$) over 18 years (2002/2003–2019/2020) indicates a low to very low bycatch risk of Campbell ($n=75$) and grey-headed ($n=1$) albatrosses within the New Zealand Exclusive Economic Zone (Ministry for Primary Industries 2022). While the dietary data indicates little sign of interaction with fishing activity for adults feeding chicks, these two species are however known to spend time in areas of intense fishing activity in the New Zealand EEZ, accounting for their high risk rating in analysis of seabird overlap with fisheries (ACAP 2012; Richard et al. 2020). Moreover, a limitation of our work is that food samples were collected during a single month period (January 1996 and 1997) more than 25 years ago, meaning that more recent dietary information is needed. In addition, Campbell and grey-headed albatrosses may be more vulnerable to negative interactions with human activities in the high-seas, especially during the inter-breeding period (Thompson et al. 2021; Goetz et al. 2022).

In conclusion, our results highlight the nutritional importance of young-of-the-year *M. australis* to both our study species, building on preliminary findings obtained from a few food samples of Campbell albatross chicks (Cherel et al. 1999). Hence, the nutritional importance of juvenile *M. australis* for seabirds has to be taken into account for a sustainable management of the resource, its predators and the fishery targeting adult fish.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00227-023-04267-4>.

Acknowledgements The authors thank G. Hedley, S. Kalish and B. Thompson for assistance in the field, G. James for his help to build a reference collection of fish otoliths and bones, and C. Trouvé for her help in food sample analysis. We also thank Invercargill-based staff from the Department of Conservation, including A. Cox and C. West for their assistance with field preparations. Special thanks to Ngai Tahu and their Murihiku iwi representatives for providing their consent for the work at Motu Ihupuku Campbell Island. The PhD thesis of S.M. Waugh was supervised by P.M. Sagar (NIWA Ltd, Christchurch) and H. Weimerskirch (CNRS, Villiers-en-Bois).

Author contributions YC and SW conceived and designed the research. SW collected food samples in the field. YC and SW analyzed food samples, and YC identified prey items. YC drafted the manuscript, and both authors edited, read, and approved it.

Funding The project was funded by the National Institute of Water and Atmospheric Research (NIWA Ltd., New Zealand), Department of Conservation (DOC, New Zealand), including the Conservation

Services Levy paid by the New Zealand Commercial Fishing Industry, New Zealand Lottery Science Commission, France-New Zealand Cultural Agreement, and the Centre National de la Recherche Scientifique (CNRS, France).

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 Department of Conservation (DOC, New Zealand).

References

- ACAP, Agreement on the Conservation of Albatrosses and Petrels (2012) <http://www.acap.aq/>. Accessed 23 Jan 2023
- Anderson OF, Bagley NW, Hurst RJ, Francis MP, Clark MR, McMillan PJ (1998) Atlas of New Zealand fish and squid distributions from research bottom trawls. NIWA technical report 42
- Arata J, Xavier JC (2003) The diet of black-browed albatrosses at the Diego Ramirez Islands, Chile. *Polar Biol* 26:638–647
- Arata J, Robertson G, Valencia J, Xavier JC, Moreno CA (2004) Diet of grey-headed albatrosses at the Diego Ramirez Islands, Chile: ecological implications. *Antarct Sci* 16:263–275
- Arkhipkin AI, Laptikhovsky VV (2010) Convergence in life-history traits in migratory deep-water squid and fish. *ICES J Mar Sci* 67:1444–1451
- Bagley NW, Anderson OF, Hurst RJ, Francis MP, Taylor PR, Clark MR, Paul LJ (2000) Atlas of New Zealand fish and squid distributions from midwater trawls, tuna longline sets, and aerial sightings. NIWA technical report 72
- Bailey RS (1982) The population biology of blue whiting in the North Atlantic. *Adv Mar Biol* 19:257–355
- Begon M, Harper JL, Townsend CR (1990) Ecology: individuals, populations and communities, 2nd edn. Blackwell, Cambridge
- Bentley LK, Kato A, Ropert-Coudert Y, Manica A, Phillips RA (2021) Diving behaviour of albatrosses: implications for foraging ecology and bycatch susceptibility. *Mar Biol* 168:36
- Berrow SD, Croxall JP (1999) The diet of white-chinned petrels *Procellaria aequinoctialis*, Linnaeus 1758, in years of contrasting prey availability at South Georgia. *Antarct Sci* 11:283–292
- Boltovskoy D (1999) South Atlantic zooplankton, vol 2. Backhuys Publishers, Leiden
- Burg TM, Croxall JP (2001) Global relationships amongst black-browed and grey-headed albatrosses: analysis of population structure using mitochondrial DNA and microsatellites. *Mol Ecol* 10:2647–2660
- Burg TM, Catry P, Ryan PG, Phillips RA (2017) Genetic population structure of black-browed and Campbell albatrosses, and implications for assigning provenance of birds killed in fisheries. *Aquat Conserv Mar Freshw Ecosyst* 27:1156–1163
- Catry P, Phillips RA, Phalan B, Silk JRD, Croxall JP (2004) Foraging strategies of grey-headed albatrosses *Thalassarche chrysostoma*: integration of movements, activity and feeding events. *Mar Ecol Prog Ser* 280:261–273
- Cherel Y (2020) A review of Southern Ocean squids using nets and beaks. *Mar Biodivers* 50:98

- Cherel Y, Bocher P (2022) Diet of the soft-plumaged petrel (*Pterodroma mollis*) at Kerguelen Islands and a review of the food of gadfly petrels (*Pterodroma* spp.) worldwide. *Mar Biol* 169:31
- Cherel Y, Klages N (1998) A review of the food of albatrosses. In: Robertson G, Gales R (eds) Albatross biology and conservation. Surrey Beatty and Sons, Chipping Norton, pp 113–136
- Cherel Y, Weimerskirch H (1995) Seabirds as indicators of marine resources: black-browed albatrosses feeding on omastrephid squids in Kerguelen waters. *Mar Ecol Prog Ser* 129:295–300
- Cherel Y, Waugh S, Hanchet S (1999) Albatross predation of juvenile southern blue whiting (*Micromesistius australis*) on the Campbell Plateau. *N Z J Mar Freshw Res* 33:437–441
- Cherel Y, Weimerskirch H, Trouvé C (2000) Food and feeding ecology of the neritic-slope forager black-browed albatross and its relationships with commercial fisheries in Kerguelen waters. *Mar Ecol Prog Ser* 207:183–199
- Cherel Y, Weimerskirch H, Trouvé C (2002) Dietary evidence for spatial foraging segregation in sympatric albatrosses (*Diomedea* spp.) rearing chicks at Iles Nuageuses, Kerguelen. *Mar Biol* 141:1117–1129
- Cherel Y, Xavier JC, de Grissac S, Trouvé C, Weimerskirch H (2017) Feeding ecology, isotopic niche, and ingestion of fishery-related items of the wandering albatross *Diomedea exulans* at Kerguelen and Crozet Islands. *Mar Ecol Prog Ser* 565:197–215
- Chiswell SM, Bostock HC, Sutton PIH, Williams MJM (2015) Physical oceanography of the deep seas around New Zealand: a review. *N Z J Mar Freshw Res* 49:286–317
- Clark MR (1985) The food and feeding of seven fish species from the Campbell Plateau, New Zealand. *N Z J Mar Freshw Res* 19:339–363
- Clark MR, King KJ, McMillan PJ (1989) The food and feeding relationships of black oreo, *Allocyttus niger*, smooth oreo, *Pseudocyttus maculatus*, and eight other fish species from the continental slope of the south-west Chatham Rise, New Zealand. *J Fish Biol* 35:465–484
- Clarke MR (1986) A handbook for the identification of cephalopod beaks. Clarendon Press, Oxford
- Clelland JB, Alderman R, Bindoff A, Lea MA, McMahon CR, Phillips RA, Raymond B, Sumner MD, Terauds A, Wotherspoon SJ, Hindell MA (2019) Factors influencing the habitat use of sympatric albatrosses from Macquarie Island, Australia. *Mar Ecol Prog Ser* 609:221–237
- Cohen DM, Inada T, Iwamoto T, Scialabba N (1990) FAO species catalogue. Vol 10. Gadiform fishes of the world (Order Gadiformes). An annotated and illustrated catalogue of cods, hakes, grenadiers and other gadiform fishes known to date. FAO Fisheries Synopsis 125, FAO, Rome
- Collins MA, Xavier JC, Johnston NM, North AW, Enderlein P, Tarling GA, Waluda CM, Hawker EJ, Cunningham NJ (2008) Patterns in the distribution of myctophid fish in the northern Scotia Sea ecosystem. *Polar Biol* 31:837–851
- Connan M, McQuaid CD, Bonnevie BT, Smale MJ, Cherel Y (2014) Combined stomach content, lipid and stable isotope analyses reveal spatial and trophic partitioning among three sympatric albatrosses from the Southern Ocean. *Mar Ecol Prog Ser* 497:259–272
- Croxall JP, McCann TS, Prince PA, Rothery P (1988) Reproductive performance of seabirds and seals at South Georgia and Signy Island, South Orkney Islands, 1976–1987: implications for Southern Ocean Monitoring studies. In: Sahrhage D (ed) Antarctic Ocean and RESOURCES VARIABILITY. Springer, Berlin, pp 261–285
- Cunningham DM, Moors PJ (1994) The decline of rockhopper penguins *Eudyptes chrysocome* at Campbell Island, Southern Ocean and the influence of rising sea temperatures. *Emu* 94:27–36
- Daponte MC, Palmieri MA, Casareto BE, Esnal GB (2013) Reproduction and population structure of the salp *Iasis zonaria* (Pallas, 1774) in the southwestern Atlantic Ocean (34°30' to 39°30' S) during three successive winters (1999–2001). *J Plankton Res* 35:813–830
- de Baker AC, Boden BP, Brinton E (1990) A practical guide to the euphausiids of the world. Natural History Museum Publications, London
- Delord K, Cotté C, Péron C, Marteau C, Pruvost P, Gasco N, Duhamel G, Cherel Y, Weimerskirch H (2010) At-sea distribution and diet of an endangered top predator: relationship between white-chinned petrels and commercial longline fisheries. *Endanger Species Res* 13:1–16
- Delord K, Barbraud C, Bost CA, Cherel Y, Guinet C, Weimerskirch H (2013) Atlas of top predators from French Southern Territories in the Southern Indian Ocean. CEBC-CNRS, France. https://doi.org/10.15474/AtlasTopPredatorsOI_CEBC-CNRS_FrenchSouthernTerritories
- Dias MP, Martin R, Pearmain EJ, Burfield IJ, Small C, Phillips RA, Yates O, Lascelles B, Borboroglu PG, Croxall JP (2019) Threat to seabirds: a global assessment. *Biol Conserv* 237:525–537
- Duffy DC, Jackson S (1986) Diet studies of seabirds: a review of methods. *Colon Waterbirds* 9:1–17
- Duhamel G, Gasco P, Davaine P (2005) Poissons des Iles Kerguelen et Crozet. Guide régional de l'océan Austral. Muséum national d'Histoire naturelle, Paris
- Escobar-Flores PC, Décima M, O'Driscoll RL, Lacroix Y, Roberts J (2022) Multiple sampling methods to develop indices of mid-trophic levels abundance in open ocean ecosystems. *Limnol Oceanogr Methods* 20:789–810
- Esnal GB (1990) Pyrosomatida. In: Boltovskoy D (ed) South Atlantic zooplankton, vol 2. Backhuys Publishers, Leiden, pp 1401–1408
- Favier V, Verfaillie D, Berthier E, Menegoz M, Jomelli V, Kay JE, Ducret L, Malbêteau Y, Brunstein D, Gallée H, Park YH, Rinterknecht V (2016) Atmospheric drying as the main driver of dramatic glacier wastage in the southern Indian Ocean. *Sci Rep* 6:32396
- Fenwick GD (1978) Plankton swarms and their predators at the Snares Islands. *N Z J Mar Freshw Res* 12:223–224
- Fisheries New Zealand (2022) Fisheries Assessment Plenary, May 2022: stock assessments and stock status. Vol 3: red gurnard to yellow-eyed mullet. Compiled by the Fisheries Science Team, Fisheries New Zealand, Wellington
- Goetz KT, Stephenson F, Hoskins A, Bindoff AD, Orben RA, Sagar PM, Torres LG, Kroeger CE, Sztukowski LA, Phillips RA, Votier SC, Bearhop S, Taylor GA, Thompson DR (2022) Data quality influences the predicted distribution and habitat of four Southern-Hemisphere albatross species. *Front Mar Sci* 9:782923
- Guilford T, Padgett O, Maurice L, Catry P (2022) Unexpectedly deep diving in an albatross. *Curr Biol* 32:R26–R28
- Hanchet SM, Uozumi Y (1996) Age validation and growth of southern blue whiting, *Micromesistius australis* Norman, in New Zealand. *N Z J Mar Freshw Res* 30:57–67
- Harper PC (1987) Feeding behaviour and other notes on 20 species of Procellariiformes at sea. *Notornis* 34:169–192
- Hedd A, Gales R (2001) The diet of shy albatrosses (*Thalassarche cauta*) at Albatross Island. *J Zool Lond* 253:69–90
- Hunter S, Klages NTW (1989) The diet of grey-headed albatrosses *Diomedea chrysostoma* at the Prince Edward Islands. *S Afr J Antarct Res* 19:31–33
- Hurst RJ, Bagley NW, Anderson OF, Francis MP, Griggs LH, Clark MR, Paul LJ, Taylor PR (2000) Atlas of juvenile and adult fish and squid distributions from bottom and midwater trawls and tuna longlines in New Zealand waters. NIWA technical report 84

- Imber MJ (1992) Cephalopods eaten by wandering albatrosses (*Diomedea exulans* L.) breeding at six circumpolar localities. J R Soc N Z 22:243–263
- Imber MJ (1999) Diet and feeding ecology of the royal albatross *Diomedea epomophora*—King of the shelf break and inner slope. Emu 99:200–211
- Imber MJ, Russ R (1975) Some foods of the wandering albatross (*Diomedea exulans*). Notornis 22:27–36
- IUCN red list of threatened species (2023) <https://www.iucnredlist.org/>. Accessed 23 Jan 2023
- James GD, Stahl JC (2000) Diet of southern Buller's albatross (*Diomedea bulleri bulleri*) and the importance of fishery discards during chick rearing. N Z J Mar Freshw Res 34:435–454
- Jereb P, Roper CFE (2010) Cephalopods of the world. An annotated and illustrated catalogue of cephalopod species known to date. Vol 2. Myopsid and oegopsid squids. FAO Species Catalogue for Fishery Purposes 4, FAO, Rome
- Jones MRL (2008) Biology and diet of *Coryphaenoides subseriatus* and *Etmopterus baxteri* from the Puysegur region, southern New Zealand. N Z J Mar Freshw Res 42:333–337
- Lourenço S, Saunders RA, Collins M, Shreeve R, Assis CA, Belchier M, Watkins JL, Xavier JC (2017) Life cycle, distribution and trophodynamics of the lanternfish *Kreftlichthys anderssoni* (Lönnberg, 1905) in the Scotia Sea. Polar Biol 40:1229–1245
- Mauchline J (1980) The biology of mysids and euphausiids. Part II. The biology of euphausiids. Academic Press, London
- McGowan CP, Allan N, Servoss J, Hedwall S, Woolridge B (2017) Incorporating population viability models into species status assessment and listing decisions under the US Endangered Species Act. Glob Ecol Conserv 12:119–130
- McInnes JC, Raymond B, Phillips RA, Jarman SN, Lea MA, Alderman R (2016) A review of methods used to analyse albatross diets—assessing priorities across their range. ICES J Mar Sci 73:2125–2137
- McInnes JC, Alderman R, Lea MA, Raymond B, Deagle BE, Phillips RA, Stanworth A, Thompson DR, Catry P, Weimerskirch H, Suazo CG, Gras M, Jarman SN (2017) High occurrence of jellyfish predation by black-browed and Campbell albatross identified by DNA metabarcoding. Mol Ecol 26:4831–4845
- Mills WF, Xavier JC, Bearhop S, Cherel Y, Votier SC, Waluda CM, Phillips RA (2020) Long-term trends in albatross diets in relation to prey availability and breeding success. Mar Biol 167:29
- Ministry for Primary Industries (2022) <https://protectedspeciescaptiveures.nz/PSCv6/>. Accessed 14 Dec 2022
- Moore PJ, Taylor GA, Amey JM (1997) Interbreeding of black-browed albatross *Diomedea m. melanophris* and New Zealand black-browed albatross *D. m. impavida* on Campbell Island. Emu 97:322–324
- Moore PJ, Burg TM, Taylor GA, Millar CD (2001) Provenance and sex-ratio of black-browed albatross, *Thalassarche melanophrys*, breeding on Campbell Island, New Zealand. Emu 101:329–334
- Nakamura I, Parin NV (1993) FAO species catalogue. Vol 15. Snake mackerels and cutlassfishes of the world (Families Gempylidae and Trichiuridae). An annotated and illustrated catalogue of the snake mackerels, snoeks, escolars, gemfishes, sackfishes, domine, oilfish, cutlassfishes, scabbardfishes, hairtails, and frostfishes known to date. FAO Fisheries Synopsis 125, FAO, Rome
- Nel DC, Lutjeharms JRE, Pakhomov EA, Anson IJ, Ryan PG, Klages NTW (2001) Exploitation of mesoscale oceanographic features by grey-headed albatross *Thalassarche chrysostoma* in the southern Indian Ocean. Mar Ecol Prog Ser 217:15–26
- Pages F, White MG, Rodhouse PG (1996) Abundance of gelatinous carnivores in the nekton community of the Antarctic Polar Frontal Zone in summer 1994. Mar Ecol Prog Ser 141:139–147
- Phillips RA (2006) Efficacy and effects of diet sampling of albatross chicks. Emu 106:305–308
- Phillips RA, Gales R, Baker GB, Double MC, Favero M, Quintana F, Tasker ML, Weimerskirch H, Uhart M, Wolfaardt A (2016) The conservation status and priorities for albatrosses and large petrels. Biol Conserv 201:169–183
- Prince PA (1980) The food and feeding ecology of grey-headed albatross *Diomedea chrysostoma* and black-browed albatross *D. melanophris*. Ibis 122:476–488
- Provencher JF, Borrelle SB, Bond AL, Lavers JL, van Franeker JA, Kühn S, Hammer S, Avery-Gomm S, Mallory ML (2019) Recommended best practices for plastic and litter ingestion studies in marine birds. FACETS 4:111–130
- Reid K, Croxall JP, Prince PA (1996) The fish diet of black-browed albatross *Diomedea melanophris* and grey-headed albatross *D. chrysostoma* at South Georgia. Polar Biol 16:469–477
- Richard Y, Abraham ER, Berkenbusch K (2020) Assessment of the risk of commercial fisheries to New Zealand seabirds, 2006–07 to 2016–2017. NZ Aquat Environ Biodivers Rep 237:1–57
- Richoux NB, Jaquemet S, Bonnevie BT, Cherel Y, McQuaid CD (2010) Trophic ecology of grey-headed albatrosses from Marion Island, Southern Ocean: insights from stomach contents and diet tracers. Mar Biol 157:1755–1766
- Ridoux V (1994) The diets and dietary segregation of seabirds at the subantarctic Crozet Islands. Mar Ornithol 22:1–192
- Rodhouse PG (1997) Large and meso-scale distribution of the omnistrephid squid *Martialis hyadesi* in the Southern Ocean: a synthesis of information relevant to fishery forecasting and management. Korean J Polar Res 8:145–154
- Rodhouse PG, Boyle PR (2010) Large aggregations of pelagic squid near the ocean surface at the Antarctic Polar Front, and their capture by grey-headed albatrosses. ICES J Mar Sci 67:1432–1435
- Sallée JB (2018) Southern Ocean warming. Oceanography 31:52–62
- Saunders RA, Collins MA, Foster E, Shreeve R, Stowasser G, Ward P, Tarling GA (2014) The trophodynamics of Southern Ocean *Electrona* (Myctophidae) in the Scotia Sea (Southern Ocean). Polar Biol 37:789–807
- Smale MJ, Watson G, Hecht T (1995) Otoliths atlas of southern African marine fishes. Ichthyological Monographs of the JLB Smith Institute of Ichthyology, Grahamstown
- Stevens DW, Dunn MR (2011) Different food preferences in four sympatric deep-sea macrourid fishes. Mar Biol 158:59–72
- Sztukowski LA, van Toor ML, Weimerskirch H, Thompson DR, Torres LG, Sagar PM, Cotton PA, Votier SC (2017) Tracking reveals limited interactions between Campbell albatross and fisheries during the breeding season. J Ornithol 158:725–735
- Thompson KR (1992) Quantitative analysis of the use of discards from squid trawlers by black-browed albatrosses *Diomedea melanophris* in the vicinity of the Falkland Islands. Ibis 134:11–21
- Thompson KR (1993) Variation in Magellanic penguin *Spheniscus magellanicus* diet in the Falkland Islands. Mar Ornithol 21:57–67
- Thompson KR, Riddy MD (1995) Utilization of offal and discards from “finfish” trawlers around the Falkland Islands by the black-browed albatross *Diomedea melanophris*. Ibis 137:198–206
- Thompson DR, Goetz KT, Sagar PM, Torres LG, Kroeger CE, Sztukowski LA, Orben RA, Hoskins AJ, Phillips RA (2021) The year-round distribution and habitat preferences of Campbell albatross (*Thalassarche impavida*). Aquatic Conserv Mar Freshw Ecosyst 31:2967–2978
- Vinogradov ME, Volkov AF, Semenova TN (1996) Hyperiid amphipods (Amphipoda, Hyperiidea) of the world oceans. Science Publishers, Lebanon

- Voskoboinikova OS, Zhukov MY (2021) Comparative osteology of the superfamily Congiopoidea (Pisces: Scorpaenoidei). *Zoomorphology* 140(373):385
- Wakefield ED, Phillips RA, Trathan PN, Arata J, Gales R, Huin N, Robertson G, Waugh S, Weimerskirch H, Matthiopoulos J (2011) Habitat preference, accessibility, and competition limit the global distribution of breeding black-browed albatrosses. *Ecol Monogr* 81:141–167
- Waldron JL, Bennett SH, Welch SM, Dorcas ME, Lanham JD, Kalinowsky W (2006) Habitat specificity and home-range size as attributes of species vulnerability to extinction: a case study using sympatric rattlesnakes. *Anim Conserv* 9:414–420
- Warham J (1990) The petrels, their ecology and breeding systems. Academic Press, London
- Waugh SM, Weimerskirch H, Cherel Y, Shankar U, Prince PA, Sagar PM (1999) Exploitation of the marine environment by two sympatric albatrosses in the Pacific Southern Ocean. *Mar Ecol Prog Ser* 177:243–254
- Waugh SM, Weimerskirch H, Cherel Y, Prince PA (2000) Contrasting strategies of provisioning and chick growth in two sympatrically breeding albatrosses at Campbell Island, New Zealand. *Condor* 102:804–813
- Waugh SM, Poupart TA, Miskelly CM, Stahl JC, Arnould JPY (2017) Human exploitation assisting a threatened species? The case of muttonbirders and Buller's albatross. *PLoS ONE* 12:e0175458
- Weimerskirch H, Guionnet T (2002) Comparative activity pattern during foraging of four albatross species. *Ibis* 144:40–50
- Weimerskirch H, Jouventin P, Stahl JC (1986) Comparative ecology of the six albatross species breeding on the Crozet Islands. *Ibis* 128:195–213
- Weimerskirch H, Collet J, Corbeau A, Pajot A, Hoarau F, Marteau C, Filippi D, Patrick SC (2020) Ocean sentinel albatrosses locate illegal vessels and provide the first estimate of the extent of non-declared fishing. *Proc Natl Acad Sci USA* 117:3006–3014
- West JA, Imber MJ (1986) Some foods of Buller's mollymawk *Diomedea bulleri*. *N Z J Zool* 13:169–174
- Xavier JC, Cherel Y (2021) Cephalopod beak guide for the Southern Ocean: an update on taxonomy. British Antarctic Survey, Cambridge
- Xavier JC, Croxall JP, Cresswell KA (2005) Boluses: an effective method for assessing the proportions of cephalopods in the diet of albatrosses. *Auk* 122:1182–1190
- Xavier JC, Phillips RA, Cherel Y (2011) Cephalopods in marine predator diet assessments: why identifying upper and lower beaks is important. *ICES J Mar Sci* 68:1857–1864
- Xavier JC, Walker K, Elliot G, Cherel Y, Thompson D (2014) Cephalopod fauna of South Pacific waters: new information from breeding New Zealand wandering albatrosses. *Mar Ecol Prog Ser* 513:131–142

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Springer Nature or its licensor (e.g. a society or other partner) holds exclusive rights to this article under a publishing agreement with the author(s) or other rightsholder(s); author self-archiving of the accepted manuscript version of this article is solely governed by the terms of such publishing agreement and applicable law.